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Habitat- and region-specific reproductive biology of female red snapper (Lutjanus campechanus) in the Gulf of Mexico

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HABITAT- AND REGION-SPECIFIC REPRODUCTIVE BIOLOGY OF FEMALE RED SNAPPER (*LUTJANUS CAMPECHANUS*) IN THE GULF OF MEXICO

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This work is dedicated to my parents, sister and grandparents and to those who cherish the living sea and the nourishment it provides.

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ABSTRACT

This study compares reproductive biology estimates of female red snapper among three habitat types (natural shelf-edge banks, standing petroleum platforms and toppled petroleum platforms) and among six regions in the Gulf of Mexico (central Florida, northwest Florida, Alabama, Louisiana, north Texas and south Texas). In both studies, batch fecundity and spawning frequency increased with length, weight and age, and batch fecundity was best correlated with maternal length. Gulf-wide, 75% maturity was achieved by age-3 and 100% maturity was reached by age-8. Sizes- and ages-at-maturity differed among habitat types and regions. Females from natural habitat reached 50% maturity the slowest (age-5, 450 mm TL), while fish from toppled platforms reached this benchmark the fastest (age-3, 400 mm TL). Among regions, 100% maturity was reached fastest in north Texas (age-6, 625 mm TL), followed by conspecifics in Alabama (age-6, 675 mm TL), while this benchmark was reached slowest in northwest Florida (age-9, 775 mm TL). Mean batch fecundity was significantly greater in Alabama (283,051 ± 35,761) compared to the other regions. Spawning frequency was significantly greater in north Texas (1.9-3.4 days) compared to the other regions. The differences in reproductive biology estimates among habitat types and regions presented here exemplify the diversity of intraspecific life history traits, which may be influenced by varying ecologies, environments and/or fishing pressures. These findings may supplement managers with important knowledge regarding red snapper vital rates, which may be useful for future management decisions.

CHAPTER 1: GENERAL INTRODUCTION

1.1 Life History, Ecology and Reproductive Traits of the Gulf Red Snapper

The red snapper (*Lutjanus campechanus*) is a demersal reef fish, which inhabits U.S. waters at temperate and tropical zones from the South Atlantic Bight to the Yucatan Peninsula (White and Palmer 2004; Wells and Cowan 2007). Greatest abundance occurs in the northern Gulf as well as on the Campeche Banks off of Mexico (GMFMC 2004). Red snapper occupy natural embankments, ridges and reefs across the continental shelf out to the shelf-edge, and peak biomass occurs at depths of 50-100 m (Patterson et al. 2001; Walter and Ingram 2009). The red snapper is a reef-associated species, which displays an affinity for structures offering vertical relief as refuge (Wells and Cowan 2007). Foraging occurs over soft bottom areas mostly at night away from reefs, and diet consists mainly of fishes, squid, crustaceans, and pelagic zooplankton (GMFMC 2004; McCawley and Cowan 2007).

Two centers of red snapper abundance presently exist in the northern Gulf. The largest occurs off of southwest Louisiana, and the other off of Alabama (Patterson et al. 2001). The widest age-distribution exists in the western Gulf (Fitzhugh et al. 2004). In the north-central Gulf, older fish are less frequent in age frequencies compared to the west. The lowest population density exists in the eastern Gulf, where red snapper are considerably younger compared to the other regions; this eastern population is considered a relic of spawning populations found elsewhere in the Gulf (Fitzhugh et al. 2004).

The red snapper is a marine broadcast spawner that exhibits a periodic life-history strategy (Winemiller and Rose 1992). It is capable of reaching ages in excess of 50 years (Wilson and Nieland 2001), and females do not reach full reproductive potential until 12 to 15 years of age (Goodyear 1995; Jackson et al. 2007). Sexual maturity is first reached at age-2, and

the majority (>50%) of fish are mature by age-4 (Schirripa and Legault 1999). Complete maturation (100% of all fish) is typically reached between 5 and 8 years of age (Fitzhugh et al. 2004; White and Palmer 2004; Jackson et al. 2007). Eggs are small (<1 mm diameter), but clutch sizes are large, ranging from hundreds in small, young fish to millions in larger, older fish (Nelson 1988; Render 1995; Collins et al. 2001; Woods 2003). At the beginning of the spawning season, fecundity is indeterminate because oocytes (i.e., egg cells) continuously develop within the ovary in an asynchronous fashion and are released in several batches over an extended spawning season. In the unpredictable, patchy marine environment, such spawning characteristics promote year class success when larvae encounter ideal conditions conducive to growth and survival (Winemiller and Rose 1992, 1993). Despite this, during most years, a female red snapper may not produce a single surviving progeny. Thus, this species depends on occasional strong recruitment years to maintain population stability (Cowan et al. 2010).

In the northern Gulf, spawning season lasts for approximately 150 days, extending from May through September (Render 1995, Woods 2003) and peaks in June, July and August (Bradley and Bryan 1976, Collins et al. 1996, Render 1995). Spawning occurs offshore on the shelf and upper continental slope between 16 and 29°C (Szedlmayer and Furman 2000; Collin et al. 2001; Woods 2003; Fitzhugh et al. 2004) over sand or mud bottom areas away from reefs (GMFMC 2004). Red snapper exhibit a distinct diel reproductive periodicity, whereby oocytes become hydrated in the morning and spawning occurs in the afternoon (Jackson et al. 2006). Eggs and larvae are pelagic and are transported inshore to coastal nursery grounds by ocean currents (Richards et al. 1993; Johnson et al. 2009). Metamorphosis occurs at 26-30 days, after which time recruits settle over sand, shell and mud bottoms (Szedlmayer and Conti 1999; Wells 2007).

An ontogenetic shift in depth and habitat preference is evident for red snapper (Allman and Fitzhugh 2007). Age-0 recruits settle over low-relief areas made of sand, mud and shell ridges, while juveniles and adults migrate to deeper waters and inhabit structures providing greater vertical relief including natural reefs, rocky ledges, petroleum platforms and artificial reefs (Patterson et al. 2001). Older adults (>8 to 10 years) are less dependent on structured habitat, and can move large distances over the shelf (Patterson et al. 2001; Gallaway et al. 2009).

The largest artificial reef system in the world exists in the northern Gulf of Mexico, where ~4,000 petroleum platforms serve as de facto artificial reefs on the outer shelf (Stanley and Wilson 2003). These structures provide an extra 12.1 km^2 of hard-bottom habitat area to a system mostly composed of mud and sand (Stanley and Wilson 2003). The majority of petroleum platforms in the northern Gulf exists off Louisiana (~90%) and Texas (Stanley and Wilson 2003). Red snapper are one of the dominant species associated with these structures (Stanley and Wilson 2003).

1.2 Current Status and Management of the Gulf Red Snapper Stock

Red snapper constitute one of the most economically valuable reef fish stocks in the northern Gulf of Mexico (Gulf). The fishery began in the northeastern Gulf in the mid-1800's, and following major advancements in fishing technologies in the mid-20th century, suffered collapse in the late 1980's (Hood et al. 2007). The first Reef Fish Fishery Management Plan was implemented in 1984, and management efforts to rebuild the stock are ongoing. However, rebuilding the stock age structure has proved a challenging feat. While struggling to restore the population to a sustainable harvest size in a reasonable amount of time, fishery managers have attempted to maintain economic stability of both the directed fishery, as well as the shrimp trawl fisheries where young red snapper are captured as bycatch (the two primary sources of fishing

mortality for red snapper) (Hood et al. 2007). In recent years, the stock has slowly begun to show some signs of recovery but remains below critical thresholds for sustainable yield (SEDAR 7 2005, SEDAR 7 Update 2009), and the 2012 NMFS Status of Stocks Report to Congress indicates that Gulf red snapper are overfished and that overfishing still is occurring (NOAA 2012).

Currently, different management strategies are used to constrain harvest levels by different sectors of the directed fishery, and in the shrimp trawl fishery in efforts to reduce fishing mortality for red snapper. The commercial fishery is allotted 51% of the Annual Catch Limit (ACL) for the directed fishery and currently operates under an individual fishing quota (IFQ) program (Strelcheck and Hood 2007). Since the implementation of the IFQ program, annual catches for the commercial fishery have been under the ACL; however, discard mortality rates remain high (GMFMC 2011). The recreational sector is allotted 49% of the yearly ACL and is restricted by bag limits, minimum size limits and seasonal closures (Strelcheck and Hood 2007). However, fishery managers continue to face problems with overharvesting as well as high discard mortality associated with the recreational fishery (Strelcheck and Hood 2007). Recent reductions in the size of the shrimp fishery and the use of bycatch reduction devices (BRD's) have had positive impacts on red snapper abundance; however, BRD's are not as effective as once hoped and shrimp trawl bycatch mortality of age-0 and age-1 red snapper continues to adversely impact the stock (SEDAR 7 2005).

Substantial declines in the size of the Gulf red snapper stock and the removal of older individuals have led to phenotypic stress responses including early maturity (Jackson et al. 2007), faster growth (Fischer et al. 2004; Nieland et al. 2007; Saari 2011) and smaller sizes-at-age (Nieland et al. 2007; Saari 2011). Across the Gulf, red snapper age-10 and older are rare, and

fish age-6 and younger comprise greater than 90% of the stock in the north-central and western Gulf (SEDAR 7 2005; Nieland et al. 2007; SEDAR 7 Update 2009; Cowan 2011). Increased dependence on younger, smaller fish limits stock reproductive potential and resilience, and slows recovery from overfishing (Trippel 1995).

The current rebuilding strategy for red snapper states that an end to overfishing should have occurred by 2009/2010, and that rebuilding of the stock should be completed by 2032 (GMFMC 2007). This allotted time frame is based on 19.6 year estimated generation time (Hood et al. 2007). Restoration to 26-27% spawning potential ratio (SPR), a benchmark associated with maximum sustainable yield and the minimum acceptable level for stock productivity, has not yet been reached (GMFMC 2007; GMFMC 2010). A new benchmark assessment for Gulf red snapper is scheduled for 2013 (GMFMC 2011).

1.3 The Importance of Understanding Habitat- and Region-Specific Differences Among a Unit Stock

In the northern Gulf, red snapper are currently managed as a single unit stock. Genetic research and tagging studies support the hypothesis that the stock is genetically homogeneous (Gold and Saillant 2007), and mixing likely occurs through larval transport via oceanic currents, and adult migratory movements which can be dramatic in response to hurricanes (Patterson et al. 2001; Johnson et al. 2009). While not found to be genetically distinct, red snapper subpopulations in the Gulf exhibit distinctive physiological qualities including different sizes at age (Fischer et al. 2004; Saari 2011) and different maturation rates (Jackson et al. 2007), and these differences may influence life history traits including growth, fecundity and recruitment (Woods 2003). Recognition of the physiological and demographic differences in this species among complex habitats and regions, and their potential influences on reproductive dynamics, would contribute greatly to effective management of the fishery (Young et al. 2006).

Furthermore, knowledge of habitat- and region-specific differences may reduce future risks of overexploitation and economic losses for the fishery (Mace 1994).

1.4 Project Objectives

In Chapter 2 of this thesis, the objective of my research was to investigate whether or not reproductive estimates were similar among female red snapper collected from natural shelf-edge bank habitat when compared to two different types of artificial reef habitat (standing and toppled platforms, each providing different levels of vertical relief) over two consecutive spawning seasons. My research was part of a collaborative Marine Fisheries Initiative (MARFIN) project designed to better understand the role that natural habitat plays in red snapper ecology. This was accomplished by estimating habitat-specific age, growth, reproductive biology, fish abundance and community structure by using hydroacoustics, vertical longlines and fish trap, diet via. gut content and nutritional condition analyses, trophic ecology via. stable isotopes of C, N, and S, and estimation of mixing rates and natal origins using otolith microchemistry. My work concentrates on the reproductive biology aspect of that project.

In Chapter 3 of this thesis, my goal was to determine whether or not reproductive estimates were similar among female red snapper sampled from six recreational fishing regions in the U.S. Gulf of Mexico. My research was part of a large-scale project designed to examine population demographics of the Gulf red snapper stock. This was accomplished through comparison of age, growth and reproductive biology from Clearwater, Florida, to South Padres, Texas, over the course of two consecutive spawning seasons. My work focuses on the reproductive biology component of that project.

In each of these studies, gonadosomatic indices, sizes- and ages-at-maturity, batch fecundity, spawning frequency and annual fecundity were estimated and compared.

Reproductive biology estimates among sizes and ages also were examined. Implications of these results with regard to life history and stock dynamics are discussed in each chapter.

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CHAPTER 2: HABITAT-SPECIFIC REPRODUCTIVE BIOLOGY OF FEMALE RED SNAPPER ON THE CONTINENTAL SHELF OF COASTAL LOUISIANA

> Despite the large volume of information in the literature concerning reproductive rates and survival probabilities, few studies directly compare the demographic rates of the same species in different habitats. —Pulliam and Danielson 1991

> Little studied … is the influence of habitat characteristics on demographic rates such as survival, growth and reproduction. —Crowder et al. 2000

2.1 Introduction

The red snapper, *Lutjanus campechanus*, is an economically valuable reef fish species that inhabits the waters of the Gulf of Mexico continental shelf. This stock supported a thriving fishery from the 1840's (Hood et al. 2007) until its collapse in the 1980's and has been intensely managed since 1989 (Strelcheck and Hood 2007). Efforts to restore this resource to sustainable harvest levels have been shrouded in great controversy, and matters are further complicated by the delayed recovery of this stock (Cowan et al. 2010). Recently, progress toward recovery has become evident; however, the red snapper stock remains overfished and may still be undergoing overfishing (SEDAR 7 Update 2009; NOAA 2012).

Depletions in spawning stock biomass (SSB) are attributed to the directed fishing sectors as well as the shrimp trawl fishery (SEDAR 7 2005). While a spawning potential ratio (SPR) of 20% is indicative of stock recovery (Fischer et al. 2004), restoration to 26% SPR, a biomass that can support maximum sustainable yield, is anticipated by 2032 (SEDAR 7 2005; GMFMC 2010). Currently SPR for red snapper remains below this benchmark.

Relatively little information exists on the reproductive ecology of red snapper in the northern Gulf of Mexico (Gulf). Current knowledge is based largely upon individuals collected from artificial reefs, petroleum platforms, or unspecified habitats reported by the directed fishery (SEDAR 7 2005). However, artificial structures (artificial reefs, oil platforms, gas platforms, sunken wreckage) constitute less than 5% of suitable habitat area on the continental shelf

(Stanley and Wilson 2003; Cowan et al. 2010). Thus, the current lack of information on red snapper life history characteristics at natural habitat elicits a gap in general understanding of the natural ecology of this species and its relation to artificial reef habitats.

For reef fish, stock size is primarily limited by recruitment success, predation, fishing mortality and habitat availability (Richards and Lindeman 1987; Macreadie et al. 2011). Habitat may promote or constrain fish populations according to amount of shelter space and food availability (Bohnsack 1989). Approximately 1,578 km^2 of natural reef area of >1 m relief exists in the northern Gulf (Gallaway et al. 2009). The shelf is characterized by silt, mud and sand with very little vertical relief (GMFMC 2004; Dufrene 2005; Wells 2007; Wells and Cowan 2007). Off Louisiana, the greatest amount of relief occurs on the shelf-edge, where natural banks, ledges, salt domes and reef peaks exist (Patterson and Cowan 2003). Natural habitat composition on the continental shelf transitions to the east and west off Louisiana. To the east, the outer shelf and upper slope of the northeastern Gulf off Mississippi and Alabama are covered by silts and clays from the Mississippi River delta, and sediment composition transitions to grainy quartz sands as the eastern direction is approached; relict hard-bottom pinnacles and ledges are present there, although no current-day reefs exist in that area (Thompson et al. 1999). To the west, high-relief natural reef pinnacles, salt dome uplifts and sprawling hard-bottom habitat support a diverse array of marine life, culminating at the Flower Garden Banks off the Louisiana-Texas border where hermatypic corals are abundant (Gledhill 2001). However, several of the shelf-edges banks support complex habitat including corals (e.g., Stetson, Bright, and McGrail Banks).

In the northern Gulf, an estimated 4,000 petroleum platforms exist today, providing an additional 4.1% (12.1 km^2) of suitable habitat area on the continental shelf; approximately 90% of these structures (~3,600) occur off the coast of Louisiana (Stanley and Wilson 2003). While

this additional substrate may have the potential to increase carrying capacity, stock abundance remains low (Cowan et al. 2010). Based on the amount of natural habitat available to red snapper in the Gulf, habitat availability likely does not constrain population size or recruitment (Strelcheck et al. 2007; Cowan et al. 2010). Others disagree, claiming that habitat limitation is in fact a central issue in red snapper management (Gallaway et al. 2009; Shipp and Bortone 2009). Regardless, while artificial reefs aggregate fish allowing for increased catch rates, few studies have demonstrated evidence of biomass production at these sites (Patterson and Cowan 2003; Strelcheck et al. 2007; Cowan et al. 2010).

When new petroleum platforms are built, plans for their removal are already in place (Bull and Kendall 1994). Off Louisiana and Texas, decommissioned platforms are either discarded, transferred to an alternate location for re-use, or recycled and used as artificial reefs through state-legislated rigs-to-reefs programs (Bull and Kendall 1994; GMFMC 2004). Repurposing obsolete platforms as artificial reefs addresses concerns about habitat loss with the removal of these structures and reduces costs associated with platform removal (Bull and Kendall 1994; GMFMC 2004). In the northern Gulf, approximately 50% of decommissioned platforms located at sufficient depths (~10% total) are used as artificial reefs through these programs (GMFMC 2004). Most commonly, conversion of retired platforms to artificial reefs involves placement of the jacket on its side (Macreadie et al. 2011), and 50 ft. of clearance between the ocean surface and the highest point on the structure is required (GMFMC 2004). However, this practice cannot continue forever as many of the areas set aside for reef deployment are nearing capacity.

This study establishes baseline data on red snapper reproductive biology variables at three habitat types (natural shelf-edge bank, standing platform and decommissioned toppled

platform), each of which offer different levels of vertical relief, and provides incite on the mechanisms that may drive the different biological expressions observed. Knowledge about the quality and ecological function of a habitat can be obtained through information on demographic rates including growth, mortality and reproduction. Basic evaluation of the unique attributes of red snapper reproductive rates at natural habitats will aid fishery managers in understanding the value of these areas in terms of function and quality as well as its impact on stock production in the northern Gulf of Mexico. With a clearer view of habitat-specific characteristics of red snapper ecology, information from this study will also aid fishery managers in attempts to establish spatial management practices in the Gulf of Mexico, furthering efforts to achieve an SPR of 26% by 2032.

2.2 Materials and Methods

Red snapper (*Lutjanus campechanus*) were collected at offshore oil fields/natural embankments called Eugene Island (EI) and Shipp Shoal Blocks (SS) near the continental shelf-edge (Figure 2.1). These areas are located approximately 80-100 miles south of Port Fourchon, Louisiana. Fish were collected from three habitat types (natural hard-bottom shelf-edge banks, standing petroleum platforms and decommissioned toppled platforms) from November 2008 to October 2010 (Appendix A, Table 1). Red snapper were collected by vertical longline and by baited chevron trap. Vertical longlines were constructed according to NMFS survey specifications for red snapper, and chevron traps were of standard MARMAP configuration (dimensions = 150 cm width x 180 cm length x 60 cm height; opening = 44.5 cm x 10 cm; mesh = 3.8 plastic coated wire). Chevron traps were deployed for 2 hours per site. At standing and toppled platforms, Chevron traps were deployed at 0.5, 1.0 and 1.5 km distances north and south of standing and toppled. At natural shelf-edge banks, Chevron traps were deployed randomly.

