Abstract.—The vermilion snapper, *Rhomboplites aurorubens*, is an important species in headboat and commercial reef fisheries in the southeastern United States, especially in the Carolinas. The reproductive biology of vermilion snapper was determined from samples collected on biweekly research cruises (April to August 1992 and May 1993) and from samples collected from commercial vessels (September to April 1992–93). Vermilion snapper did not exhibit a 1:1 sex ratio; 63% of the specimens were female. The reproductive season of vermilion snapper is April through late September in the southeastern United States. All vermilion snapper examined were mature, with the smallest female at 165 mm FL, the smallest male at 179 mm FL. The smallest fish aged (165 mm FL) was two years old. Length was the best predictor of batch fecundity (BF=0.0438$FL^{2.508}$). Vermilion snapper spawn approximately every five days or about 35 times a year. Atresia did not significantly affect fecundity estimates. Vermilion snapper is an indeterminate spawner; its oocytes mature continuously during the spawning season and there is no hiatus between the size distribution of the oocyte classes. Total fecundity did not decline over the spawning season. Rather, it gradually increased through August and then declined in September. Mean oocyte diameter stayed constant over the reproductive season. The order of spawning batches was not consistent with the determinate fecundity prediction.

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Reproductive seasonality, maturation, fecundity, and spawning frequency of the vermilion snapper, *Rhomboplites aurorubens*, off the southeastern United States*

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The vermilion snapper, *Rhomboplites aurorubens*, is a small lutjanid distributed from North Carolina and Bermuda, through the West Indies and the Gulf of Mexico, and south to southeastern Brazil (Böhlke and Chaplin, 1968). It is associated with two distinct habitats on the outer continental shelf near the Carolinas: shelf-edge habitat (64–183 m) and inshore "live-bottom" habitat (26–56 m) (Grimes, 1976). This lutjanid attains a maximum total length of approximately 600 mm (24 in) and a maximum weight of 2.8 kg (6 lb) (Grimes, 1978).

Vermilion snapper is an important species in the headboat and commercial reef fish fisheries of the Carolinas. Despite an increase in landings in North Carolina, South Carolina, and Georgia from 6.8 metric tons (t) (15,000 lbs) in 1988 to 499 t (1.1 million lbs) in 1991, catch per unit of effort (CPUE) exhibited a marked decline (Zhao and McGovern[1]); there was also a significant decrease in mean length of vermilion snapper taken by fishery independent sampling and by headboat and commercial fisheries (Collins and Sedberry, 1991; Zhao and McGovern[1]) over the same period.

Declines in CPUE and mean size in fishery-independent samples indicate that vermilion snapper is overfished (Collins and Sedberry, 1991). Owing to the importance of vermilion snapper in the southeastern U.S. fisheries, current information on all aspects of its reproduction is needed to manage the vermilion snapper fishery effectively. Fecundity and sexual maturity information is essential for management of any fishery of economic consequence to a region (Hunter et al., 1992). Fecundity data are needed to calculate a spawning stock ratio (SSR) in annual stock assessments for use in evaluating management regulations. To quantify fecundity

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[1] Zhao, B., and J. C. McGovern. 1996. Population characteristics of the vermilion snapper, *Rhomboplites aurorubens*, from the southeastern United States. In preparation.

and spawning frequency more accurately, new techniques, such as the hydrated oocyte method for fecundity estimates (Hunter et al., 1985) and the postovulatory follicle method (Hunter and Goldberg, 1980; Hunter and Macewicz, 1985) for determining spawning frequency, need to be used. There is considerable information on the reproductive biology of over 40 lutjanids (Grimes, 1987); however, there is only one recent study (Davis and West, 1993) that uses the new assessment methods on a lutjanid.

Recent studies of the reproductive biology of vermilion snapper in the southeastern U.S. are quite limited. Current management of the vermilion snapper fishery is based on age, growth, and reproductive data collected in the early to mid-1970's, prior to the rapid expansion of the fishery (Grimes, 1978; Grimes and Huntsman, 1980). Grimes (1976) and Grimes and Huntsman (1980) examined aspects of the reproductive biology of vermilion snapper in this area in the early 1970's, but neither used a histological technique to assess reproductive season, spawning frequency, or maturity. Collins and Pinckney (1988) reported on the maturity of vermilion snapper in the southeastern United States from 1978 to 1980 but used only scales to age fish. The reproductive biology of vermilion snapper has also been studied in the Gulf of Mexico. Nelson (1988) examined the sex ratio, size at maturity, spawning frequency, and fecundity of vermilion snapper off Flower Garden Banks, Gulf of Mexico, from 1980 to 1982 but did not use a histological technique. These data need to be supplemented with more recent information, including histological criteria and more accurate assessment methods.

Although vermilion snapper is considered a multiple spawner on the basis of its prolonged spawning season, variation in the gonadosomatic index for similarly sized fish, and variation in the number of maturing ova types found in the ovary (Grimes and Huntsman, 1980), a reassessment of the reproductive biology of vermilion snapper, using recently developed techniques, is necessary 1) to quantify the annual reproductive cycle; 2) to determine age and size at maturity and to detect changes that may have occurred because of the fishery; 3) to estimate spawning frequency; 4) to describe vermilion snapper as either a determinate or indeterminate spawner; and 5) to calculate fecundity (corrected for atresia) of the vermilion snapper in the southeastern United States.

Materials and methods

Specimens were obtained between April 1992 and May 1993 on research cruises conducted as part of a fishery-independent survey of reef fishes. Scientists of the MARMAP (Marine Resources Monitoring, Assessment, and Prediction) program (see Collins and Sedberry [1991] and Zhao and McGovern[1]) conducted biweekly cruises to randomly selected reef sites, from Cape Lookout, North Carolina, to Jacksonville, Florida (Fig. 1). Sampling in 1992 was conducted from April through August, and in 1993 from May through August by using baited chevron-shaped (arrowhead) fish traps (Collins, 1990) soaked for 90 min during daylight only. The time of trap deployment was recorded as time of catch. Some (n=24) fish were collected with hook-and-line gear fished at dawn or dusk (Collins and Sedberry, 1991). Measurements taken from the vermilion snapper catches were lengths in mm (total length [TL] and fork length [FL])

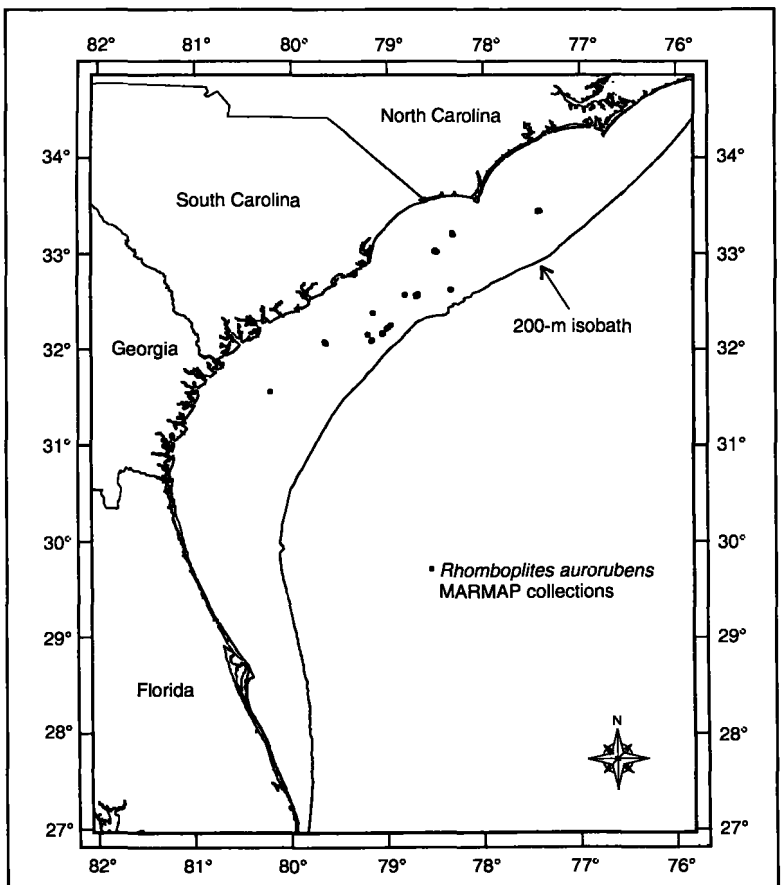

Figure 1

MARMAP station locations of vermilion snapper, *Rhomboplites aurorubens*, captured from April to August 1992 and in May 1993. (n=110)

and weights (g/total body weight and g/ovary-free body weight [OFWT] ±1 g). Ovaries were removed, blotted dry, and weighed and fixed in 10% buffered seawater formalin. After fixation, samples of ovarian tissue were weighed with an Ohaus digital balance (±0.001 g) for fecundity determination. Conversion factors were developed for samples taken during the first three months of the study because fresh gonad weight and OFWT were not measured. When sampling was not untertaken (September to April), additional samples were purchased from the commercial hook-and-line catch landed in Georgetown, South Carolina. Commercial samples were used for histological examination (see below), both to define the spawning season and to gather atresia measurements.

