REPRODUCTIVE BIOLOGY OF THE VERMILION SNAPPER, *RHOMBOPLITES AURORUBENS*, FROM NORTH CAROLINA AND SOUTH CAROLINA

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ABSTRACT

The vermilion snapper, *Rhomboplites aurorubens*, a species often associated with Caribbean reefs and banks, is an important recreational fish of the outer continental shelf of North Carolina and South Carolina. Serial spawning occurs from late April through September off the Carolinas at depths ranging from 31 to 91 m. Most females spawn in the third or fourth year at about 205-275 mm total length. Larger, older females (age 5-10; up to 530 mm total length) appear to spawn longer each reproductive season, which may be an optimal strategy for maximizing reproductive biomass (balancing the physiological costs of somatic and gonadal growth).

Overall sex ratio is unequal in favor of females (approximately 60%), but the ratio is 1:1 for small fish (less than 150 mm total length) and heavily in favor of large females (69-100% for fish greater than 500 mm total length) because they live longer than males. Fecundity of first spawners is estimated at 17-42 thousand eggs, and large females produce 1.5 million eggs.

The vermilion snapper, *Rhomboplites aurorubens*, is a small lutjanid which grows to 600 mm total length (TL) and 2,600 g (illustrated in Böhlke and Chaplin 1968). It occurs from Cape Hatteras, N.C., to Bermuda, southward throughout the Gulf of Mexico and Caribbean Sea to southeastern Brazil. The species is abundant, ranking second or third in weight and numbers in the Carolina headboat[3] fishery (which landed between 590 and 730 metric tons of demersal fishes annually) between 1972 and 1975 (Huntsman 1976).

Vermilion snapper and other reef fishes normally associated with deep (>70-90 m) Caribbean reefs and banks occur in two habitats of the outer continental shelf of the Carolinas (Figure 1). The most spectacular of the habitats, the shelf break zone (Struhsaker 1969), occurs at the edge of the continental shelf (55-180 m) where the gently sloping bottom plunges abruptly downward as the continental slope. It is an area of jagged peaks, precipitous cliffs and rocky ledges associated with drowned Pleistocene reefs (MacIntyre and Milliman 1970). The second habitat (inshore live bottom) occurs at 25-55 m and consists of broken reefs and rock outcroppings, rocky ledges, and coral patches dispersed over the continental shelf shoreward of the shelf break zone.

Knowledge concerning reproduction of the vermilion snapper is lacking. Longley and Hildebrand (1941) reported gravid specimens about the Tortugas, Fla., in July and concluded that spawning takes place in midsummer. Breder (1929) wrote that vermilion snapper probably spawn in early spring along the South Atlantic coast of the United States, and Walker (1950) reported spawning off North Carolina in February. Monroe et al. (1973) collected a ripe female off Jamaica in November, and Fahay (1975) and Laroche (1977) recorded larvae off Georgia in July and August. Erdman (1976) found ripe fish from February through June in the northeastern Caribbean.

In this paper we describe the seasonality, spawning frequency, sex ratio, age and size at maturity, and fecundity of the vermilion snapper and discuss possible adaptive strategies for its reproduction.

The study area (Cape Hatteras, N.C., to Charleston, S.C.) was stratified by depth (i.e., inshore and offshore, the dividing depth being 55 m), and specimens were collected throughout. Most fish were obtained from the recreational fisheries throughout the Carolinas; however, some specimens were collected by hook and line or trawl from

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[3]Headboats are recreational fishing vessels which charge anglers for a day's fishing on an individual, thus "per head," basis.