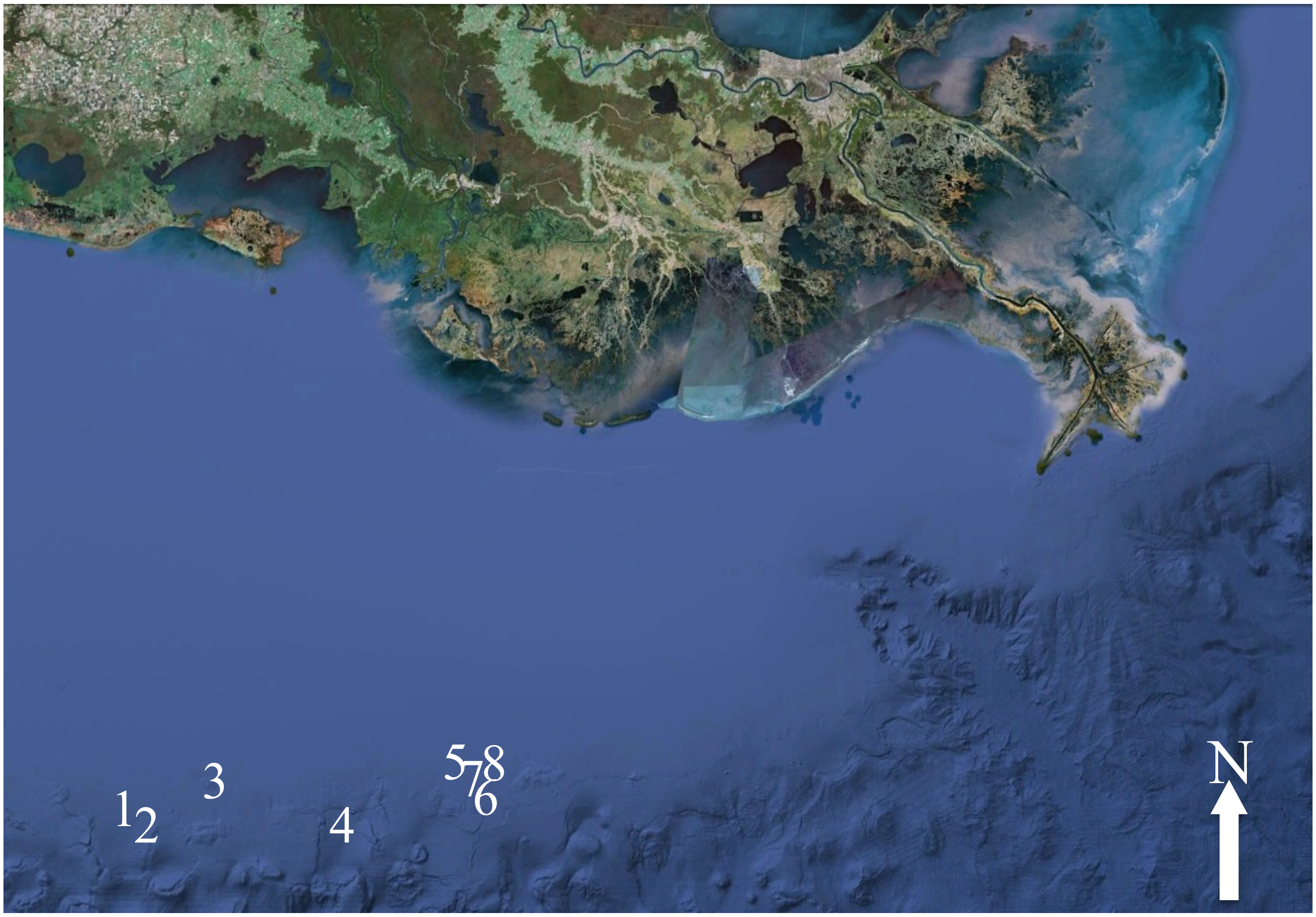


Figure 2.1 Sampling sites along Louisiana's continental shelf edge. Red snapper were collected from 4 natural shelf-edge bank sites (1=Bouma Bank, 2=Rezak/Sidner Bank, 3=Alderdice Bank, 4=Jakkula Bank), from 2 standing platform sites (5=EI-325, 6=EI-346), and from 2 toppled platform sites (7=EI-324, 8=EI-322). Map courtesy of Google Earth.

Only female red snapper were considered for reproductive analysis. Sample collection during spawning season occurred over 2 consecutive years, in June and July 2009 and in July 2010. An additional 57 females were collected in April and October 2010 to look for signs of oocyte maturation outside of the peak reproductive season. Unfortunately, sampling efforts during the 2010 spawning season were reduced due to the Deepwater Horizon oil spill, which began on April 20 off of Venice, LA, was capped on July 15, and the well was officially sealed on September 19 of that year (GMFMC 2011).

Upon capture, females were fitted with labeled cable ties and placed on ice until expiration. Total length (nearest mm) and total weight (nearest 0.01 g) were recorded, and sagittal otoliths were removed for age analysis. Otoliths were processed and sectioned following the methods of Cowan et al. (1995). Ovaries were excised and extraneous visceral and adipose tissues were trimmed away. Then, gonads were placed into labeled plastic freezer bags and frozen. Samples were transported on ice to the LSU Fisheries Science Laboratory.

2.2.1 Ovarian Tissue Processing

In the laboratory, gonad tissues were thawed, blotted with a paper towel and weighed (nearest 0.01 gram) and fixed in a 10% formalin solution (37% formaldehyde diluted with deionized water) for a minimum of 2 weeks. For red snapper, ovarian lobes are symmetric (Collins et al. 1996) and oocytes are homogenously distributed throughout the gonad (Wilson et al. 1994; Collins et al. 1996). Thus, sampling from one location on each ovary was adequate to determine all existing oocyte maturation stages. Post-fixation, a cross-section of ovary tissue (2 mm thickness) was removed at random (a die was cast) from one of six subsections comprising each pair of ovaries (Appendix B, Figure 1). Subsamples were secured in labeled histology cassettes, and deposited into histology jars filled with 10% formalin. Subsample jars were topped with 10% formalin to prevent samples from dessicating, sealed tightly and transported to the LSU School of Veterinary Medicine histology laboratory for slide preparation.

2.2.2 Histology Slide Preparation

Ovarian tissue subsamples were processed at the LSU School of Veterinary Medicine by histology laboratory staff and myself. Histology cassettes containing tissue samples were vacuum infiltrated (Sakura Tissue-Tek VIP model number VIP 5A-F1; Code 5215) and embedded in paraffin wax (Sakura Tissue-Tek TEC model number 5CMA-1). A microtome

(Leica RM2255) was used to cut embedded samples to 4 µm thickness. Embedded tissue slices were mounted on labeled slides in a warm water bath, allowed to dry, then stained and counterstained (Leica Autostainer XL) with hematoxylin and eosin (H and E), respectively. Coverslips were affixed with Permount.

2.2.3 Oocyte Stage Analysis

Maturity was determined by microscopic examination of gonads (Olympus BX41 microscope, 40x magnification). The 4 stages of oocyte development for heterochronal fishes (i.e., , various oocyte stages within the ovary at a given point in time during the reproductive season) are defined by Wallace and Selman (1981): primary growth (PG), cortical alveoli (CA), vitellogenic (V) and hydrated (H) (Table 2.1; Appendix B, Figures 2 & 3).

The immature ovary contains only un-yolked oocytes: primary growth oocytes and cortical alveoli (Hunter and Macewicz 1985a), while an ovary containing vitellogenic oocytes (i.e., coalesced yolk) is capable of reproduction (Brown-Peterson et al. 1988). Therefore, the benchmark for maturity in this study was vitellogenesis (Hunter and Goldberg 1980; Jackson et al. 2007; Brown-Peterson et al. 2011). The presence of hydrated oocytes indicated imminent (within the next 24 hours) spawning.

Two post-developmental oocyte stages were also identified: post-ovulatory follicles (POF) and atretic oocytes (Table 2.1). The occurrence of fresh POF (Appendix B, Figure 4) indicated spawning had recently occurred (within the past 24 hours); after a 24 hour period, POF disintegrate quickly and are no longer easily identified (Hunter and Macewicz 1985a). Atresia

Table 2.1 Biological descriptions and histological features of oocyte developmental stages for female red snapper (*Lutjanus campechanus*), a heterochronal and asynchronous batch spawner. PG=primary growth; CA=cortical alveoli; V=vitellogenic; H=hydrated; POF=post-ovulatory follicle.

Oocyte Stage	Biological Description	Histological Features
PG	Small size; thin, highly basophilic cytoplasm; less basophilic nucleus; the prominent oocyte stage during the "immature" phase of life	Dark purple/blue color; lighter-color core
CA	Small/med. size; less basophilic than previous stage; release of "gonadotropin" protein initializes formation of yolk vessicles; first appears during the "developing" phase	Purple/blue cytoplasm; light-color core is visible
V	Med/large size; acidophilic cytoplasm; numerous highly acidophilic yolk vessicles form with the uptake of "vitellogenin" (yolk protein); nucleus migrates toward pole; present during the "spawning capable" phase yolk vessicles coalesce during late vitellogenesis just prior to full hydration;	Deep red/pink, grainy vessicles in cytoplasm, yolk may be visible; or pink, smooth just before hydration
H	Very large size; characteristic smooth cytoplasm due to coalescence and yolk plate formation; final stage prior to ovulation; present during the "spawning capable" phase	Pink; smooth; yolk not easily visible; wrinkled shape
POF	Small/med. size; acidophilic collapsed follicle layers; composed of cord-like strings of cuboid epithelial granulosa cells and outer thecal connective tissue cells; present up to 24 hours post-ovulation; present during the "spawning capable" phase	Red/pink; consists of many collapsed folds; blue nuclei visible
Atresia	Variable size; hypertrophying granulosa follicle cells; yolk is resorbed; appears in the all spawning phases with the exception of the "immature" phase; occurs in mass during the "regressing phase" at the end of the spawning season	Discolored; not smooth; general deterioration of the cell and its follicle

(Appendix B, Figure 5) marks the degeneration and resorption of oocytes in the ovary prior to being spawned (Hunter and Macewicz 1985a). Atresia occurs during all phases of the reproductive cycle with the exception of the immature phase; atretic oocytes appear in greatest

abundance during the regressing phase of the reproductive cycle, when the spawning season is completed (Brown-Peterson et al. 2011).

2.2.4 Reproductive Biology Analyses

Gonadosomatic indices, spawning phases, size- and age-at-maturity, batch fecundity estimates, spawning frequency estimates and annual fecundity estimates were examined in this study to evaluate red snapper reproductive biology on Louisiana's continental shelf edge. An index of reproductive importance was constructed from a portion of these estimates to approximate the reproductive value of different age groups in the spawning stock. This study occurred over 2 consecutive spawning seasons and is the first to assess red snapper reproductive biology variables on natural habitats.

2.2.4.1 GSI

Gonadosomatic indices (GSI) indicate spawning readiness in fish populations. GSI is a ratio of gonad weight (grams) to eviscerated/gutted body weight (grams):

$$\text{GSI} = (\text{Weight}_{\text{ovary}})/(\text{Weight}_{\text{eviscerated body}}) \times 100 \qquad \text{(Eq. 1)}$$

GSI is plotted on a monthly scale and values greater >1 coincide with peak reproductive readiness during the annual spawning cycle (Hunter and Macewicz 1985a). Reproductive samples were not taken from November through March because numerous previous studies agree upon nominal and low GSI values from early fall to early spring in the northern Gulf (Render 1995; Collins et al. 2001; Woods et al. 2003).

2.2.4.2 Spawning Phase

Previous analyses in the Gulf have determined that the reproductive season for red snapper occurs from April/May through September/October in the Gulf of Mexico, peaking in June, July and August (Moseley 1966; Nelson 1988; Wilson et al. 1994; Woods et al. 2003;

Fitzhugh et al. 2004). Therefore, reproductive analyses were conducted during June and July to minimize errors in distinguishing immature fish from resting or spent specimens. All females were classified by spawning phase of the annual reproductive cycle, defined by Brown-Peterson et al. (2011): immature, mature, developing, spawning capable, regressing and regenerating. An additional portion of females (n=57) collected in April and October 2010 were also histologically examined for signs of spawning and classified according to spawning phase.

2.2.4.3 Size- and Age-at-Maturity

As mentioned above, the benchmark for maturity was the presence of vitellogenic oocytes. Reproductively mature females were sorted into nearest-50-mm TL size classes and annual age classes. Sizes- and ages-at-50%, -75% and -100% maturity were determined and compared among habitat types.

2.2.4.4 Batch Fecundity

Batch fecundity refers to the number of eggs one female produces during one spawning episode. The mature red snapper ovary contains two symmetric lobes (Collins et al. 1996) and oocytes at all stages of development are uniformly distributed (Wilson et al. 1994; Collins et al. 1996). Therefore, three subsamples (0.03-0.05 g weighed to 0.0001 g) were taken from randomly selected ovary regions and placed into petri dishes with a 3:7 glycerin-water solution. Subsamples were separated gently with a spatula (Render and Wilson 1992; Wilson et al. 1994; Woods 2003) taking care to avoid cross-contamination. Glycerin spreads of subsamples were examined under a compound microscope (Olympus BX41, 10x magnification) and hydrated oocytes were enumerated. Batch fecundity estimate (BFE) was determined gravimetrically for each subsample according to the hydrated oocyte method described by Hunter et al. (1983):

$$BFE = (n \text{ hydrated oocytes/ tissue sample weight})*(\text{total ovary weight}) \quad \text{(Eq. 2)}$$

For each hydrated female, the BFE was average of the estimates derived from the three subsamples.

2.2.4.5 Spawning Frequency

A spawning frequency estimate (SFE) is the average number of days between consecutive spawning events. SFE determines how often a serial heterochronal spawner releases ova during one reproductive season (Hunter and Macewicz 1985a). Specimens were categorized based upon histological observations. Fully hydrated females and those showing signs of the beginning of hydration were classified as “day-0” imminent spawners and were expected to spawn within the next 24-hour time period. Females exhibiting fresh POF were classified as “day-1” as these individuals had spawned less than 24 hours prior to capture. Spawning frequency was then estimated using three standard methods: 1) the hydrated oocyte method (H method) described by Hunter and Macewicz (1985a), 2) the post-ovulatory follicle method (POF method) described by Hunter and Macewicz (1985a) and 3) the time-calibrated method (TC method) described by Wilson and Nieland (1994):

$$SFE_{\text{H Method}} = (\text{total \# mature females})/(\text{total \# day-0}) \quad \text{(Eq. 3)}$$

$$SFE_{\text{POF Method}} = (\text{total \# mature females})/ (\text{total \# day-1}) \quad \text{(Eq. 4)}$$

$$SFE_{\text{TC Method}} = (\text{total \# mature females})/((\text{total \# day-0} + \text{total \# day-1})/2) \quad \text{(Eq. 5)}$$

Estimates of spawning frequency using the hydrated oocyte method are not reported in this study due to small sample size of hydrated individuals (n=8).

2.2.4.6 Annual Fecundity

Annual fecundity (AFE) is the number of ova a mature female releases over the course of one spawning season. AFE were determined according to Nieland and Wilson (1993) for all hydrated females as follows:

AFE = (# days in the reproductive season)/(SFE)*(BFE) (Eq. 6)

For red snapper in the northern Gulf of Mexico, the best-estimated duration of one spawning season is 150 days (Woods 2003; Fitzhugh et al. 2004).

2.2.4.7 Index of Reproductive Importance

An index of reproductive importance (IRI) was developed in effort to determine spawning potential per recruit (Woods 2003). This system is based upon percent maturity and annual fecundity estimates (this study), as well as percent-at-age estimates of the Gulf red snapper stock through updated 1998 (Schirripa and Legault 1999). IRI estimates were determined for ages 0 through 9+ years old. When annual fecundity estimates were not available for given age groups (ages 2, 6, 8 and 9+), Woods' (2003) AFE for female red snapper sampled from Louisiana waters were used.

2.2.5 Statistics

All statistical analyses were performed using Statistical Analysis System software (SAS Institute 2008). ANOVA (i.e., analysis of variance) and the Mann-Whitney U-test (used for mean frequencies of non-parametric data) were used to evaluate equality of sample means for age, total length and total weight between habitat types and sampling years. Linear regression (GLM) was used to evaluate the significance of length-weight relationships, and ANCOVA (i.e., analysis of covariance) was used to compare length-weight regression parameters between habitats. Chi-square analyses were used to test male-to-female ratio and spawning frequency between habitat types. All tests were considered significant if $p<0.05$.

2.3 Results

2.3.1 Year-Round Sampling: A General Synopsis

A total of 1,282 red snapper (*Lutjanus campechanus*) were collected for this study at Eugene Island (EI) and Shipp Shoal Blocks (SS) off the coast of Louisiana from November 2008 through October 2010 (Appendix A, Table 1). Fish were caught at depths ranging from 230 to 280 feet (70.1 to 85.3 m). While sex could not be determined for 66 individuals, 587 male and 629 female red snapper were identified, measured and sampled. Overall, the male-to-female ratio (M:F) was 1:1.07 (Table 2.2); this ratio was not significantly different from 1:1 (χ^2=1.5869, p=0.2078). Proportions of females were marginally greater than that of males at natural shelf edge banks and toppled platform sites, while the male population was slightly larger at standing platforms.

Table 2.2 Male-to-female ratio for red snapper, *Lutjanus campechanus,* sampled from natural bank (Bank), standing platform (Standing) and toppled platform (Toppled) sites on the Louisiana continental shelf.

Site	Unknown Sex	Male	Female	M:F
Bank	5	137	171	1 : 1.248
Standing	37	262	251	1 : 0.958
Toppled	24	188	207	1 : 1.101
All	66	587	629	1 : 1.072

For the remainder of this chapter, analyses were performed for female red snapper only. At all sites combined, ages ranged from 1.31 to 12.28 years, and the average individual sampled (± Standard Error (SE)) was 4.18 ± 0.06 years old (Table 2.3A). Fish sampled from standing platforms were significantly younger (mean=4.00 ± 0.10 years) than specimens collected from toppled platform (p=0.0012) and natural shelf-edge bank sites (p=0.0001) (Appendix A, Table 3). No significant difference in mean age was found between samples from natural shelf-edge banks and toppled platforms. Mean total length for females at all sites combined was 500.28 ± 4.00

Table 2.3 Mean A) age (years), B) total length (mm) and C) total weight (g) of female red snapper, *Lutjanus campechanus,* sampled from natural bank (Bank), standing platform (Standing), toppled platform (Toppled) sites on the Louisiana continental shelf edge. For each habitat type, similar superscripted letters denote no difference in mean age (α=0.05).

A		Age			
Site	n	Mean ± SE	Min	Max	95% CI
Bank	157	4.54 ± 0.12^{A}	2.01	11.01	(4.30, 4.78)
Standing	248	4.00 ± 0.10^{B}	1.31	12.28	(3.81, 4.19)
Toppled	207	4.11 ± 0.07^{A}	1.80	8.03	(3.98, 4.24)
All	612	4.18 ± 0.06	1.31	12.28	(4.07, 4.29)
B		Total Length			
Site	n	Mean ± SE	Min	Max	95% CI
Bank	171	480.09 ± 7.87^{A}	320	807	(464.66, 495.52)
Standing	251	499.81 ± 6.90^{B}	235	864	(486.29, 513.33)
Toppled	207	517.53 ± 5.73^{C}	307	740	(506.31, 528.75)
All	629	500.28 ± 4.00	235	864	(492.44, 508.12)
C		Total Weight			
Site	n	Mean ± SE	Min	Max	95% CI
Bank	170	1683.92 ± 98.82^{A}	414	7071	(1490.23, 1877.61)
Standing	251	2020.04 ± 90.48^{B}	176	9527	(1842.70, 2197.38)
Toppled	207	2004.28 ± 69.56^{B}	384	5718	(1867.94, 2140.62)
All	628	1923.86 ± 50.75	176	9527	(1824.39, 2023.33)

n=sample size; SE=standard error; Min=minimum; Max=maximum; CI=confidence interval

mm (range: 235-864 mm) (Table 2.3B). Mean total length differed significantly between sites (p=0.0269; p<0.0001; p=0.0042) with specimens from toppled habitat being the longest, followed by specimens from standing platforms, and fish from the natural shelf-edge banks were the shortest (Appendix A, Table 3). Mean total weight for female red snapper was 1923.86 ± 50.75 g (range 176-9527 g) at all sites combined (Table 2.3C). Specimens from standing and toppled platform structures were significantly larger than those collected from natural shelf-edge bank sites (p=0.0002; p<0.0001) (Appendix A, Table 3). Mean total weight did not differ between standing and toppled platform sites (p=0.0574).

Eviscerated body weight (g) and total length (mm) was used in all length-weight regression analyses. A power curve (R^2=0.9680) was used to fit raw length-weight data (Appendix B, Figure 6). When eviscerated body weight values were not available, a predictive linear function (R^2 = 0.9814) was used for approximation (Appendix B, Figure 7). Length-weight data were $\log_{10}$-$\log_{10}$ transformed and regressed per habitat and overall. Regression coefficients and logarithmic relationships are listed in Table 2.4.

All relationships between $\log_{10}$-$\log_{10}$ regressed total length and eviscerated body weight were significant ($p<0.0001$) (Appendix A, Table 4) with highly positive regression coefficients (all $R^2 > 0.90$) (Figure 2.2). The following length-weight regression is representative for female red snapper sampled during this study (R^2=0.9664):

$$W=(2.03*10^{-5})*L^{2.9252}$$

where W=eviscerated body weight (g), and L=total length (mm) (Table 2.4). Females from natural shelf-edge bank sites produced a significantly greater regression slope than those collected from standing (p=0.0014) and toppled (p=0.0106) platforms, albeit natural bank specimens also produced a significantly lower initial weight value than those sampled from standing (p=0.0004) and toppled (p=0.0081) platform sites (Appendix A, Table 4). Length-weight slopes (p=0.7331) and y-intercepts (p=0.8460) were not different between standing and toppled platform sites.