A modified gonadosomatic index (GSI) was used to quantify the reproductive cycle. The GSI was calculated as $GSI = (gonad\ weight/OFWT) \times 100$ (Nieland and Wilson, 1993; Nikolsky, 1963). In order to make comparisons with the findings of Grimes (1976), the following gonad index (GI) equation was used:

$$K_G = (WT_G / TL^3) \times 10^6,$$

where WT = preserved weight of the gonad (g), and
TL = total length (mm).

GI values from Grimes (1976) were compared with GI values from the present study to evaluate possible differences between the two studies in reproductive timing and size and age at maturity.

A chi-square test was used to evaluate the sex ratio of vermilion snapper. A 2 × 2 contingency table was used to compare the sex ratios in Grimes (1976) with those in the present study and to compare MARMAP samples with commercial samples (Zar, 1984). Sex-ratio data were also analyzed by 50-mm length classes by using a 2 × 4 contingency table (Zar, 1984).

Histological analysis was used to assess maturity and spawning activity and to verify whole-oocyte staging. Gonad sections were prepared according to the methods of Wenner et al. (1986). The developmental stage of each ovary was identified by using the criteria of Hunter et al. (1992) (Table 1). Each ovary was also examined for the presence or absence of the two stages of postovulatory follicles (POF's). Testes were classified by means of the modified criteria of Wyanski and Pashuk[2] (Table 2).

Maturity definitions I–V from Hunter et al. (1992) were used to classify females. Mature females included the following: all active females; all inactive mature females; inactive females with early yolked oocytes and with alpha, beta, or no atresia; and inactive females with unyolked oocytes and with alpha or beta atresia (Table 1). If testes were developing, ripe, spent, or resting, they were considered mature (Table 2).

Transverse sections of otoliths were made with a Buehler Isomet low-speed saw. Sections were mounted on slides, immersed in cedarwood oil, and viewed under a dissecting microscope. The dissecting microscope was linked by a video camera to a MATROX frame grabber and personal computer with OPTIMAS image analysis software.

The following fecundity definitions from Hunter et al. (1992) were used in the present study:

Determinate fecundity	Annual fecundity is fixed prior to the onset of the spawning season.
Indeterminate fecundity	Annual fecundity is not fixed prior to the onset of the spawning season, and unyolked oocytes continue to mature and are spawned during the spawning season.
Annual fecundity (AF)	Total number of eggs spawned per year.
Total fecundity (TF)	Standing stock of advance-stage yolked oocytes (AYO's).
Potential fecundity (PF)	Total AYO's that mature per year. Potential fecundity was considered to be equivalent to the standing stock of AYO's in fully developed prespawning females.
Batch fecundity (BF)	Total number of hydrated oocytes (HO's) released in one spawning.

If vermilion snapper is a determinate spawner, then the following are expected: a hiatus will develop in the frequency distribution of oocyte diameter between the oocytes that mature for the season and the reservoir of less advanced oocytes present year round; TF declines over the spawning season; mean oocyte diameter (MOD) increases over the spawning season; and the spawning order of batches is consistent with the determinate fecundity definition (see Hunter et al., 1992).

To determine whether AYO's were randomly distributed throughout the ovary, the densities of AYO's at six locations within the ovaries of nine fish were

[2] Wyanski, D. M., and O. Pashuk. 1996. Processing and interpretation of fish reproductive tissue at the Marine Resources Research Institute of the South Carolina Department of Natural Resources. In preparation.

compared. The locations were anterior, center, and posterior in both the left and right lobes of the ovary. A wedge from the exterior of the ovary to the interior of the ovary was taken for each location sampled. A two-way ANOVA was run to test for effects of location and individual fish on oocyte density.

Whole oocytes were staged by using the criteria of Hunter et al. (1992). Yolk density was used to discriminate between the different developmental stages of oocytes, with counts of stage-3 AYO's (Fig. 2A) being the basis of TF estimates. The definitions of each stage were as follows:

Stage 1 Initial layer of yolk along the periphery of the oocyte appearing as a narrow band but not extending over 20% of the distance

Table 1

Histological stages of female vermilion snapper, *Rhomboplites aurorubens*, modified from Hunter et al. (1992).

Inactive	Active
Not capable of spawning now or in the near future.	Capable of spawning now or in the near future. Ovary contained enough advanced yolked-oocytes (AYO's) for one spawning.
Mature Ovaries show clear evidence of past spawning or past maturation of AYO's.	**Mature** AYO's present with no or minor (<49%) alpha atresia of AYO's.
Postspawning. Contains either postovulatory follicles (POF's) and no AYO's, or contains POF's with mostly atretic AYO's.	Spawning. Evidence of past spawning (POF's) or imminent spawning (hydrated oocytes [HO's]) or migratory nucleus-stage oocytes (MNO's).
Major atresia. AYO's present, alpha atresia of AYO's ≥50%.	Nonspawning. No evidence of recent or imminent spawning, but fish are capable of spawning in the near future.
Uncertain maturity No AYO's present.	
Early yolked. Early yolked oocytes present. May have alpha, beta, or no atresia of early yolked oocytes.	
Unyolked. Unyolked oocytes present. Alpha or beta atresia of unyolked oocytes evident.	
Immature Unyolked oocytes present with no atresia.	

Table 2

Histological staging of male vermilion snapper following modified criteria developed by Wyanski and Pashuk (1990).

Inactive	Active
Not capable of spawning now or in the near future.	Capable of spawning now or in the near future.
Mature Spent. No spermatogenesis; some residual sperm in tubules and lumina.	**Mature** Developing. A few primary and secondary spermatocytes through tubules and lumina (no spaces) with spermatozoa.
Resting. Large cross section compared to immature male; little or no spermatocyte development; empty tubules and lumina evident.	Ripe. Predominance of spermatozoa; areas of spermatogenesis toward outer surface of testes in some specimens.
Immature Small cross section compared to resting male; little or no spermatocyte development; empty tubules and lumina not evident.	

between the nucleus and the zona pellucida (egg diameter ~0.15–0.25 mm)

Stage 2 Lightly packed yolk possibly extending from the periphery to the nucleus with the nuclear area still evident (~0.25–0.35 mm)

Stage 3 Yolk dense enough to occlude the nucleus (~0.35–0.45 mm)

Stage 4 Parts of the dense yolk become translucent usually beginning at the periphery (~0.45–0.60 mm)

Stage 5 Oocyte is translucent except for the oil droplet (~0.60–1.25 mm).

Alpha-atretic AYO's were not included in TF estimates.

To estimate total fecundity, whole oocytes were examined by using a modified version of the hydrated oocyte method of Hunter et al. (1985). Each sample weighed approximately 50 mg and consisted of about 100 to 150 oocytes. Three diameter measurements per oocyte were taken and then averaged to obtain a mean oocyte diameter (MOD). A mean of the MOD's of all AYO's in the two samples taken from each female was calculated for 138 females and then analyzed for TF. Oocytes on each gridded slide were counted, measured, and staged with GLOBAL LAB image analysis software linked by a video camera system to a compound microscope. The following fecundity equation was used to assess TF:

$$TF = Z \times C,$$

where Z = ovary weight in grams, and
C = oocyte density (number of AYO's per gram of ovarian tissue).

To see if time had an impact on TF, TF was regressed on OFWT and on days elapsed since 15 April. Also, an ANCOVA was performed on monthly TF regression equations to see if there was a temporal effect on TF.

To see if atresia had any effect on fecundity estimates, the proportion of atretic oocytes was calculated for each whole oocyte sample that was counted. The number of alpha atretic AYO's in a sample was divided by the total number of AYO's in that sample (Hunter et al., 1992). Atresia subclasses were defined by Bretschneider and Duyvene de Wit (1947) and Hunter and Macewicz (1985). Alpha atresia involves the reabsorption of the entire oocyte, and beta atresia involves the major degeneration and reabsorption of the follicle (Hunter and Macewicz, 1985). Three subclasses of alpha atretic AYO's were noted: no atresia, minor atresia (1–49%), and major atresia (50–100%).

