Preliminary Results from a Continuing Study of Spawning and Fecundity in the Red Snapper (Lutjanidae: *Lutjanus campechanus*) from the Gulf of Mexico, 1998-1999

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ABSTRACT

In response to increased management concerns by the National Marine Fisheries Service in early 1998, we analyzed red snapper (Lutjanidae: *Lutjanus campechanus*) gonads and otoliths from the U. S. Gulf of Mexico coasts of Texas, Louisiana, Mississippi, Alabama and west Florida (TX, LA, MS, AL and FL, respectively). Our main objective related to reproduction was to provide size and age-specific estimates of fecundity (batch fecundity and frequency of spawning) for large red snapper. We previously provided estimates of fecundity (n=66, from 349 to 820 mm total length, TL) from northeastern Gulf of Mexico red snapper. However, in order to complete size/age matrices of spawning frequency, more samples of larger females were needed. We therefore greatly expanded our sampling area and number of samplers. Most samples were provided by headboat samplers stationed from South Padre Island, TX, to St. Petersburg, FL, beginning in late June 1998 and ending in October 1999. Large red snapper (at least 500 mm TL) were non-randomly selected in an attempt to provide adequate sample numbers of large fish. The sex ratio of all 1517 fish sampled was 1:1. The spawning season off TX and LA began and ended in the same months as in the northeastern Gulf: April - May and September - October, respectively. The presence of hydrated oocytes in ovaries of some large females indicated that spawning began in April 1999 off TX and LA. A few females had hydrated oocytes in October 1998 to signal the end of the spawning season in all areas. Batch fecundity for 1998 (n = 59, from 359 to 901 mm TL) ranged from an extremely low value of 13 (in a 417 mm TL, 4 year-old TX fish) to an extremely high value of 3.4 million (in a 851 mm TL, 11 year-old LA fish). Both age and TL had an exponential relationship with batch fecundity, but age was the best predictor. Spawning frequency estimates by age (for those ages or age ranges with at least 36 females sampled in 1998) were about 50% greater for age 6-35 females than for ages 3, 4 or 5 females. Several spawning locations around the northern Gulf were also identified using headboat and fishery independent data along with histology.

KEY WORDS: Fecundity, snapper, spawning

INTRODUCTION

In early 1998, the National Marine Fisheries Service (NMFS) expressed increased concern with the management of red snapper commercial and recreational fisheries in the Gulf of Mexico. Commercial catches had peaked in 1983 and then steadily declined through 1989 (Bennett [1998]). Commercial quotas have been used since 1990 to close the fishery early (= before the end of the fishing year) every year. While red snapper commercial catches since 1983 have remained stable or increased from the northwestern and north-central Gulf (Texas, Louisiana, Mississippi and Alabama), catches from the west coast of Florida have steadily decreased since 1983 to an all-time low (a total decrease of two orders of magnitude) in 1997 (Bennett 1998). Some regional changes in landings may have been affected by the commercial quota. Recreational fishery landings in the Gulf have been somewhat more stable, but quotas also closed that fishery early in recent years and increasing minimum size limits have also affected the catch (Schirripa and Legault 1999).

Research on reproductive biology of reef fishes is important to assessing stocks, testing management tools, and evaluating habitat. Spawning potential ratios (SPRs) require age-specific fecundity estimates to determine if stocks are overfished. Reproduction studies also help to gauge the success of marine reserves as a management tool. Reef fishes are usually aggregate spawners and little is presently known about the structure and function of those aggregations. The identification of spawning sites also helps to delineate essential fish habitat.

Extensive sampling and study of both age/growth and reproduction from the north-central and northwestern Gulf was requested by NMFS to improve stock assessment of this species. We had previously studied red snapper reproduction and published our results on histology and fecundity estimates from the northeastern Gulf of Mexico (Collins, et al. 1996). Samples from the north-central and northwestern Gulf of Mexico were more difficult to obtain and required the assistance of all Gulf samplers from the NMFS Beaufort, NC, Headboat Survey Program.