2.3.2 Spawning Season

A total of 391 female red snapper were sampled from natural shelf-edge banks (n=174), standing platforms (n=145), and toppled platforms (n=72) in June and July 2009 and July 2010 (Table 2.5). Additionally, 57 females were collected in April (n=28) and October (n=29) 2010 at

Table 2.4 Estimated length-weight regression coefficients for Louisiana female red snapper, *Lutjanus campechanus*, sampled from natural shelf-edge banks (Bank), standing platforms (Standing), toppled platforms (Toppled) and all habitats combined (All).

Habitat	Slope (m)	Intercept (b)	Power Function
Banks	3.0212	-4.9712	$W=(1.07*10^{-5})*L^{3.0212}$
Standing	2.8790	-4.5508	$W=(2.81*10^{-5})*L^{2.8790}$
Toppled	2.8583	-4.5161	$W=(3.05*10^{-5})*L^{2.8583}$
All	2.9252	-4.6932	$W=(2.03*10^{-5})*L^{2.9252}$

W=eviscerated body weight; L=total length

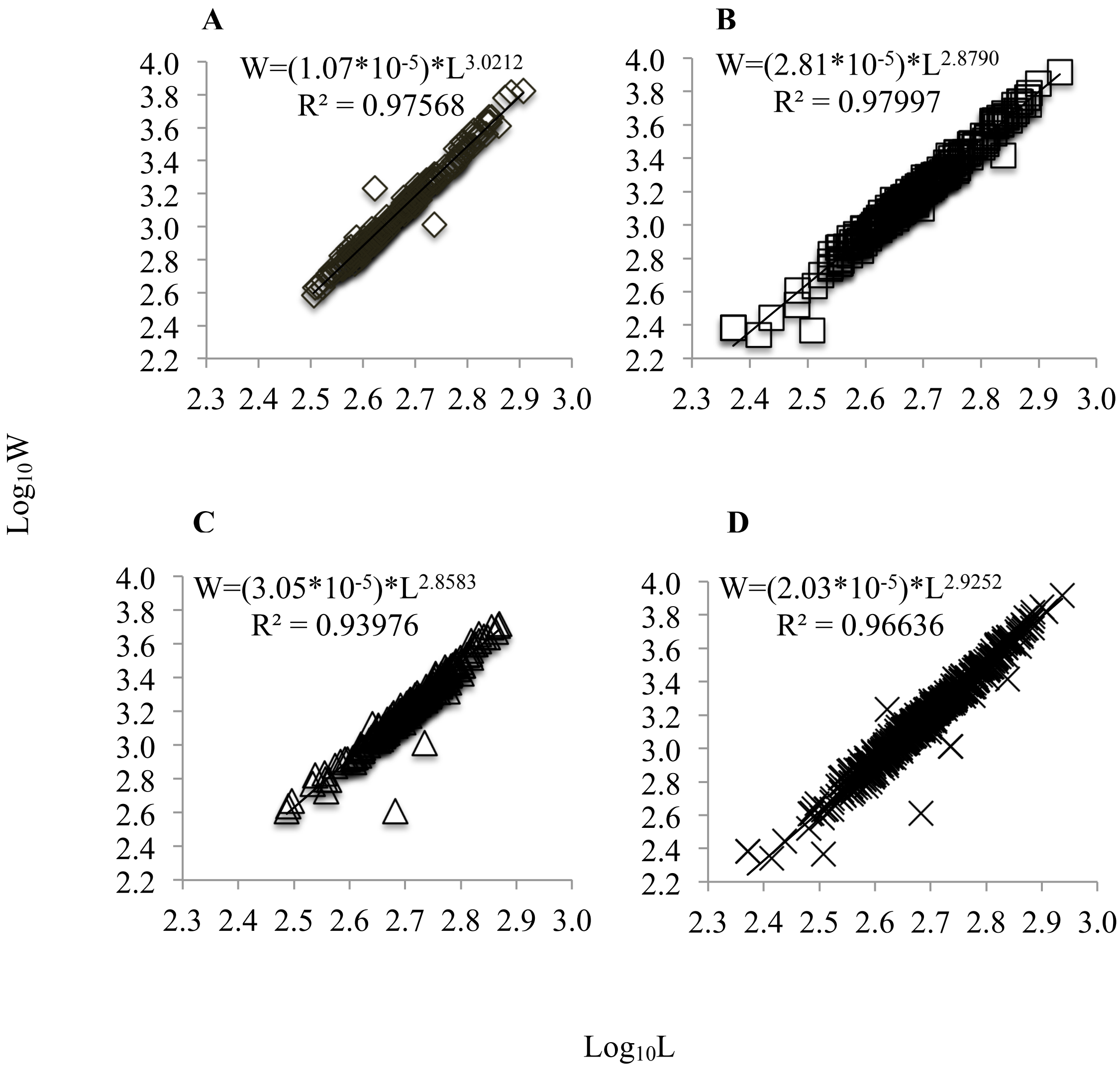


Figure 2.2 Length-weight regressions for female red snapper, *Lutjanus campechanus*, sampled at the continental shelf edge off Louisiana at A) natural shelf edge banks B) standing platforms C) toppled platforms and D) all habitats combined. W=eviscerated body weight (mm); L=total length (g).

Table 2.5 Female red snapper, *Lutjanus campechanus,* sampled in 2009 and 2010 at natural bank (Bank), standing platform (Standing), toppled platform (Toppled) sites on the Louisiana continental shelf.

Site	Jun 2009	Jul 2009	Apr 2010	Jul 2010	Oct 2010	Total
Bank	63	80	-	31	-	174
Standing	49	43	15	11	27	145
Toppled	-	47	13	10	2	72
Total	112	170	28	52	29	391

standing and toppled structures. All fish were examined for signs of oocyte maturation and categorized according to phase in the reproductive cycle.

Minimum observed age-at-maturity on the Louisiana continental shelf was 1.97 years old and was found at a standing platform site. The minimum size-at-maturity was 320 mm total length (TL), and this individual was found at the natural shelf edge bank habitat. Among hydrated and recently-spawned females (evident by the presence of fresh POF), minimum age was 2.96 years old, and the smallest sizes were 366 mm and 359 mm TL. The youngest specimens with hydrated oocytes or POF were collected from the natural shelf edge banks. The shortest females retaining hydrated oocytes or POF were sampled from toppled and standing platforms, respectively.

Size frequency at both natural bank and standing platform sites was greatest at 400 mm TL, while the most common size class for fish sampled from toppled structures was 500 mm TL (Figure 2.3A). No difference in mean total length was observed between standing and toppled platforms (p=0.3309) (Appendix A, Table 5). However, mean total length was significantly smaller at natural shelf-edge banks than at standing (p=0.0116) and toppled (p=0.0009) platforms.

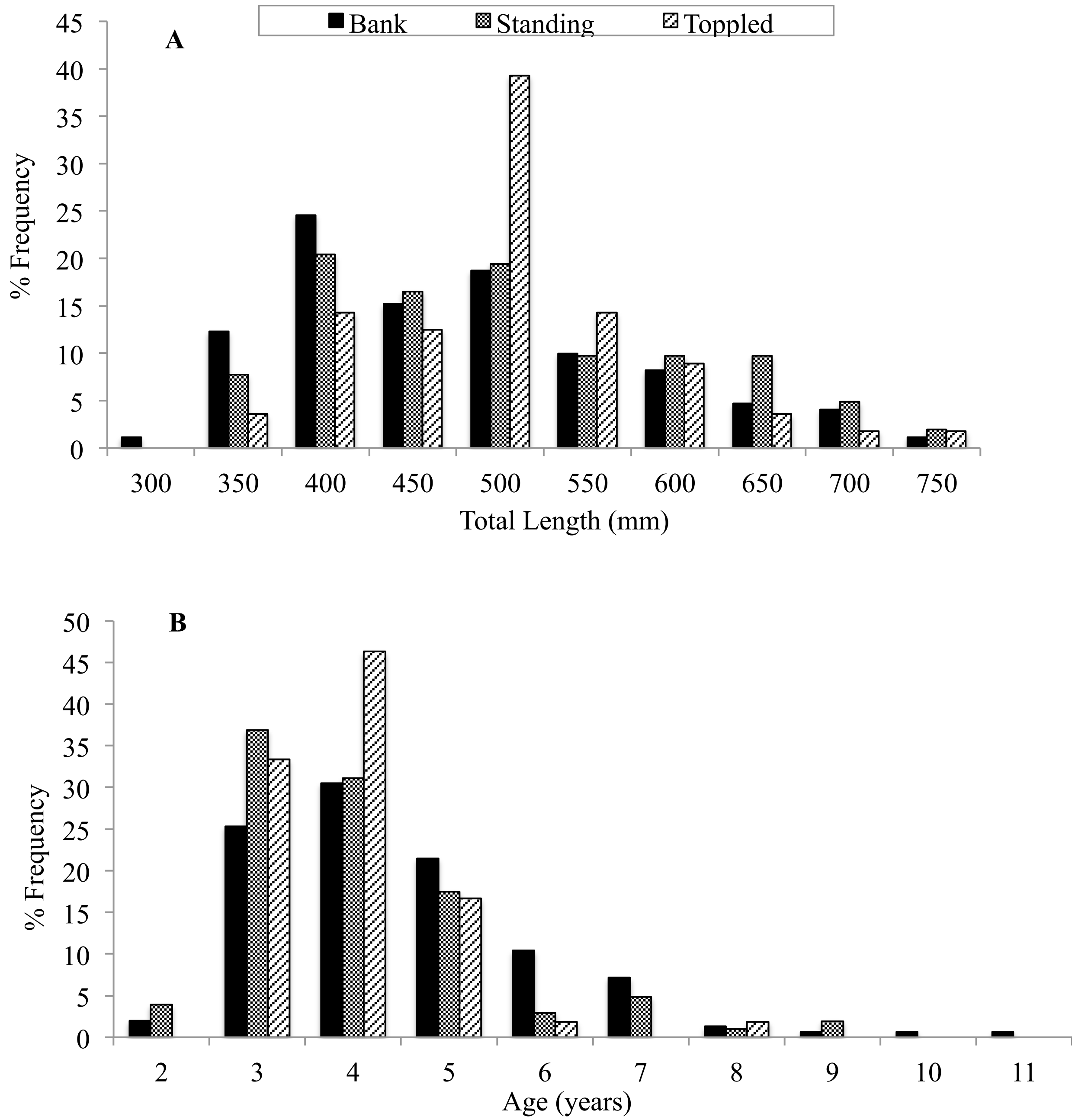


Figure 2.3 Frequency distributions of (A) total length and (B) age for female red snapper, *Lutjanus campechanus*, sampled from natural banks (Bank), standing platforms (Standing) and toppled platforms (Toppled) during spawning season on Louisiana's continental shelf.

At all habitats, the most frequently observed ages were 3 to 5 years (Figure 2.3B). The most frequently encountered age group at standing platforms was age-3, while at both natural

shelf-edge bank and toppled platform sites 4-year-olds were most frequently observed. Age-2 individuals were scarce at all habitats combined (n=6), indicating that shelf-edge habitat was not functioning as a recruitment area.

No significant differences in mean age were found between sites during the spawning season ($p>0.05$) (Table 2.6A; Appendix A, Table 5). Red snapper sampled in June-July 2009 and April-October 2010 had a collective mean age of 4.33 ± 0.08 years. Females at natural bank sites were shorter than those from platform sites (Table. 2.6B; Appendix A, Table 5), while mean total length standing and toppled platforms was sufficiently similar ($p=0.3309$). Mean total weight at natural shelf- edge banks was significantly lighter on average than that observed at standing ($p<0.0001$) and toppled platforms ($p=0.0001$) (Table. 2.6C; Appendix A, Table 5). However, no difference in mean total weight was observed between standing and toppled platform sites ($p=0.6397$).

At all habitats combined, the majority of female red snapper sampled in 2009 (69.5%) were 3 and 4 years old (2005 and 2006 cohorts), followed by age-5 fish (17.7%; 2004 cohort) (Table 2.7). In 2010, the female sample population was primarily composed of 4- and 5-year-olds (52.0% collectively; 2005 and 2006 cohorts), followed by age-6 and 7-year-olds (28.0% collectively; 2003 and 2004 cohorts). For both years combined, fish ages 3- to 5-years-old comprised 83.2% of sampled females, with individuals outside of the 3- to 5-year-old age range collectively comprising the remaining 16.8% of the sample population.

Results for annual effects should be regarded with caution, as sample sizes were much smaller in 2010 due to difficulty sampling during the BP oil spill. Fish were significantly older in 2010 at both natural bank ($p=0.0002$) and standing platform sites ($p=0.0015$) compared to

those sampled in 2009, while no difference in mean age was detected in between years for toppled samples (p = 0.1286) (Appendix A, Table 6). Fish were significantly longer in 2010 at natural shelf-edge bank sites (p<0.0001) and at toppled platforms (p=0.0232) compared to those collected in 2009, but differences were not detected at standing platforms between sampling years (p=0.0980). Specimens were significantly heavier in 2010 at both natural bank (p<0.0001) and toppled platform sites (p=0.0027), but no annual difference in total weight was found at standing platforms (p=0.1144).

Table 2.6 Mean age (years), total length (mm) and total weight (g) of female red snapper, *Lutjanus campechanus,* sampled at A) natural banks, B) standing platforms and C) toppled platforms on the Louisiana continental shelf (June - July 2009 and April - October 2010). For each habitat type, similar superscripted letters denote no difference in mean age, total length or total weight (α=0.05).

A		Age			
Site	n	Mean ± SE	Min	Max	95% CI
Bank	157	4.54 ± 0.12^{A}	2.01	11.01	(4.30, 4.78)
Standing	143	4.17 ± 0.13^{B}	1.31	12.28	(3.92, 4.42)
Toppled	74	4.19 ± 0.12^{AB}	1.8	8.03	(3.95, 4.43)
All	374	4.33 ± 0.08	1.31	12.28	(4.18, 4.48)
B		Total Length			
Site	n	Mean ± SE	Min	Max	95% CI
Bank	170	480.24 ± 4.71^{A}	320	807	(464.72, 495.76)
Standing	145	509.89 ± 4.97^{B}	260	864	(491.64, 528.15)
Toppled	71	518.44 ± 3.88^{B}	309	740	(497.90, 538.98)
All	386	498.40 ± 4.71	260	864	(487.90, 508.90)
C		Total Weight			
Site	n	Mean ± SE	Min	Max	95% CI
Bank	170	1670.36 ± 97.67^{A}	414	7071	(1478.92, 1861.80)
Standing	145	2139.19 ± 122.55^{B}	176	9527	(1898.99, 2377.39)
Toppled	71	2042.39 ± 128.42^{B}	414	5718	(1790.70, 2294.08)
All	386	1914.91 ± 68.05	176	9527	(1781.53, 2048.29)

n=sample size; SE=standard error; Min=minimum; Max=maximum; CI=confidence interval

Table 2.7 Frequency at age for female red snapper, *Lutjanus campechanus,* collected at Eugene Island off Louisiana's coast during the 2009 (n=266) and 2010 (n=50) spawning seasons. Year=sampling year; Freq=frequency; % n=percent of sample population. Bold font indicates greatest frequencies-at-age per sampling year.

Year	Age	Freq	% n	Cohort
2009	2	6	2.3	2007
	3	**93**	35.0	2006
	4	**92**	34.6	2005
	5	47	17.7	2004
	6	13	4.9	2003
	7	9	3.4	2002
	8	2	0.8	2001
	9	3	1.1	2000
	10	1	0.4	1999
	11	-	-	1998
2010	2	1	2.0	2008
	3	5	10.0	2007
	4	**12**	24.0	2006
	5	**14**	28.0	2005
	6	7	14.0	2004
	7	7	14.0	2003
	8	3	6.0	2002
	9	-	-	2001
	10	-	-	2000
	11	1	2.0 %	1999

2.3.2.1 Reproductive Seasonality

Histological Characterization of Oocyte Stages

Oocyte stages were classified for a total of 337 female red snapper collected during the spawning seasons of 2009 and 2010 (June-July 2009 and July 2010) (Table 2.8). Overall, 55.2% of specimen collected possessed vitellogenic oocytes, indicating capability of spawning, and 12.4% of sexually mature individuals showed signs of eminent or recent spawning activity, indicated by the presence of hydrated oocytes (H) and/or post-ovulatory follicles (POF). Fish sampled from toppled platforms produced the highest ratio of mature individuals (66.1%), followed by those collected from natural banks (55.0%) and standing platform structures (49.5%).

Highest incidence of POF and hydrated oocytes also occurred at toppled platform sites (POF=12.5%; H=8.9%), while the lowest incidence of each was observed in fish sampled from natural shelf-edge banks (POF=7.6%; H<1.0%).

Table 2.8 Characterization of oocyte maturation for female red snapper, *Lutjanus campechanus,* collected from natural shelf edge bank, standing platform and toppled platform sites during the reproductive season on Louisiana's continental shelf.

Site	n	Unknown Sex	Immature	Mature	LV	POF	H
Bank	175	4	45.0%	55.0%	4.1%	7.6%	<1.0%
Standing	105	2	50.5%	49.5%	1.9%	11.7%	2.9%
Toppled	57	1	33.9%	66.1%	8.9%	12.5%	8.9%
All	337	7	44.8%	55.2%	4.2%	9.7%	2.7%

n=sample size; LV=late vitellogenic; POF=post-ovulatory follicles; H=hydrated

Gonadosomatic Index (GSI)

A predictive linear function was used to generate eviscerated weight (EBW) estimates for 71 females when only total length and total weight information was available (R^2=0.9946) (Appendix B, Figure 8). Mean GSI values greater than 1.0 occurred at all sites in June and July of 2009 and July of 2010, with the exception of toppled platforms in July 2010 (Table 2.9). The highest observed GSI estimates occurred at the natural banks. Individuals from toppled platform sites produced the lowest GSI values during the spawning season.

Mean GSI values were less than 1 during the months of April and October 2010 (GSI=0.80 and 0.69, respectively), indicating that overall the mature portion of the female population was not capable of producing optimal batch sizes during these months (Table 2.9). However, GSI greater than 0.5 in April indicated the onset of the spawning season (Fitzhugh et al. 2004).

Table 2.9 Mean monthly gonadosomatic index (GSI) values for female red snapper, *Lutjanus campechanus,* sampled from natural shelf edge banks (Bank), standing platforms (Standing) and toppled platforms (Toppled) on the Louisiana continental shelf.

Bank

Month	n	Mean GSI	SE	StDev	95% CI
Jun-09	26	1.48	0.200	1.018	(1.09, 1.87)
Jul-09	37	1.45	0.196	1.194	(1.07, 1.84)
Apr-10	-	-	-	-	-
Jul-10	25	2.06	0.300	1.498	(1.47, 2.65)
Oct-10	-	-	-	-	-

Standing

Month	n	Mean GSI	SE	StDev	95% CI
Jun-09	20	1.33	0.209	0.935	(0.92, 1.74)
Jul-09	20	1.24	0.210	0.937	(0.83, 1.65)
Apr-10	3	0.80	0.149	0.257	(0.51, 1.09)
Jul-10	9	1.35	0.331	0.993	(0.70, 2.00)
Oct-10	6	0.69	0.268	0.657	(0.16, 1.22)

Toppled

Month	N	Mean GSI	SE	StDev	95% CI
Jun-09	-	-	-	-	-
Jul-09	27	1.07	0.171	0.889	(0.74, 1.41)
Apr-10	-	-	-	-	-
Jul-10	8	0.94	0.166	0.470	(0.61, 1.27)
Oct-10	-	-	-	-	-

n=sample size; StDev=standard deviation; SE=standard error; CI=confidence interval

Spawning Phase

The majority of mature females sampled in April 2010 (77.8%) was experiencing the regenerating phase of the annual reproductive cycle and were reproductively inactive; this was indicated by the presence of only primary growth (PG) oocytes in conjunction with atresia and thick ovarian walls (Table 2.10). Another 25.0% of April samples were classified as "developing," indicated by the presence of PG oocytes and cortical alveoli (CA), and early pre-vitellogenic oocytes. Only one individual sampled in April 2010 was reproductively active.

Table 2.10 Spawning phases of female red snapper, *Lutjanus campechanus,* sampled from three habitats on the Louisiana continental shelf in April and October 2010 (n=38). Capable=spawning capable. Asterisk indicates n<5.

