Size and Age at Maturity of Female Red Snapper *Lutjanus campechanus* in the Northern Gulf of Mexico

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ABSTRACT

Red snapper, *Lutjanus campechanus*, support important recreational and commercial fisheries in the Gulf of Mexico (Gulf). Both fisheries have been intensely managed since the early 1990s after perceptions of overfishing in both sectors surfaced during the 1980s. Due to incomplete or missing life history data, particularly in regard to the species' reproductive behavior and output, certain assumptions have been made as regulations to promote the species' recovery have been designed. To provide information on the size and age of female red snapper at the onset of reproductive maturity, specimens from the Gulf off Alabama and Louisiana were examined for evidence of spawning activity during the spawning seasons of 1999, 2000, and 2001. The progression of oocyte maturation to vitellogenesis as observed in histological sections of ovarian tissues was used to define sexual maturity. The smallest red snapper having either hydrated oocytes or postovulatory follicles, definitive evidence of imminent or recent spawning, was 267 mm FL and was two years old. Female red snapper in Alabama reached maturation at a smaller size and younger age than those in Louisiana and growth rates did not differ between the regions.

KEY WORDS: Maturation, population demographics, red snapper

INTRODUCTION

The red snapper, *Lutjanus campechanus*, has supported important recreational and commercial fisheries in both the United States and Mexico for over a century. Both fisheries have been intensely managed in the U.S. since the early 1990s after perceptions of overfishing in both sectors surfaced during the 1980s. The Reef Fish Management Plan was developed in 1990 to provide for assessments of the status of the red snapper stock in the northern Gulf of Mexico (hereafter Gulf) and to adopt measures to rebuild the stock, ultimately to a sustainable yield. These recommendations are based principally upon the assumption that the red snapper population is one continuous or unit stock. However, data concerning stock structure (Camper et al. 1993, Chapman et al. 1995, Gold et al. 1997, Heist and

Gold 2000) are inconclusive and the unit stock hypothesis has yet to be tested. Despite management efforts, red snapper in the Gulf remain overfished (Goodyear 1995, Schirripa and Legault 1999).

The red snapper is a long-lived reef fish that can grow to be greater than 1000 mm TL and can live more than 50 years (Wilson and Nieland 2001). It is restricted to the Atlantic coast of the southeastern United States and the Gulf of Mexico (Rivas 1966). In the Gulf, adult red snapper are commonly found at depths ranging from 30 to 130 m (Fischer 1978). This gonochoristic species spawns multiple times during a prolonged season. Though many publications on red snapper exist, none addressing spawning and reproductive biology of the species in the wild have been published in the peer-reviewed literature. Studies presented in available publications differ in the spatial and temporal scales and in sampling protocols and methodologies (Table 1). Previous studies of more than one year have been restricted to a single state, while those studies incorporating larger regions only lasted a year. This study covers a greater region for a greater time period than any previous study.

Camber (1955), Moseley (1966), and Futch and Bruger (1976) all presented limited data on red snapper length- or age-at- maturity and the duration of the spawning season in the Gulf of Mexico. Length at maturity has been reported to be 320 mm FL (Camber 1955) and 190-300 mm SL (Mosely 1966). Wilson et al. (1994) presented preliminary estimates of maturation at 290 mm FL. Age at maturity has been reported as greater than 2 years old (Futch and Bruger 1976). Duration of spawning season has been reported differently among studies (Camber 1955, Mosely 1966, Bradly and Bryan 1975, Futch and Bruger 1976, Wilson et al. 1994, Collins et al. 1996). It has been described to occur for as long as seven months, lasting from May until January (Bradly and Bryan 1975), and as short as two months, lasting from July until September (Camber 1955); one study included April in the spawning season (Wilson et al. 1994).

Ovary analyses also vary among studies. While authors prior to 1976 (Camber 1955, Bradly and Bryan 1975, and Mosely 1966) used macro-assessment of gonad condition and maturation, later authors (Collins et al. 1996, Futch and Bruger 1976, and Wilson et al 1994) used histological techniques to determine distinct oocyte maturation. Histology is a more effective method for staging oocytes because it allows a detailed view of cross-sectioned and stained oocytes and thus, precise descriptions of oocyte maturation stages can be most clearly defined (West 1990). Despite this precision, problems still exist in the histology technique due to differences in terminology among authors, as well as subtle differences in oocyte maturation among species.