Our objectives were threefold: (1) to acquire greater numbers of large female red snapper that could be used for estimating fecundity; (2) to determine if spawning times for this species were similar in the eastern and western Gulf of Mexico; (3) to identify red snapper spawning sites using histology and catch location data from fishers.

METHODS

Our methods were identical to those in Collins et al. (1996), except that field sampling was much more extensive and we specifically selected larger (>499 mm total length, TL) fish in the present study. Fish <500 mm TL were randomly sampled. Red snapper gonads and otoliths were sampled mainly from recreational headboats out of west Florida (FL), Alabama (AL), Louisiana (LA), and Texas (TX). Charterboats from Panama City, FL, and tournaments in FL and Mississippi (MS) were sampled to a lesser extent. A few fishery-independent samples came from NMFS scientific surveys off Panama City, FL, and MS.

For each fish sampled in the field, fork length (FL) and TL were first measured to the nearest mm, and total wet weight was usually taken to the nearest 0.01 kg. Gonads were then removed, placed dry in heavy-plastic bags and kept on ice until processed. A sagittal otolith was also removed from each fish. Samplers in TX, LA, and AL shipped otoliths and gonads on ice to our lab in Panama City by overnight mail.

In the laboratory, gonads were processed as soon as possible (usually within four hours of shipment-arrival). Excess tissue was removed and a small sample of each gonad was examined at 250x to determine final sex and preliminary stage of gonad maturation (1-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 small sample was recorded for each female. All gonads were weighed to the nearest 0.1 g before most samples were placed in 10% buffered formaldehyde solution (mixed according to Hunter 1985) inside a sealed plastic bag.

A gonadosomatic index (GSI = 100 * gonad weight/ total weight), the MAXOD, and preliminary gonad stages were used to generally delineate the spawning season, as well as to compare to the final staging from histology. After at least two weeks in 10% formaldehyde solution, tissue samples were used for standard histological slides (Fitzhugh, et al. 1993). Slides were then viewed at our laboratory in order to record sex, stage and quality of preservation. Histological-stages for females were determined by the most-advanced stage of oocyte development found in each fish: 1-primary growth; 2-cortical alveolar; 3-vitellogenic; 4-early coalescing or nucleus migrating ; 5-fully hydrated; 6-spawning or recently spawned (with fresh post-ovulatory follicles, POFs); 7-at least 50% atretic. Histological-stages for males were: 1-inactive; 2-active, with many secondary spermatocytes; 3-developing ,with some spermatids in ducts; 4-ripe, with large pools of spermatozoa in ducts.

Batch fecundity and spawning frequency were estimated using the hydrated oocyte method of Hunter, et al. (1985) and Hunter and Macewicz (1985), respectively. Only histological stage 4 and 5 females were used for batch fecundity estimates. We used the length of the smallest hydrated female as a

benchmark for selecting fish included in the spawning frequency estimate: histological stage 1,2, 3 and 7 females were counted as not spawning while stage 4, 5 and 6 females were counted as spawning. Batch fecundity was regressed on TL and age using linear and non-linear models.

Age was determined from sections of sagittal otoliths following the methods of Fitzhugh, et al. (1999). Nelson (1980) validated rings on red snapper otoliths as annular marks.

Spawning sites were identified as those locations where at least one female with hydrated oocytes or fresh POFs was found. Locating these sites required the catch-coordinates from fishers and a histological slide from each fish.

RESULTS

A total of 1,517 red snapper have been sampled between Port Isabel, TX, and St. Petersburg, FL, during the period February 13, 1998, through October 16, 1999. Sex ratio was 1:1 by chi-square analysis (Zar 1984) and 51.6% of all fish collected were females. Headboat samples outnumbered those from all other modes with n = 954 (62.9%) and charterboat samples were the next most-dominant mode with n = 340 (22.4%). Most samples (42.8%) came from FL, followed by TX (31.6%), LA (12.6%), AL (11.7%) and MS (1.3%).