Apr-10

Site	n	Immature	Mature	Developing	Capable	Regressing	Regenerating
Bank	-	-	-	-	-	-	-
Standing	14	14.3%	85.7%	25.0%	8.3%	-	66.7%
Toppled	8	25.0%	75.0%	-	-	-	100%
All	22	18.2%	81.8%	13.6%	4.5%	-	77.8%

Oct-10

Site	n	Immature	Mature	Developing	Capable	Regressing	Regenerating
Bank	-	-	-	-	-	-	-
Standing	15	13.3%	86.7%	-	38.5%	61.5%	38.5%
Toppled	1	-	*100%	-	-	*100%	-
All	16	12.5%	87.5%	-	35.7%	64.3%	35.7%

*All spawning capable fish sampled in October 2010 exhibited late vitellogenic oocytes in conjunction with significant atresia.

Mature fish collected in October were largely undergoing the regressing phase (64.3%; n=9) of the reproductive cycle; this was indicated by mass atresia in combination with the presence of PG, CA and vitellogenic oocytes. Some of these regressing fish (35.7%; n=5) also displayed late vitellogenic oocytes indicating the capability of spawning to some degree. All remaining mature fish in this sample population were in the regenerating phase; that is, incapable of reproduction.

2.3.2.2 Size- and Age-at-Maturity

Female red snapper sampled from toppled platform structures reached the 50%-maturity benchmark the earliest of the three habitats at the 400 mm TL size-class (Figure 2.4A; Appendix A, Table 7), while the natural bank and standing platform samples each reached 50% maturity in the 450 mm TL size-class. Samples from all sites combined reached 100% maturity by the 700 mm TL size class.

Fish sampled at toppled platforms reached the 50% maturity benchmark earliest of the three habitat types, at age-3 (Figure 2.4B; Appendix A, Table 8). However, age at 100% maturity could not be determined for toppled samples due to age gaps in the data. At standing platforms, 50% maturity was achieved at age-4, followed by the banks at age-5. Despite the slow progression to 50% maturity at the natural banks, this group reached 100% maturity quickly, at age-6. At all sites combined, 100% maturation was reached by age-8 (Appendix B, Figure 9).

2.3.2.3 Batch Fecundity

Batch fecundity was estimated for all fully hydrated (n=8) red snapper (Appendix A, Table 9). Fully hydrated individuals ranged from 366 to 666 mm TL (mean=532 mm TL) and from 3.05 to 7.05 years (mean=4.80 years) in age. All fully hydrated fish were found during the 2009 spawning season, and no hydrated females displayed simultaneous signs of post-ovulatory follicles (POF). Overall, mean batch fecundity was 219,258 ± 113,749 ova per spawning event (Table 2.11). Red snapper sampled from standing platforms and the natural banks spawned the highest estimated number of ova, while batch fecundity estimates (BFE) for specimens collected at toppled sites were ~2/3 lower. Only one female sampled from the natural banks was found in hydrated condition.

Positive trends in batch fecundity estimates (BFE) emerged when the natural logarithm (ln_e) of BFE was plotted against the natural logs of total length (TL), eviscerated body weight (EBW) and age (Appendix B, Figure 10). Best-fit regression relationships are shown in Table 2.12. Due to small sample sizes of hydrated fish, mean batch fecundity estimates could not be statistically compared between sites. However, a general positive exponential trend between batch fecundity and total length was evident (Figure 2.5).

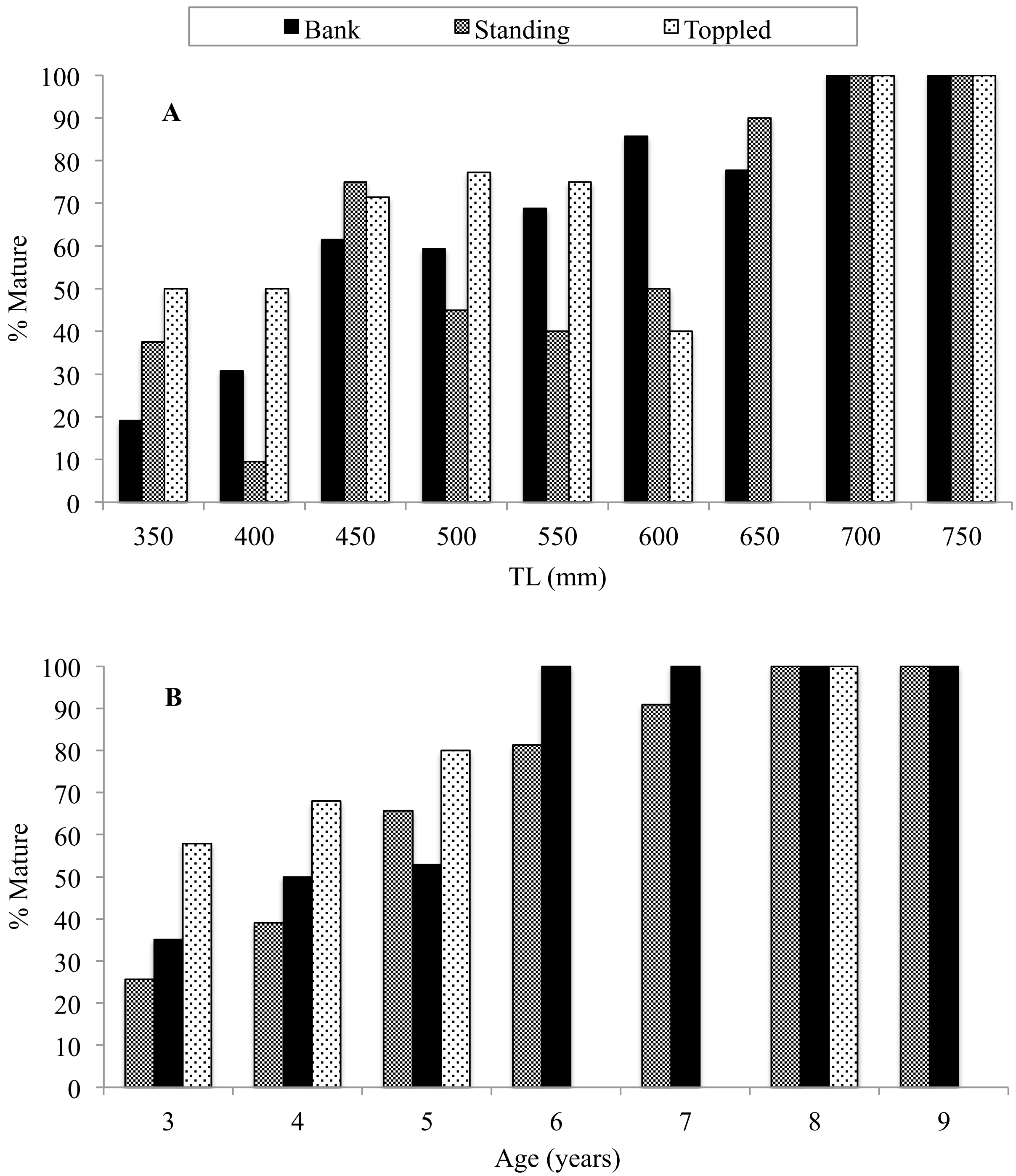


Figure 2.4 Percent maturity at (A) total length and (B) age for female red snapper, *Lutjanus campechanus*, sampled from natural shelf edge banks, and standing platforms and toppled platforms on the Louisiana continental shelf. Females in the 650 mm size class collected from toppled platforms (n=2) were not in spawning condition when sampled, creating a gap in the data. At toppled platforms, females from the 6, 7, and 9-year-old age groups were not collected.

Table 2.11 Batch fecundity estimates (BFE) for female red snapper, *Lutjanus campechanus,* sampled from three habitat types on Louisiana's continental shelf edge.

Site	n	Mean ± SE	Min	Max
Bank	1	326734	-	-
Standing	3	327955 ± 308584	16363	945114
Toppled	4	110867 ± 70259	4631	316514
All	8	219258 ± 113749	4631	945114

n=sample size; SE=standard error; Min=minimum; Max=maximum;

Table 2.12 Best-fit batch fecundity regression relationships for Louisiana female red snapper, *Lutjanus campechanus*, from natural shelf-edge bank, standing platform, and toppled platform habitats and from all habitats combined.

Logarithmic Function	p-value	R^2
$Ln_eBFE = 8.4559 * Ln_eL - 41.7636$	<0.0001	0.9578
$Ln_eBFE = 2.9382 * Ln_eW - 10.8473$	<0.0001	0.9553
$Ln_eBFE = 4.9398 * Ln_eAge + 3.6934$	0.0015	0.8344

Ln_e=natural logarithm; BFE=batch fecundity estimate; L=total length; W=eviscerated body weight; A=age

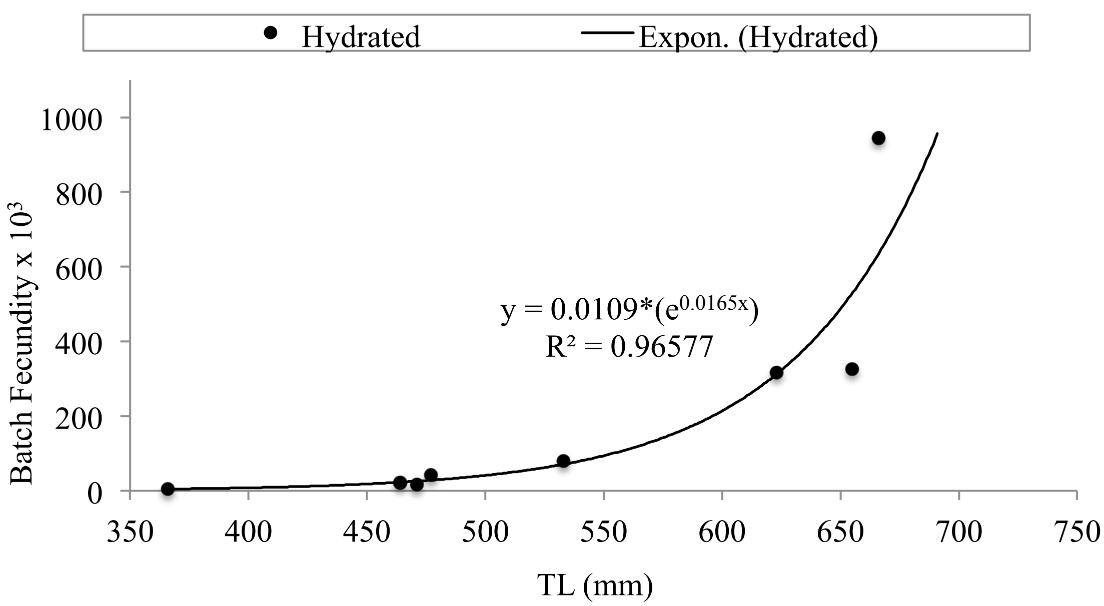


Figure 2.5 Relationship between batch fecundity and total length (TL) for female red snapper, *Lutjanus campechanus,* collected on the Louisiana continental shelf from three habitat types: natural banks (n=1), standing platforms (n=3) and toppled platforms (n=4).

2.3.2.4 Spawning Frequency

Spawning frequency was estimated for 180 mature female red snapper (Table 2.13). In total, twenty-one females showed signs of yolk coalescence and/or hydration, while 30 individuals displayed fresh POF. Three fecund females simultaneously displayed both early signs of hydration and POF demonstrating back-to-back spawning. Back-to-back spawners were sampled between 0900 and 1900 hours.

On average, spawning occurred once every 6.0 to 7.1 days and 21 to 25 times per reproductive season (Table 2.13) and spawning frequency estimates (SFE) did not differ between habitats ($p>0.05$) (Appendix A, Table 10). Specimens collected from toppled platforms spawned marginally more often, which was similar to individuals from standing platforms. Fish sampled at natural bank sites ovulated slightly less often.

Spawning frequency was assessed by age and total length (Appendix A, Tables 11 and 12, respectively) for each habitat type. At natural banks, spawning frequency was lowest for fish inthe 450 mm and 500 mm TL size classes (SFE=6.8-8.5 and 6.3-9.5 days, respectively). Three

Table 2.13 Spawning frequency estimates (SFE) for female red snapper, *Lutjanus campechanus,* collected from three habitat types on the Louisiana continental shelf. Spawning frequency estimates are based on the Post-Ovulatory Follicle Method (POF method) and the Time-Calibrated method (TC method).

Site	n day-0	n day-1	n Mature	SFE_{POF}	SFE_{TC}	Spawns* season^{-1} (SFE_{POF})	Spawns* season^{-1} (SFE_{TC})
Bank	8	14	94	6.7	8.5	22	18
Standing	5	9	49	5.4	7.0	28	21
Toppled	8	7	37	5.3	4.9	28	30
All	21	30	180	6.0	7.1	25	21

n=sample size; day-0=late vitellogenic or hydrated; day-1=POF present; SFE_{POF}= spawning frequency estimate based on the POF method; SFE_{TC}=spawning frequency estimate based on the time-calibrated method

females from standing platforms in the 350 mm TL size class were excluded due to small sample size; two of these samples exhibited POF. Spawning frequency increased for natural bank samples that were ≥575 mm TL (SFE=2.0-6.0). At standing platforms, spawning frequency estimates were lowest for the 450 mm TL size class (SFE=7.3-11.0); however, spawning seemed to occur more regularly by the time fish reached 500 mm TL (SFE=4.5-6.0 days). At toppled platforms, no mature females in the 450 mm TL size group (n=4) displayed POF or hydrated oocytes. Samples in the 500 mm TL group from toppled platforms spawned once every 5.7 to 6.0 days; spawning rate greatly increased by the time these females reached ≥575 mm TL (SFE=1.0-2.0).

Overall, age-3 females yielded the lowest SFE values on the Louisiana continental shelf (SFE=11.7-17.5 days; 9 to13 spawning events per season) (Table 2.14; Appendix A, Table 11). Fish in the 4- and 5-year age groups spawned at nearly double this rate (age-4: SFE=5.3-8.2; age-5: SFE=6.2-7.4). Fish ages 6-, 7- and 8-years old spawned the most frequently (age-6: SFE=3.0-

Table 2.14 Mean spawning frequency estimate at age for female red snapper, *Lutjanus campechanus*, sampled on the Louisiana continental shelf. SFE are based on the post-ovulatory follicle method (POF) and the time-calibrated method (TC). Asterisk indicates n < 10.

Age	n Mature	n Day-0	n Day-1	SFE (POF)	SFE (TC)	Spawns* $season^{-1}$ (POF)	Spawns* $season^{-1}$ (TC)
2	2	0	0	-	-	-	-
3	35	4	2	17.5	11.7	9	13
4	53	3	10	5.3	8.2	28	18
5	37	7	5	7.4	6.2	20	24
6	12	0	4	3.0	6.0	50	25
7	15	5	4	3.8	3.3	40	45
8	7	0	2	3.5	*7.0	43	21
≥9	5	1	0	-	*10.0	-	15

n=sample size; Day-0=hydrated females; Day-1=females with POF

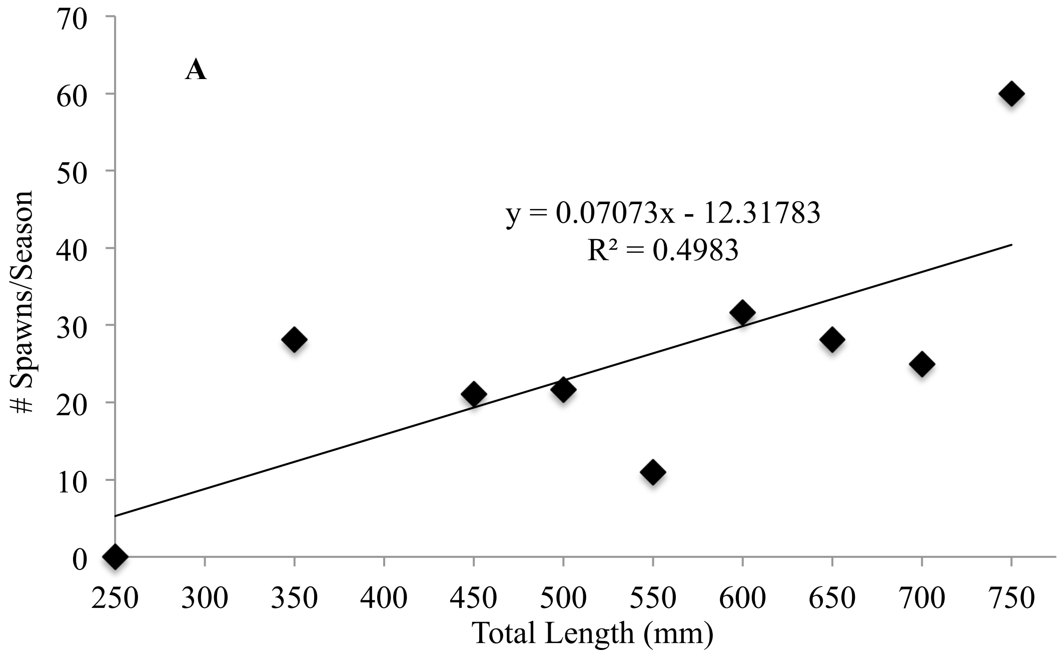
6.0; age-7: SFE=3.3-3.8; age-8: SFE=3.5-7.0). Age-2 females were excluded from spawning frequency analyses due to small sample size (n=7) and because no fish in this age group were found with POF or hydrated oocytes.

At all sites combined, spawning occurred most frequently for fish that were 725 mm total length or greater (SFE=2.5 days, 60 spawning events per season) (Table 2.15). In contrast, females in the 325-374 mm total length group spawned at roughly half that rate (SFE=4.0-5.3 days, 28 to 38 times per season). Spawning frequency estimates were highly variable for fish less than 574 mm total length (SFE=4.0-21.0 days). Variability in spawning frequency estimates diminished by the time females reached 575 mm total length (SFE=2.5-6.0), although these larger individuals spawned between 25 and 60 times per season. Number of spawning events per season appeared to be related to length (p=0.0336; R^2=0.4983) and age up to 7 years (p=0.0006; R^2=0.9228) among all habitats combined (Figure 2.6)

Table 2.15 Average spawning frequency estimates (SFE) at total length for female red snapper, *Lutjanus campechanus*, sampled on Louisiana's continental shelf. SFE are based on the post-ovulatory follicle method (POF) and the time-calibrated method (TC).

TL (mm)	n Mature	n Day-0	n Day-1	SFE (POF)	SFE (TC)	Spawns* $season^{-1}$ (POF)	Spawns* $season^{-1}$ (TC)
275-324	1	0	0	-	-	-	-
325-374	8	1	2	4.0	5.3	38	28
375-424	18	0	0	-	-	-	-
425-474	32	6	3	10.7	7.1	14	21
475-524	45	5	8	5.6	6.9	27	22
525-574	21	2	1	21.0	14.0	7	11
575-624	19	2	6	3.2	4.8	47	32
625-674	16	2	4	4.0	5.3	38	28
675-724	12	1	3	4.0	6.0	38	25
725-774	5	2	2	2.5	2.5	60	60
>775	1	0	0	-	-	-	-

n=sample size; TL=total length; n=sample size; Day-0=hydrated females; Day-1=females with POF



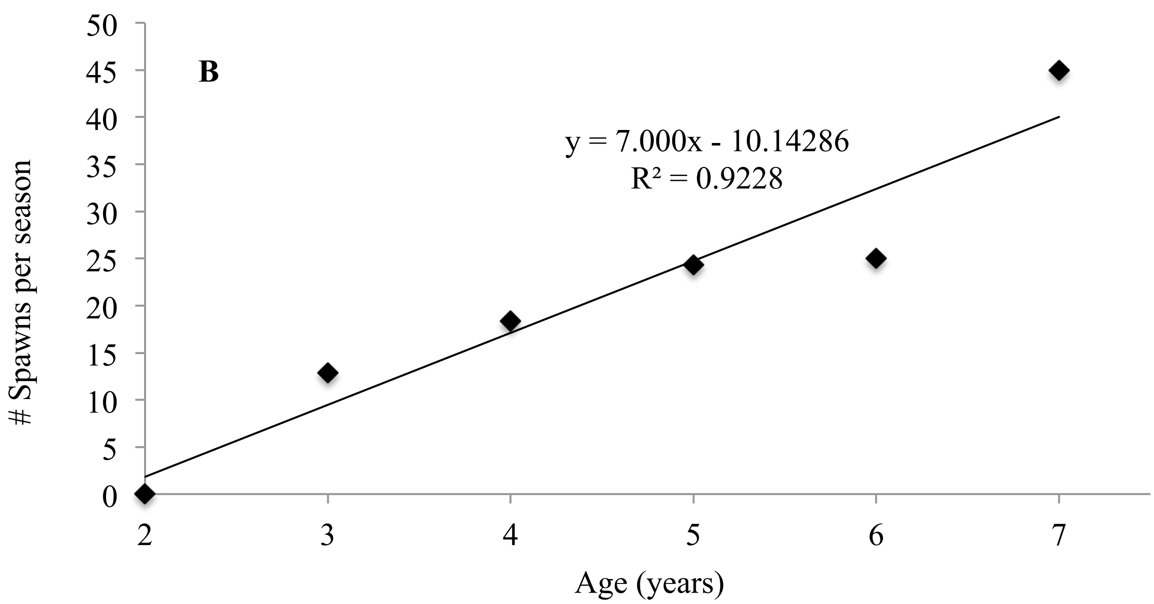


Figure 2.6 Spawning events per season at A) total length (TL) and B) age for female red snapper, *Lutjanus campechanus,* collected on the Louisiana continental shelf. Spawning events per season were based on the inverse of spawning frequency (time-calibrated) and a best-estimated 150-day spawning season.

