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Reproduction of vermilion snapper (Lutjanidae: *Rhomboplites aurorubens*) from the northern and eastern Gulf of Mexico, 1991-2002

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Introduction

The typically-small size of vermilion snapper (Lutjanidae: *Rhomboplites aurorubens*) belies the fish's importance to both commercial and recreational fisheries along the southeastern U. S. Atlantic Ocean and Gulf of Mexico coasts. The species grows to approximately 63 cm total length (TL), ranges from North Carolina to Brazil, and is widespread along the coast of the Gulf of Mexico (Anderson 2002). Vermilion snapper is reported to reach a maximum age of 26 years (Allman et al. 2005) and has a high variance in size-at-age (Hood and Johnson 1999).

Two important studies on reproduction, including histology, of this gonochoristic and multiple-spawning species with indeterminate fecundity have been published in the last decade. A one-year study published on vermilion snapper from South Carolina by Cuellar et al. (1996) included the first estimates of batch fecundity and spawning frequency on fish <300 mm TL. Hood and Johnson (1999) also conducted a one-year study and provided information on age, growth and reproduction including the first published batch fecundity estimates for vermilion snapper <300 mm TL from the eastern Gulf of Mexico.

Herein we provide more information on reproduction of vermilion snapper from the Gulf of Mexico (subsequently referred to as the Gulf) over more than a decade. Our objectives were to : (1) obtain basic data on sex ratio and gonad maturation from various areas of the Gulf over multiple years, using histology and other methods; (2) estimate annual fecundity in fish >299 mm TL for the first time in any area; (3) estimate annual fecundity in fish <300 mm TL to compare with previous studies; (4) determine spawning time-of-day/location/depth from diel sampling for the first time in any area; and (5) examine geographic and temporal differences in reproductive parameters both within our study and between our study and previous studies.

Methods and Materials

Collections

We sampled vermilion snapper from fishery-dependent and fishery-independent sources in port and at sea from commercial boats, headboats, charterboats, private boats and research vessels. Sampling was usually random but some females and larger fish were selected for fecundity estimates and to provide data for large specimens. Only randomly sampled fish were used for calculations of length frequency, gonadosomatic index (gonad weight as a percentage of total weight, GSI), maximum oocyte diameter (MAXOD), and sex ratio. We targeted fish >299 mm TL from Panama City, Florida, west through Texas from 2000 through 2002, collecting gonads and otoliths from large specimens that were sampled mainly from recreational headboats. All random and selected samples were used for estimates of maturity and fecundity.

We recorded TL measured to the nearest mm and total wet weight to the nearest 0.01 kg. A two-sample z-test for means (Excel 2000) was used to test for differences in lengths. Gonads were excised, placed "dry" in plastic bags and kept on ice until processed. Gonad samples were usually processed within 24 hours of collection. Samples collected at remote locations were sent to us on ice by overnight mail. A sagittal otolith was also removed from each fish to determine age (Allman et al. 2005).

Gonad processing and analysis

Macroscopic and microscopic examinations for sex, gonad stage, MAXOD, and GSI were used to generally delineate the spawning season and to compare with histological results. Connective tissue was removed from each gonad and a small cube (approximately 2 mm on

each side) was cut from the central region of one lobe (Hood and Johnson 1999). This material was examined at 250X to determine preliminary sex and stage of gonad maturation (1-immature/resting; 2-early developing; 3-late developing; 4-ready to spawn or spawning; 5-recently spawned or spawned-out; West, 1990). The diameter of the largest oocyte (MAXOD) found in the sample was also recorded for each female in order to test if that was an effective method of determining maturation. The sex was classified as male if no oocytes were visible in gonadal tissue microscopically at 250X. Male Stages 1-3 were assigned according to testis thickness and Stage 4 had milt when cut. All gonads were then weighed (not including the small sample cut from one ovarian lobe) to the nearest 0.1 g before most samples were placed in 10% buffered formalin solution (Hunter, 1985). GSI used gonad-free total weight (Hood and Johnson 1998). Chi-square analysis was used to test for differences in sex ratio (Ambrose and Ambrose, 1987).

We used histology for final gonad staging and determination of maturation. After at least two weeks in formalin, tissue samples were cut in thin sections and used for standard histological slides (Fitzhugh et al. 1993) which were then examined to assign the final sex, stage of gonad maturation, presence of hydrated oocytes and postovulatory follicles (POF), presence of atresia, and quality of preservation. Histological stages for females and males were similar to those given in Hood and Johnson (1999); ovarian stages were determined by the most advanced oocyte development found in each fish: 1-primary growth; 2-cortical alveolar; 3-vitellogenic; 4-lipid coalescence/migratory nucleus (the first phase in final oocyte maturation or early FOM (Brown-Peterson et al. 1988)) or early hydrated; 5-late hydrated; 6-at least 50% atretic (or spent). Histological stages for males were: 1-inactive, with few secondary spermatocytes; 2-active, with many secondary spermatocytes; 3-developing, with some spermatids in ducts; 4-ripe, with large pools of spermatozoa in ducts. Reference to stage from this point on refer to histological stage unless noted otherwise. Immature females had small Stage 1 or 2 ovaries with no atresia. Mature females were Stage 1-2 (inactive) with at least a trace of atresia, or Stage 3-6 (active) with yolked oocytes. Immature males were Stage 1-2 with no brown bodies (Hood and Johnson 1999), while mature males were Stage 1-2 with brown bodies or Stage 3-4 with spermatids or spermatozoa.