As expected (see Figure 17 in Schirripa and Legault 1999), most large specimens (>499 mm TL; n = 517) came from the northwestern/north-central Gulf of Mexico. These TX and LA fish made up 56.1 % of this high-priority size-group for fecundity estimates, with Florida fish making up 26.9%. Texas and LA also produced 74.2 % of the largest fish (700 to 972 mm TL; n = 120). Sex ratio of these largest fish was about the same as for the total sampled (1:1 by chi-square analysis (Zar 1984), with 53.3% female.

The spawning season for red snapper from FL to TX in this study was April or May through September or October, according to GSI (Figure 1), MAXOD, preliminary gonad-staging and histological gonad-staging. Our sampling of TX, LA, MS and AL in 1998 did not start until early July, so the onset of spawning in those states is based on 1999 sampling only. The end of spawning in those same states to the west of FL also was shown by one year's data (1998) because headboat sampling ceased in late August 1999 due to the fishery being closed in all federal waters.

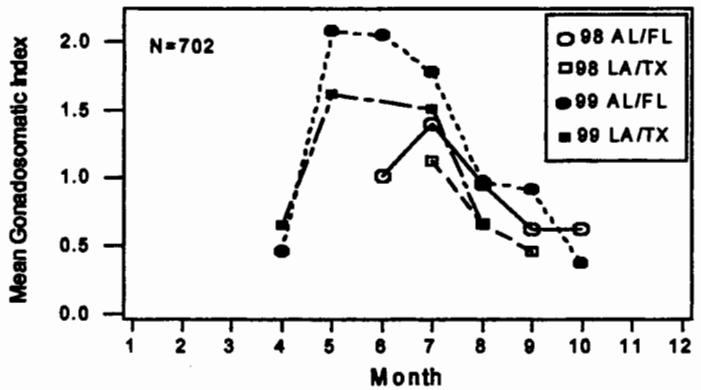

Figure 1. Mean GSI of female red snapper collected by all gear types from northeastern (FL/AL) and north-central/northwestern (LA/TX) Gulf of Mexico, 1998-1999. Only months with n > 10 are shown.

Some locations of spawning activity off TX, LA, AL and FL were determined by the use of coordinates provided to the Headboat Survey Program by headboat-captains (pers. comm., R. Dixon, NMFS Beaufort, NC July 1999) and also from NMFS fishery independent sampling (Figure 2). Headboat catch locations were 10' by 10' grids where at least one day's catch (mostly during 1998) included at least one female red snapper with hydrated oocytes. Catch coordinates from most 1998-1999 headboat trips were not available. Fishery independent sampling that revealed the location of females with hydrated oocytes off AL and FL was conducted on a "R/V Ferrell" longline cruise and on several day-trips by NMFS Panama City personnel. Scientists on board those vessels (Pers. comm., D. DeVries, A. David , NMFS Panama City, October 1999) provided data on exact catch-location, catch depth, total red snapper caught and bottom temperature (Table 1). Headboat data on 1999 red snapper spawning sites off west-central FL are shown in Table 2.

Batch fecundity was estimated for all females (n = 59) that contained intact ovaries with hydrated oocytes and no fresh POFs. Dates of catch on these fish ranged from late June to mid-September. All Gulf states except MS were represented in these subsamples. Total length and total weight ranged from 359 to 901 mm and 0.77 to 8.08 kg, respectively. Due to the small sample size

by state, all fish on which batch fecundity was estimated were combined for analysis.