2.3.2.5 Annual Fecundity

Annual fecundity estimates (AFE) were determined for all hydrated females (n=8) (Appendix A, Table 13). On average, hydrated fish were 4.8 years old and spawned once every 7.1 days (Table 2.16). The lone hydrated female sampled at the natural shelf-edge banks was capable of producing an estimated 5,765,893 ova per year (age: 7.04 years).

Table 2.16 Mean batch and annual fecundity estimates (± standard error) for female red snapper, *Lutjanus campechanus,* collected from three habitat types off the coast collected on the Louisiana continental shelf. Spawning frequency was estimated with the time-calibrated method.

Site	n	SFE	BFE ± SE	AFE ± SE	CI
Bank	1	8.5	326734	5765893	-
Standing	3	7.0	327955 ± 308584	7027605 ± 6612523	12960308
Toppled	4	4.9	110867 ± 140518	3393876 ± 2150780	4215451
All	8	7.1	219258 ± 113749	4632217 ± 2467934	4837062

n=sample size; SFE=spawning frequency estimate; BFE=batch fecundity estimate; AFE=annual fecundity estimate

2.3.2.6 Index of Reproductive Importance

The most significant contributors among the adult female spawning stock were specimens ages 9 years old or greater, with an IRI value of 0.71 (Table 2.17). Following the 9+ age group with an IRI value of 0.10, eight-year-old females were the second-highest producers. Five-, 6-, and 7-year-olds yielded IRI values of 0.06, 0.05 and 0.06, respectively. The index for four-year-olds was 0.012, while age-2 and -3 individuals collectively contributed even less to the spawning population (IRI=0.005). No mature age-0 or age-1 female red snapper were found in this study.

Table 2.17 Index of reproductive importance for female red snapper, *Lutjanus campechanus,* sampled on the Louisiana continental shelf. Age-specific proportions of the red snapper population in the Gulf (%n) were based on estimates developed by Schirripa and Legault (1999). Asterisk indicates AFE was borrowed from Woods' 2003 data on coastal Louisiana female red snapper.

Age	n	Mature	BFE	AFE	%n	IRI
0	0	0%	0	0	0.5684	0
1	0	0%	0	0	0.3257	0
2	6	33.33%	-	1004250*	0.0075	0.0030
3	95	35.79%	13509	173691	0.0276	0.0020
4	103	49.51%	29292	538868	0.0387	0.0121
5	59	64.41%	198307	4823686	0.0156	0.0568
6	33	36.36%	-	23032584*	0.0053	0.0518
7	16	93.75%	635924	28616571	0.0019	0.0601
8	8	87.50%	-	55609114*	0.0018	0.1035
9+	5	100%	-	80938769*	0.0075	0.7107

n=sample size; AFE=annual fecundity estimate; IRI=index of reproductive importance

2.4 Discussion

Overview

Prior to this study, little previous work has directly compared life history characteristics of adult red snapper between natural bank and platform (i.e., artificial) habitats. In a recently completed comprehensive study, fish abundance and species composition, trophic dynamics (Daigle 2011), diet analysis (Simonsen, in preparation), size and age composition and growth rates (Saari 2011), natal origins (Sluis 2011) and reproductive biology (this thesis) were examined with the goal of gaining valuable knowledge on the natural ecology of this species. Here, I examined size and age at maturity, batch fecundity, spawning frequency, annual fecundity and index of reproductive importance. Other parameters were included as well. Sex ratio was determined, and female size, age and length-weight regressions were compared between habitat types.

2.4.1 Year-Round Sampling: Sex Ratio, Age Structure and Length-Weight Relationships for Female Red Snapper on Louisiana's Continental Shelf-Edge

Sex Ratio

For sexually reproducing species, a 1:1 male-to-female ratio is typically observed among populations in nature. For this study, a total of 1,216 red snapper were sexed, producing a 1:1.07 male-to-female ratio. While the proportion of females was slightly greater, it did not deviate significantly from 1:1. Numerous other studies on this species conducted in the Gulf of Mexico and the Atlantic coast demonstrate this same pattern (Nelson 1988; Patterson et al. 2001; Collins et al. 2001; Fischer et al. 2004; White and Palmer 2004; Brulé et al. 2010).

Age Structure

Most of the females sampled in this study were very young considering the potential lifespan of red snapper (mean = 4.18 ± 0.06 years; range = 1 to 12 years). Combined data showed that 90.1% of the female red snapper collected for this project were 3 to 6 years old (Appendix A, Table 2). Two-year-olds comprised 3.3% of the total catch, while fish age 9+ comprised 1.5% of the total catch. This agrees with previous studies, which indicate that the stock age structure consists mainly (>90%) of fish age-6 or younger on the Alabama, Louisiana and Texas shelves (Wilson and Nieland 2001; Woods 2003; Fischer et al. 2004; SEDAR 7; Nieland et al. 2007a; Nieland et al. 2007b). In addition, most fish sampled in this study were members of the 2004-2006 cohorts. This agrees with recent reports that relatively strong year classes were produced in 2004, 2005 and 2006 (Cowan 2011; Saari 2011).

The maximum ages observed in this study was relatively young (age-12 for females, age 21 for males). Similarly, Nieland et al. (2007b) reported a maximum age of 14 years for red snapper sampled from the commercial fishery off Louisiana (n=2,900). This agrees with numerous other studies, which report a scarcity of older red snapper (>9 or 10 years old) in the

northern Gulf of Mexico (Wilson et al. 1994; Render 1995; Wilson and Nieland 1998; Patterson 1999; Wilson and Nieland 2001; Woods 2003; Fischer et al 2004; Nieland et al. 2007a; SEDAR 7 Update 2009; Cowan et al. 2010; Cowan 2011; Saari 2011). In contrast, Woods (2003) and Wilson et al. (1994) reported much older maximum ages for female red snapper off Louisiana (37 and 53 years, respectively). This may be explained by much larger sample sizes in Woods (2003)'s and Wilson et al. (1994)'s studies (n=1,863 and n=1,865, respectively) compared to this study (n=629 females).

Size, Age and Length-Weight Comparisons Among Habitat Types

Sizes, ages and length-weight regression relationships differed among the three habitat types. Females at standing platforms were significantly younger compared to fish at the natural banks and toppled platforms, while females at the toppled platforms were significantly longer compared to fish sampled from the other two habitat types. At the natural banks, females were significantly smaller in both length and weight compared to fish at standing and toppled platforms. Length-weight regression coefficients in this study were consistent with other reports (Futch and Bruger 1976; Moran 1988; Patterson et al. 2001; Fischer et al. 2004; Saari 2011). Females at natural bank habitat exhibited a significantly larger slope and a significantly smaller intercept compared to conspecifics sampled from the other two habitat types, indicating that they were shorter but heavier than fish on the artificial habitats.

Length-weight coefficients are frequently used to measure and compare fish condition (i.e., the volume of fish relative to its length); a larger slope generally implies greater energy reserves and healthier body condition (Pitcher and Hart 1982). Some suggest that a positive correlation exists between fish condition and reproductive output such that better maternal condition may positively influence recruitment and maturation (Neumann and Murphy 1992;

Blackwell et al. 2000; Morgan 2004; Dieckmann and Heino 2007). Contrarily, females in poor condition may negatively influence recruitment due to lower fecundity, production of less viable larvae, and higher rates of atresia and skipped spawning (Morgan 2004). Others argue that condition itself may not directly influence fecundity, but rather its correlation with maternal age, length and weight (Bromley et al. 2000; Marteinsdottir and Begg 2002; Koops et al. 2004; Morgan 2004).

In discussing length-weight relationships, it is important to note potential biases that may affect their interpretation. First, allocation of energy reserves may fluctuate with season, and this could influence fish condition (Blackwell et al. 2000). The females in the year-round portion of this study were collected on a quarterly basis each year; thus seasonal changes in body weight may potentially influence length-weight relationships, to some degree. Second, another potential bias in length-weight regressions may arise when fish lengths are not uniform among compared fish populations (Blackwell et al. 2000; Ranney et al. 2010). In this study, significant differences in mean total length were evident among all three habitat types. Furthermore, in a companion study, red snapper at natural bank habitat consisted of a significantly lower proportion of longer (≥550 mm TL) individuals compared to conspecifics at standing and toppled platforms, and the frequency of longer fish was significantly greater at toppled platforms compared to standing platforms and natural banks (Saari 2011). Therefore, biases among length-weight relationships in this study may exist through seasonal fluctuations in fish condition or through different size compositions among habitat types.

Relatively older but significantly shorter females at the natural banks, in addition to significantly different length-weight regression coefficients, may reflect different adaptive responses to the environment. More specifically, these distinctions and may reflect variations in

energy allocation, feeding or metabolic demands between females at natural bank habitat versus the platform habitats (Lambert and Dutil 1997; Blackwell et al. 2000; Nunes et al. 2011).

Regarding feeding, preliminary results for red snapper diet analysis on Louisiana's continental shelf edge indicate that food was not scarce at any of the three habitats in this study, and food items at natural bank and standing platform habitats were of high caloric density, consisting primarily of fishes; conversely, at toppled platform habitats, diet was markedly less nutritious and included a large quantity of less digestible prey items (Simonsen, personal communication[1]). Despite observations of a less nutritious diet at toppled platforms, Saari (2011) found that the fastest growth rates occurred in fish from that habitat type. Moreover, Saari (2011) found that rapid somatic growth attenuates earlier (by age 5 or 6) for red snapper at the natural banks compared to standing and toppled platforms, where growth attenuates at age 6 or 7. Therefore, smaller sizes at natural bank habitat may not be a function of quantity or quality of food but may instead imply an energetic trade-offs between growth and reproduction.

Additionally, Saari and Simonsen (personal communication [2]) proposed that red snapper at the natural shelf edge banks may have greater habitat-specific metabolic requirements. The Louisiana shelf is largely covered by sprawling mud-bottom, and natural reefs are relatively scarce (Bull and Kendall 1994; Chesney et al. 2000; Patterson and Cowan 2003). Potentially, increased metabolic requirements on the natural shelf-edge banks could be related to swimming behavior and/or the influence of Gulf currents (see Emery et al. 2006 and Crout 2009). However, surface currents attenuate approaching the seafloor on the outer shelf (Merrell et al. 1983). Thus, the influence of currents on a demersal fish like red snapper may, for the most part, be negligible.

2.4.2 Reproductive Effort on Louisiana's Continental Shelf-Edge

During the spawning season, 3, 4 and 5-year-olds were the most commonly observed age groups, and total length peaked at 400, 450 and 500 mm TL on Louisiana's continental shelf edge. Similarly, Woods (2003) reported peak lengths of 400, 450 and 500 mm FL (~427, 480 and 533 mm TL) for female red snapper sampled mainly from the recreational fishery off Louisiana. In contrast, Wilson et al. (1994) described a smaller primary modal length of 350 mm FL (~374 mm TL) for red snapper mostly sampled from the commercial fishery off Louisiana.

Gonadosomatic Index

Off Louisiana, hydrated oocyte and post-ovulatory follicle production, indicative of imminent spawning and immediate post-spawning, respectively, appear in late May or early June and persist through early or mid-September; peak months of spawning activity occur from May/June through July/August (Wilson et al. 1994; Woods 2003; Fitzhugh et al. 2004). As expected, the vast majority of mature females collected during the June and July sampling months in this study displayed vitellogenic and hydrated oocytes. High mean monthly GSI values corresponded well with these histological observations, confirming peak spawning activity during these months, corresponding well with a wide range of mean monthly GSI values reported for red snapper. Estimates from this study were consistent with Woods (2003) andWhite and Palmer (2004), who reported mean monthly GSI values <3.0 during the peak months of spawning season. Conversely, the maximum mean monthly GSI value in this study (GSI=2.1) was less than half of those estimates reported by others (Brown-Peterson et al. 2009;

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[1] Simonsen, K.A. 2011. Louisiana State University. Department of Oceanography and Coastal Sciences.

[2] Saari, C.S. and K.A. Simonsen. 2011. Louisiana State University. Department of Oceanography and Coastal Sciences.

Wilson et al. 1994), and more than double that recently reported during the peak of spawning season off the Campeche Banks (GSI=1.0) in Mexico (Brulé et al. 2010).

In April and October, histological observations indicated mass regeneration and regression spawning phases, respectively. These observations, in conjunction with GSI values less than 1, confirmed suboptimal spawning activity during these months. Conversely, Woods (2003) reported GSI values greater than 1 during the month of April for female red snapper caught off the Louisiana coast. This could be a result of a larger sample size in that study, or it could be a possible indication that spawning schedules are different for this species between inshore/mid-shelf and shelf-edge areas off Louisiana.

Maturation

A considerably slower progression to sexual maturity was evident on the outer shelf compared to previous reports for the northern Gulf (Appendix A, Table 14). In this study, 50% maturity was reached at age-4, 75% maturation was reached at age-6 and 100% maturity was achieved by age-8. Results for age-at-50% maturity should be regarded with caution because very few age-2 females were collected on the outer shelf, so maturity rates could not be determined for that age group. Contrary to my results, previous reports indicate that Louisiana red snapper reach 50% maturity by 2 or 2.5 years of age (Woods et al. 2003; Jackson et al. 2007). Somewhat consistent with females on the outer shelf off Louisiana, Fitzhugh et al. (2004) reported that 75% maturity was reached at age-6 in the eastern Gulf and by age-8 in the western Gulf. Also consistent with my findings, Fitzhugh et al. (2004) reported that 100% maturity occurred at age-8 in the northern Gulf. Contrarily, others have reported that 100% maturity occurs between 4.5 and 6.5 years of age in red snapper (Wilson et al. 1994; Woods et al. 2003; White and Palmer 2004; Jackson et al. 2007).

Much larger sizes at maturity were also observed on the outer shelf compared to all previous reports to date. For ease of comparison, reported fork lengths from other studies were converted to total length using the equation developed by Allman et al. (2002). The 50% maturity benchmark was reached at 450 mm TL. Somewhat similarly, Nelson (1988) reported that length-at-50%-maturity was reached at 375 mm FL (401 mm TL) for females sampled from the east and west Flower Garden Banks. In contrast, females sampled off the Louisiana and Texas coasts by Wilson et al. (1994) and Woods et al. (2003) reached this same benchmark at the much smaller sizes of 290 and 300 mm FL (310 and 321 mm TL), respectively. Others have reported length-at-50% maturity ranging from 292 mm FL (312 mm TL) to 378 mm TL from the Southeast Atlantic and across the Gulf from Florida to Mexico's Campeche Banks (White and Palmer 2004; Jackson et al. 2007; Brown-Peterson et al. 2009; Brulé et al. 2010). The 75% maturity benchmark was reached at 650 mm TL on Louisiana's shelf-edge. In contrast, 75% maturity was attained at 350 mm FL (374 mm TL) in the western Gulf (Fitzhugh et al. 2004). The 100% maturity benchmark occurred at 700 mm TL on Louisiana's shelf-edge. Some have reported similar values for length-at-100%-maturation have been reported in the northern the Gulf (Woods et al. 2003; Fitzhugh et al. 2004). Conversely, other reports indicate that 100% maturity occurs at smaller sizes, between 448 and 666 mm TL in the northern Gulf (Wilson et al. 1994; Woods 2003; Jackson et al. 2007).

On Louisiana's shelf-edge, slower progressions to maturity may reflect a more natural maturation pattern for red snapper. Differences in vital rates such as natural mortality (M) and fishing mortality (F) are known to influence life history characteristics such as size- and age-at-maturity (Trippel 1995). If fishing mortality is reduced on the outer shelf, higher red snapper density may result in a slower maturation rate. This is, perhaps, expected given that the shelf

edge banks have long been considered the center of abundance in the Gulf (Goodyear 1995). For instance, much faster maturation rates are evident off Alabama, where red snapper are heavily harvested from artificial reefs (Woods 2003). Earlier maturation off Alabama signifies a stress-induced compensatory response and/or genetic selection resulting from extreme declines population size through overexploitation (Trippel 1995; Woods et al. 2003). If mortality rates are reduced on Louisiana's shelf-edge compared to areas further inshore, then understanding their correlations with the slower maturation rates observed in this study would provide valuable incite on stock reproductive dynamics and could be useful for future stock assessments.

Slower maturation rates on the outer shelf could also indicate a potential inshore/offshore effect for red snapper off Louisiana, whereby significantly different reproductive biology characteristics may exist between inshore and offshore areas. If an inshore/offshore effect on maturity does exist, then progression to maturity seems to shift in a positive direction (i.e., maturation rates are slower) as one approaches the shelf-edge. Further research is necessary to explore this concept.

Batch Fecundity

Batch fecundity estimates (BFE) increased exponentially when plotted against length, weight and age. Similarly, previous research suggests that both size and age are good predictors of batch fecundity (Collins et al. 1996, 2001). Natural-log linear regression relationships between batch fecundity and eviscerated weight as well as total length each yielded relatively high correlation coefficients, suggesting that either weight or length values may be used to provide relatively stable estimates of batch fecundity. These findings are consistent previous research, which indicates that for indeterminate spawners, batch fecundity progresses geometrically with fish size (Bagenal 1978; Hunter et al. 1985a; Murua et al. 2003; Porch et al.

2007). A slightly greater correlation between batch fecundity and total length may be explained by greater seasonal fluctuations in body weight compared to length. While age was also positively correlated with batch fecundity, regression analyses indicated that age had a less significant influence on egg production. This is consistent with Porch et al. (2007), who reported that age may have a less direct effect on batch fecundity compared to length and weight.

Maximum batch fecundity estimates in this study were relatively low; even the highest BFE was less than 1 million ova. These estimates are reasonable for this species at those ages (Collins et al. 2001). However, an older female red snapper can produce millions of ripe ova in a single spawning event. For instance, Woods (2003) reported a BFE of 7.9 million ova for a 13-year-old red snapper off Louisiana. Other studies across the Gulf have reported a wide range of BFE minima (ranging from 458 to 450,000 ova) and maxima (ranging from 1.7 million to 7.8 million ova) for female red snapper sampled from artificial reef structures (Nelson 1988; Wilson et al. 1994; Render 1995; Collins et al. 1996; Collins et al. 2001). These studies clearly illustrate the powerful influence on egg production that older, larger females contribute to the spawning stock in comparison to smaller, younger conspecifics (Claramunt et al. 2007; Nunes et al. 2011).

Spawning Frequency

Generally, spawning frequency appeared to increase with female size and age. Although very few mature age-2 fish (n=2) were found on Louisiana's shelf edge banks, age-3 females spawned far less frequently than any of the older age groups in this study. Age 4 and 5 individuals spawned 2-3 times more frequently on averaged than age 3 fish. Females age 6-7 years old spawned ~50% more frequently than 3-5 year olds. Similarly, Collins et al. (2001) reported that SFE was about 50% greater for females that were age 6 to 35 years old, than for individuals between ages 3 and 5 years. It should be noted that due to a small sample size for

age 9+ fish, a representative spawning frequency estimate for this age group was not possible. In comparison, Woods (2003) reported that the 2, 6 and 9+ age groups were the most frequent spawners in her analyses. For iteroparous fishes, spawning frequency is correlated with size and age (Chesney and San Fillipo 1994; Ganias et al. 2003; Claramunt et al. 2007; Porch et al. 2007; Fitzhugh et al 2004; Jackson et al. 2007).

Spawning frequency was also roughly correlated with length in this study. Individuals in the 350 mm TL size class spawned once every 4.0-5.3 days (28-38 spawning events per season). Estimates for spawning frequency varied greatly in females up to 574 mm TL (7-38 spawning events per season). By the time females reached 575 mm TL, SFE were more consistent, and spawning occurred on a more frequent basis (SFE=2.5-6.0 days). Individuals in the 750 mm TL size class spawned the most often, although no data were available for fish of greater sizes. Similarly, Woods (2003) reported that females in the 750 mm FL (798 mm TL) size class were the most frequently spawning size group off Louisiana, releasing ova batches 54 times per year.