This research sought to gain a better understanding of red snapper population dynamics for optimum management. Our objectives were to provide data on age and size at reproductive maturity of red snapper in the northern Gulf of Mexico and to determine if differences exist east and west of the Mississippi River over a time span of three years.

Table 1. Results of this study and past studies pertaining to reproductive biology of red snapper.

Reference	Year of study	Location	female:male	length range	length/age at 50 % maturity	spawn season	peak spawn
Camber 1955	1955	Campeche Banks	1.1:1	250-800 mm FL	320mm FL	July-Sept	July-Aug
Moseley 1966	1964-65	NW Gulf	1:1.3	200-700 mm SL	190-300mm SL	June-mid-Sept	Aug
Bradley & Bryan 1975	1970-72	Texas	1:1	200-845 mm FL	255mm FL	May-January	June-July
Futch & Bruger 1976	1972-75	Clearwater, Florida	1.2:1	100-941 mm FL	2+ years	July-October	Aug-Sept
Wilson et al. 1994	1989-93	Louisiana	------	340-850 mm FL	290mm FL	April-Sept	June-Aug
This Study	1999 – 2001	Alabama - Louisiana	------	239-916 mm FL	AL: 275mm FL/ 2 LA: 300mm FL/ 2	May-Sept	May-July

METHODS

During the recreational fishing season of 1999, 2000, and 2001 red snapper were sampled by hook and line from the Gulf of Mexico west of the Mississippi River off Louisiana waters, and east of the Mississippi River off Alabama (Figure 1). Between the months of May and October, a minimum of 600 individuals per region were targeted in 1999 and 2000 and 300 individuals per region were targeted in 2001. Minimum size (406 mm TL) of the recreational harvest was dependent upon federally controlled size limits. In addition to these targeted fish, a National Marine Fisheries Service permit allowed us to collect undersized red snapper. In this study only female individuals are considered.

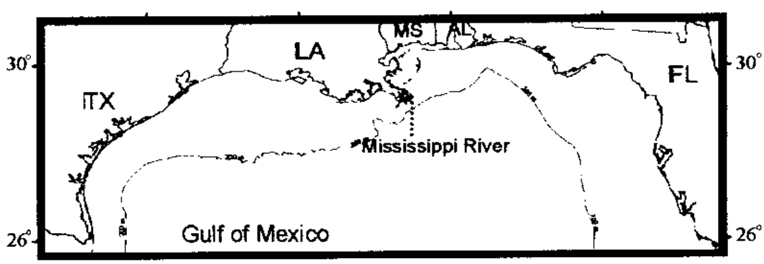

Figure 1. Red snapper were collected east of the Mississippi River off Alabama (AL) and west of the River off Louisiana (LA)

Fork length (FL) (to the nearest mm), and total (TW) and eviscerated weights (EW) (to the nearest 0.01 kg) were recorded for each fish sampled. Sagittal otoliths were removed as described by Beckman et al. (1990) and processed for age analysis following Cowan et al. (1995). Gonads were excised, placed in individually labeled plastic resealable bags, and transported on ice to the laboratory. After the gonads were weighed (nearest 0.1 g), the ovaries were stored in 10% formalin until further analysis.

We analyzed several reproductive characteristics of female red snapper to determine age and size at maturity. These characteristics include gonadosomatic indices (GSI), oocyte maturation stages, and duration of spawning season.

GSI was calculated as gonad weight as a function of body weight (Htun-Han 1978): GSI= (100) (gonad weight in g / ovary free body weight in g). A peak in the GSI suggests a peak in seasonal spawning.

Oocyte maturation stages were determined by histological analysis. The lobes of the ovaries are symmetrical (Collins et al. 1996); therefore, a subsample of formalin fixed ovarian tissue (30-50 g) was dissected from one randomly chosen region of the two lobes. Each subsample was embedded in Paraplast and sectioned to 3μm thickness. Sections were mounted on microscope slides, stained in Gill hematoxylin, and counterstained in eosin Y.