Fecundity

In order to facilitate batch fecundity estimates, we used a two-way analysis of variance, (ANOVA; SAS, 1988) to determine if hydrated oocytes were homogeneously distributed within and between ovaries. Hydrated oocytes were counted in weighed samples (0.086 - 0.250 g) from each of three ovarian regions (anterior, middle and posterior) in each lobe for six Stage 4 or 5 fish. If distribution of hydrated oocytes was not significantly different among regions and between lobes (at alpha = 0.05) , then batch fecundity could be estimated from just one sample. Batch fecundity samples were wedge-shaped, representing the ovary in cross section from the center to the tunica, in order to allow for possible differences in hydrated oocyte concentrations between the periphery and the center of the ovary.

Batch fecundity and spawning frequency were estimated using the hydrated oocyte method of Hunter et al. (1985) and Hunter and Macewicz (1985), respectively. Only Stage 5 females were used to estimate batch fecundity but both Stage 4 and 5 were used to estimate spawning frequency. We used the length of the smallest fully hydrated female as a benchmark for selecting fish sizes included in the spawning frequency estimate. Batch fecundity was regressed on length and age using linear and non-linear models to identify which model best explained the variation in batch fecundity (according to the coefficient of determination). Batch

fecundity of small (< 300 mm) and large (> 299 mm) females were determined in order to test for significant differences. The estimate of spawning periodicity (= the number of days between spawns) was the reciprocal of the average proportion of females that were hydrated (Hunter et al. 1985). The estimate of spawning frequency (the number of spawns per year for each female) was the duration of the spawning season in days divided by the spawning periodicity (Hunter and Macewicz 1985).

We determined spawning time-of-day, location and depth using histology and catch data. The time-of-day that spawning occurred was determined from diel hook and line sampling during 2000-2001. The fish were considered to be spawning at the time when Stage 5 ovaries ceased to occur and new POFs were first visible. During this specialized sampling, the fish were separated by time of catch and quickly iced down on the boat. When possible, gonads were preserved in 10% formalin at sea, mainly to ensure that the fragile POFs did not undergo post-mortem decay (which would make new POFs look like old ones and confuse the estimates of spawning time). Spawning sites were identified as those locations where at least one female with hydrated oocytes was collected. Locating these sites required catch coordinates from fishery-independent surveys or from cooperative commercial and recreational fishers. We investigated geographic and temporal differences in fecundity and other reproductive parameters using graphs and regression analysis. Large scale geographic differences were compared among our results and those of Cuellar, et al. (1996) off South Carolina during 1992-1993 and Hood and Johnson (1999) off west-central Florida during 1995-1996, assuming no annual variations in the latter two areas. Small scale spatial variations were analyzed using 2000-2001 data from fishery-independent sampling off Panama City, Florida, our best source for catch location data. Some temporal differences were analyzed for the years in which we sampled the greatest numbers of fish.

Results

Collections

We sampled gonads from a total of 3,412 vermilion snapper (153-555 mm TL) from Key West, Florida, to Port Aransas, Texas, from February 1991 through November 2002. Most fish (66 %) were 201 – 325 mm. Although we sampled every year during 1991-2002, about half of all samples were collected during each of two four-year periods: 1991-1994 (46 %) and 1999-2002 (50 %). Both commercial and recreational fisheries were sampled in all years except 1997-1999, when only one of those fisheries were represented in each year. Most fishery-dependent samples (65.1 % of 2,356 fish) were collected during 1991-1994. Most fishery-independent samples (81.3 % of 1,056 fish) were collected during 2000-2001.

Samples came from all Gulf coastal states except Mississippi, but the vast majority of all samples (3,193 fish) came from the west coast of Florida. Most Florida samples (83.5 %) came from Panama City, followed by Cape San Blas/Apalachicola (3.2 %), northeastern Gulf shelf (3.0 %), Fort Myers (2.9 %), Homosassa (2.5 %), St. Petersburg (1.8 %), and elsewhere (1.6 %).

Though comparatively small in number, and largely selected rather than random, the samples from Alabama (n=125), Louisiana (n=62), and Texas (n=30) were important mainly because many of them were large specimens upon which little information on reproduction has been reported. Alabama samples were mostly collected from Mobile and Orange Beach. Louisiana samples usually came from Cameron and south of the main pass of the Mississippi River. Texas samples came mostly from Freeport and Port Aransas.

Length frequency by source, sex, and both sexes for all areas combined

The commercial fishery produced the largest vermilion snapper of each sex, and fishery-independent sources produced the smallest (Figure 1). Modal lengths for recreational, commercial, and fishery- independent samples were 225-274, 300-374 and 225-274 mm, respectively. A two sample z-test (alpha = 0.05) showed that mean length was significantly different among all three data sources: 308 mm for recreational, 352 mm for commercial, and 263 mm for fishery-independent sources. Median length was < 11 mm of mean length for each data source.

The smallest and largest fish (153 and 555 mm) were females, while males of 161-525 mm were collected. Modal lengths were slightly greater for males (250-274 mm versus 225-249 mm) (Figure 2). Mean length was similar for females (296 mm, SE=1.65, n=1692) and males (302 mm, SE=1.87, n=1140). Median TL was < mean TL for both sexes: 272 mm for females and 293 mm for males.

Modal length of all fish sampled for gonads from all areas was 225-274 mm (Figure 3).

Sex ratio

Overall female: male sex ratio from all fishery sources and areas was significantly female-dominated (1.48:1; X^2=107 with critical value = 3.8, n = 2833, df = 1, and alpha = 0.05). Sex ratio was usually > 1:1 for recreational (1.72:1) and fishery-independent (1.87:1) samples and 1:1 for commercial samples (1.08:1).

Length at maturation/spawning

Histology indicated that both sexes of vermilion snapper at all lengths sampled (153–555 mm; 1384 females and 391 males) were mature. Only one female was immature. Relatively few fish < 200 mm were collected (n=33), but four out of five females and all three males at 150-174 mm were mature, and all 17 females and all 8 males at 175-199 mm were mature. The smallest female that we sampled (153 mm) was Stage 6; no Stage 1 females and few Stage 2 females were found during the spawning season. The smallest male (161 mm) was Stage 4; no males of Stage 1, 2 or 3 were found during the spawning season.