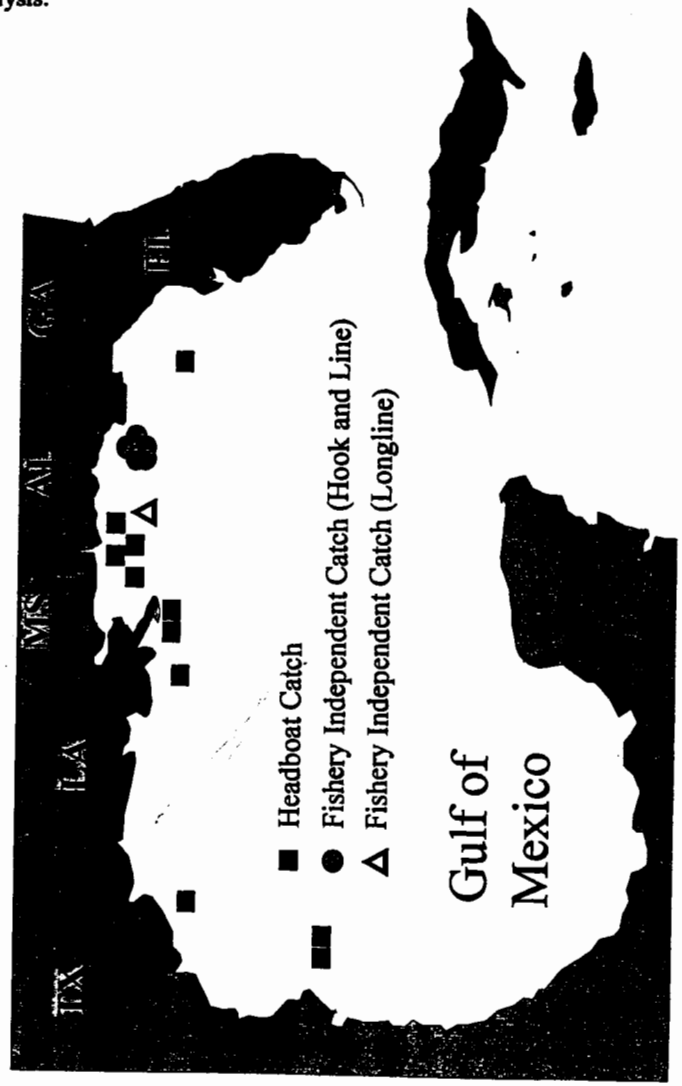

Figure 2. Red snapper spawning locations, 1998-1999.

Table 1. Fishery independent data on 1999 red snapper spawning sites off Alabama (AL) and northwest Florida (FL).

State	Date	Degrees Latitude (N)	Degrees Longitude (W)	Depth (m)	Bottom Temperature (°C)
AL	5/18	29.557	87.460	122.0	20.6
FL	7/15	29.733	86.127	47.2	27.0
FL	7/28	29.816	65.914	38.4	26.8
FL	7/28	29.882	85.832	32.9	26.5
FL	9.29	29.618	86.052	61.0	29.0
FL	10/13	29.825	85.998	40.2	29.0

Table 2. Headboat data on 1999 red snapper spawning sites shown by occurrence of females in the Florida Middle Ground. Approximate location = 28°N latitude and 84°W longitude)

Date	Approx. Depth (m)	N	TL range (mm)	Max. oocyte Dia. (mm)	Histological stage of ovary
5/21	23.8	6	420-490	0.52	Late vitellogenic
8/5	not given	6	440-601	1.94	Full hydrated

Batch fecundity estimates ranged widely from nearly zero (in a 4 year old fish) to more than 3 million (in an 11 year old fish) (Figure 3). Most fish sampled, aged 8 years or less, showed batch fecundities of less than 1 million. Some fish, aged 4 years or less, showed extremely low batch fecundities of less than 200.

Both age and TL had an exponential (third order polynomial) relationship with batch fecundity, but age was the best predictor (Figure 3). Older individuals are potentially much more highly fecund. The TL relationship was: batch fecundity = $(8.0*10^{-9}TL^3) - (8.0*10^{-6}TL^2) + (2.2*10^{-3}TL)$; ($r^2 = 0.34$, n = 59).

Estimates of spawning frequency are incomplete, but age 6-35 females seemed to spawn about 50% more times than age 3,4 or 5 females did in 1998. Some spawning frequency estimates were made difficult by postmortem decay in some samples. The decay caused a problem separating some stage 3 and stage 4 ovaries. However, all ovaries can still be staged.