More frequent spawning observed among older females may be associated with a transition period in red snapper growth, where growth rates shift from rapid and linear among younger fish to slower and asymptotic among older fish. In a companion study, Saari (2011) demonstrated that rapid growth began to attenuate for red snapper between the ages of 5 and 7 years on Louisiana's outer shelf. Thus, as the function of size-at-age shifted from linear to asymptotic, spawning also appeared to occur more frequently. This may be possible because once the period of rapid somatic growth ends, more energy is made available for investment in gonadal growth and reproductive output.

Annual Fecundity

Overall, the average hydrated female red snapper in this study produced 3-7 million ova each year. This range is quite low compared to yearly maxima reported by others, but these results should be regarded with caution due to the small sample size (n=8) of hydrated females in this study. Contrary to my findings, Woods (2003) reported that on average, with all age groups combined, one female red snapper off Louisiana spawns 19-23 million ova per year. Woods (2003)'s estimate was derived from a much larger sample size and age range compared to my study. Additionally, off northwest Florida, Collins et al. (1996) reported that red snapper ages 3- to 12-years-old produced 12 million to 60 million ova each year. It should also be noted that Collins et al. (1996) collected their samples in the early 1990s when the red snapper population was significantly overexploited, perhaps reflecting a compensatory response in reproductive output.

Due to the small sample size and high variation in fecundity estimates, standard error values were large, especially at standing platform habitat, making it difficult to directly compare age-specific annual fecundity estimates with other previous assessments. However, on average, the 3-year-old females in this study produced <1 million ova per year, a small fraction of the number of eggs that older, larger fish are capable of yielding. This estimate is smaller than what Woods' (2003) estimated for both 2- and 3-year-old Louisiana red snapper, which annually produced 1 million and 1.5 million ova, respectively. Age-4 produced <1 million to 1.3 million ova per year in this study. In contrast, Woods (2003) found that Louisiana 4-year-olds produced at least 4-5 times more ova annually (AFE=5.6 million ova). Five-year-olds produced between 2.5 million and 9.7 million ova per year in this study, while Woods (2003) found the same age group produced at least twice this much (18.4 million ova/yr). The fish with the highest annual

fecundity estimate in this study was 7 years old and was sampled from a standing platform; this fish was capable of producing an average 20.3 million ova per year. One other hydrated age-7 fish was found in this study; this female was collected from natural shelf edge bank habitat and its average AFE was only 5.8 million ova. By comparison, Woods (2003) estimated an AFE of 41.1 million ova for 7-year-old fish. While no hydrated specimens older than age-7 were present in this study, Woods (2003) reported that on average, age 9+ females produced 80-106 million ova annually, a far greater estimate than any of the younger age groups in her study.

Differences in AFE between among members of the same age group demonstrate the high variability in batch sizes. For the two hydrated 7-year-olds in this study, 2 possible reasons may account for the difference in AFE. First, the 7-year-old from natural bank habitat was slightly smaller in both length and weight than the 7-year-old from standing platform habitat. Since fecundity is correlated with maternal size (Bagenal 1973), the smaller female from the natural banks may not have been large enough to produce as many oocytes as the female from standing platform habitat. Second, spawning frequency estimates were higher at natural bank habitat, meaning that fish from natural banks spawned less often than those from standing platforms. Each of these factors would contribute to decreased annual fecundity. It is important to note that while reproductive biology estimates in this study were relatively low compared to previous reports (Nelson 1988; Wilson et al. 1994; Render 1995; Collins et al. 1996, 2001; Woods 2003), those studies were conducted at times when population size estimates were perhaps much lower than they are today. Variable sample sources among studies may also account for some of these differences. For example, most of the fish accounted for in Woods (2003)'s study were sampled dockside and were predominantly captured at artificial reefs or on

platforms. These factors may contribute to some of the differences between results from this study and other research.

Index of Reproductive Importance

Based on an index of reproductive importance (IRI), older female red snapper, especially those in the 8+ age group, contribute a great deal more to the spawning stock compared to younger conspecifics (this study). This is consistent with previous reports (Schirripa and Legault 1999; Woods 2003). In the absence of fishing mortality, when natural mortality is equal to 0.10, Schirripa and Legault (1999) demonstrated that the age of greatest egg production likely occurs at age-14 for red snapper, after which age relative importance declines due to decreased expected survivorship among older age groups.

IRI estimates in this study should be considered with caution, as they may not be representative of the Gulf spawning population. First, females in this study were sampled from a restricted area (the shelf-edge off Louisiana) rather than across the Gulf. Second, extremely low sample sizes of hydrated females (n=8) made it particularly difficult to accurately estimate mean fecundity-at-age. Third, the sample sizes for maturity-at-age estimates were highly variable, especially for fish older than 6 years, because the age distribution in this study was highly truncated. The truncated age structure evident in this study is attributable to overfishing (Fischer et al. 2004; SEDAR7 2005; Nieland et al. 2007a; Cowan 2011). The elimination of older spawners through overfishing decreases stock reproductive potential because spawning production becomes increasingly reliant upon younger individuals to produce sufficient numbers of offspring to maintain or increase population size (Trippel 1995).

2.4.3 Reproductive Biology Comparisons Among Habitat Types

Differences in GSI, maturity and spawning frequency were detectable among habitat types. Unfortunately, habitat-specific comparisons of batch fecundity and annual fecundity estimates were not possible due to the limited sample size of hydrated females (n=8).

Fish from toppled platforms produced the lowest GSI values of the three habitat types. This observation was surprising for a variety of reasons. First, the highest percentages of mature, hydrated and recently spawned females occurred at toppled platforms. Second, females at toppled platforms were relatively older and significantly longer than conspecifics from the other two habitat types. Typically, larger sizes-at-age translate to better physical condition among fishes; thus, there is reason to infer that reproductive output should also be enhanced in fish that are larger-at-age (Powers et al. 2003). However, reduced GSI values at toppled platforms show that fish at those sites seem to be investing more energy in somatic growth, while placing less emphasis on reproductive output.

At standing platforms, females also yielded relatively low GSI estimates. This may be explained by a significantly younger mean age at standing platforms. Yet, at the natural banks, females consistently yielded the highest GSI values of the three habitat types. Greater GSI among females at the natural banks indicates greater energetic investment in reproduction, where mature female red snapper appear to sacrifice body length in order to boost egg production during the spawning season. An energetic trade-off between somatic growth and reproduction (Rijnsdorp 1990; Stearns 1992; Nunes et al. 2011) at the natural banks is further supported by the fact that red snapper captured at the natural banks were significantly smaller-at-age and heavier-at-length compared to conspecifics from the other two habitat types (Saari 2011). Furthermore, the period of rapid linear growth attenuated earlier (by age 5-6) at the natural banks compared to

the other two habitat types (by age 6-7), and growth generally seemed to occur at a slower pace (Saari 2011). These patterns are perhaps more typical of a population less influenced by exploitation.

While regional differences in maturity schedules for red snapper have been shown to exist in the northern Gulf (Woods et al. 2003; Fitzhugh et al. 2004), no prior studies have investigated whether or not habitat-specific differences in maturation rates exist for this species. In this study, maturity rates varied among habitat types. Females from the natural banks reached maturity at a slower pace compared to fish standing and toppled platforms. At the natural banks, females reached 50% maturity by age 5 and 450 mm TL, while fish from standing platforms reached the same maturity benchmark at a similar size, but at a younger age (4 years). At toppled platforms, 50% maturity was attained the fastest, by age-3 and 400 mm TL. Natural bank and standing platform habitats each produced the same size-at-100%-maturity estimate of 700 mm TL, however an estimate for 100% maturity at toppled platform habitat could not be determined due to a small sample size.

Different sizes- and ages-at-maturity may indicate real differences in life history patterns among habitat types. In nature, maturity is a phenotypically plastic trait, which fluctuates slowly over time (Trippel 1995). However, differences in maturity schedules among habitat types may indicate dissimilar mortality rates or environmental factors such as feeding, predation rates, or physical stress (Ricklefs and Wikelski 2002). Fishing pressures may differ for red snapper among natural banks, standing platforms and toppled platforms. Off Louisiana, petroleum platforms are a preferred place to fish by the directed fishery due to their ease in being located and high abundances of marketable reef fish species (Chesney et al. 2000). While recreational fishers don't typically venture out to the outer shelf, the commercial fishery has a larger capacity

to fish areas on the shelf edge for extended periods of time throughout the year, but commercial fishers generally target smaller red snapper farther inshore because they command a better press. Thus, if fishing mortality is increased at petroleum platforms, then fish at the natural banks may exhibit a progression to maturity more typical of population that is less heavily exploited.

No statistical difference was found for spawning frequency between habitats in this study. However, slight dissimilarities were apparent. Females from the natural banks spawned less frequently (SFE=6.7-8.5 days) than did fish from the other habitat types, followed by fish from standing platforms (SFE=5.4-7.0 days). The most frequent spawners were those from toppled platforms (SFE=4.9-5.3 days). Three other studies have estimated spawning frequency at artificial reefs in the northern Gulf of Mexico. These estimates are similar to Render (1995), who reported that spawning occurs once every 5 to 8 days for red snapper. Contrarily, Woods (2003) reported that spawning occurred much more frequently off Louisiana, once every 4.2-4.5 days. Woods (2003)'s estimate was close to that observed at toppled platforms in this study, but notably more frequent than that observed at the natural banks. It should be noted, however, that the large majority of fish Woods (2003) sampled at dockside were captured at artificial reefs off Alabama and at standing platforms off Louisiana.

At standing platforms, spawning likely occurred slightly less frequently than at toppled structures because specimens inhabiting standing platforms were smaller and younger. This is further supported by similar length-weight regression parameters between those two habitat types, indicating comparable body condition between females at standing and toppled platforms. At the natural banks, increased metabolic demands may contribute to reduced spawning frequency.

2.5 General Summary and Conclusion

Data from this study demonstrate that habitat-specific differences in the reproductive parameters, sizes and ages of female red snapper exist in the northern Gulf. These findings suggest that phenotypic plasticity is employed as a mechanism to control the balance between somatic growth and reproduction according to food availability, metabolic demands, habitat composition and/or exploitation. The potential for less fecund females on the natural banks as well as slower maturation rates further offshore should be considered, and fishery managers could work to incorporate these life history parameters into future stock assessments as a means in increase SPR to benchmark levels and maintain maximum sustainable yields.

Furthermore, a truncated age distribution is evident on Louisiana's shelf-edge (Saari 2011; this study). This finding is contrary to speculation that a sub-population of older, larger red snapper occupies deeper waters of the Gulf and is in agreement with a study recently conducted by NMFS (SEDAR 7 Update 2009). Numerous others have documented age truncation of Gulf red snapper due to emigration, natural mortality or fishing exploitation (Goodyear 1988; Wilson et al. 1994; Nieland and Wilson 2000; Wilson and Nieland 2001; Fischer et al. 2004; Nieland et al. 2007b; Saari 2011). Other compensatory responses indicative of overfishing have been noted for the stock as well, including increased growth rates (Fischer et al. 2004), declining size-at-age (Nieland et al. 2007a) and smaller sizes and ages at maturity (Fitzhugh et al. 2004; Jackson et al. 2007; Cook et al. 2009).

Rebuilding the red snapper stock's age distribution would indeed support the increase of SPR and support stock recovery. Older females are highly valuable contributors to the spawning stock because they spawn more often (Chesney and San Filippo 1994; Claramunt et al. 2007; Ganias et al. 2011), are exponentially more fecund (Bagenal 1973; Marteinsdottir and Begg

2002; Porch 2004; Porch et al. 2007; Somarakis 2004), produce more viable eggs (Bagenal 1973; Rijnsdorp 1994; Trippel 1998; Johnston and Leggett 2002) and spawn for longer periods over the duration of the spawning season (Trippel 1998). Therefore, protection of older age groups should be heavily considered (Cowan 2011). Furthermore, decreased juvenile fishing mortality would also contribute greatly to the future survival of older age classes.

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CHAPTER 3: REGIONAL COMPARISONS OF THE REPRODUCTIVE BIOLOGY OF FEMALE RED SNAPPER IN THE GULF OF MEXICO

3.1 Introduction

Red snapper are among the most economically valued finfish species in the Gulf of Mexico (Gulf). Red snapper supported a thriving fishery from the mid-nineteenth century until the 1980's, when stock depletion became undeniable (Goodyear 1988). In both the eastern and western Gulf, stock declines are attributed to direct harvest by the commercial and recreational fisheries, and to bycatch of juveniles by the shrimp trawl fishery (SEDAR 7 2005). The Gulf Reef Fish Fishery Management Plan, which includes red snapper, was implemented in 1984. Despite intense management efforts ever since, the stock remains overfished (SEDAR 7 Update 2009) and recent evidence suggests that overfishing is still occurring (NOAA 2012). Presently, restoration to a spawning potential ratio (SPR) of 26-27%, a biomass that can support maximum sustainable yield, is anticipated by 2032 (SEDAR 7 2005; GMFMC 2010). In both the eastern and western Gulf, SPR remains below this benchmark at this time.

The red snapper is a long-lived, highly fecund species, which exhibits a periodic ("bet-hedging") life history strategy (Winemiller and Rose 1992). Adults may live to >55 years old, and females do not reach full reproductive potential until 14 to 15 years of age (Cowan et al. 2010). A single female of optimal reproductive capacity may produce millions of eggs in a single spawning event, and multiple batches are spawned over a protracted spawning season (Nelson 1988; Render 1995; Woods 2003; Collins et al. 1996, 2001). While the likelihood that an egg will survive to produce a mature adult is remarkably low (most females don't even produce one single surviving progeny in a given year), producing large numbers of offspring several times throughout an extended spawning period improves chances of strong year-classes and thus maintenance of population size (Houde 1987).

Red snapper are currently managed as a unit stock in the Gulf of Mexico. Two centers of abundance currently exist in the northern Gulf, the larger off southwest Louisiana and the smaller off Alabama (Patterson 2001; Gold and Saillant 2007). In general, older and larger red snapper are found in the western Gulf (Allman et al. 2004; SEDAR 7 Update 2009). Genetic studies indicate that the stock is a genetically homogeneous metapopulation, which consists of regionally independent subpopulations, and gene flow intermittently occurs among subpopulations through migration or ocean currents (Gold et al. 1997, 2001; Gold and Saillant 2007). Regional variations in size or life history probably stem from differences between local environments or fishing pressures (Fischer et al. 2004; Gold and Saillant 2007; Jackson et al. 2007).

Many reproductive traits, including maturation rates, spawning season and fecundity vary between fish populations (Morgan 2008). In the Gulf of Mexico, regional differences in spawning and maturation schedules have been documented for red snapper. For instance, spawning season in the northern Gulf occurs May/June through August/October with a peak in June and July (Render 1995; Woods 2003; Fitzhugh et al. 2004). Contrarily, in the southern Gulf off the Campeche Banks of Mexico, the reproductive season occurs throughout most of the year (Brulé et al. 2010). Additionally, Woods (2003) found that female red snapper east of the Mississippi River off Alabama consistently reached reproductive maturity at younger ages and smaller sizes compared to conspecifics west of the river, off Louisiana. Similarly, Fitzhugh et al. (2004) reported that female red snapper in the eastern Gulf reach maturity earlier than females in the west. Taking variations like these into account enables more accurate estimates of reproductive potential and stock productivity (Morgan 2008).

This study aims to provide managers of the Gulf of Mexico red snapper fishery with updated information about region-specific reproductive biology parameters including sex ratio, gonadosomatic index, maturity, batch fecundity, spawning frequency, and annual fecundity. To better understand stock dynamics, the reproductive characteristics of female red snapper were examined and compared among six primary fishing regions in the Gulf of Mexico. This study also establishes baseline data on reproductive estimates for female red snapper in central Florida and south Texas.

3.2 Materials and Methods

Red snapper (*Lutjanus campechanus*) were sampled from recreational landings in six regions in the US the Gulf of Mexico: Clearwater, Florida (Central Florida), Destin Florida (Northwest Florida), Dauphin Island, Alabama (Alabama), Port Fourchon, Louisiana (Louisiana), Galveston, Texas (North Texas) and South Padre Island, Texas (South Texas) (Figure 3.1). My goal was to sample 100 female red snapper from each region per year. After sampling goals were met for a companion age and growth study, which included random sampling of both males and females, if 100 females had not yet been sampled, extra fish were randomly sexed and only females were kept. These extra females (n=78) were excluded from sex ratio analysis; however they were included in reproductive biology analyses.

Sampling from the recreational fishery occurred in June, July and August 2009 and in June 2010. Originally, plans for sampling included only Central Florida, Northwest Florida, Alabama, Louisiana and South Texas during the 2009 and 2010 fishing seasons. Samples were collected according to plan in 2009. However, the Deepwater Horizon Oil Spill prompted fishery closures in Alabama and Louisiana during the summer of 2010. Therefore, North Texas was included in 2010 (along with Central Florida, Northwest Florida and South Texas).

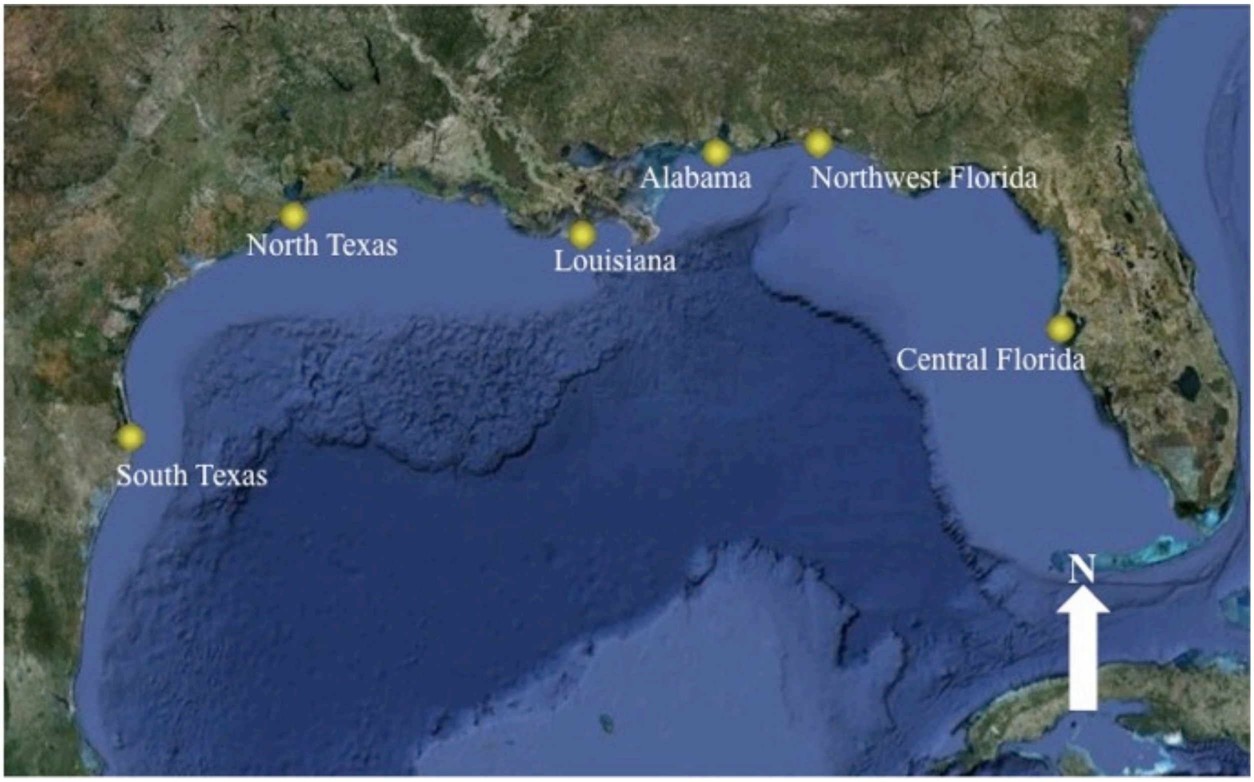


Figure 3.1 Sampling sites. Red snapper were sampled from six primary recreational fishing regions in the Gulf of Mexico. Map courtesy of Google Earth.

Additionally, 52 females sampled in July 2010 are included for the Louisiana region; these fish were collected by hook and line (under Federal Permit) from oil platforms off the coast of Louisiana.

Stock reproductive potential is limited by egg production, therefore only female red snapper were considered for reproductive analysis in this study. At the time of collection, red snapper were fitted with labeled cable ties, and total weight (nearest 0.01 g) and total length (nearest mm) were measured and recorded. Gender was determined, and sagittal otoliths were removed and placed into labeled envelopes for a companion study on age and growth (Saari 2011). Otoliths were processed and sectioned following the methods of Cowan et al. (1995). Ovaries were removed from females, and visceral and adipose tissues were trimmed away.