Oocyte development by lobe and region

Comparison of counts of hydrated oocytes by lobe and region indicated that hydrated oocytes were distributed evenly (ANOVA, F = 0.9944). We therefore randomly selected the region of ovary used for batch fecundity estimates.

Spawning season

The spawning season for vermilion snapper determined by female and male GSI and MAXOD (Figure 4A-C) was March or April through September or October. Histological ovary stage (Figure 4D) and testis stage indicated the spawning season was mid-April through mid-September. GSIs > 2.0 mainly occurred from late March through early or mid-October for females and males (Figure 4A, B); low GSIs for females were rare from May through early September. MAXODs >0.40 mm mainly occurred from late March through early October (Figure 4C) and low MAXODs were rare during late April through late September. Stage 5 ovaries, the best indicator of spawning, occurred from mid-April through mid-September (Figure 4D). All testes were ripe from late March through late October.

Spawning time-of-day

Peak spawning occurred at 2100-2359 hr according to ovarian histology during our intensive day/night fishery-independent sampling off Panama City in 2000 and 2001 (Figure 5). In both years, early hydration occurred as early as 0905 hr and late hydration did not begin until

1200 -1300 hr. At approximately 2230 hr during one sampling trip in 2000, fully hydrated oocytes were not visible in the sampled females and some new POFs appeared to mark the time of spawning (Figure 3 in Collins et al. 2001). During 2001, fully hydrated oocytes appeared from 1330 to 2240 hr and new POFs appeared from 2200 to 0130 hr. Two "running ripe" females collected at 2200 and 2210 spewed large, clear eggs on the deck of a headboat during sampling, and their ovaries contained both Stage 5 oocytes and new POFs when viewed in the laboratory.

Spawning sites

Forty-two spawning sites were identified for 239 vermilion snapper caught at known fishing locations offshore between Dry Tortugas, Florida, and Cameron, Louisiana. Most of these sites were within 40 miles of Panama City, Florida, in 30 to 60 m as identified by our intensive fishery-independent sampling in 2000-2001. Most sampling occurred off Panama City. Most of the females with late hydrated ovaries (n=160) were caught at depths of 40-49 m (Figure 6). Headboat samplers from just west of Panama City, Florida, through Texas sampled gonads from large female vermilion snapper that were early hydrated, but these fish were not used to identify spawning areas because they were not close enough to actual spawning and only a general catch location was available.

Batch fecundity

Batch fecundity from all fishery sources and areas combined was estimated as 7,385 to 407,570 hydrated oocytes (mean=73,388, SE=6,968, median=47,098) from 123 females collected in 1993-1994 and 2000-2001 (Figure 7). Total length was an effective predictor of batch fecundity for all fish, with an exponential function explaining 66% of the variation in batch fecundity (Figure 7). Dates of catch on all fish ranged from late April to early September. Depths and times of catch were 30 to 114 m and 1300 to 2240 hours, respectively. Sample weights for estimation of batch fecundity were 0.079 - 0.252 g per fish.

A z-test indicated that batch fecundity was significantly greater in large (>299 mm) fish ($z = -7.20$, $P < .0001$). Mean batch fecundity for small (<300 mm) fish was 41,051 (n=83, SE=1,764, median=39,941) and for large fish was 152,788 (n=40, SE=15,408, median=103,606). Batch fecundity was variable for both small and large females.

Age was not an effective predictor of batch fecundity for fish ranging from 2 to 14 yr (n=80, Figure 8). Ages were not available for 1993 fish.

Spawning frequency

We estimated spawning frequency to be 33 to 87 spawns per year but we had the most confidence in the estimate of 87 (Table 1). Although we estimated spawning frequency for four years, there was strong sampling bias for 1993, 1994, and 2001. Although the spawning frequency estimate of 81 during 1993 was similar to what we considered our best estimate of 87 during 2000, two main factors cause the 1993, 1994, and 2001 estimates to be questioned. The samples for those three years did not cover the whole spawning season or did not cover one area adequately. Our most complete sampling year was 2000, when we had good coverage over the entire spawning season from one known spawning area.

The only variable not represented well by our spawning frequency estimate during 2000 was fish size: there were only two females > 299 mm sampled (Table 1). However, the proportion of hydrated fish (62.5 %) and the estimate of spawning periodicity (every 1.6 days) for large fish in 2001 were very similar to those for small fish in 2000 (63.8 % and 1.6 days). Therefore, we used the same spawning frequency estimate of 87 for all fish sizes.

Annual fecundity

Annual fecundity estimates ranged from 0.64 to 35.5 million hydrated oocytes over all data (Figure 9). Since a constant of 87 was used for spawning frequency in all four years, the regressions of batch and annual fecundity on length were almost identical (Figures 7 and 9).

Discussion

Our sampling for gonads was probably not as random as that of the sampling for otoliths, although we excluded selected samples from our reproduction analyses that required random samples. Our Figures 1-3 describe the most random samples taken for reproduction studies. We recommend that anyone wanting better random representation of vermilion snapper length frequency by area, year and fishing mode for 1994-2004 should see Allman et al. 2001 and Allman et al. 2005.