Oocytes were categorized into one of four oocyte stages by microscopic examination of the prepared histology slides at 40x and 100x magnification. The four stages of oocyte maturation described by Wallace and Selman (1981) are primary growth (PG), cortical alveoli (CA), vitellogenic (V), and hydrated (H). Progression of oocyte maturation to vitellogenesis was used to define and identify mature females (Figure 2A) (Hunter and Goldberg 1980, Brown-Peterson et al. 1988, Nieland and Wilson 1993). Immature ovaries contained only PG and CA oocytes (Figure 2B).

Females were classified as mature by size and by age. Females were grouped into size classes of 25 mm and 50 mm FL and age classes. Differences in defined reproductive characteristics between regions were tested by chi-square analysis. The Benferroni technique was used to adjust for the possibility of a Type I error. A weighted log regression was used to determine if differences in growth rates existed between regions.

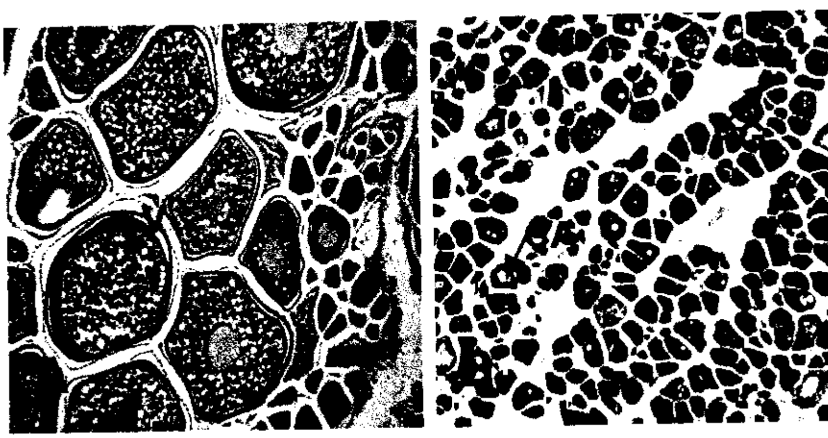

Figure 2. Image of mature (A) and immature (B) ovaries of red snapper. V indicates a vitellogenic oocyte. PG indicates a primary growth oocyte. CA indicates a cortical alveoli oocyte.

RESULTS

A total of 1681 female red snapper were collected from the northern Gulf: 1029 from Alabama and 653 from Louisiana. Alabama females ranged from 237-916 mm FL, Louisiana females ranged from 292-910 mm FL. Ages of Alabama and Louisiana females ranged from 1-34 years and 2-37 years, respectively. Age data from 2001 was not included in this analysis because fish collected in 2001 had not been aged as of this writing.

Gonadosomatic index indicated that spawning began in May and ended by September. The peak months of the spawning season appeared to be May, June, and July. Only individuals captured during June, July, and early August were considered in determining size- and age-at-maturity. Individuals captured in May were not analyzed in order to insure 'truly immature', as opposed to apparent immaturity resulting from the beginning of the spawning season. A total sample size of 1,247 females was used for comparisons of length-at-maturity, and 864 for comparisons of age-at-maturity.

The smallest mature Alabama fish was 267 mm FL and the smallest with hydrated oocytes, indicative of imminent spawning, and POF, indicative of recent spawning, were 280 mm and 267 mm FL, respectively. The smallest mature Louisiana fish was 292 mm FL and the smallest with hydrated oocytes and POF were 304 and 324 mm FL, respectively. All of these fish were 2 years old.

Combined data showed that all fish greater than 590 mm FL, and all greater than age 5 years were mature, with one exception. A 720 mm FL, 7 year old captured off Alabama was immature. A comparison of the maturity schedules for each region indicated that fish captured east of the Mississippi River in Alabama reached 50% maturity at 275 mm FL and 2 years old and 100% maturity by 600 mm FL and 5 years old; fish captured to the west in Louisiana reached 50% maturity before 300 mm FL and 2 years old and 100% maturity by 600 mm FL and 6 years old (Figures 3 and 4). Compared to Alabama, Louisiana females progressed to maturity over size and age classes more slowly. Chi-square analyses indicated that Alabama size classes between 300 mm – 500 mm, and age classes between 3 – 5 years, had significantly more mature females than in Louisiana (Tables 2 and 3). Weighted linear regression on $\log_{10}$-transformed data of length at age indicated no significant differences between growth rates of these two regions (ANCOVA test for equal slopes, $p = 0.56$).