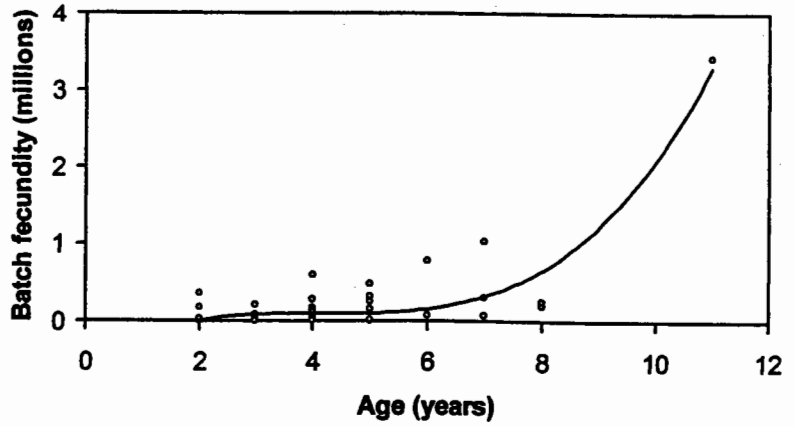

Figure 3. 1999 NW Florida red snapper spawning locations.

DISCUSSION

Our results on spawning months, locations and temperatures (assuming that spawning takes place near the bottom) and batch fecundity estimates generally agree with published studies. We recorded spawning from April - May through September - October and similar results were reported for the northeastern Gulf (Moe 1963, Futch and Bruger 1976, Collins, et al. 1996), the northwestern Gulf (Moseley 1965, and Bradley and Bryan 1976) and in the southern Gulf (Camber 1955). Collins, et al. (1980) also reported larval red snapper off Texas during May, July through September, and November. Bottom temperatures recorded at our spawning sites were 20.6 and 26.5 to 29.0°C. (Table 1); similar temperatures for spawning in captivity were reported by three studies (23 to 25°C. by Arnold, et al. 1978; 25 to 27°C. by Minton, et al. 1983, and 24 to 27°C. by Chesney and Filippo 1994). Our batch fecundity range of 13 (for a 417 mm TL, 4 year old fish) to 3.4 million (for a 851 mm TL, 11 year old fish) compares favorably to those in Collins, et al. (1996) (their range of batch fecundity was 458, for a 349 mm TL fish that couldn't be aged, to 1.7 million for a 820 mm TL fish that was 12 years old).

Although we increased the number of large red snapper on which batch fecundity has been estimated by sampling a much greater area of the Gulf of Mexico in 1998, many of the larger specimens we sampled could not be used for batch fecundity estimation because they were either males or non-hydrated females. We were, however, able to find almost as many fish (of all lengths) on which batch fecundity was estimated in our first year of this new sampling program (n = 59) as we had previously (off northwest FL) in 3 years (n = 66, in Collins, et al. 1996).

Although we requested larger fish from the port samplers, older-aged fish (i.e. > age 5) were rare in accordance with findings from a complementary aging study (Fitzhugh, et al. 1999). With the inclusion of some fish aged 6-8 and a single 11 year old into the reproductive analysis, it is apparent that batch fecundity increases exponentially with age and that some younger fish (e.g., < age 4 or 5) are showing extremely low batch fecundities (i. e., thousands or less). Batch fecundities typically range from tens of thousands to millions in some other demersal commercial-sized fishes (Fitzhugh, et al. 1993, Nieland and Wilson 1993, Wilson and Nieland 1994). The documentation of extremely low batch fecundities and good estimates of their proportions among age classes within a given spawning year would be of great interest in estimation of spawning potential and as a factor in monitoring recruitment variability.

We are not aware that extremely low batch fecundities are often reported in the fisheries literature. Loss of ova upon sampling and improper preservation of gonads have been suspected causes for biased estimation of fecundity; these are not uncommon problems among fishery-dependent dockside sampling programs.