To estimate PF, only females from the beginning of the spawning season that showed no recent signs of spawning (presence of HO's or POF's) were used in analyses. Because PF is estimated at the beginning of the season, some oocytes may not have yet been recruited into the stock of advanced yolked oocytes. To find the size at which oocytes are fully recruited, a series of stepwise multiple regressions was run on 59 females (Table 3). Data were removed by 0.005 mm increments beginning with the lowest diameter class of 0.360 mm. Analysis indicated that the threshold for a significant effect of diameter on PF occurred between 0.445 mm and 0.450 mm. The regression coefficient for oocyte diameter was significant for females with a MOD equal to or less than 0.445 mm but insignificant for females with a MOD

Figure 2

Photographs of whole oocytes of vermilion snapper at 40×: (**A**) stage-3 advanced yolked oocyte (AYO), in which the oocyte is completely opaque except the perivitelline border; (**B**) late migratory nucleus-stage oocyte (MNO), in which some droplets of the peripheral yolk have coalesced and become translucent; and (**C**) hydrated oocyte (HO), in which the whole oocyte is translucent.

Table 3

Results of a stepwise multiple regression of the total fecundity of vermilion snapper on ovary-free weight and mean oocyte diameter for a succession of oocyte diameter classes. Dashed line separates oocyte diameter classes, where diameter is a significant variable, from those where it is not.

	Multiple regression coefficient and t-ratio						
	Constants		Fish weight		Oocyte diameter		
Oocyte diameter class (mm)	n	a	b_1	t	b_2	t	r^2
0.360–0.470	59	–271,217	83.5	2.73	720,838	5.86	0.405
0.365–0.470	58	–273,751	84.0	2.71	726,434	5.57	0.384
0.370–0.470	57	–274,239	84.1	2.66	727,502	5.24	0.357
0.375–0.470	55	–267,604	84.1	2.56	712,304	4.56	0.306
0.380–0.470	52	–228,103	87.9	2.54	620,040	3.34	0.230
0.385–0.470	50	–242,944	106	2.95	645,696	3.31	0.260
0.400–0.470	48	–239,170	112	3.04	634,478	2.98	0.248
0.405–0.470	47	–229,442	189.3	4.15	578,788	2.87	0.347
0.410–0.470	41	–247,829	210.5	4.47	611,076	2.55	0.385
0.415–0.470	40	–233,730	214.7	4.48	577,705	2.33	0.389
0.420–0.470	34	–295,305	222.9	5.24	711,614	2.86	0.506
0.425–0.470	27	–312,154	355.1	6.66	694,250	2.52	0.684
0.430–0.470	24	–300,087	364.1	6.45	663,948	2.09	0.680
0.435–0.470	18	–501,504	389.7	6.64	1,093,714	2.63	0.750
0.440–0.470	16	–510,147	398.6	6.74	1,108,996	2.40	0.782
0.445–0.470	13	–700,475	551.9	5.41	1,462,344	2.85	0.770
0.450–0.470	7	–652,740	536.4	2.37	1,365,795	.855	0.749

greater than 0.445 mm. Thus, only females with a MOD greater then 0.445 mm were used to estimate PF. Fecundity was regressed on OFWT to evaluate the predictability of the relationship.

Batch fecundity was determined by calculating the number of migratory nucleus-stage oocytes (MNO's; Fig 2B) or hydrated oocytes (HO's; Fig. 2C) in two weighed subsamples from each female (Hunter et al., 1992). Ovaries that contained hydrated oocytes loose in the lumen were eliminated from BF analyses. A modified version of the hydrated oocyte procedure of Hunter et al. (1985) was also used in BF estimates. Definitions from Hunter et al. (1992) were used to separate each spawning batch (Table 4). To see if batch size varied with the order of spawning, a one-way ANOVA was run on 49 females. To evaluate the temporal effects on BF, ANCOVA was run on monthly equations of BF.

Exact ages of POF's were not known because sampling on MARMAP cruises occurred only from dawn through dusk and because trap deployment time was assigned to the catch, regardless of when the fish entered the trap. Therefore, we defined POF's in terms of "new" and "old," on the basis of data from reports in the literature and from our observations. There is limited work on other lutjanids (Davis and West, 1993); thus, descriptions from Hunter and Macewicz (1985) were also used to define POF's. New POF's were generally large and had an orderly arrangement of distinct columnar granulosa cells with prominent nuclei intact (Fig. 3A). New POF's resembled the early stage POF of *Lutjanus vittus* (Davis and West, 1993). Old POF's were small, coiled, eosin-

Table 4

Batch number classification for vermilion snapper following Hunter et al. (1992).

Batch number	Definition
1	Nonhydrated advanced yolked oocytes (AYO's) present and post-ovulatory follicles (POF's) absent.
2	One class of POF's and nonhydrated AYO's present.
3	Two classes of POF's and nonhydrated AYO's present.
4	Only one batch of migratory nucleus-stage oocytes (MNO's) and one batch of hydrated oocytes (HO's) present, no other AYO's present.
5	Only one batch of HO's present, no other AYO's present.

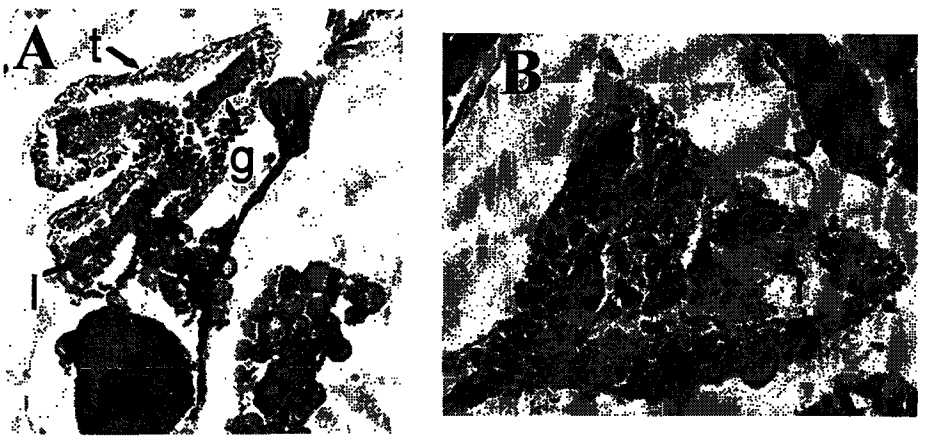

Figure 3

Photographs of histological section of the ovary of vermilion snapper, showing (**A**) new postovulatory follicle (POF) at 100×, in which the columnar granulosa cells with prominent nuclei are distinct and the lumen is visible, and (**B**) old POF at 400× with a typical triangular shape, in which most of the granulosa cells without nuclei are disintegrating. (g=granulosa layer, t=thecal layer, l=lumen)

y–stained structures with approximately half to very few of the granulosa cells intact (Fig. 3B). Old POF's resembled 1-day-old POF's of *Engraulis mordax* (Hunter and Macewicz, 1985). To confirm temporal trends in the occurrence of hydrated females, the samples collected for this study were supplemented with additional histological slides (from spawning females collected on MARMAP research cruises in 1991 and June to August 1993) for examination of POF age.

To calculate spawning frequency, the method of Fitzhugh et al. (1993) was used to calculate overall percentages of HO's, new POF's, and old POF's. A proportion was computed for each category by dividing the total number observed in each category by the total number of mature females. An overall average was computed by summing the three category proportions and by dividing by three. The overall average was then multiplied by number of days in the spawning season to determine spawning frequency. We defined the spawning season as the date (15 April 1992) when spawning condition was histologically evident until the date (24 September 1992) when major atresia of AYO's first occurred. If the proportions for each criterion were independent of those of other criteria and similarly distributed, then they could be combined to increase the sample size (Alheit et al., 1984). If spawning frequencies are to be combined, they must not be statistically different; therefore, we used the Mann-Whitney test to examine differences between frequencies of the HO's versus new POF's and between new POF's versus old POF's.

Results

Sex ratio, ovarian development, maturity, and spawning season

Vermilion snapper did not exhibit a 1:1 sex ratio; females were 63% of the samples (Table 5). Comparisons of sex ratio by 5-cm length classes revealed significant differences from a 1:1 ratio for every length class. Trap and hook-and-line samples collected during MARMAP cruises and samples collected by the commercial hook-and-line fishery yielded similar sex ratios. The sex ratio from Grimes (1976) was comparable to the sex ratio for all samples of vermilion snapper in this study.