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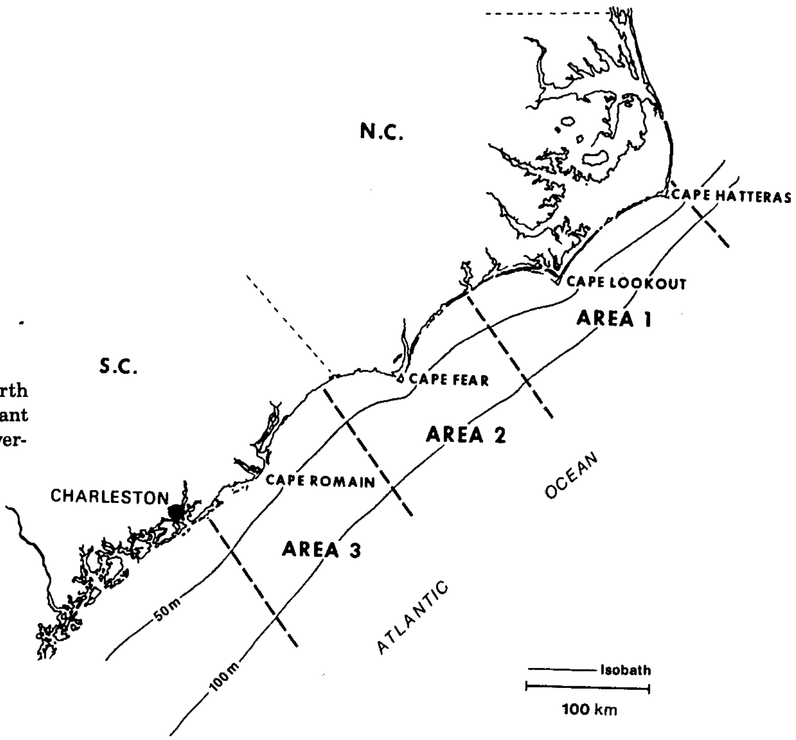

FIGURE 1.—Continental shelf off North Carolina and South Carolina and important bathymetric features that relate to the vermilion snapper study.

the RV *Onslow Bay* and the RV *Eastward*; most juveniles were trawled from RV *Dolphin*.

Temperature was taken by expendable bathythermograph, and photoperiod was obtained from the National Ocean Survey tide tables (U.S. Department of Commerce 1971, 1972, 1973). Specimens were weighed (nearest gram) and measured (nearest millimeter). Gonads were removed, preserved in 10% Formalin[4] for at least 1 wk, washed in tap water for several days, and then placed in 70% isopropyl alcohol. Frequency distributions of ovum diameters were plotted by month to determine seasonality, frequency, and duration of spawning (Hickling and Rutenberg 1936; Fahay 1954). The diameters of approximately 100 randomly selected ova from each of two females per month were measured to the nearest 0.05 mm by dissecting binocular microscope at 25×. To validate measuring ova from any portion of an ovary, we determined by analysis of variance that ova sizes were distributed uniformly (indicating uniform development) throughout the ovaries (Table 1).

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Later, the gonads were removed from preservative and weighed (nearest 0.1 g) after surface moisture was absorbed by blotting.

A gonosomatic index was used as a measure of reproductive development (Finkelstein 1969) for determining spawning seasonality and maturity. The index was calculated according to the formula $KG = W/TL^3$ where KG = gonad index, W = preserved (blotted dry) gonad weight in grams, TL = total length in millimeters. We realize that assuming the cubic relationship is arbitrary. Quast (1968) has shown for kelp bass, *Paralabrax clathratus*, that the percentage of body weight contained in gonads increases with fish length. Therefore, the true exponent is undoubtedly >3, but data limitations preclude more accurate formulation.

Ovaries used for fecundity studies were preserved in modified Gilson's fixative (Bagenal and Braum 1968). The ovarian tunic was removed and washed free of adhering ova. Additional washings separated developing ova from undifferentiated oöcytes and follicular material. A small subsample of ova (about 1,000 or less) was stored wet for later counting in a gridded Petri dish under a binocular dissecting scope. Subsamples and origi-

TABLE 1.—Analysis of variance testing the hypothesis that there is no difference in ovum diameters between anterior, posterior, and center sections of ovaries from three vermilion snapper. NS = not significant.

Fish no.	Source of variation	df	MS	*F*
1	Between sections	2	1.0769	0.46 NS
	Within sections	309	2.341	
2	Between sections	2	0.5417	0.97 NS
	Within sections	309	0.5770	
3	Between sections	2	29.907	1.09 NS
	Within sections	309	27.3512	

nal ova samples (total sample minus counting subsample) were drained and dried for 24 h at 40° C. Subsample and original ova sample dry weights were determined to 0.001 g on a beam balance, and the sum of these two weights provided the total ova sample dry weight. Fecundity was determined by proportionality where:

$$\frac{\text{fecundity}}{\text{total ova dry weight}} = \frac{\text{number of ova in subsample}}{\text{subsample dry weight}}.$$

Fecundity models were fitted by semilog transformation (log fecundity = $a + b \times$ length, weight, or age) and regressions are the functional regressions of Ricker (1973). The semilog formulation of fecundity models was used instead of more traditional log-log models because they fit the data best.