Hydration of ova occurs within a diel cycle and spawning likely occurs after dusk (Chesney and Filippo 1994). Sampling partially hydrated females during daylight hours may also result in estimates of batch fecundity that are biased (low).

Extremely variable (i.e. low) batch fecundity data are also likely to be closely scrutinized, and eliminated as biologically unreasonable outliers when a goal is to provide "good" equation fits to fecundity data (see Schirripa and Legault 1999). However, we also noticed that these extremely low batch fecundities were detected from ovaries that were small in size, light in weight, and low in corresponding GSI value (hydrated ovaries < 20 g and with GSI < 0.7). This could not be explained by artifacts of sampling. Improper preservation and loss of running-ripe ova are likely to explain decreases of ovary weight (and batch fecundity) of only a few percent. Red snapper are known to mature very early (age 2) given their estimated longevity (about age 50) (Futch and Bruger 1976, Wilson et al. 1994). Relatively low ovarian weight occurring naturally among some females classified as mature seems to coincide with extremely low batch fecundity.

An examination of red snapper induced to spawn by hormone injection also revealed extremely low batch fecundities (hundreds to a few thousand) among the smallest fish (presumably age-2, based on expected size at age) in contrast to larger and presumably older females (Chesney and San Filippo 1994). Lacking more detailed reproductive information for a stock assessment, Schirripa and Legault (1999) looked at the Chesney and Filippo report and postulated a case where the fecundity-length relationship could be a two-tiered function with a steep initial slope for the first maturing females. Our initial findings based on field samples highlights the relevancy of Chesney and Filippo's observations of extremely low batch fecundity and provides support for the two-tier case presented in Schirripa and Legault (1999).

Although red snapper is one of the most studied fishes from the Gulf of Mexico, there are very few positive identifications of spawning sites and depths. Moe (1963) published habitat descriptions and fishermen's observations of red snapper spawning sites (determined from running ripe fish) at 13 - 16 fathoms (24 - 29 m) due south of Panama City, FL. Subsequently, research publications have reviewed anecdotal information, distribution of larvae and juveniles, and provided suppositions about larval transport pathways to advance what was known about possible spawning locations and depths (Moseley 1965, Beaumariage and Bullock 1976, Futch and Bruger 1976, Collins, et al. 1980). Bradley and Bryan (1975) report the only other fishermens' observation which increased the known depth of spawning (off TX) to about 20 fathoms (37 m). Futch and Bruger (1976) and Bradley and Bryan (1976) conducted surveys to specifically identify spawning locations and failed to find actively spawning red

snapper. Collins et al. (1980) gave catch locations of 225 larvae and early juveniles, suggesting a general spawning area and depth range off TX. Our limited results to date indicate that spawning may be occurring at depths greater than previously reported. We have found actively spawning fish (occurrence of at least one hydrated female within a catch) from 24 to 60 m using hook and line gear. One hydrated female (out of 7 total red snapper) was collected during a fishery-independent long-line survey at 122 m depth. A hook-and-line fishery independent survey of the Texas Flower Gardens (Nelson, 1988) is also notable for the deeper depth distribution of "ripe" red snapper females. By interpolation of results in Nelson (1988) it can be estimated that about 10 ripe females captured from a total of 53 females during summer cruises were likely to have come from depths deeper than 50 m (99% of the red snapper captured). These findings, that red snapper spawning is not commonly detected and can occur across a broad depth zone (mid-shelf to slope), clearly reflect that we don't know enough about conditions and habitats important for red snapper reproduction.

Of special interest are some spawning sites off west-central FL shown by samples from headboats out of St. Petersburg (Figure 3, Table 2 and West 1999). Although red snapper in this area were once worthy of "a good catch" (Camber 1955) and "frequent" and "numerically dominant" (Smith, et al. 1975), catches in the 1980s and 1990s have been infrequent until the last two years (Schirripa and Legault 1999, West 1999). Red snapper may be moving back into that area from further west. Although Fable (1980) found that red snapper tagged off TX did not move far, Patterson (1999) found that this species does travel substantial distances off AL.