The sex ratio of female: male vermilion snapper generally seems to decrease from the northern half of its range (North Carolina, South Carolina and northwest Florida) to the southern half (west-central Florida and Trinidad). Both Grimes (1976) and Cuellar et al. (1996) found that females off North Carolina and South Carolina made up 63 % of the total sampled (sex ratio = 1.70:1). Fishery-independent samples from North Carolina were similar with 67 % female (sex ratio = 2.03:1), and commercial samples from the same area were also significantly different from 1:1 at 57 % female (sex ratio = 1.33:1) (Cuellar et al. 1996). Random samples from the present study were 60 % female (sex ratio = 1.5:1) which was significantly different than 1:1, although some individual locations did have sex ratios =1:1 or significantly < 1:1. Hood and Johnson (1999) found that the sex ratio off west-central Florida was not significantly different from 1:1 and our sex ratio for two locations (Homosassa and Fort Myers) near the area covered by Hood and Johnson was also 1:1. Vermilion snapper sex ratio from Trinidad was also not significantly different from 1:1 (Manickchand-Heileman and Phillip, 1999). It is also interesting to note that our combined random samples from the commercial fishery, usually collected from deeper water than samples from the recreational fishery, were also 1:1.

Our study found that vermilion snapper mature at < 200 mm TL, as did Hood and Johnson (1999) and Cuellar et al. (1996). Off North Carolina and South Carolina, Grimes (1976) found that most females first spawned at 350-400 mm but Cuellar et al. (1996) found that all females at least 165 mm were mature. Preliminary data in Collins and Pinckney (1988) also showed that 60% of females and 90% of males from North Carolina, South Carolina, Georgia and northeast Florida were mature at 160 mm. Differences in methodology and temporal variation could explain the differences in length at maturity/spawning estimates between Grimes (1976), Collins and Pinckney (1988) and Cuellar et al. (1996).

Spawning months, spawning-time-of-day, and batch fecundity for smaller fish from the present study generally agree with recently published estimates for vermilion snapper, but Cuellar et al. 1996 estimated spawning frequency off South Carolina as 35 spawns per year. Spawning months were April or May through September in the present study, agreeing with Cuellar et al. (1996) and Hood and Johnson (1998). Cuellar et al. (1996) used only daytime samples and estimated that vermilion snapper spawned in the early evening hours off South Carolina. Our day and night sampling narrowed the time of spawning to approximately 2230 hr (+/- 1 hr). Our estimate of 87 spawns per year was greater than that of Cuellar et al. (1996)

possibly due to differences in areas, years and times sampled and to different methods of estimating spawning frequency. Cuellar et al. (1996) used methods from Hunter et al. (1985) and Hunter et al. (1992) to estimate batch fecundity, but they used methods in Fitzhugh et al. (1993) to estimate spawning frequency. We chose the simplest spawning frequency estimation method, using only the presence of hydrated oocytes in Stage 4 and 5 ovaries during the period of hydration (approximately 13 hours prior to spawning). Since Cuellar et al. (1996) could not closely estimate the time of hydration and spawning from their daytime sampling, they could not use just the occurrence of hydrated oocytes during the entire period of hydration to estimate the number of spawns. Ours is not the first seemingly high estimate of spawning frequency for a snapper. Davis and West (1993) found that Brownstripe red snapper, *Lutjanus vittus*, spawn 22 times per month for seven months (154 spawns) each year in Australian waters. Further investigations into sex ratio, length at maturation and spawning frequency are ongoing (Allman et al. 2005).

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Table1. Annual spawning frequency estimates for vermilion snapper from the west coast of Florida using the hydrated oocyte method.

Year	Areas	n	Total length in mm			Estimated spawning dates (and # days)	% Hydrated (and spawning periodicity)	Spawning frequency estimate	Comments
			Mean	Range	SE				
1993	Panama City and Homosassa	100	306	218 – 514	5.62	May 16 – Sep 30 (136 d)	60% (spawned every 1.67 d)	81	Two different areas Most hydrated fish from one area No catch times recorded No histology for April – mid-May
1994	Panama City, Cape San Blas, and St. Petersburg	138	276	198 – 427	4.52	Apr 30 –Sep 4 (127 d)	36% (2.78 d.)	46	Three different areas Most fish from one area No catch times recorded Little histology for Apr or Sep
2000	Panama City	166	247	171 – 360	1.78	Apr 13 – Sep 14 (150 d)	58% (1.72 d)	87	One area (known spawning locations) Catch times recorded Good temporal coverage for histology, Mostly fish < 300 mm
2001	Panama City	178	269	153 – 435	5.13	Jun 4 – Aug 25 (82 d)	40% (2.50 d)	33	One area (known spawning locations) Catch times recorded Scant histology during hydration for Apr, May and Sep Mostly fish > 300 mm

Figure 1. Length frequency of vermilion snapper caught A). recreationally, B). commercially, and C). from fishery-independent sources during 1992-2002, and used in reproductive assessment.