RESULTS

Seasonality, Frequency, and Duration of Spawning

Several lines of evidence indicate that spawning occurs from late spring through early fall. Males and females with ripe-appearing gonads were collected from late April through September, but few females were collected with ova loose within the ovarian tunic. Microscopic examination of preserved ovaries showed three types of maturing ova present during this period (in addition to maturing ova, undifferentiated transparent oöcytes were present and were by far the most numerous): the smallest developing ova (0.11-0.2 mm in diameter) were translucent and were the most numerous developing type; the next largest ova (0.33-0.43 mm in diameter) were nearly opaque throughout and less abundant than the preceding; the largest developing ova (0.46-0.71 mm in diameter) were typical mature teleost eggs with opaque cytoplasm occupying one pole of the egg which also contained transparent to translucent yolk material and oil globules. We observed these most mature ova only in ovaries collected from May to September, although what appeared to be ripe ovaries were also seen in April; furthermore, these mature ova occurred in only 7 of 149 ripe-appearing ovaries examined.

Frequency distributions of maturing ovum diameters (Table 2) show at least two size modes of ova present from April to October (three were present in one of two June samples), while only one smaller size mode or undifferentiated oöcytes were present in November, December, and March. No ova collected in January or February were examined. These data indicate spawning begins in late April or May and continues through September or perhaps early October.

Monthly mean gonad index values for 101 sexually mature females, sampled from May 1972 to April 1974, also denote late spring to fall spawning (Figure 2). No fish were collected in January or February 1973 or 1974; however, adult females collected in February 1975 had gonad index values of 0.51 and 0.40 which are consistent with gonad index trends indicated in Figure 2. Increasing

TABLE 2.—Developing ovum diameter-frequency distributions (percent) from two female vermilion snapper that were examined during various months of the study.

0.08 mm interval (midpoint)	1972 May	June	July	Aug.	Sept.	Oct.	Nov.	1973 Mar.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	1974 Apr.
0.06				1													
0.14	40	45	39	29	35				35	16	17	28	19	80	100		26
0.22	27	13	32	15	8				21	49	22	36	38	12			17
0.30	11	7	7	2	1				10	5	5	11	16				14
0.38	11	10	6	9	12				5	9	17	10	13	6			13
0.46	4	25	2	8	41				28	15	36	9	13	2			27
0.54	4		1	13	3				1		3	6	1				3
0.62	3		5	23								2					
0.70			8							4							
0.78										2							
Total	194	198	172	214	227				179	199	209	200	197	100	100		200
Mean, mm	0.25	0.27	0.27	0.37	0.32	—	—	—	0.28	0.29	0.34	0.27	0.27	0.17	0.14	—	0.3

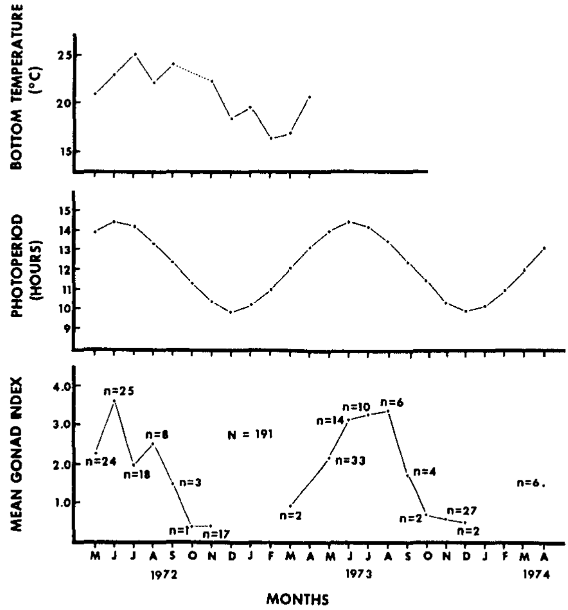

FIGURE 2.—Monthly mean gonad index of female vermilion snapper collected from May 1972 to April 1974, mean bottom temperatures at collecting sites, and photoperiod (U.S. Department of Commerce 1971, 1972, 1973).

monthly mean gonad index is well correlated with lengthening photoperiod and increasing bottom temperature.