Oocyte size-frequency (percent) distributions for five oocyte stages (Fig. 4) revealed the developmental sequence of ovary maturation. Oocyte size was correlated with stage of development; however, there was considerable overlap in size between stages. This asynchronous pattern of development means that the number of batches cannot be inferred from the size-frequency distribution of oocytes.

The mean oocyte diameter (MOD) appeared constant over the spawning season (Fig. 5). This is evidence that oocytes matured and were developing throughout the spawning season.

Table 5

A comparison of sex ratios among different groups of vermilion snapper.

Comparison group (and ratios)	χ^2	P	Result
Females vs. Males: (62.6% vs. 37.4%; 1.67:1)	6.35	$0.025<P<0.01$	Significant difference from 1:1 ratio.
MARMAP catches (67% female) vs. commercial catches (57% female)	1.72	$0.10<P<0.25$	No significant difference between the sex ratios of MARMAP catches and commercial catches.
Length-class comparison 20–24 cm TL: 62.7% female 25–29 cm TL: 66.5% female 30–34 cm TL: 64.3% female 35–39 cm TL: 68.1% female	9.92	0.0193	Significant difference from 1:1 ratio within each 5 cm length classes.
Grimes (1976) vs. present study (62.5% vs. 62.6% females, respectively)	0.01728	$0.75<P<0.90$	No significant difference between overall sex ratios of Grimes (1976) and the present study.

All vermilion snapper in this study were mature. Of the 750 females (Table 6) and 254 males (Table 7) examined histologically, the smallest female was 165 mm FL (186 mm TL) and smallest male 179 mm FL (197 mm TL). Ages of 176 females ranged from 2 to 10 yr; 87 males ranged from 3 to 11 yr (Tables 6 and 7).

Owing to gear selectivity, fish under two years old were not found in the present study; however, three- and four-year old fish were about the size of those found by Grimes (1976) (Fig. 6). After age four, fish in the present study were dramatically smaller than fish in the study by Grimes (1976).

The spawning season of vermilion snapper was from April to September (Fig. 7). The mean gonadosomatic index (GSI) for females increased in April and was high through August, decreasing in September. Mean GSI values remained constant from October through March. Spawning was first evident histologically on 15 April 1992 and no longer evident in sections taken at the end of September 1992. Gonad index (GI) values of Grimes (1976) for 1973–74 showed trends similar to those for GI values from this study (Fig. 8).

Reproductive activities of males began earlier in the year and lasted longer in the season than did the reproductive activity of females (Fig. 9). Percentages of active males and females were similar for July, August, and September. There were reproductively active portions of the population present from April through October (during which period there were correspondingly higher GSI values for females).

Table 6

Number of mature specimens by size class for 750 female vermilion snapper. Specimens with evidence of histological criteria I–V (see Hunter et al., 1992) were considered mature. All females were examined histologically.

	Age (yr)										
FL (mm)	2	3	4	5	6	7	8	9	10	11	No age
151–175											1
176–200	1	6	3	3	1	1					142
201–225	2	3	6	6	4	2	2				227
226–250	1	2	4	22	12	4	2				92
251–275		2	9	14	6	5	1	2			60
276–300	1		5	17	4	1					31
301–325			3	2	4	1	1	1			13
326–350			2	1	1	1					3
351–375				1		1	2		1		5
Total	5	13	32	66	32	16	8	3	1		574

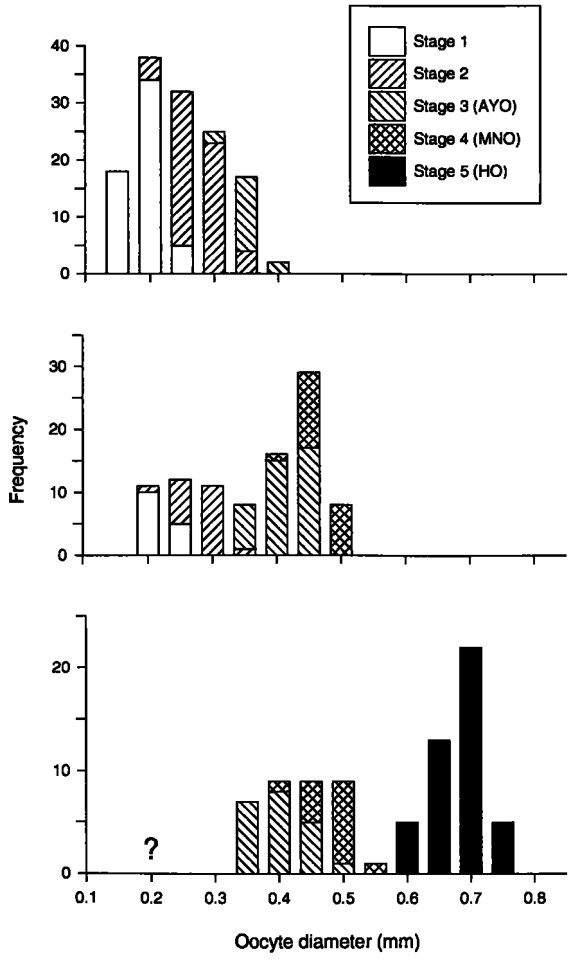

Figure 4

Oocyte size-frequency (percent) distributions and oocyte stage of three mature vermilion snapper representing the developmental sequence of maturation. Females were collected in May and length range was 192 mm to 213 mm FL. (? = stages that were not counted.)

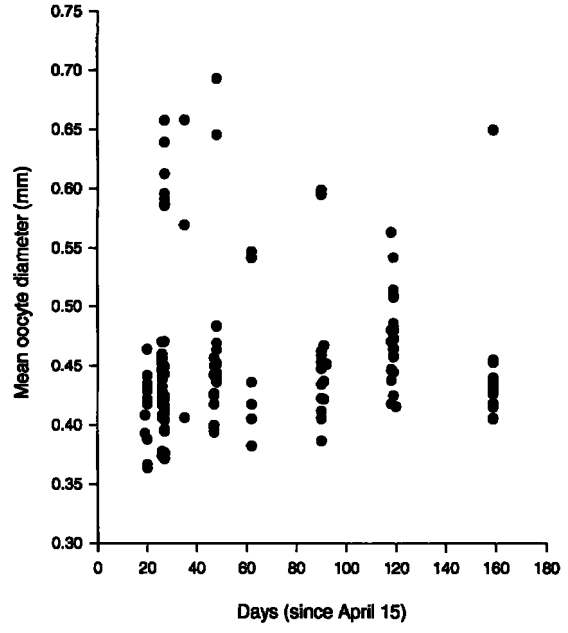

Figure 5

Mean oocyte diameter of vermilion snapper versus number of days since April 15.

Fecundity

Location of oocytes within the ovary revealed no significant effect on oocyte density (Table 8). Advanced yolked oocytes (AYO's) were randomly distributed within the ovary; samples could be taken from any location within the ovary without bias.

The relationship between ovary-free body weight (OFWT) and potential fecundity (PF) was expressed by the following equation:

$$PF = -25{,}992 + (508 \times OFWT).$$

The coefficient of determination (r^2) was 0.583 for the 13 fish used in the analysis (Fig. 10). The PF ranged from 17,374 to 122,130 oocytes for an OFWT range of 109 g to 265 g.

Monthly mean TF estimates of vermilion snapper increased from 54,100 oocytes in May (n=16, OFWT range 109–194 g) to 118,500 in August (n=25, OFWT range 108–442 g); then decreased to 58,200 in September (n=15, OFWT range 106–238 g). Analysis of covariance of monthly equations of TF on OFWT indicated that equations were similar over the spawning season (Fig. 11). The slopes of the equations were similar (F=0.02984, df=4,85, P>0.25) and, assuming a common slope, there was no significant difference in intercepts between months (F=0.02936, df=4,89, P>0.25). Regression of TF on OFWT for days elapsed since 15 April indicated that the coefficient for elapsed days was not significant (t=1.338, df=94, P=0.1842). Thus, TF did not decline continually over the spawning season.

In whole oocyte samples used to estimate fecundity, the average fraction of AYO's that were atretic was 0.011 (SD=± 0.023, n=138). Minor alpha atresia of AYO's was observed in 29% of the fish used in fecundity estimates. A stepwise multiple regression of OFWT, days, and atretic fraction of AYO's on TF, indicated that the coefficient for the atretic fraction of AYO's was not significant and thus atresia does not result in a significant loss of oocytes (Table 9).

Table 7

Number of mature specimens by size class for 254 male vermilion snapper. Males were classified as mature based on criteria in Table 2. All males were examined histologically.