Ovaries were placed into labeled plastic freezer bags and kept on ice or frozen until further processing.

Ovaries were weighed (nearest 0.01 g) and fixed in a 10% formalin solution (37% formaldehyde diluted to 10% with deionized water) for a minimum of 2 weeks. It is important to note that undamaged gonads are often difficult to obtain from recreational catches. For several females (n=75), only one intact lobe was available. In these cases, the weight of the intact lobe was doubled to estimate undamaged ovary weight. This was feasible because the red snapper ovary is comprised of 2 symmetric lobes (Collins et al. 1996).

Ovarian tissue processing, histology slide preparation, and oocyte stage analysis followed the methods described in Chapter 2 (Sections 2.2.1, 2.2.2 and 2.2.3, respectively). The following reproductive biology analyses were performed according to methods described in Chapter 2: gonadosomatic indices (GSI), size- and age-at-maturity, batch fecundity, spawning frequency, annual fecundity and index of reproductive importance (IRI) (Sections 2.2.4.1, 2.2.4.3, 2.2.4.4, 2.2.4.5, 2.2.4.6 and 2.2.4.7, respectively).

Statistics

All statistical analyses were performed using Statistical Analysis System software (SAS Institute 2008). Analysis of variance (ANOVA) with the Tukey-Kramer post-hoc test and the Mann-Whitney U-test (used for non-parametric data) were used to evaluate equality of sample means for age, length and weight among regions. Chi-square analyses were used to test sex ratio among regions, and spawning frequency among regions, sizes and ages. Linear regression was used to estimate regional relationships between batch fecundity and length, weight and age. Analysis of covariance (ANCOVA) was used to test for differences among regions in regression

relationships between batch fecundity and length, weight and age. All tests were considered significant if $p<0.05$.

3.3 Results

A total of 1811 red snapper (*Lutjanus campechanus*) were sampled during the 2009 and 2010 recreational fishing seasons from six regions in the Gulf of Mexico (Table 3.1). While sex could not be determined for 115 individuals, 740 males and 956 females were identified, measured and sampled. A significantly greater proportion of females was found in Central Florida (χ^2=31.72; $p<0.0001$), South Texas (χ^2 = 13.04; $p=0.0003$) and at all regions combined (χ^2 = 27.51; $p<0.0001$) (Appendix A, Table 15). Sex ratios were not different from 1:1 in Northwest Florida, Alabama, Louisiana or North Texas.

An additional 78 females were sampled from the recreational fishery to meet sampling goals of 100 females per region each year. A total of 1,034 female red snapper were sampled in June, July and August 2009 and in June and July 2010 (Tables 3.2 and 3.3).

3.3.1 Ages and Sizes of Female Red Snapper

For the remainder of this chapter, only female red snapper will be considered. Previously published age and growth analyses for the red snapper in this study indicated that neither the means nor the frequency distributions for age, total length and total weight differed between sexes (Saari 2011). Therefore, statistical results for regional comparisons of age, total length and total weight reported by Saari (2011) are applied to the females in this study (Table 3.4). In all regions combined, females ranged from 2 to 16 years old, while the mean age was 4.53 ± 0.04 years old (Table 3.4A, mean ± standard error (SE)). Females were significantly younger in Central Florida and Northwest Florida. Females from Central Florida and Northwest Florida

were younger than in other regions, but did not differ from one another. Mean ages among Alabama, Louisiana, North Texas and South Texas were not significantly different.

Table 3.1 Red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions in the Gulf of Mexico.

Region	Unknown Sex	Male	Female	Total
Central Florida	34	105	204	343
Northwest Florida	23	186	220	429
Alabama	3	93	117	213
Louisiana	12	111	122	245
North Texas	20	111	93	224
South Texas	23	134	200	357
All	115	740	956	1811

Table 3.2 Annual % totals for female red snapper, *Lutjanus campechanus*, sampled from the recreational fishery in 2009 and 2010.

Region	n	2009	2010
Central Florida	217	109 (50.2%)	108 (50.0%)
Northwest Florida	270	156 (57.8%)	114 (42.2%)
Alabama	120	120 (100%)	-
Louisiana	125	73 (58.4%)	52 (41.6%)
North Texas	95	-	95 (100%)
South Texas	207	86 (41.6%)	121 (58.5%)
All	1034	544 (52.6%)	490 (47.4%)

Table 3.3 Monthly % totals for female red snapper, *Lutjanus campechanus*, sampled from the recreational fishery in 2009 and 2010.

Region	n	June	July	August
Central Florida	217	217 (100%)	-	-
Northwest Florida	270	114 (42.2%)	142 (52.6%)	14 (5.2%)
Alabama	120	120 (100%)	-	-
Louisiana	125	37 (29.6%)	60 (48.0%)	28 (22.4%)
North Texas	95	95 (100%)	-	-
South Texas	207	121 (58.5%)	86 (41.6%)	-
All	1034	704 (68.1%)	288 (27.9%)	42 (4.1%)

Table 3.4 Mean A) age (years), B) total length (mm) and C) total weight (g) of female red snapper, *Lutjanus campechanus,* sampled from six recreational fishing regions in the Gulf of Mexico. Similar superscripted letters indicate no significant difference between regions according to ANOVA results with Tukey's adjusted least square means (Saari 2011).

A			Age		
Region	n	Mean ± SE	Min	Max	95% CI
Central Florida	161	4.06 ± 0.07^{A}	2.92	6.95	(3.91, 4.21)
Northwest Florida	254	4.15 ± 0.06^{A}	2.92	9.08	(4.02, 4.28)
Alabama	108	4.73 ± 0.12^{B}	2.95	15.94	(4.48, 4.98)
Louisiana	123	4.95 ± 0.11^{B}	2.01	11.01	(4.73, 5.17)
North Texas	93	4.68 ± 0.12^{B}	2.96	8.96	(4.44, 4.92)
South Texas	191	4.97 ± 0.09^{B}	3.00	12.98	(4.78, 5.16)
All	929	4.53 ± 0.04	2.01	15.94	(4.45, 4.61)
B			Total Length		
Region	n	Mean ± SE	Min	Max	95% CI
Central Florida	160	535 ± 7^{A}	394	754	(521, 549)
Northwest Florida	247	501 ± 5^{B}	389	880	(491, 511)
Alabama	109	601 ± 7^{D}	426	880	(587, 615)
Louisiana	123	560 ± 8^{C}	374	744	(545, 575)
North Texas	92	519 ± 9^{A}	418	786	(502, 536)
South Texas	189	560 ± 5^{C}	420	711	(549, 570)
All	920	543 ± 3	374	880	(537, 549)
C			Total Weight		
Region	n	Mean ± SE	Min	Max	95% CI
Central Florida	152	2186 ± 97^{A}	650	6040	(1995, 2377)
Northwest Florida	217	1996 ± 92^{A}	730	9160	(1814, 2178)
Alabama	92	3248 ± 15^{C}	1040	12700	(2947, 3549)
Louisiana	87	2743 ± 14^{B}	702	6640	(2457, 3029)
North Texas	92	2100 ± 15^{A}	910	9740	(1799, 2401)
South Texas	174	2527 ± 76^{B}	900	6140	(2376, 2678)
All	814	2378 ± 50	650	12700	(2286, 2470)

n=sample size; SE=standard error; Min=minimum; Max=maximum; CI=confidence interval

Mean total length (TL) across all regions was 543 ± 3 mm and ranged from 374 to 880 mm TL (Table 3.4B). On average, females from Northwest Florida were significantly shorter than those from all other regions. Individuals from North Texas and Central Florida were longer than those from Northwest Florida but shorter than specimens from Louisiana and South Texas.

The majority of individuals from Northwest Florida, North Texas and Central Florida were in the 450 mm TL and 500 mm TL size classes (57%, 63% and 43%, respectively) (Figure 3.2). The majority of females from Louisiana belonged to the 500, 600 and 650 mm TL size groups (19%, 23% and 19%, respectively). Specimens from Alabama were significantly longer than individuals from all other regions. Most females from Alabama (54%) and South Texas (42%) were in the 550 and 600 mm TL size classes.

Overall, the average total weight (TW) for female red snapper was 2378 g (Table 3.4C). Total weights ranged from 650 to 12700 g. Mean total weight was significantly lower among specimens from Central Florida, Northwest Florida or North Texas, and did not differ significantly among those three regions. Females from Louisiana and South Texas were similar in weight and significantly heavier, than conspecifics from Central Florida, Northwest Florida and North Texas. Alabama females were significantly heavier than fish from all other regions.

Among all regions, female red snapper in the 450 and 500 mm TL size classes were the most frequently encountered size groups and collectively constituted 40.42% of all fish sampled (Appendix A, Table 16A). Females in the 550 and 600 mm TL size classes comprised another 33.06% of the sampled catches. Females in the 650 mm TL size class made up 12.11% of the total catch across all regions. Individuals in the 400 and 700 mm TL size groups made up 6.11% and 6.32% of the specimens sampled, respectively, while specimens in the ≥750 mm TL size class accounted for only 1.79% of all samples combined.

Among all regions, the most frequently observed age groups were ages 4 and 5; these two age groups collectively comprised 70.90% of the total sample population (Appendix A, Table 16B). Age-3 females constituted 14.82% of all samples, while age-6 specimens made up 9.59% of the samples. Fish ages 7, 8 and 9+ collectively comprised 4.69% of the total sample

population (3.20%, 0.53% and 0.96%, respectively). No age-2 specimens were observed, an effect of minimum size limits imposed on the recreational fishery during both sampling years. Age distributions varied among regions (Figure 3.3). The majority of females from Central Florida (72.67%) and Northwest Florida (68.11%) were 3- and 4-year olds. Most females from Alabama (93.80%), Louisiana (72.95%), North Texas (75.26%) and South Texas (72.31%) were 4 and 5 years old.

Overall, females from the 2004, 2005 and 2006 year classes comprised 88.1% of the total catch (n=938) sampled from the recreational fishery over both sampling years (2004 cohort=25.3%; 2005 cohort=32.5%; 2006 cohort=30.2%, respectively) (Figure 3.4). Individuals from the 2003 and 2007 year-classes comprised 5.5% and 4.5% of the total catch, respectively. Females from the 1993-2002 cohorts collectively comprised 1.8%, and individuals from the 2008 cohort comprised 0.1% of the total recreational catch.

3.3.2 Reproductive Analyses

Oocyte stages were classified for all female red snapper (n=956) (Table 3.5). Overall, a total of 700 fish (73% of all samples) showed signs of vitellogenesis, indicating that they were capable of spawning. A total of 178 individuals (19% of all samples) showed signs of imminent spawning activity, indicated by the presence of late vitellogenic oocytes (LV) and/or hydrated oocytes (H). Clear evidence of recent spawning, indicated by the presence of fresh POF, was found for an additional 38 specimens (4% of all samples).

Among regions, the highest incidences of spawning females occurred in South Texas and Alabama; at least 90% of all samples from these two regions possessed vitellogenic oocytes. In Northwest Florida as well as Louisiana, 79% of females collected were reproductively active.

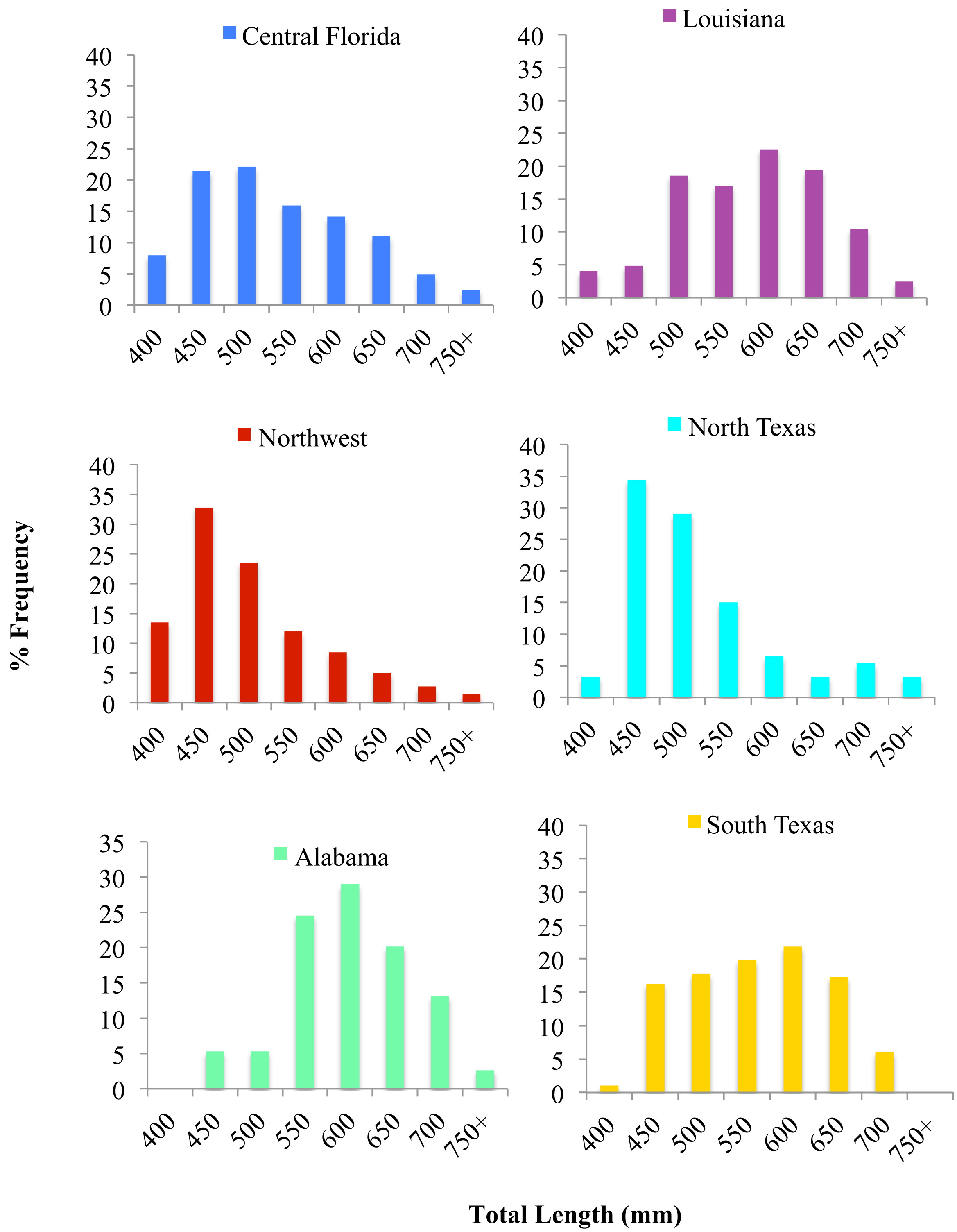


Figure 3.2 Frequency distributions for female red snapper, *Lutjanus campechanus*, at total length (mm). Females were sampled across the Gulf of Mexico from six recreational fishing regions.

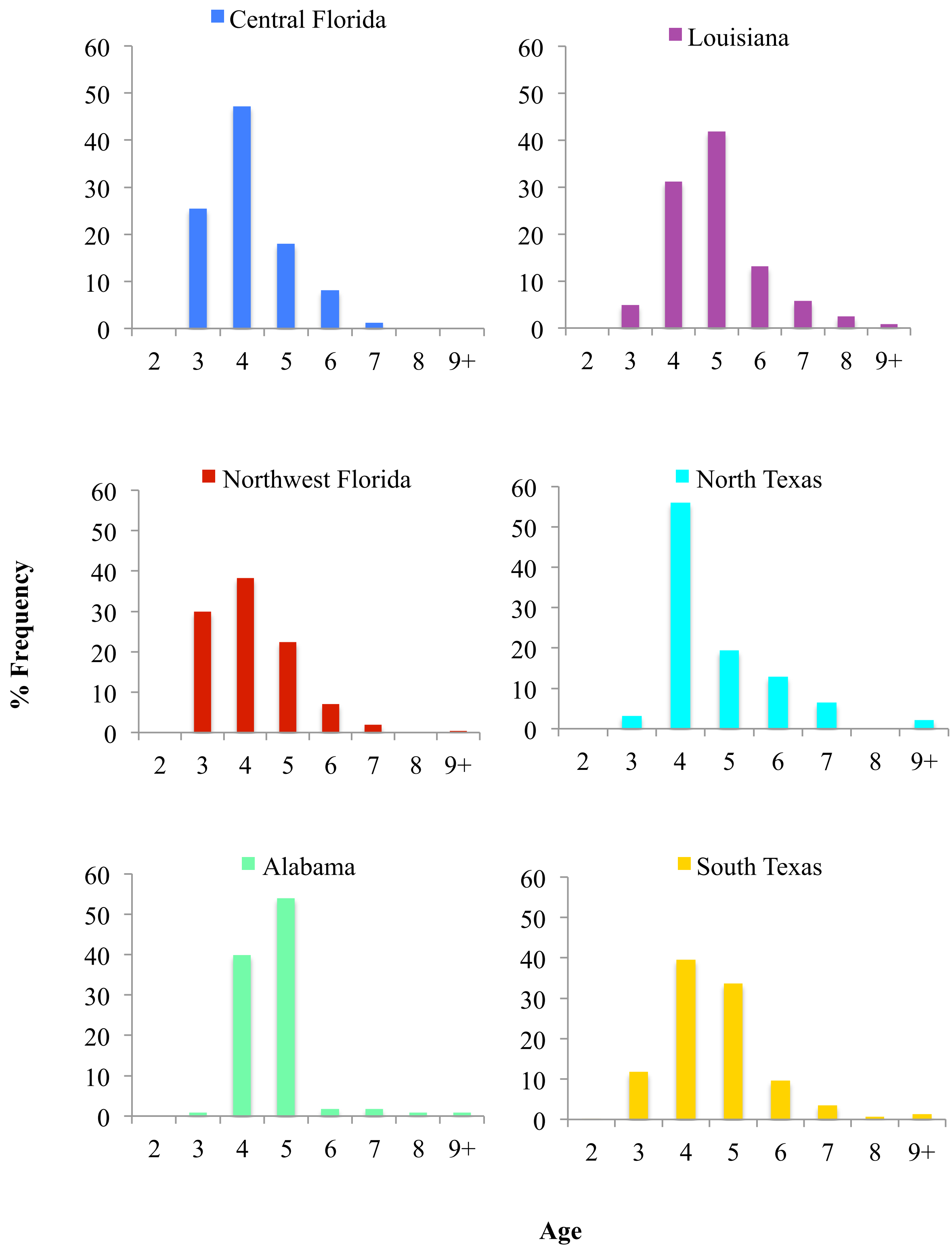


Figure 3.3 Frequency distributions for female red snapper, *Lutjanus campechanus*, at age (year). Females were sampled across the Gulf of Mexico from six recreational fishing regions.

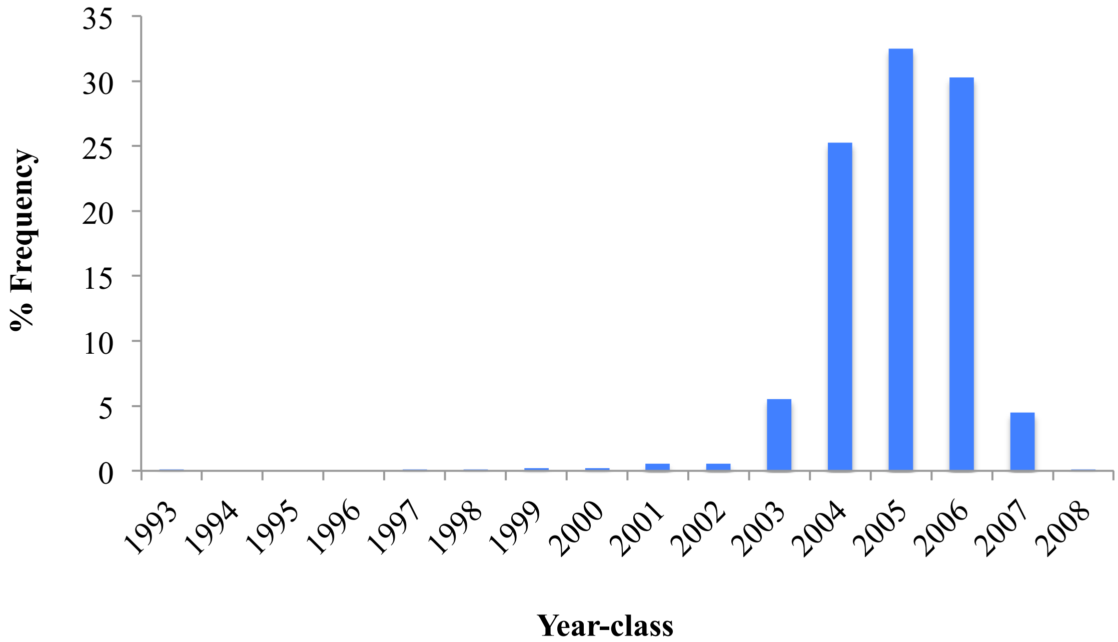


Figure 3.4 Frequency distribution by year-class for female red snapper (*Lutjanus campechanus*) sampled from the Gulf of Mexico recreational fishery. Fish were sampled from Central Florida to South Texas during the 2009 and 2010 recreational fishing seasons (n=938).