The seasonal occurrence of juveniles and the large size variation within the youngest age-group provides additional evidence of an extended summer spawning season. During October and November 1973, several hundred juveniles ranging from 53 to 227 mm TL were trawled in Long Bay, N.C. and S.C., and also off Charleston. Aging of these fish from scales showed the sample to contain mostly age-groups 0 and 1. Using the growth rate for the first year of life (Grimes 1978) for extrapolating backwards, we determined that the age 0 fish collected in October and November 1973 were spawned throughout the summer months.

Although actual spawning was never observed, it probably occurs around rough bottom from 31 to 91 m but may be more concentrated in deeper areas (55-91 m). Ripe fish were taken over rough bottom at depths of 31-91 m when bottom temperatures were 20.6°-24.8° C. In Raleigh Bay and northern Onslow Bay, ripe fish were more abundant from 55 to 91 m; however, in the southern portion of the study area (southern Onslow Bay and Long Bay) ripe individuals were more equally distributed with depth.

Reproductive synchrony within schools may be indicated by hook-and-line sampling. Fish were usually caught in sudden bursts of fishing activity; seldom were single individuals encountered. Gonad indices for fish of similar size caught over a short time interval (probably from the same school) were nearly identical, indicating that reproduction within schools may be highly synchronized.

Multiple spawnings each season are indicated by the relative abundance of ova types (described earlier) at different times during the spawning season (Table 2). Maturing ova were present April through October and spawning apparently takes place during this period. Early in the spawning season (May) all three developing ova types were present in considerable abundance. When ripe ova were present later in the season (June or July), fewer smaller developing ova occurred. In August and September (late in the spawning season) when ripe ova were present, smaller developing ova were absent. The total of the developing ova types may represent all that will be spawned that season, and at each spawning a female develops only as many ova as her abdominal capacity will allow. This process could be repeated a number of times during the season until all eggs are spawned.

Variation in gonad index during the spawning period for similar size fish may also indicate fractional spawning. This was evident during the spawning months of 1972 and 1973 when the gonad index of both males and females of similar size varied by as much as a factor of 12 (Figure 3). The small size of ripe gonads combined with high fecundity (see subsequent discussion) is additional evidence for fractional spawning. The mean percent of body weight (observed) for ovaries of mature females collected during spawning months was 2.4% (0.6-5.8%, n = 40). Mature males had testes averaging 1.1% of body weight (0.4-2.4%, n = 15) during the same months. Also, we frequently observed semiflacid ovaries with no loose ova (perhaps partially spawned) in large adult females from June through September.

Maturation

Age and growth data of Grimes (1978) and our reproductive data indicate that most fish attain sexual maturity during their third or fourth years of life (186-256 and 256-324 mm TL), but a few