	Age (yr)										
FL (mm)	2	3	4	5	6	7	8	9	10	11	No age
151–175											0
176–200			2	2							40
201–225				5	2	2	1				50
226–250		1	2		1	1					28
251–275		1	13	14	3	6	1	1	1		22
276–300			7	6	3	1					19
301–325			1	1	1						5
326–350			1	3	1					1	2
351–375				1	1						0
376–400											1
Total		2	26	32	12	10	2	1	1	1	167

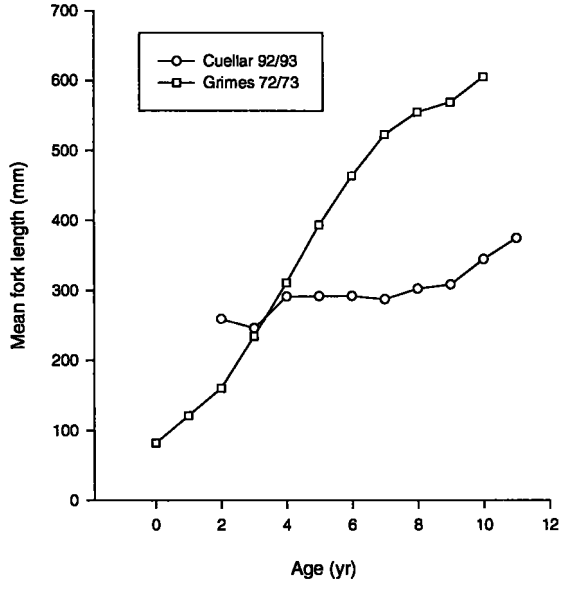

Figure 6

A comparison of mean fork length (at capture [in mm]) at age for vermilion snapper from 1972–73 (Grimes's study) with fork length at age from 1992 to 1993 (present study).

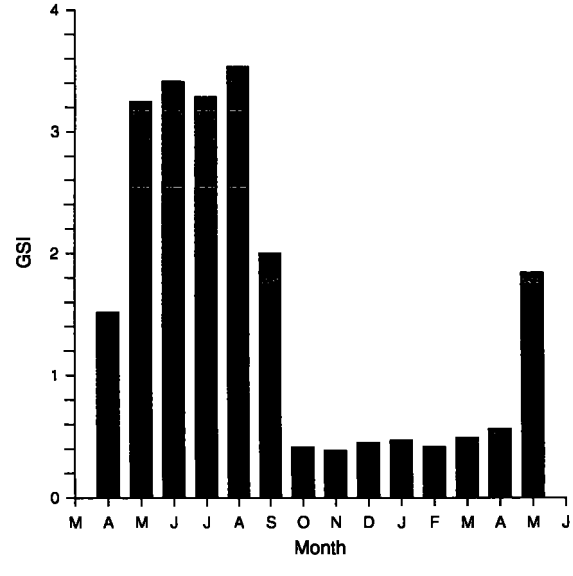

Figure 7

Gonadosomatic index (GSI) values by month for female vermilion snapper that were collected from April 1992 through May 1993. GSI = gonad weight (g)/ovary-free body weight (g).

Histological examination for alpha atresia of samples with AYO's (n=410) revealed that only 2% of all females had major alpha atresia of AYO's and that 27.5% had minor alpha atresia of AYO's (Table 10). Percentages of minor and major alpha atresia of AYO's were similar between whole oocyte samples and histological samples.

A one-way ANOVA on 49 females detected no significant difference among batch sizes (Table 11). All spawning batches were found throughout the spawning season, with batch 1 and batch 2 having the highest percentages in each month (Fig. 12). The relationship between fish length and batch fecundity was best described by the following equation, with r^2= 0.444 (Fig. 13):

Table 8

Effect of location of tissue samples within the ovary on oocyte density (number of advanced oocytes per unit sample weight) vermilion snapper for mean, standard deviation (SD), and two-way analysis of variance of results are given.

	Location of sample			Oocyte density	
Position no.	Lobe	Long. plane	*n*	Mean	SD
1	Left	Anterior	9	4470.7	3311.8
2	Left	Center	9	5730.9	4721.0
3	Left	Posterior	9	4660.6	3266.1
4	Right	Anterior	9	3619.7	2112.3
5	Right	Center	9	5746.9	2629.3
6	Right	Posterior	9	4633.3	2501.3

Analysis of variance on six locations within the ovary of vermilion snapper

Source	df	Sum of squares	Mean square	*F*	*P*
Fish	8	150,536,374.2	18,817,046.8	2.007	0.0704
Location	5	29,043,522.9	5,808,704.6	0.620	0.6855
Error	40	374,972,921.2	9,374,323.0		
Total	53	554,552,818.3	10,463,260.7		

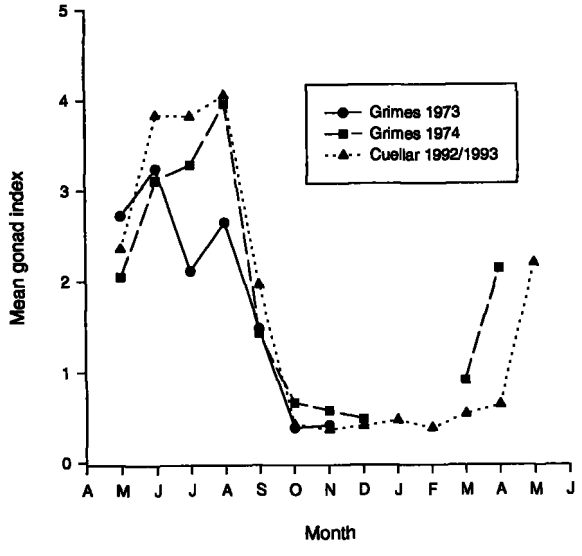

Figure 8

A comparison of mean gonad index [K_G=(WT_G/TL^3) × 10^6] by month for vermilion snapper from 1973 and 1974 (Grimes, 1976) with mean gonad index by month in the present study (1992–93).

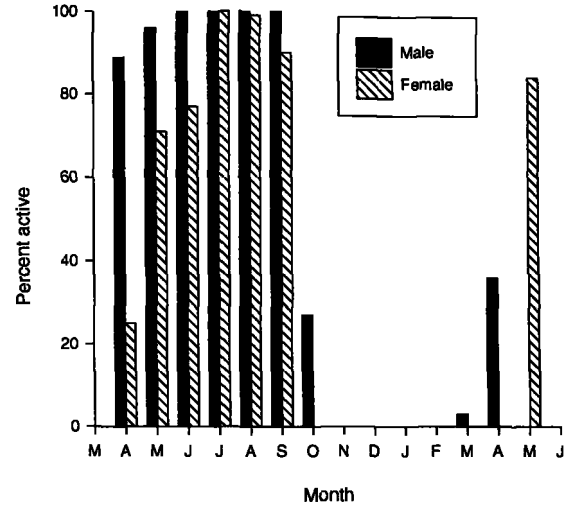

Figure 9

Percentages of reproductively active male and female vermilion snapper in each month from April 1992 through May 1993.

$BF = 0.0438FL^{2.508}$ (F=37.6, df=1,47, P <0.0001);

and the relation between OFWT and batch fecundity by the following equation, with r^2 = 0.332 (Fig. 14):

$BF = 14{,}037 + (112 \times OFWT)$ (F=23.3, df=1,47, P<0.0001).

Batch fecundity varied remarkably among fish of the same size (Table 12; Fig. 13). ANCOVA was run on monthly linear regression equations of FL on BF.

This analysis indicated that the slopes were similar between months (F=0.06548, df=4,44, P>0.25). Assuming a common slope, we concluded that there were no differences among intercepts of each month (F=1.90, df=4,44, 0.10<P<0.25). The variation of BF estimates was high (4,000–90,000 oocytes), and there was not a significant difference in BF between months.

Spawning frequency

Although no significant temporal trends in the frequencies of POF's were evident, the following observations provide a preliminary age to new POF's of vermilion snapper. MARMAP sampling occurred

Table 9

Analysis of the relation between total fecundity on ovary-free body weight (OFWT), on elapsed days since April 15, and on fraction of atretic oocytes of vermilion snapper with stepwise regression. Boldface refers to the coefficient of the atretic fraction of oocytes.

	Step		
	1	2	3
Constant	26,848.2	–6,968.8	–9,117.2
OFWT	258.8	291.7	293.7
t	6.398	7.620	7.597
P			<0.0001
Days		403.1	415.9
t		4.703	4.589
P			<0.0001
Atretic oocytes			81177.8
t			**0.445**
P			0.6574
r^2	0.2313	0.3395	0.3405
Adjusted r^2	0.2257	0.3298	0.3258

Table 10

Histological determination of number of vermilion snapper with no atresia, minor atresia (<49%), and major atresia (>50%) of advanced yolked oocytes (AYO's) expressed as a percentage of all females with AYO's during the spawning season (April–October).