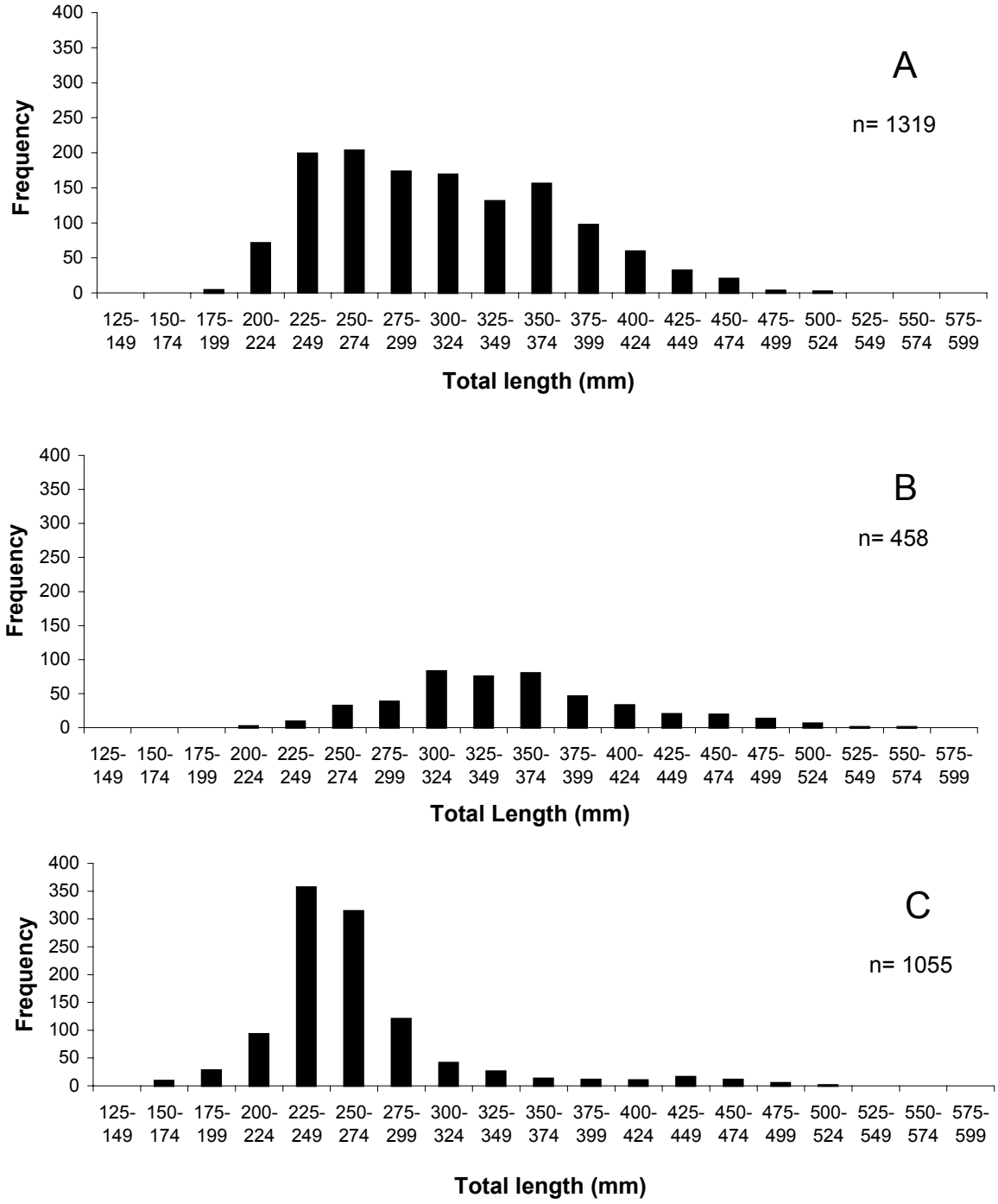
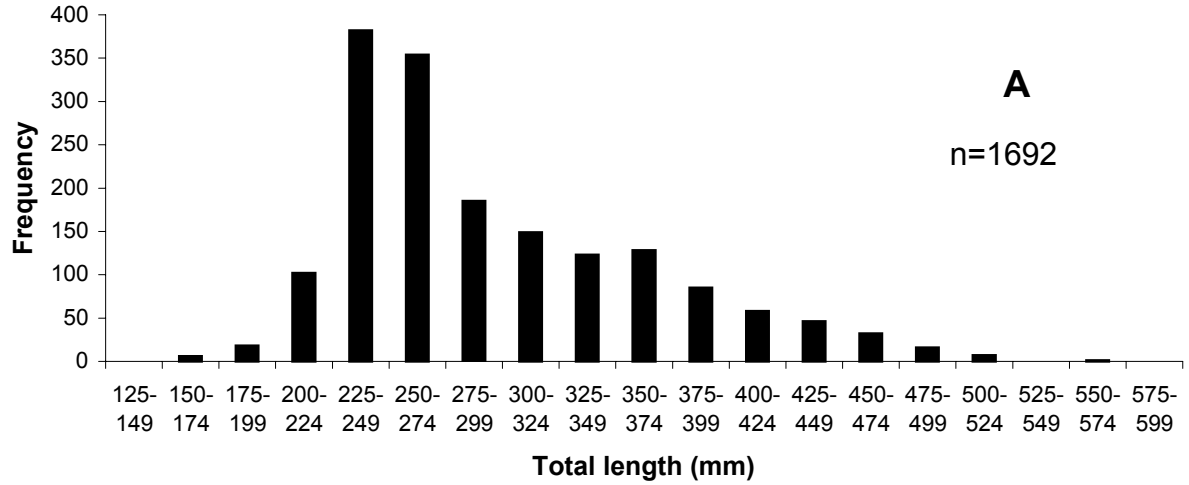


Figure 2. Length frequency of all vermilion snapper A). females and B). males used in reproductive assessment, 1992-2002.