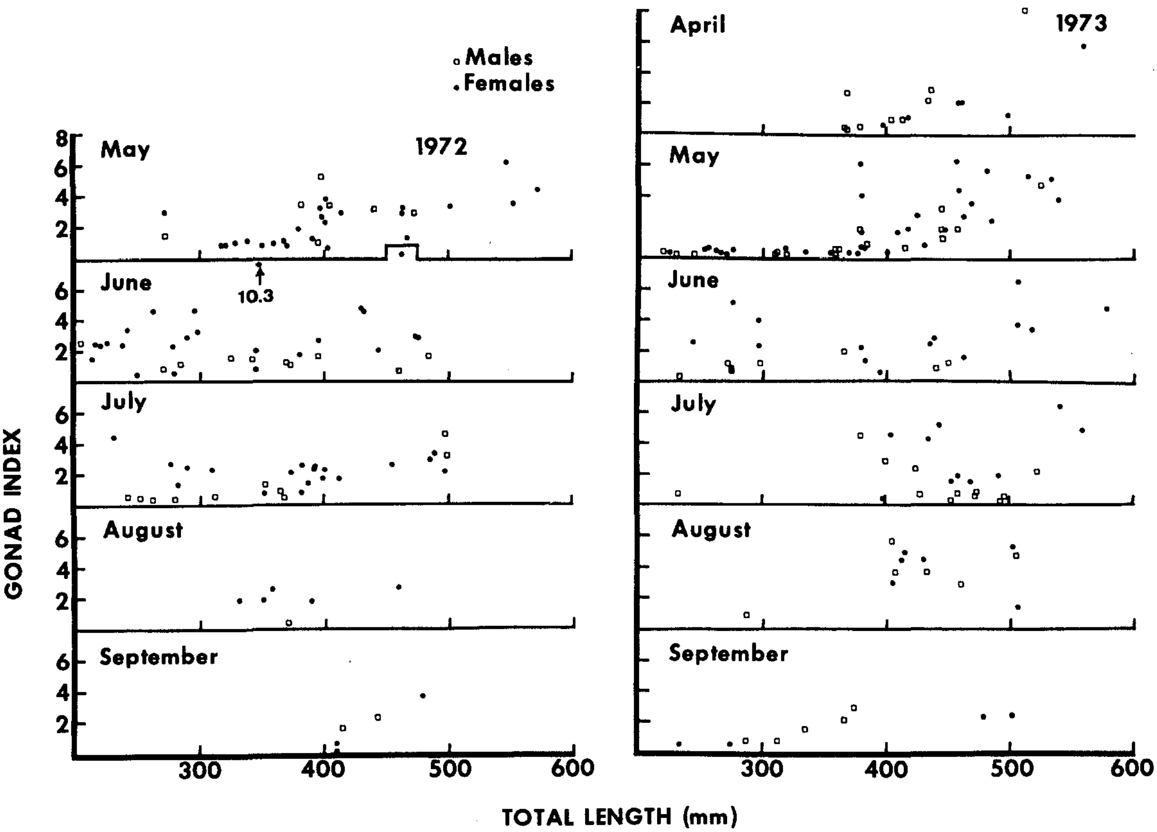

FIGURE 3.—Individual gonad index (gonad weight/(total length)[3]) values for vermilion snapper over the spawning months of 1972 and 1973 plotted against total length.

precocious individuals may mature in their second year (100-186 mm TL) at about 150 mm TL. We determined age and size at maturity by examining a plot of monthly mean gonad index of females collected in the spawning season (June-September) by total length (Figure 4). Furthermore, spawning season (April-September) gonad index values for males and females (Figure 3) and monthly mean gonad index for each age-group of fish (Figure 5) show that fish age 4-9 (>324 mm TL) ripen earlier (April or May vs. June) and remained in reproductive condition longer (April to September vs. June to August) than younger spawning fish.

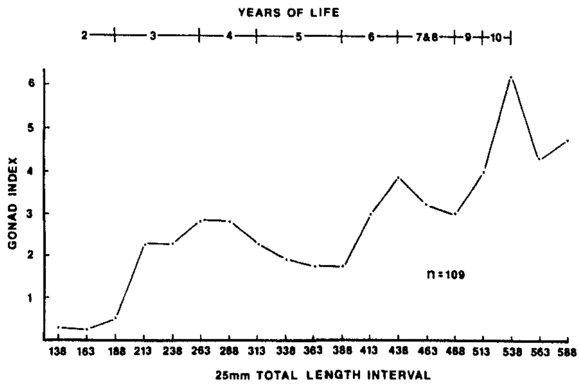

FIGURE 4.—Mean gonad index plotted by 25 mm TL intervals for female vermilion snapper during the spawning season (June-August). Approximate size at age was determined from Grimes (1978).

Sex Ratio

Sex ratio varies significantly from 1:1. From 1972 to 1974 we sexed 874 fish; 546 (62.5%) were females and 328 (37.5%) were males (1 df; χ^2 = 54.4; P<0.001). The total sample was analyzed by year of collection and sex ratios were judged significantly different from 1:1 in all years (Table 3). Higher proportions of females (62.5%) were col-