State	Atresia	Percentage	Number
Nonspawning	none	41.4	172
Nonspawning	minor	22.4	93
Spawning	none	28.2	117
Spawning	minor	5.1	21
Inactive	major	2.2	9
Total			415
Total samples without AYO's			335
Total: minor		27.5	114
Total: major		2.2	9

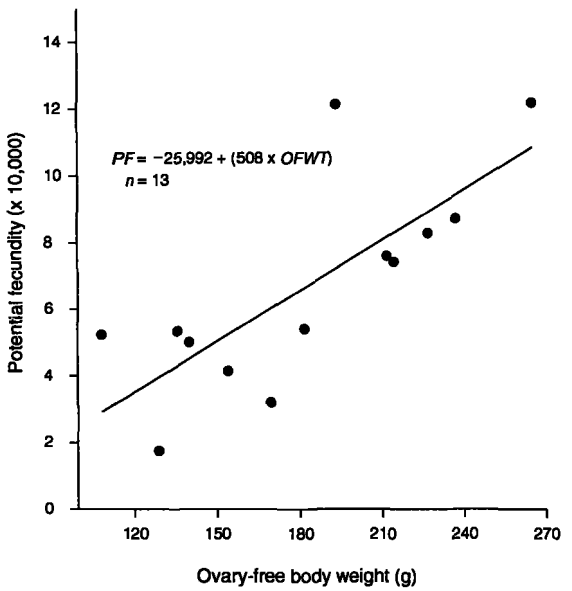

Figure 10

Linear regression of potential fecundity (PF) of vermilion snapper on ovary-free body weight (OFWT).

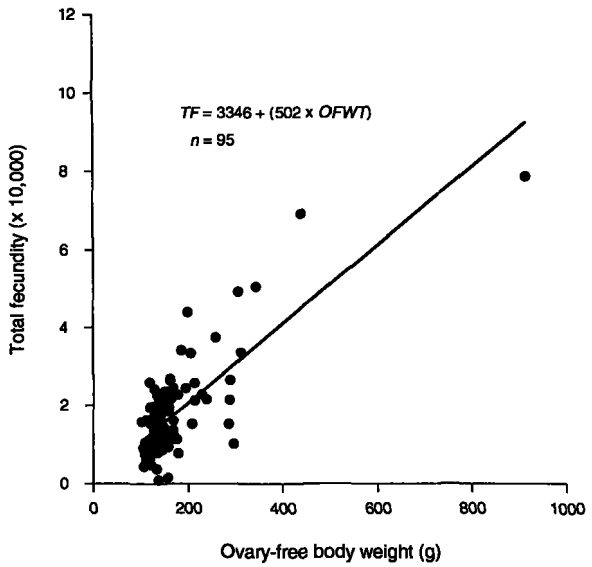

Figure 11

Linear regression of total fecundity (TF) of vermilion snapper on ovary-free weight (OFWT) in g.

from approximately 0800 to 1900 h local (Eastern) time and in all fish examined from samples collected during MARMAP cruises from 1991 to 1993, 70–100% of spawning females (i.e. those with hydrated oocytes (HO's); n=54) were captured between 1300–1900 h. During the April 1992–May 1993 sampling,

Table 11

Mean relative batch fecundity for five batch order numbers. Relative batch fecundity = number of oocytes/ovary-free body weight.

Batch number	No. of females	Relative batch fecundity Mean	SD
1	14	202	125
2	14	174	73
3	2	271	34
4	16	193	59
5	3	186	111

ANOVA on five batch orders

Source	df	Sum of squares	Mean square	F	P
Batch order	4	34,753.7	8,688.4	1.331	0.282
Error	44	189,321.1	6,528.3		
Total	48	367,605.5	7,658.4		

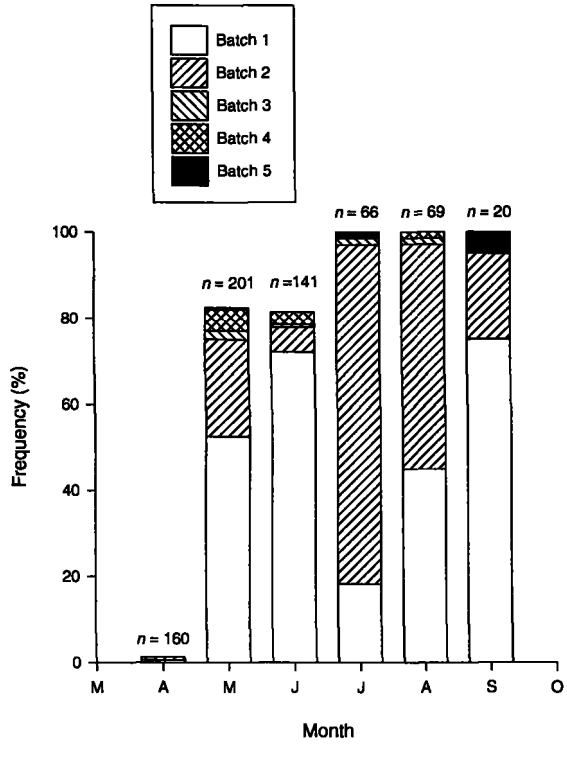

Figure 12

Percent frequencies of batch numbers by month for vermilion snapper. Definitions for batch numbers are listed in Table 4. n = total number of females collected each month.

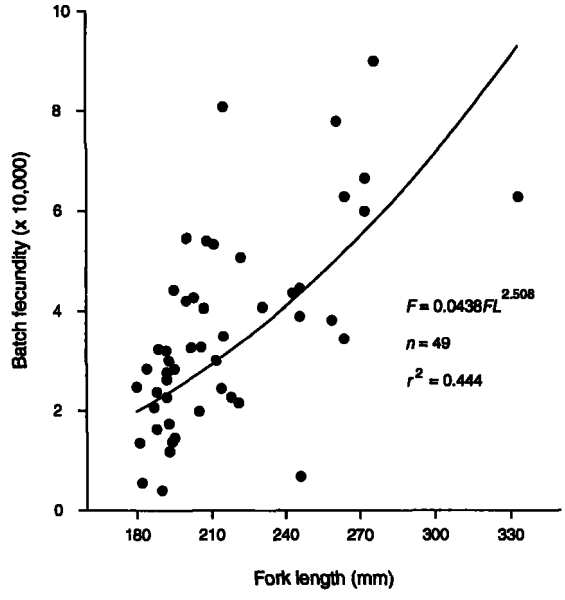

Figure 13

Nonlinear regression of batch fecundity (BF) of vermilion snapper on fork length (FL) in mm.

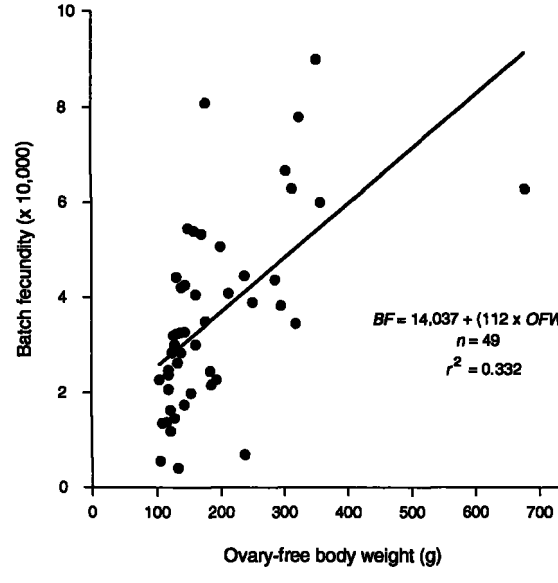

Figure 14

Linear regression of batch fecundity (BF) of vermilion snapper on ovary-free weight (OFWT) in g.

80% of hydrated females (n=10) were found between 1300–1800 h. In 1992, 70% of fish with new POF's (n=25) were collected between 0800–1200 h. Histological examination of 128 females (from April 1992 to May 1993 [MARMAP sampling]) revealed that only two fish had hydrated oocytes (HO's) as well as old POF's and that only seven fish had two classes of POF's (new and old). Because new POF's in lutjanids are ~12–24 hours old (Davis and West, 1993), these new POF's in vermilion snapper indicate that spawning took place during the previous afternoon or evening.