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LITERATURE CITED

Arnold, C.R., J.M. Wakeman, T.D. Williams and G.D. Treece. 1978. Spawning of red snapper (*Lutjanus campechanus*) in captivity. *Aquaculture* **15**:301-302.

Beaumariage, D.S., and L.H. Bullock. 1976. Biological research on snappers and groupers as related to fishery management requirements. Pages 86-94 in: H. R. Bullis, Jr., and A.C. Jones (eds.). *Proceedings: colloquium on snapper-grouper fishery resources of the western central Atlantic Ocean.* Florida Sea Grant Colloquium Report 17, 333 pp.

Bennett, J.E. [1998] Automated Landings Assessment for Responsive Management Report. National Marine Fisheries Service, Miami, FL, Sustainable Fisheries Division Contribution: SFD-98/99-39. 93 pp. Unpubl. Report.

Bradley, E., and C.E. Bryan. 1975. Life history and fishery of the red snapper (*Lutjanus campechanus*) in the northwestern Gulf of Mexico: 1970-1974. *Proc. Gulf Carib. Fish. Inst.* **27**:77-106.

Camber, C.I. 1955. A survey of the red snapper fishery of the Gulf of Mexico, with special reference to the Campeche Banks. Fl. Bd. Conserv., Tech. Ser. 12. 63 pp.

Chesney, E.J. and R. San Filippo. 1994. Size-dependent spawning and egg-quality of red snapper. Final report to U. S. Dept. Comm.,NMFS. Marine Fisheries Initiative (MARFIN) Coop. Agreement NA37FF0048-01. 17 pp.

Collins, L.A., J.H. Finucane and L.E. Barger.1980. Description of larval and juvenile red snapper, *Lutjanus campechanus. Fish. Bull.* **77**(**4**):965-974.

Collins, L.A., A.G. Johnson and C.P. Keim. 1996. Spawning and annual fecundity of the red snapper (*Lutjanus campechanus)* from the Northeastern Gulf of Mexico. Pages 174–188 in: F. Arreguin -Sanchez, J. L. Munro, M. C. Balgos and D. Pauly, (eds.) *Biology, fisheries and culture of tropical groupers and snappers.* Proc. ICLARM/EPOMEX International Workshop, Campeche, Mexico. October 1993.

Fable, W. A., Jr. 1980. Tagging studies of red snapper (*Lutjanus campechanus)* and vermilion snapper (*Rhomboplites aurorubens)* off the south Texas coast. *Contributions to Marine Science* **23**:115-121.

Fitzhugh, G.R., B.A. Thompson, and T.G. Snider III. 1993. Ovarian development, fecundity and spawning frequency of black drum *Pogonias cromis* in Louisiana. *Fish. Bull.* **91**:244-253.

Fitzhugh, G.R., L. A. Collins, L.A. Lombardi, M. R. Burnett, W.A. Fable and W.T. Walling [1999]. Report of red snapper aging and spawning/fecundity research. National Marine Fisheries Service,

Panama City, Florida. 5 pp. Unpubl. Report.

Futch, R. B., and G.E. Bruger. 1976. Age, growth, and reproduction of red snapper in Florida waters. Pages 165-184 in: H. R. Bullis, Jr., and A. C. Jones (editors), *Proceedings: Colloquium on Snapper-Grouper Fishery Resources of the Western Central Atlantic Ocean.* Fla. Sea Grant Report No. 17.

Hunter, J. R. 1985. Preservation of Northern Anchovy in Formaldehyde Solution. Pages 63-65 in: R. Lasker (ed.) *An egg production method for estimating spawning biomass of pelagic fish: an application to the northern anchovy, Engraulis mordax.* NOAA/NMFS Tech. Rep. 36.