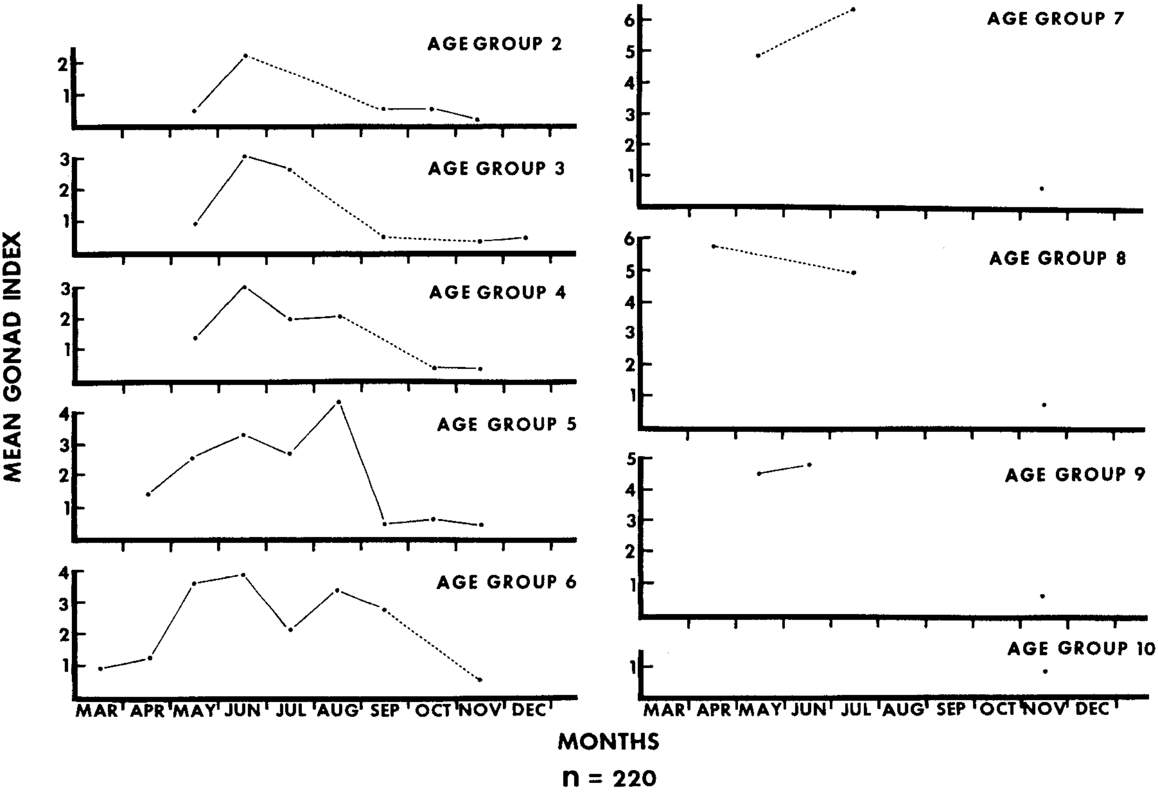

FIGURE 5.—Monthly mean gonad index (gonad weight/(total length)^3) for female vermilion snapper by age-group.

TABLE 3.—Test of the hypothesis that sex ratios of vermilion snapper did not vary significantly from 1:1 within years of collection.

Item	1972	1973	1974
Percentage of females	71.9	59.4	62.5
Sample size	135	424	315
Chi-square value	25.8*	15.1*	20.8*

*P<0.01.

TABLE 4.—Tests of the hypothesis that sex ratio of vermilion snapper did not vary significantly from 1:1 within 50 mm TL intervals.

Total length (mm)	n	Females (%)	Chi-square	Total length (mm)	n	Females (%)	Chi-square
101-150	105	49.5	0.0096	401-450	102	63.8	7.19*
151-200	117	63.4	8.83*	451-500	60	61.7	3.27
201-250	68	49.3	0.014	501-550	58	69.2	7.69*
251-300	99	61.2	4.94*	551-600	32	89.3	17.28*
301-350	90	59.4	3.38	601-650	1	100	
351-400	142	65.9	12.7*				

*P<0.05.

lected at shelf break habitats than inshore live bottom (60.5%), but the hypothesis that sex ratio and capture depth were independent was not rejected (χ^2 P>0.05, n = 852).

There is a significant difference in sex ratio throughout the life of the fish (as estimated by total length); however, differences within some size intervals were not judged significant (Table 4). Contingency-table analysis showed that sex ratio and size were dependent (χ^2 P>0.05, df = 9) (i.e., with growth sex ratios were different from 1:1 and changed significantly). In small fish (101-150 mm TL) the number of males and females was nearly equal, but at 151-200 mm TL the percentage of females increased to about 60%, where it remained somewhat stable until 501-550 mm TL, when percentage of females began to steadily increase (Table 4). Only one fish >600 mm TL was collected (618 mm) and it was a female.

Fecundity

Estimates of fecundity ranged from 8,168 to 1,789,998 ova for 41 females ranging from 229 to 557 mm TL (3-8 yr old and 136-2,293 g). Because females may spawn several times per season, fecundity estimates were from ovaries collected early in the spawning season (May and June) and all classes of maturing ova were counted.