In 23 collections, 3.5% of spawning females had HO's, 8.9% had new POF's, and 30.5% had old POF's (Table 13). This finding corresponded to a spawning periodicity of about every seven days or 23 times per

Table 12

Fork length (FL), ovary-free body weight (OFWT), batch fecundity (BF), and annual fecundity (AF) ranges by month for vermilion snapper from the southeastern United States. Annual fecundity is the batch fecundity multiplied by the spawning frequency (35 times). n = number of specimens.

Month	n	FL range (mm)	OFWT range (g)	BF range (no. of oocytes)	AF range (no. of oocytes)
May	17	180-333	109–678	4,005–90,000	140,175–3,150,000
Jun	11	187–259	119–296	16,312–54,519	570,920–1,908,165
Jul	9	182–211	105–170	5,520–53,972	193,200–1,889,020
Aug	9	195–264	124–313	28,289–80,848	990,115–2,829,680
Sep	3	188–246	119–238	6,846–23,685	239,610–828,975

Table 13

Numbers of female vermilion snapper with histological evidence of spawning used to determine spawning frequency. Hydrated oocytes (HO's), new postovulatory follicles (POF's), and old POF's were classified according to descriptions from Hunter and Macewicz (1985) and Davis and West (1993) (See Fig. 3, A and B). Sampling period in 1992 was 162 days. Total % was calculated by dividing the total of each category by the total number of mature females (282) and by multiplying by 100.

Date	Collection	No. of HO's	No. of new POF's	No. of old POF's	Total mature
15 Apr	1077			1	1
4 May	1129–1133			1	8
20 May	1169–1173	2	4		8
1 Jun	1175–1180			4	37
2 Jun	1183–1188	1	1	3	33
2 Jun	1203	1			7
16 Jun	1241			1	25
16 Jun	1246–1248	2			8
14 Jul	1312–1317		6	1	13
14 Jul	1319–1323			5	6
14 Jul	1331–1333	2		1	4
15 Jul	1336–1340		4		5
15 Jul	1342–1347		4		4
15 Jul	1351–1352			3	5
16 Jul	1355–1358		1	10	12
16 Jul	1362–1364		1	18	19
11 Aug	1371			1	1
11 Aug	1373			1	1
11 Aug	1378–1384	1		7	13
12 Aug	1388–1390			11	22
12 Aug	1395			12	24
13 Aug	1408–1410			6	6
21 Sep		1	4		20
Total		10	25	86	282
Total %		3.50	8.90	30.50	

year. From visual observations of histological slides, it appeared that the duration of HO's and new POF's might be more similar than the duration of new POF's and old POF's. Thus, we decided to test the populations statistically to see if this might be true. There was no difference in the frequencies of HO's and new POF's (Mann-Whitney, n=23, P=0.675), but there was a significant difference in the frequencies of new POF's and old POF's (Mann-Whitney, n=23, P= 0.00598). Thus, HO's and new POF's probably have similar durations that allow us to combine the categories statistically to increase the sample size. An overall average was recalculated by summing only two categories ((*HO+new POF*)/2, and *old POF*) and by dividing by two. This overall average was then multiplied by days in the spawning season to determine a new spawning frequency. Combining categories results in a spawning frequency of approximately every five days or 35 times per year. The duration between new POF's and old POF's was long enough that the combination of categories was not statistically possible.

Discussion

Hunter et al. (1992) listed four lines of evidence that indicate determinate fecundity (see Materials and Methods section). Vermilion snapper, however, is an indeterminate spawner because it does not demonstrate any of the four characteristics given for determinate fecundity. Each line of evidence is addressed in detail in the following section.

The oocyte size-frequency distribution is continuous in vermilion snapper (without a hiatus between any oocyte stages) except for the hydrated batch. Traditional evidence for determinate fecundity is 1) the obvious gap in oocyte maturity stages or size classes among the oocytes that are maturing during the season and 2) the reservoir of less mature oocytes present year-round in the ovary (Yamamoto, 1956). Although the absence of such a hiatus is evidence for indeterminate fecundity, in some cases fish with a continuous oocyte distribution are still considered to have determinate fecundity (Hunter and Macewicz, 1985). In such cases, the product of batch fecundity multiplied by spawning frequency needs to be compared with the standing stock of mature oocytes at the beginning of the season. For example, a 300-g vermilion snapper in this study produces approximately 126,408 oocytes on the basis of the potential fecundity equation, whereas a 300-g female produces approximately 1.7 million oocytes according to the product of BF multiplied by spawning frequency. It is quite obvious from this study that the product of BF multiplied by spawning frequency must be used to estimate annual fecundity.

The mean oocyte diameter of vermilion snapper stayed constant over the spawning season. Species with determinate fecundity would produce larger oocytes as the season progressed because, as maturation continued during the spawning season, no new oocytes would be recruited into the advanced stock, and eggs that were present would be developing and increasing in size. In contrast, indeterminate spawners are continually producing oocytes during the spawning season, with smaller immature oocytes replacing those that mature and are spawned, resulting in a constant MOD.

Total fecundity and BF in vermilion snapper did not consistently decline over the spawning season as would be expected if the vermilion snapper was a determinate spawner. Total fecundity and BF actually increased through August and declined in September in this study. No trends in TF existed over the months of the spawning season. Atresia also had no significant effect on fecundity estimates to account for a decrease in the number of oocytes. Similarly, Davis and West (1993) found that the BF of *Lutjanus vittus* did not decline over the spawning season. Vermilion snapper in the northern central Gulf of Mexico appear to have a similar trend of peak spawning in late summer according to larval abundances found in that area (Comyns and Lyczkowski-Shultz[3]). Grimes (1976) found peak spawning activity (according to gonsomatic index [GSI] values) in August off the Carolinas, and Nelson (1988) found peak activity in the Gulf during the summer. This trend toward peak spawning during middle to late summer would be expected for an indeterminate spawner with continuous development of oocytes over the reproductive season.

The order of spawning batches was not consistent with the determinate fecundity prediction. Of 750 females examined histologically, three had hydrated oocytes (HO's) in the ovary in the absence of any other advanced-stage yolked oocyte (AYO) batch, and only 16 had a batch of early migratory nucleus-stage oocytes (MNO's) and a late HO batch. Many of the females sampled from September contained all mature oocyte stages, except in the HO batch.

According to Hunter and Macewicz (1985), determinate fecundity is generally found in species in cooler climates and with shorter spawning seasons. Many fishes (snappers, grunts, jacks, dolphin, some

[3] Comyns, B. H., and J. Lyczkowski-Schultz. 1993. Spawning and early life history of snappers in the northcentral Gulf of Mexico. Proceedings of the sixth annual MARFIN conference; Atlanta, Georgia, 12–13 October 1993, p. 1–3.

porgies, and sea basses) in the Carolinas have a protracted spawning season extending from early spring to early fall (Hardy, 1978; Johnson, 1978; Grimes, 1987). The southeastern United States has temperate and tropical characteristics, with surface water temperatures from about 22°C to 29°C (Mathews and Pashuk, 1986) and bottom temperatures of 15°C to 25°C on the middle continental shelf (18–60 m) during summer (present study). Vermilion snapper fit the expectation of being indeterminate spawners on the basis of the temperate and tropical characteristics of this area and on the basis of their long spawning season.

Length was the best predictor of batch fecundity, but great variability was seen in BF estimates for same-size fish, perhaps because some oocytes may have been spawned. This is not likely, however, because fish with hydrated oocytes free in the lumen and fish with postovulatory follicles (POF's) were not used in BF estimates. The monthly average BF appeared to peak in August and decline in September. However, time (months) did not have a significant effect on BF estimates, and it is unlikely that differences in station locations within the sampling area could account for the variation in BF. Davis and West (1993) suggested that the variation seen in BF estimates of *Lutjanus vittus* might be due to the collection of samples during various phases of the lunar cycle. *Lutjanus vittus* seemed to follow a lunar rhythm in spawning, as do many lutjanids (Grimes, 1987; Carter and Perrine, 1994). Thresher (1984) suggested that lunar periodicities are probably universal in lutjanids. Environmental cues of spawning events were not examined in this study; however, Grimes (1976) found that vermilion snapper spawning correlated with temperature and photoperiod, but not with the lunar cycle.

Because of differences in fecundity estimation methods, comparisons between the present study and that of Grimes (1976), or with most other studies on lutjanids, are not particularly useful (Grimes, 1987). For example, Grimes (1976) estimated fecundity on vermilion snapper taken off the Carolinas early in the season. He counted all developing oocytes in each female (the total count is approximately equivalent to a PF estimate in this study). His fecundity equation for a 300-g fish results in a fecundity estimate of 49,152 oocytes, compared with a PF of 126,408 oocytes for the same size fish in the present study.