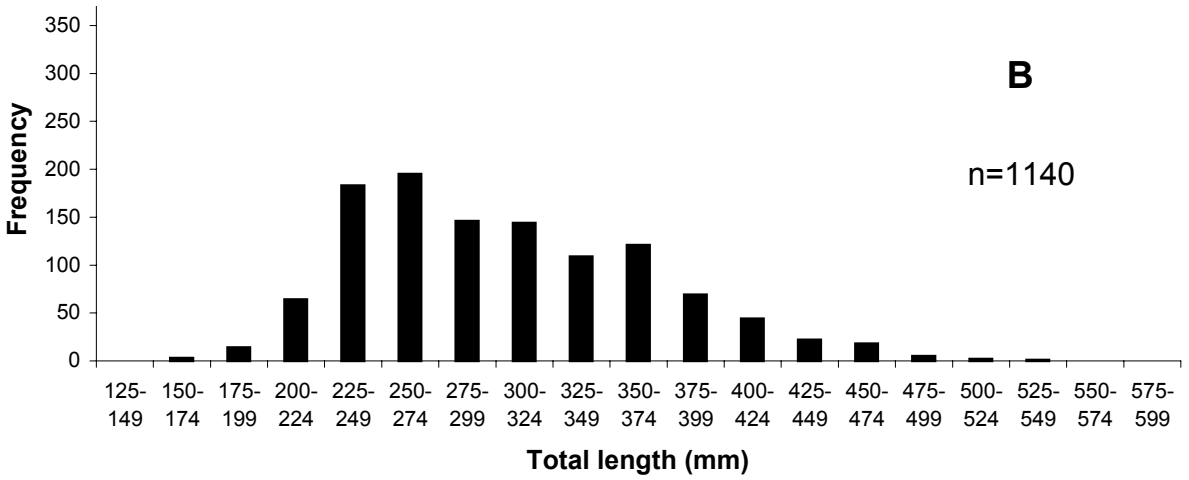


Figure 3. Length frequency of all vermilion snapper from all areas used in reproduction assessment, 1992-2002 (n=2832).

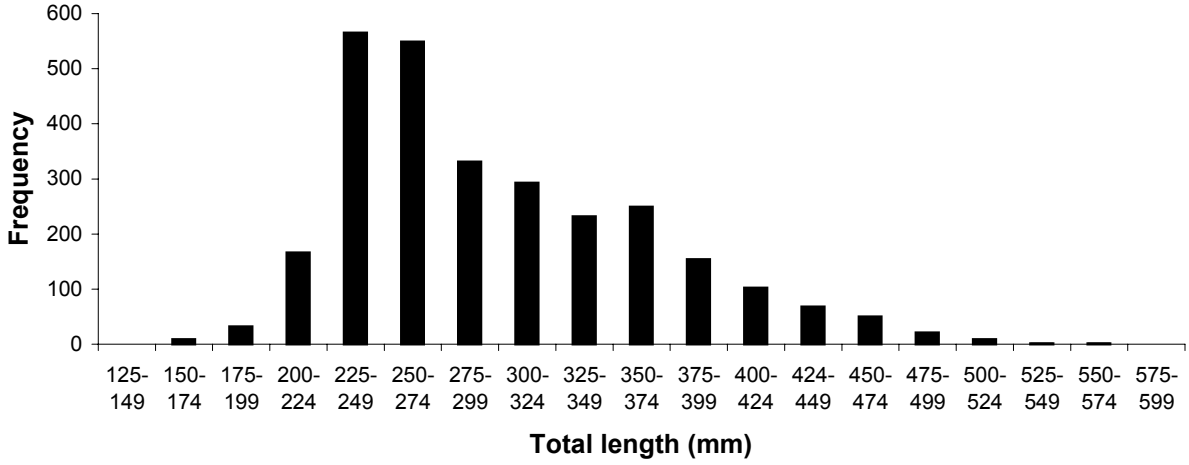
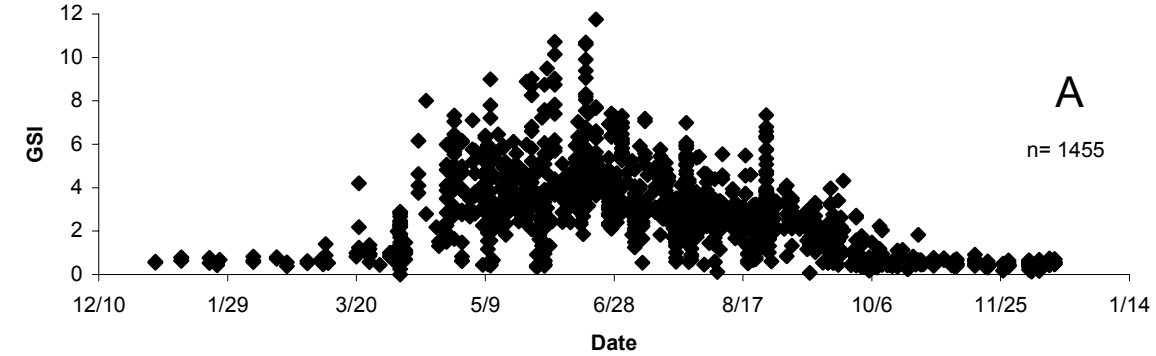
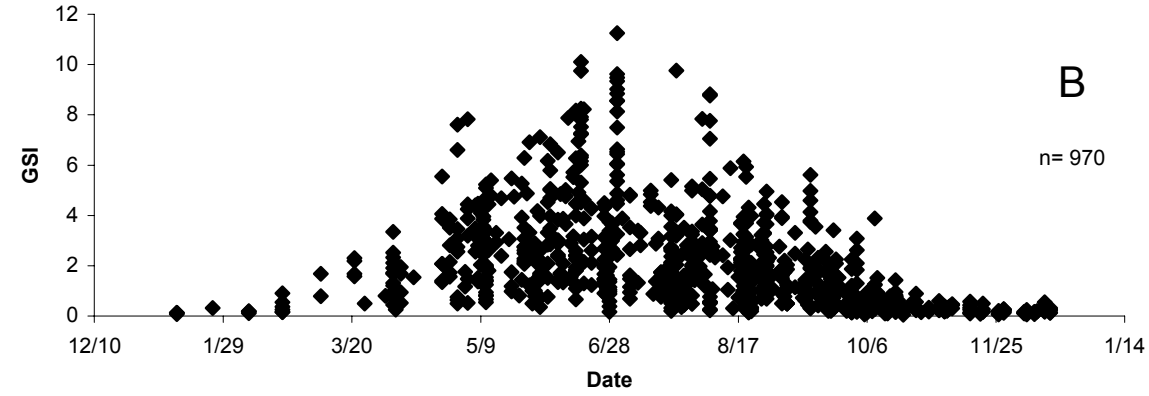
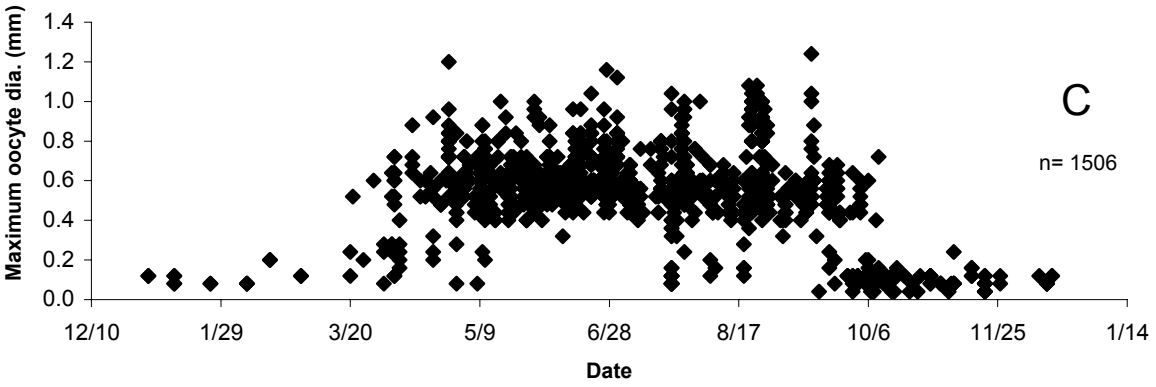