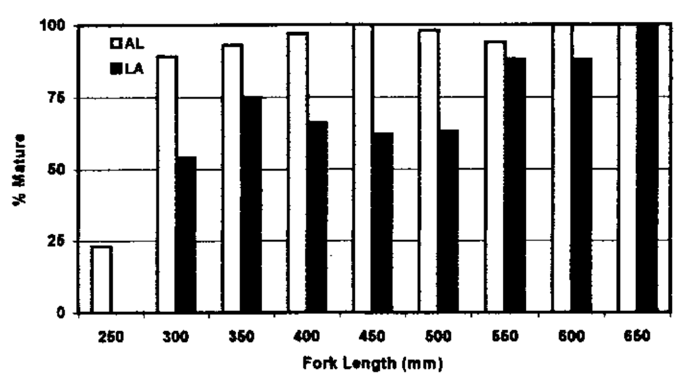

Figure 3. Percent of mature female red snapper by fork length (mm) for Alabama (AL) and Louisiana (AL)

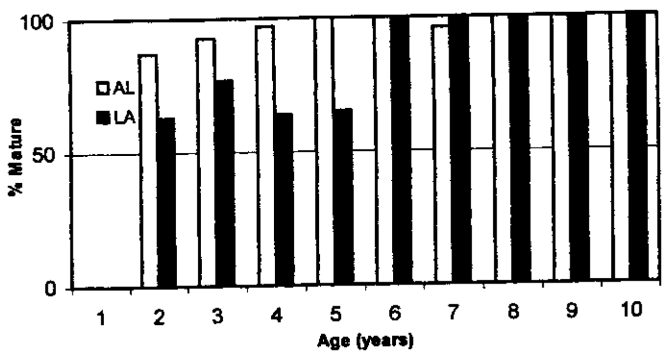

Figure 4. Percent of mature female red snapper by age) for Alabama (AL) and Louisiana (AL)

Table 2. Percent of mature females and sample size N by size class in 25 mm increments for Alabama and Louisiana. Size classes having significantly different proportions of mature females are indicated by (*).

Size Class	Alabama		Louisiana	
FL (mm)	% Mature	N	% Mature	N
250	0	7		
275	65	17		
300	92	38	67	9
325*	94	34	43	7
350*	94	31	70	20
375*	95	62	70	27
400*	97	65	70	27
425*	99	79	61	28
450*	100	78	69	54
475*	100	55	50	34
500*	96	46	67	24
525*	100	37	74	19
550	94	33	100	6
575	92	24	75	4
600	100	16	100	4
625	100	24	100	4
650	100	30	100	4

Table 3. Percent of mature females and sample size N by age classes for Alabama and Louisiana. Age classes having significantly different proportions of mature females between states are indicated by (*).

Age Class	Alabama		Louisiana	
years	% Mature	N	% Mature	N
1	0	8		
2*	87	55	63	16
3*	93	75	77	117
4*	97	200	65	99
5*	100	86	65	54
6	100	29	97	34
7	96	25	100	8

DISCUSSION

While our estimates of size- and age-at-50 %maturity do fall within the range of estimates of past studies (Camber 1955, Moseley 1966, Futch and Bruger 1976, and Wilson et al. 1994), only one other study has reported maturation schedule to 100% maturity and it was not similar to our results. Wilson et al. (1994) reported that females sampled from Louisiana reached 100% maturity by 420 mm FL.

Regional differences in red snapper age- and size-at-maturation could represent a real difference in population demographics of the red snapper east and west of the Mississippi River. Maturity schedules of a species generally are not static, and it is rare for all individuals in a fish stock to mature at the same age. However, a decline in age-at-maturity can be an indication of a stressed population and is often caused by compensatory responses to declining population size and/or by genetic selection (Trippel 1995).

Maturation schedules can change in response to fishing pressure, predator and prey abundance, stock composition, and other biotic and abiotic environmental factors (Wooton 1990). Zhao and McGovern (1997) identified changes through time in age- and length-at-maturity and in growth rate of vermilion snapper *Rhomboplites aurorubens* in the South Atlantic Bight; changes were probably due to gradual fishing pressure increases ultimately resulting in growth overfishing. A preliminary study indicated that, compared to fish sampled from the region five years earlier (Grimes and Huntsman 1980), vermilion snapper decreased in size and age at maturation; however, length at age for one and two year old fish changed little (Collins and Pinckney 1988). A temporal comparison of the stock in 1979-80 to 1985-87 also concluded that vermilion snapper declined in size- and age-at-maturity through time (Zhao and McGovern 1997) and that growth rate decreased through time (Zhao et al. 1997). Because growth rates decreased with time, the decrease in size at maturity probably is not part of a density-dependent compensatory response to harvesting; more likely, it is a response to growth overfishing caused by the selective removal and incomplete replacement of faster-growing, later-maturing fish by harvesting (Zhao and McGovern 1997).