Hunter, J.R., N.C.H. Lo, and R.J.H. Leong.1985. Batch fecundity in multiple spawning fishes. Pages 67-77 in: R. Lasker (ed.) *An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, Engraulis mordax.* NOAA/NMFS Tech. Rep. 36.

Hunter, J. R. and B. J. Macewicz. 1985. Measurement of spawning frequency in multiple spawning fishes. Pages 79-94 in: R. Lasker (ed.) *An egg production method for estimating spawning biomass of pelagic fish: an application to the northern anchovy, Engraulis mordax.* NOAA/NMFS Tech. Rep. 36.

Minton, R. V., J.P. Hawke and W.M. Tatum. 1983. Hormone induced spawning of red snapper, *Lutjanus campechanus*. *Aquaculture*, **30**: 363-368.

Moe, M. A., Jr. 1963. A survey of offshore fishing in Florida. Fla. St. Bd. Conserv. Mar. Lab., Prof. Pap. Ser. No. 4, 117 pp.

Moseley, F.N. 1965. Biology of the red snapper, *Lutjanus aya* Bloch, of the northwestern Gulf of Mexico. *Publ. Inst. Mar. Sci. Univ. Tex.* **11**:90-101.

Nelson , R. S. 1980. Growth and mortality aspects of natural populations of the red snapper, Lutjanus campechanus, in the west central Atlantic and Gulf of Mexico. M.S. Thesis, Louisiana State University, Baton Rouge, La. 73 pp.

Nelson, R. S. 1988. *A study of the life history, ecology, and population dynamics of four sympatric reef predators (Rhomboplites aurorubens, Lutjanus campechanus,Lutjanidae; Haemulon melanurum, Haemulidae; and Pagrus pagrus, Sparidae) on the East and West Flower Garden Banks.* Ph. D. Dissertation. North Carolina State University. 197 pp.

Nieland, D.L., and C.A. Wilson. 1993. Reproductive biology and annual variation of reproductive variables of black drum in the northern Gulf of Mexico. *Trans. Am. Fish. Soc.* **122**:318-327.

Patterson, W.F. 1999. *Aspects of the population ecology of red snapper, Lutjanus campechanus, in an artificial reef area off Alabama*. Ph. D.

dissertation, University of South Alabama, Mobile, Al.

Schirripa, M.J. and C.M. Legault [1999] Status of the red snapper in U. S. waters of the Gulf of Mexico: updated through 1998. National Marine Fisheries Service, Miami, FL, Sustainable Fisheries Division Contribution: SFD-99/00-75.106 p. Unpubl. Report.

Smith, G.B., H.M. Austin, S.A. Bortone, R.W. Hastings, and L H. Ogren. 1975. Fishes of the Florida Middle Ground with Comments on Ecology and Zoogeography. Florida Marine Research Publication No. **9**, Florida Dept. of Nat. Resources, Marine Research Laboratory, St. Petersburg, Florida.

West, G. 1990. Methods of assessing ovarian development in fishes: a review. *Aust. J. Mar. Freshwater Res.* **41**:199-222.

West, J. 1999. Red snapper revival. *Florida Sportsman* , August 1999:16-25.

Wilson, C.A., and D.L. Nieland. 1994. Reproductive biology of red drum, *Sciaenops ocellatus*, from the neritic waters of the northern Gulf of Mexico. *Fish. Bull.* **92**:841-850.

Wilson, C.A., J.H. Render, and D.L. Nieland. 1994. Life history gaps in red snapper (*Lutjanus campechanus*), swordfish (*Xiphias gladius*), and red drum (*Sciaenops ocellatus*) in the northern Gulf of Mexico; age distribution, growth, and some reproduction biology. Final report to U. S. Dept. Comm., NMFS, Marine Fisheries Initiative (MARFIN) Coop. Agreement NA17FF0383-02. 79 pp.

Zar, J. H. 1984. Testing for Goodness of Fit. Pages 40–60 in: B Kurtz (ed.) *Biostatistical Analysis*, Prentice Hall, Englewood Cliffs, NJ.

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