Figure 4. Spawning season of vermilion snapper (1992-2002) in the Gulf of Mexico as show by: A). female GSI, B). male GSI, C). Maximum oocyte diameter and D). ovarian histological stage.







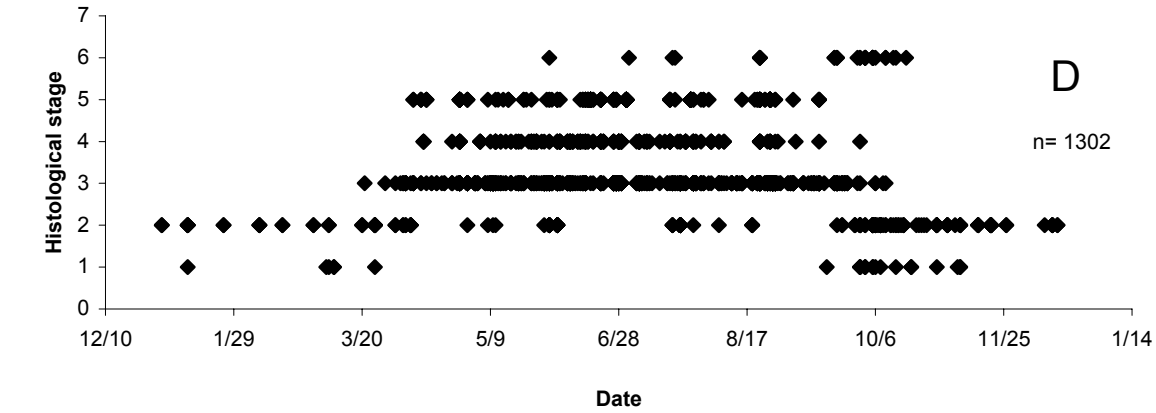


Figure 5. Spawning time (arrow) off Panama City, Florida, shown by frequency of females with early hydrated oocytes (EH: n=42), late hydrated oocytes (LH: n=105), and new postovulatory follicles (POF: n=98) by time interval, April-September 2000-2001.

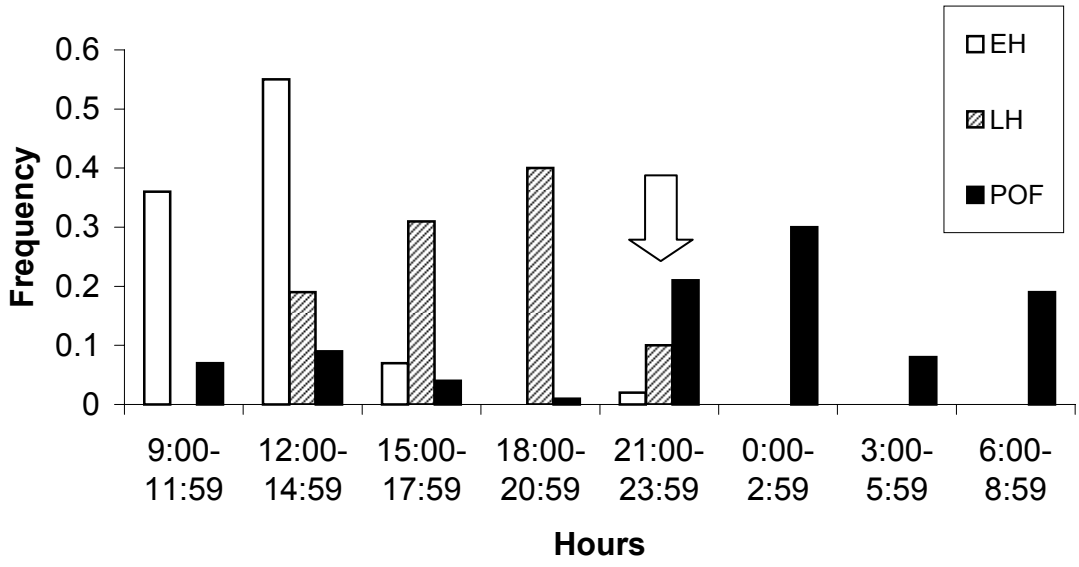


Figure 6. Frequency of spawning females (with late-hydrated oocytes) by depth from the northern and eastern Gulf of Mexico from off Cameron, Louisiana, to off Dry Tortugas, Florida, 1991-2002 (n=160).