In Table 5, fecundity was separately regressed on total length (millimeters), weight (grams), and age (years) and, as expected, fecundity increases as a function of all three correlates. Fecundity increases so markedly in larger (older) fish (Figure 6) that semilog models were needed to adequately describe the relationship between fecundity and length, weight, and age. Length and weight are approximately equally good predictors of fecundity (r = 0.864 and 0.863, respectively). First spawners probably are about 205-275 mm TL and produce between 16,800 and 41,700 eggs. This estimate assumes that spawning extends from late June through September for young fish (age 2-4), that first spawning occurs in the third or fourth year (186-256 or 256-324 mm TL), that scale annuli form in March (Grimes 1978), and that approximately 25% of annual growth occurs from annulus formation to late June.

TABLE 5.—Functional equations for fecundity in vermilion snapper. Age (A) determined from scales.

Predictor	Equation	r	n
Total length (mm)	F = exp (7.07 + 0.013TL)	0.863	41
Age (yr)	F = exp (7.57 + 0.873A)	0.853	41
Weight (g)	F = exp (10.21 + 0.002W)	0.864	41

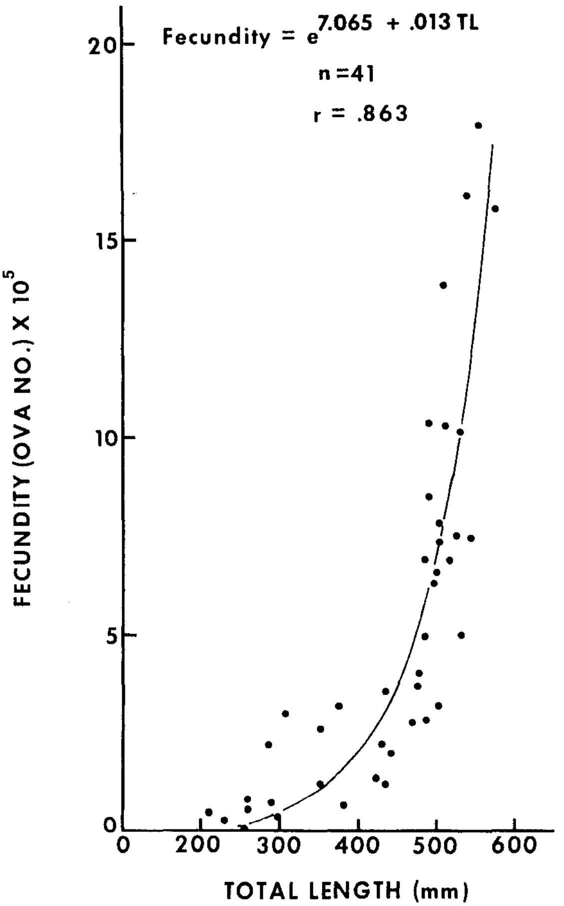

FIGURE 6.—The relationship of fecundity to total length of female vermilion snapper.

DISCUSSION

Spawning Seasonality

The conclusion that spawning occurs from late April through September is corroborated by Longley and Hildebrand's (1941) statement that spawning took place in summer around the Tortugas. Powles[5] and Fahay (1975) reported that larvae were collected at the surface off South Carolina and Georgia in June and July, and Laroche (1977) described a larval series collected off Georgia in August. Walker (1950), however, reports collecting vermilion snapper in spawning condition off North Carolina in February. Erdman (1976) sampled 400 vermilion snapper in the northeastern Caribbean and found fish in spawning condition January through June. Monroe et al. (1973) collected a ripe female in November off Jamaica and suggested, on the basis of these and more extensive data for other reef species, that spawning probably occurs year-round in the Caribbean, but that peak spawning is in winter where surface temperature is about 26.5° C. The larvae reported on by Fahay (1975) and Laroche (1977) were collected at 27° and 26.5° C, respectively, and we collected ripe fish off North Carolina when sea surface temperature was between 26° and 27° C.

It appears that spawning of vermilion snapper off North Carolina and South Carolina is restricted to warm months (late April or May-September), yet spawning may occur almost year-round in the Caribbean (Monroe et al. 1973; Erdman 1976). Similar life history variations in response to local environmental conditions are reported by Leggett and Carscadden (1978) for American shad.