Jørgensen (1990) observed changes through time in age at maturity and growth rate of Arctic cod *Gadus morhua* to be a density-dependent compensatory response to harvesting. The cod population has been intensely exploited for the past 50 years and cod stocks have undergone severe population declines. Jørgensen determined that despite high fishing pressures, it is the age distribution and not the size distribution of the population that has changed. It is likely that in response to increased mortality, fish grow faster and mature at a younger age; implicitly, there is a minimum threshold for size-at-maturity (Jørgensen 1990). If this idea is correct, then declines in size and in age at maturity should not occur simultaneously.

In contrast, Reznick et al. (2001) presented a case in which populations of guppies experiencing high and low predation pressures had different population demographics. Guppies experiencing high predation rates had a smaller size and younger age at maturity and a faster growth rate than fish experiencing low predation pressure because higher levels of resource availability existed as an indirect consequence of high predation. The populations experienced different mortality, lived in different environments, and due to mortality and environmental differences, food availability differed. Guppies at sites of low-predation did not have a greater density per unit area but had more large, old fish and fewer small, young fish, and thus, a greater biomass.

Similarly, red snapper populations could vary by region due to a compensatory response. If mortality rates are different and/or if the environments in areas off Alabama and Louisiana coastlines differ, then population demographics could also differ. Greater fishing pressure off Alabama could decrease the density of fish per unit area, thereby decreasing intra-specific competition and allowing for an increase in resource availability. If red snapper in the Gulf have reached their maximum physiological growth potential, then the increased available energy in Alabama's system could be allocated to reproduction. This would allow fish to reproduce at a smaller size, and therefore, younger age in Alabama waters. However, there are no reliable estimates to compare mortality rates east and west of the Mississippi River.

Environmental differences could also exist between the regions. Both have a great number of artificial reefs which red snapper are known to inhabit. While Alabama's artificial reefs are predominantly small, low-vertical-relief structures, Louisiana's artificial reefs are predominantly oil and gas platforms. Compared to the smaller artificial reefs of Alabama, it is unknown as to whether platform reefs are more productive as habitat for red snapper. Regardless of these artificial reef structure differences, there is a vast amount of natural hard bottom off each the coastlines (Gore 1992) and differences in habitat are likely to be negligible.

Shifts in maturation schedule in red snapper may be attributable to genetic selection coincident with increased mortality (Roff 1992). Tagging studies have implied that red snapper movement may be sufficient to facilitate stock mixing in the stock in the northern Gulf have not strongly supported genetic differences in the stock (Camper et al. 1993, Gold et al. 1997, Heist and Gold 2000, but see Chapman et al. 1995). However, these genetic tests would not indicate differences in a maturity genotype. A genotype for smaller size and younger age at maturity can be selected for in some species (Trippel 1995). Early maturing genotypes reproduce before being fully recruited to the fishery. Genotypes that mature at larger sizes or older ages are likely to be removed before reproduction. In contrast, fish that mature early may participate in one or more spawning seasons before being captured. The progeny for later maturing fish would be selected out of the population over time. Therefore, it may be that the late-maturing genotypes have been removed from the Alabama population due to high fishing pressure. This process would explain the lesser abundance of larger and older immature fish (if it is true that Alabama has fewer large and old individuals than Louisiana) in the Alabama region and would account for differences in size and age at maturity.

It is unclear what is causing differences in size- and age-at-maturity in regions east of the Mississippi River off Alabama and west of the River off Louisiana. It is evident that differences in population demographics exist between the two regions. This study is part of a larger effort to gain a better understanding of the red snapper population in the northern Gulf. Although a difference in mortality due to fishing is likely to be the cause of the differentiation in reproductive demographics that we observed, results of ongoing studies will bolster these preliminary results.

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