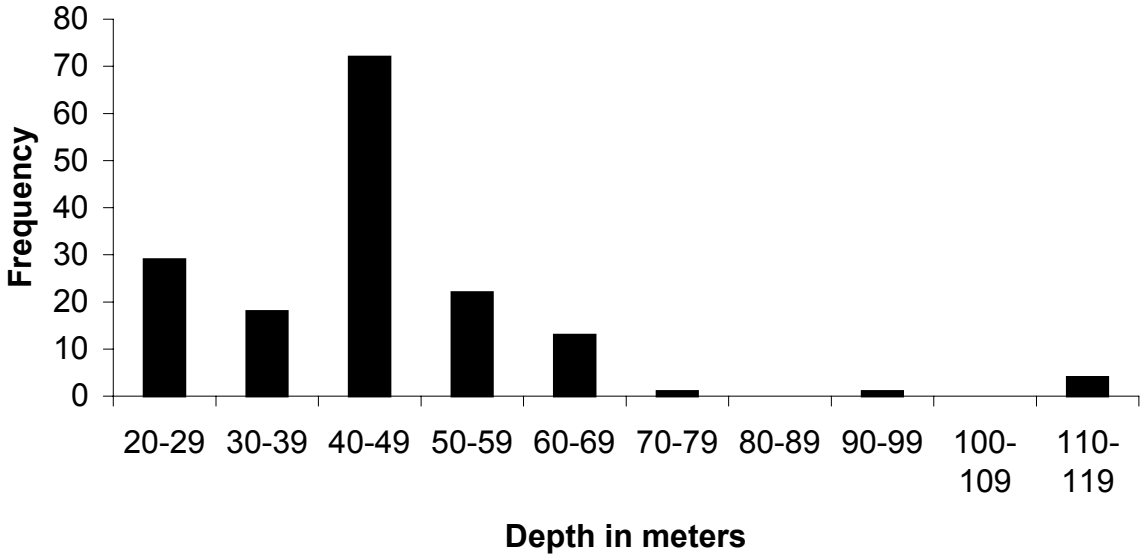


Figure 7. Batch fecundity estimates regressed on total length for the Florida west coast, 1993-1994 and 2000-2001 (n=123).

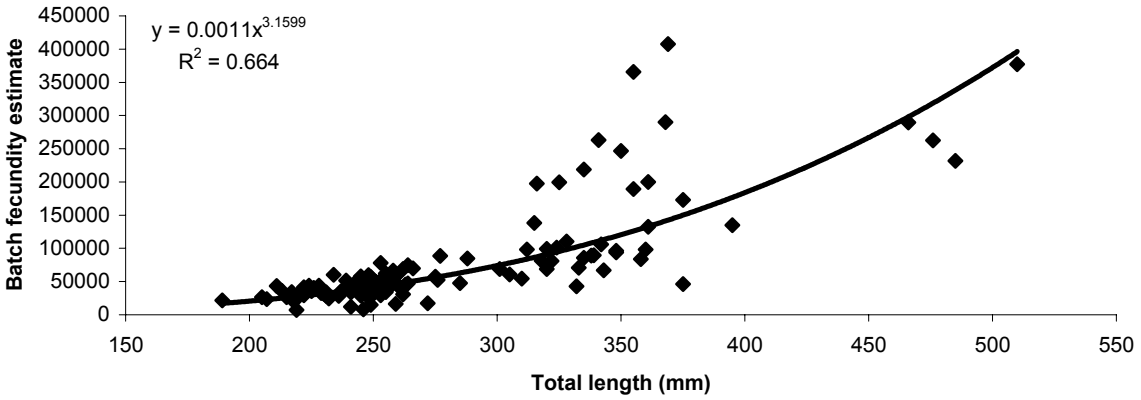


Figure 8. Batch fecundity regressed on age of vermilion snapper from the west coast of Florida, 1994 and 2000-2001 (n=80).

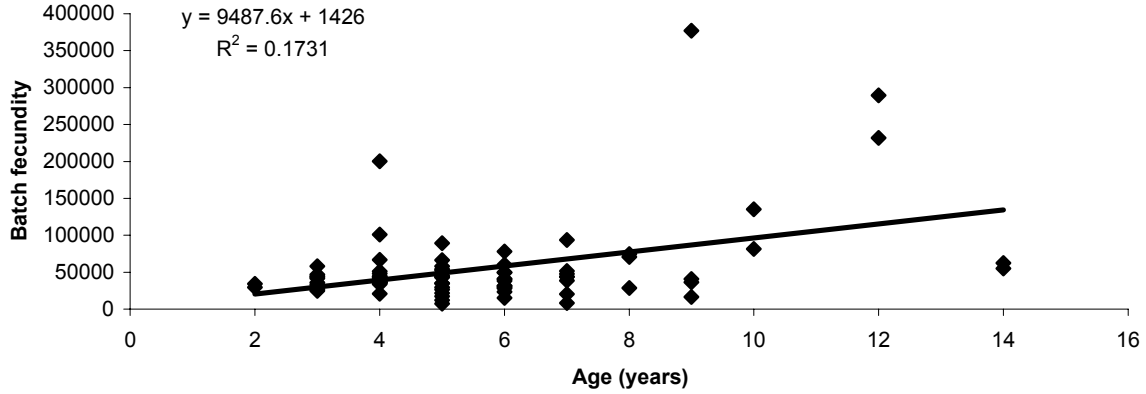


Figure 9. Annual fecundity estimates in millions (assuming an average spawning frequency of 87) regressed on total length of vermilion snapper from the west coast of Florida, 1993-1994 and 2000-2001 (n=123).