Collins and Johnson[4] used the hydrated oocyte method (Hunter et al., 1985; Hunter and Macewicz, 1985) for spawning frequency and annual fecundity measurements of vermilion snapper in the northeastern Gulf of Mexico. The spawning frequency (44 times per year) of vermilion snapper in the Gulf exceeded spawning frequency in this study (35 times per year). Also, the annual fecundity of the vermilion snapper in the Gulf (1.32 to 21.9 million eggs) was much higher than the annual fecundity determined in the present study for vermilion snapper in Atlantic waters off the southeastern United States (140,175 to 3.2 million eggs). The spawning season of vermilion snapper in the Gulf is slightly longer than the spawning season of vermilion snapper in the southeastern United States (April to late September), and this additional time in the warmer waters of the Gulf may result in the differences in annual fecundity estimates between the two regions. The use of the hydrated oocyte method instead of the postovulatory method to estimate spawning frequency may also account for the difference between the two studies.

Larger fish in the Gulf study may also account for some of the differences in annual fecundity estimates between the two studies; however, the sizes of fish studied by Collins and Johnson[4] were not available. The largest female in the present study was 440 mm TL, but the majority of the vermilion snapper were between 200 mm TL and 300 mm TL. It is generally accepted that larger females produce more oocytes. Grimes and Huntsman (1980) found that fecundity increased dramatically in larger (older) vermilion snapper.

Davis and West (1993), using new assessment techniques, found that the annual fecundity of a 300-mm *Lutjanus vittus* was about 4.5 million oocytes (if it spawned 90 times a season) or 7.6 million oocytes (if it spawned 150 times a season) on the northwest shelf of Australia. This annual fecundity estimate for *Lutjanus vittus* is closer to the annual fecundity estimate for vermilion snapper (140,175 to 3.2 million eggs) in this study than to the estimate for vermilion snapper calculated by Collins and Johnson.[4] Examination of the annual fecundity estimates reveals that the major difference between vermilion snapper and *Lutjanus vittus* is spawning frequency. Batch sizes were relatively similar: a batch size for a 300-mm *L. vittus* was about 71,000 oocytes and a batch size for a similarly sized vermilion snapper was about 50,000 oocytes. The spawning season for *Lutjanus vittus* is year round, and most spawning occurs from September to April. The longer spawning season of *L. vittus* accounts for a major portion of the large difference in spawning frequency between the two species.

In the vermilion snapper of our study, POF's could not be given an exact age because of a lack of 24-h sampling and because of small sample sizes; therefore time of day for spawning could not be deter-

[4] Collins, L. A., and A. G. Johnson. 1994. Spawning and annual fecundity of gag, red snapper and vermilion snapper in the northeastern Gulf of Mexico. Southeastern U.S. and Caribbean reef fish workshop: Charleston, South Carolina, 15–16 September 1994 [abstract].

mined. Because of these limitations the spawning-frequency estimate calculated in this study should be considered preliminary. More detailed work needs to be done to calculate a more representative spawning-frequency estimate for the population in this region. Additional work should include sampling over a 24-h period for a series of days during the spawning season to define POF age from a larger number of fish.

In spite of limitations, a preliminary estimate of spawning time and POF duration can be derived from the literature and our observations. Postovulatory follicles in *Lutjanus vittus* persist for only about 24 h (Davis and West, 1993), and POF's in vermilion snapper may be similar in duration owing to the higher temperature of shelf waters during the spawning season, which may accelerate reabsorption of POF's (Hunter and Macewicz, 1985). Most lutjanids appeared to spawn at dusk (Wicklund, 1969; Starck and Schroeder, 1971; Thresher, 1984) but recently some lutjanids were found to spawn in the mid-afternoon (Davis and West, 1993; Carter and Perrine, 1994). In addition, vermilion snapper are nocturnally active (Grimes, 1979; Sedberry and Cuellar, 1993); thus spawning activity may continue into the night. In the present study, some vermilion snapper appeared to spawn from mid-afternoon to early dusk, as do other lutjanids; when the majority spawn was not determined.

A comparison of the sex ratio, based on present data and Grimes (1976), indicated that the sex ratio of vermilion snapper had not changed in 20 years (62.6 and 62.5% females, respectively). Sex ratios for western Atlantic snappers often deviate from 1:1, with males outnumbering females in more cases than the reverse (Grimes, 1987). MARMAP data collected with standardized methods over a 15-yr period revealed an increase in the percentage of females in the vermilion snapper population in the region from about 60% in 1978–79 to about 72% in 1991–93 (Zhao and McGovern[1]). This change in sex ratio has occurred in spite of no significant difference in fishing mortality (F) between males and females (Zhao and McGovern[1]). Temperature changes have been known to induce change in sex ratio in fish (Lagomarsino and Conover, 1993) but summer water temperatures on the middle and outer continental shelf off the southeastern United States have been remarkably uniform for the 17 years preceding this study (National Environmental Satellite, Data, and Information Service[5]). Decreases in mean size of vermilion snapper in recent years are well documented (Collins and Sedberry, 1991; Zhao and McGovern[1]). This change in size may be caused by intense fishing, which is believed to have resulted in fewer individuals and smaller fish size (Collins and Pinckney, 1988; Bas and Calderon-Aguilera, 1989; Sutherland, 1990) and, hence, reduced fecundity (PDT, 1990). Unknown compensatory mechanisms may be at work under the intense selection pressure exerted by fishing on vermilion snapper; these mechanisms may result in altered sex ratios to compensate for reduced individual fecundity.

All vermilion snapper in this study were mature, with the smallest fish measuring 186 mm total length (TL). The smallest aged fish was two years old at 186 mm TL. Grimes (1976) found most mature fish at age three were 186–256 mm TL and at age four were 256–324 mm TL; only a few individuals matured in their second year at approximately 150 mm TL. After age four, vermilion snapper in our study were much smaller than those in the study by Grimes (1976). The size difference could, again, be explained by increased fishing pressure or by the fact that Grimes (1976) used scales and whole otoliths, not sectioned otoliths, to determine age. Collins and Pinckney (1988), like Grimes (1976), used scales rather then sectioned otoliths and found that 60% of females and 90% of males mature at 160 mm TL. Recently, Zhao and McGovern[1] found mature vermilion snapper at an even a smaller size, with 100% of males and females mature at 140 mm TL. This change in size at maturity may be a result of fishing pressure.

Vermilion snapper has a protracted spawning season throughout the summer months in the southeastern United States. The gonad index used by Grimes (1976) indicated that vermilion snapper in this area spawn from late April to September. In the Carolinas and Georgia, Powles (1977) and Fahay (1975) found high abundances of larvae during July–September, although they did not sample beyond that period of time. Nelson (1988) and Collins and Johnson[4] found that the spawning season of vermilion snapper occurred during spring and summer in the Gulf of Mexico. Also in the Gulf of Mexico, Comyns and Lyczkowski-Shultz[3] indicated that spawning occurred from May through September on the basis of abundance of larvae. However, in Puerto Rico, Boardman and Weiler (1979) found that vermilion snapper spawned year round, and Munro et al. (1973) found a ripe female vermilion snapper in November in Jamaica. Restricted spawning and year-round spawning in the same species may reflect a difference between temperate and tropical locations, or as Grimes (1987) suggested, a difference between con-

[5] National Environmental Satellite, Data, and Information Service. 1992. Oceanographic monthly summary, July 1978–July 1992. U.S. Dep. Commer., National Ocean Service, National Weather Service. Ocean Products Division, Camp Springs, MD.

tinental versus insular populations of snappers. Vermilion snapper in this study had a spawning season similar to many other continental populations of snappers as reviewed by Grimes (1987).

Grimes (1987) suggested that restricted spawning in continental species may be linked to the production cycle of the environment. Off the southeastern United States, upwelling occurs year-round, but it increases dramatically in spring and summer as the Gulf Stream moves farther offshore, allowing deep waters to upwell near the shelf break (Atkinson et al., 1985; Mathews and Pashuk, 1986). Topographic features in this area (i.e. the Charleston Bump) also cause upwelling events that bring nutrient-rich bottom water to the shelf areas (Mathews and Pashuk, 1986). Periodic meanders and eddies from the Gulf Stream add to the mechanism in which productivity of the shelf increases over the summer months. Phytoplankton blooms develop rapidly within the surface nutrient-rich water (Atkinson et al., 1984), thereby providing a large food source for larval and juvenile fishes. Spawning during this time of high productivity maximizes the survival of the larvae and juveniles of many of the reef fishes of the southeastern United States.

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