[5]H. Powles, Fishery Biologist, South Carolina Marine Resource Center, Charleston, S.C., pers. commun. May 1975.

Several authors report fractional spawning in marine fishes (Starck and Schroeder 1971; Beaumarriage 1973; de Silva 1973; Macer 1974). Our inference that variation in gonad index during a spawning month for similar size fish suggests fractional spawning is supported by Starck and Schroeder's (1971) findings on a related species, *Lutjanus griseus*, the gray snapper. They concluded, from variation of ovary lengths and weights from fish of similar size, that spawning probably occurs more than once in the same season in south Florida waters.

In the results, we described three types of maturing ova and concluded that they indicate fractional spawning, yet the most mature ova type was found only in a few ripe-appearing females. Evidently final ova maturation occurs nearly simultaneously with spawning so that the probability of catching a completely ripe fish is low.

Maturation

There are no published reports on maturation in vermilion snapper, but Starck and Schroeder's (1971) results on gray snapper agree closely. They wrote that females are mature at age 3 and 190-200 mm SL. Results for vermilion snapper also agree with Starck and Schroeder's findings that *L. griseus* females >375-400 mm SL probably spawn more times each year than smaller ones, and Mosley (1966) observed (from a sample of fish 223-456 mm SL) that early in the spawning season, smaller red snapper, *L. campechanus*, showed less gonad development than larger ones, perhaps indicating earlier spawning by larger fish. Also similar to our results, Quast (1968) showed earlier and longer seasonal gonad maturation with growth in kelp bass.

Earlier spawning by older fish can probably be explained via the interplay between somatic and gonad growth and maintenance. Sexual maturity marks diminished growth in many fishes (Hubbs 1926; Magnuson and Smith 1963; Iles 1974). Female vermilion snapper older than 5 yr (390 mm TL) are beyond the years of most rapid somatic growth (Grimes 1978) and undoubtedly can afford to put more energy into gonad development, even though the energy costs of maintenance are greater for larger fish as well.

Cohen (1976), using a theoretical mathematical model, predicts that if reproductive success depends upon maximizing reproductive biomass, the change in the fraction of reproductive growth (diminished somatic growth and beginning reproductive growth) will occur at a time and mass just prior to maximum growth rate. We used annual length increments and a length-weight relation (Grimes 1978) to derive annual increments in mass, so that we could evaluate how well vermilion snapper fit the optimal timing of reproduction model. The greatest annual growth increment (weight) occurs between age 6 and 7. Age 5, then, is the year of life the model predicts the growth change, and Figure 5 shows that fish age 5 and older reflect the growth change by maturing earlier and being mature for a longer time each reproductive season.

Sex Ratio

The literature on other lutjanids provides little help in interpreting our findings that sex ratios of vermilion snapper vary significantly from 1:1 overall, and throughout life (as measured by length). Camber's (1955) data on red snapper showed a greater proportion of males when small (200-400 mm TL) but a higher percentage of females among larger fish (400 mm TL). Mosley (1966) reported 56% males and 44% females among red snapper (200-400 mm TL). Bradley and Bryan (1974), however, reported a 1:1 ratio for 1,129 adult red snapper (no size range reported), and Starck and Schroeder (1971) gave a 1:1 ratio for 772 gray snapper (including small juveniles to adults).

Wenner (1972) suggested several possibilities to account for unequal sex ratios (i.e., differential mortality, growth, and longevity; sex reversal; sex difference in activity; and in or out migiration from sampling area by one sex). There is no evidence to support any of these explanations in vermilion snapper, except differential mortality and longevity. Our results show conclusively that relative numbers of females begin to increase (to about 60%) at about 250-300 mm TL, further increase to about 70% at 500-550 mm TL, and eventually reach 90% above 550 mm TL (Table 2). These results indicate that males experience greater mortalities above 250-300 mm TL, and Grimes (1978) demonstrated greater longevity for females (no male was older than 8 yr, but females reach at least age 10). It is interesting to note that differential mortality commences approximately coincidentally with the onset of sexual maturity.

Our fecundity estimates agree reasonably well with published results for other lutjanids. Starck and Schroeder (1971) estimated fecundity for gray snapper and found a 354 mm SL female to contain about 550,000 ova. Using length conversion equations for vermilion snapper (Grimes 1978), the 354 mm SL is approximately equivalent to a 450 mm TL vermilion snapper which would contain about 410,000 ova.

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