Fewer individuals displayed vitellogenic oocytes in North Texas (65%), and less than half of the females from Central Florida (41%) were spawning capable.

The greatest incidence of hydrated individuals was observed in North Texas (H=32%) followed by Alabama (H=25%) (Table 3.5). Central Florida had the smallest number of fish in hydrated condition (H<1%). Louisiana and South Texas each had the highest frequency of fish with post-ovulatory follicles among all regions (POF=9%). The lowest occurrence of POF was observed in samples from Central Florida (POF<1%).

3.3.2.1 Gonadosomatic Index

Among all regions, a mean GSI (± standard error) of 1.6 ± 0.1 indicated significant spawning activity across the northern Gulf (range: 0.2-7.9) (Table 3.6; Appendix A, Table 17).

Table 3.5 Characterization of oocyte maturation for female red snapper, *Lutjanus campechanus,* collected from six recreational fishing regions in the Gulf of Mexico.

Region	n	Immature	Mature	LV	POF	H
Central Florida	204	121 (59.3%)	83 (40.7%)	15 (7.4%)	1 (0.5%)	1 (0.5%)
Northwest Florida	220	46 (20.9%)	174 (79.1%)	13 (5.9%)	3 (1.4%)	28 (12.7%)
Alabama	117	12 (10.3%)	105 (89.7%)	5 (4.3%)	3 (2.6%)	29 (24.8%)
Louisiana	122	26 (21.3%)	96 (78.7%)	10 (8.2%)	11 (9.0%)	8 (6.6%)
North Texas	93	33 (35.5%)	60 (64.5%)	2 (2.2%)	3 (3.2%)	30 (32.3%)
South Texas	200	18 (9.0%)	182 (91.0%)	7 (3.5%)	17 (8.5%)	30 (15.0%)
All	956	256 (26.8%)	700 (73.2%)	52 (5.4%)	38 (4.0%)	126 (13.2%)

n=sample size; LV=late vitellogenic; POF=post-ovulatory follicles; H=hydrated

A maximum GSI estimate of 15.0 was observed for one extremely fecund Alabama female (total weight=2020 g). With and without this individual included in the analysis, Alabama by far produced the highest mean GSI estimate (GSI=2.4, GSI=2.3, respectively), followed by Northwest Florida (GSI=1.8). North Texas produced the third highest GSI estimate (GSI=1.6), while Louisiana and Central Florida each produced the fourth highest GSI estimate (GSI=1.4). South Texas produced the lowest mean GSI estimate overall (GSI=1.1).

A clear trend in GSI values among regions was evident, where mean GSI tended to increase at higher latitudes (Figure 3.5). Hydrated females were excluded from Figure 3.5 to avoid overestimation of energetic investment in reproduction via extra water weight. Females sampled during the month of August were also excluded from Figure 3.5 to prevent underestimation of reproductive effort because peak spawning occurs in June and July in the northern Gulf, and spawning efforts tend to decline by August (Woods 2003).

3.3.2.2 Size- and Age-at-Maturity

The Gulf red snapper recreational fishery is currently managed under a 16-inch TL (406 mm TL) size limit. Thus, the sizes and ages at which smaller and younger female red snapper attained first maturity as well as 50% maturity could not be determined from this data set.

Table 3.6 Mean gonadosomatic index (GSI) values for vitellogenic female red snapper, *Lutjanus campechanus,* sampled from six recreational fishing regions in the Gulf of Mexico. An asterisk indicates one extremely fecund female from Alabama (GSI = 15.03) was excluded from this analysis.

Region	n	Mean GSI	Min GSI	Max GSI	StDev	SE	95% CI
Central Florida	54	1.41	0.34	7.23	1.23	0.17	(1.08, 1.74)
Northwest Florida	101	1.83	0.32	7.92	1.39	0.14	(1.56, 2.10)
Alabama*	78	2.28	0.35	7.92	1.67	0.19	(1.91, 2.65)
Alabama	79	2.44	0.35	15.03	2.19	0.25	(1.80, 2.92)
Louisiana	66	1.38	0.27	4.72	1.20	0.15	(1.09, 1.67)
North Texas	56	1.56	0.23	3.93	1.01	0.13	(1.30, 1.82)
South Texas	151	1.08	0.27	3.91	0.67	0.05	(0.97, 1.19)
All*	506	1.55	0.23	7.92	1.25	0.06	(1.44, 1.66)
All	507	1.57	0.23	15.03	1.39	0.06	(1.45, 1.69)

n=sample size; StDev=standard deviation; CI=confidence interval; SE=standard error

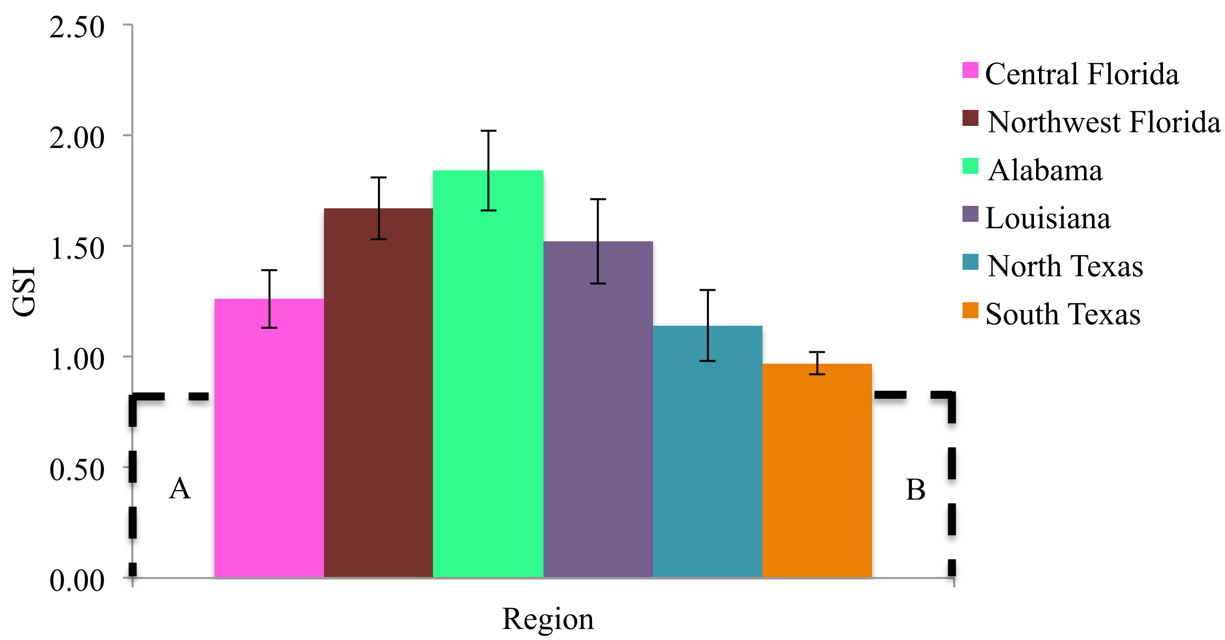


Figure 3.5 Regional mean gonadosomatic index (GSI) values for all non-hydrated female red snapper sampled during the months of June and July 2009 and 2010 in the Gulf of Mexico. Empty columns indicate unknown GSI values for non-hydrated females during the months of June and July from: A) South Florida and B) Mexico.

Females from all sampling regions had reached the 50% maturity benchmark by the 400 mm TL size class (Table 3.7). A Gulf-wide estimate for size-at-100% maturity could not be determined due a high occurrence of non-vitellogenic females in the larger size classes (700 mm TL size class: 17% inactive; 750+ mm TL size class: 24% inactive).

Alabama females reached 100% maturation by 450 mm TL (Table 3.7). Fish from South Texas had a very small sample size (n=2) for the 400 mm TL size class, both of which were sexually mature. By 500 mm TL, thirty-five of 36 females (97%) from South Texas had reached sexual maturity; the one immature fish from this group was a 6-year-old female of 524 mm TL. Females from the other regions took longer to reach the 100% maturity benchmark. For North Texas, 100% maturity was achieved at 650 mm TL, while females from Louisiana reached 100% maturation by 700 mm TL. Specimens from the Florida regions reached 100% maturity the slowest. For Northwest Florida, 100% maturation was achieved by 800 mm TL. The size at which 100% maturity was reached in Central Florida could not be determined. However, it should be noted that for Central Florida <35% of the 600, 650, 700 and 750 mm TL size classes demonstrated spawning capability; these are considerably low percentages of vitellogenic females compared to the other regions.

Maturity-at-age could not be determined for red snapper younger than age-3. However, among all regions, 50% maturity was reached by age-3 (Table 3.8). Gulf-wide, 100% maturity was achieved by age-8 (n=879), with the exception of one 9-year-old female from North Texas lacking vitellogenic oocytes. Age-at-100% maturation varied among regions. Specimens from South Texas appeared to achieve 100% maturity by age-3 (n=10); however, slightly less than 100% of South Texas females in the 4, 5 and 6 age groups were spawning-capable, giving reason to speculate that 100% maturation may not occur until age-7 in South Texas. Females in all

other regions reached this same benchmark at similar ages. In Alabama and North Texas, 100% maturity was reached by age-6, and in Louisiana this benchmark was reached by age-7. In Northwest Florida, 100% maturity was evident for individuals age-9 and older, however no data were available for 8-year-olds in that region. For Central Florida, the age-at-100%-maturation could not be determined due to an absence of individuals in the 8 and 9+ age groups. However, a strikingly low percentage of reproductively active females was evident for Central Florida after age-3 as less than 50% of females in the 4, 5, 6 and 7 age groups produced evidence of spawning activity.

For both the eastern and western Gulf, 75% maturity was reached by age-3 and by the 400 mm TL size class (Appendix A, Table 17). Females in the western Gulf reached 100% maturity slightly earlier, by age-7 and by the 750 mm TL size class. Females in the east reached 100% maturity by age-8 and at ≥775 mm TL.

Table 3.7 Percent maturity at total length for female red snapper, *Lutjanus campechanus,* sampled from recreational landings at six regions in the Gulf. Bold font marks the size at which 50% maturity was reached for a given size class. An asterisk indicates n<5.

Total Length (mm)	Central Florida (n=158)	Northwest Florida (n=212)	Alabama (n=113)	Louisiana (n=120)	North Texas (n=91)	South Texas (n=191)	All (n=884)
375-424	**58**	**90**	-	**67***	**67***	**100***	**78**
425-474	54	91	100	67	65	90	78
475-524	50	87	100	86	52	97	77
525-574	27	76	93	45	46	87	67
575-624	32	55	79	82	83	87	72
625-674	17	46	91	83	100*	91	73
675-724	29	43	100	100	100	92	83
725-774	25*	50*	100*	100*	100*	-	76
>775	-	100*	100*	-	100*	-	-

n=sample size

Table 3.8 Percent maturity at age for female red snapper, *Lutjanus campechanus*, sampled from six regions of the Gulf recreational fishery. Bold font marks the size at which 50% maturity was reached for a given age class. An asterisk indicates n<5.

Age Class (yr)	Central Florida (n=157)	Northwest Florida (n=214)	Alabama (n=109)	Louisiana (n=119)	North Texas (n=91)	South Texas (n=189)	All (n=879)
3	**56**	**89**	**100***	**67**	**67***	**100**	77
4	33	85	95	75	49	94	70
5	43	71	86	78	76	86	77
6	31	41	100*	75	100	90	71
7	0*	50*	100*	100	100	100	86
8	-	-	100*	100*	-	100*	100
9+	-	100*	100*	100*	50*	100*	100

n=sample size

3.3.2.3 Batch Fecundity

Batch fecundity was estimated for all fully hydrated (n=102) red snapper (Table 3.9). Overall, hydrated individuals ranged from 366 to 786 mm TL (mean=562 mm TL) and from 3 to 7 years (mean=4.7 years) in age. Two females displaying concurrent signs of hydrated oocytes and post-ovulatory follicles (POF) were removed from this analysis to avoid underestimation of BFE. Among all regions, the average female red snapper produced 158,182 ± 17,540 ova per spawning event. A possible regional trend among batch fecundity estimates (BFEs) was evident, where mean BFEs tended to increase with latitude (Figure 3.6).

Red snapper sampled from Alabama spawned significantly more ova per batch (mean=283,051 ± 35,761 ova) than any other region (Table 3.9). Specimens collected from South Texas yielded the lowest BFE, producing ~2/3 fewer ova per batch on average than fish from Alabama. Only one female from Central Florida was found in hydrated condition. Therefore, Central Florida was excluded from batch fecundity regression analyses.

Batch fecundity increases exponentially with total length, eviscerated body weight and age (Figure 3.7). To meet the normality and homogeneity of variance assumptions for

Analysis of Variance (ANOVA) and regression, batch fecundity data was natural log (ln) transformed. ANOVA results indicate that mean batch fecundity differed significantly among regions ($p<0.0001$). The Tukey- Kramer post-hoc test showed that mean BFE was significantly greater in Alabama compared to the other regions (Table 3.9). No significant differences in mean BFE were found between Northwest Florida, Louisiana, North Texas and South Texas.

Regression analyses indicated highly significant positive relationships between ln batch fecundity and ln total length, ln eviscerated body weight, and ln age (all $p<0.0001$) (Table 3.10). In general, ln BFE correlated the best with ln total length ($R^2=0.38$), followed by ln weight ($R^2=0.35$). Ln age correlated the least well with ln BFE ($R^2=0.19$).

ANCOVA analyses indicated no significant differences among regions for regressions of ln batch fecundity and ln total length (n=97); overall, slopes (p=0.1236) and y-intercepts (p=0.1126) among regions were not significantly different (Appendix A, Table 19; Figure 3.8). Natural-log transformed batch fecundity plotted against ln eviscerated body weight (n=92) was also not different among regions; slopes (p=0.0796) and y-intercepts (p=0.0620) were similar. Regression parameters for ln batch fecundity and ln age (n=92) did not differ among regions either; slopes (p=0.1458) and y-intercepts (p=0.0832) were not different.

3.3.2.4 Spawning Frequency

Spawning frequency was estimated for a total of 700 sexually mature female red snapper using three different methods: the hydrated oocyte method (H method), the post-ovulatory follicle method (POF method) and the time-calibrated method (TC method) (Table 3.11). Among all regions, 25% of all mature females displayed signs of hydration (n=177), while only 6% showed signs of fresh POF (n=39). Back-to-back spawning was evident for 0.6% females,

which were found with simultaneous signs of hydrated oocytes and POF (n=4). All four back-to-back spawners were 5-year-olds and ranged from 434-519 mm TL and from 1130-1892 g TW.

Table 3.9 Mean batch fecundity for female red snapper, *Lutjanus campechanus,* sampled from the recreational fishery at six regions in the Gulf of Mexico. For each region, similar superscripted letters denote no significant difference in mean batch fecundity estimates according to the Tukey-Kramer post-hoc test for Analysis of Variance (α=0.05).

Region	n	Mean ± SE	Min	Max	95% CI
Central Florida	1	14,939	-	-	-
Northwest Florida	15	115,369 ± 26,301^{A}	7,339	297,789	(63820, 166918)
Alabama	25	283,051 ± 35,761^{B}	45,817	615,702	(212960, 353142)
Louisiana	13	144,386 ± 73,561^{A}	4,631	945,114	(209, 288563)
North Texas	24	118,746 ± 33,683^{A}	3,279	557,502	(52728, 184764)
South Texas	24	107,745 ± 21,187^{A}	2,683	378,084	(66220, 149270)
All	102	158,182 ± 17,540	2,683	945,114	(123804, 192560)

n=sample size; SE=standard error; Min=minimum; Max=maximum; CI=confidence interval

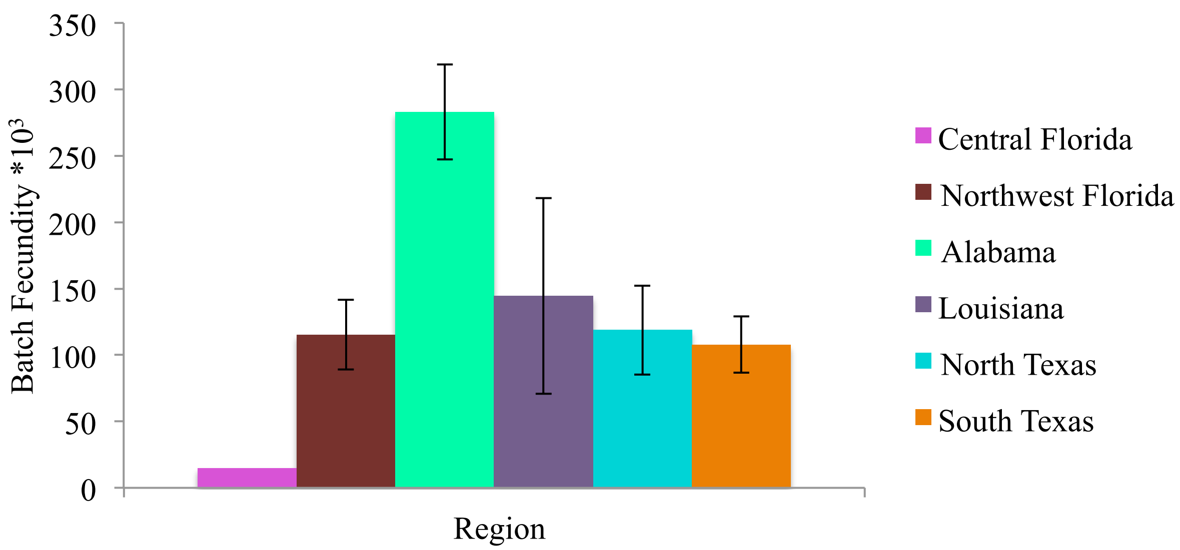


Figure 3.6 Mean batch fecundity for female red snapper, *Lutjanus campechanus*, sampled from six recreational fishing regions during the 2009 and 2010 spawning seasons (June, July and August).

Spawning frequency estimated by using the POF method is shown but was not used to compare SFE among regions due to the very low frequency of females observed with fresh (<24 hours old) POF. Across all regions, female red snapper spawned once every 3.9 to 6.5 days according to spawning frequency estimated by using the H method and the TC method (Table 3.11). Specimens from North Texas spawned the most often according to both the H method (SFE_H=1.9 days) and the TC method (SFE_{TC}=3.4 days), followed by females from Alabama (SFE_H=3.1 days; SFE_{TC}=5.7 days). Fish from Northwest Florida spawned slightly less often: once every 4.2 to 7.7 days. Spawning frequency estimated for South Texas was 4.9 to 6.7 days. Louisiana specimens spawned once every 5.3 to 6.6 days. Females from Central Florida spawned the least often, once every 5.2 to 9.8 days.

The average number of spawning events per year was estimated based on a 150-day spawning season (Woods 2003). For all regions combined, the average female red snapper spawned between 23 and 38 times per season (Table 3.12). Among regions, specimens from North Texas spawned the most often, 44 to 80 times per season. Alabama specimens spawned 26 to 49 times per season. In Northwest Florida, the average female spawned between 19 and 35 times per season. In South Texas spawning occurred 22 to 30 times per reproductive season. Louisiana fish spawned 23 to 28 times per season. Females from Central Florida spawned the least often, 15 to 29 times per season.

The number of spawning events per season positively correlated with both age and total length according to all three methods for spawning frequency estimation (Figure 3.9; Appendix A, Tables 20 & 21). The number of spawning events per season correlated best with total length according to spawning frequency estimated by using the hydrated oocyte, POF and time-calibrated methods (R^2=0.68, R^2=0.57 and R^2=0.70, respectively). Spawning events per season

Table 3.10 Regression relationships between natural log-transformed batch fecundity estimates and natural log transformations of total length, eviscerated body weight and age for female red snapper, *Lutjanus campechanus*. Fish were sampled from the recreational fishery in the northern Gulf of Mexico.

Logarithmic Function	p-value	R^2
Ln (BFE) = 4.9637 * Ln (L) - 20.1038	<0.0001	0.3757
Ln (BFE) = 1.5824 * Ln (W) - 0.8876	<0.0001	0.3535
Ln (BFE) = 2.8791 * Ln (Age) + 6.9766	<0.0001	0.1852

Ln=natural logarithm; BFE=batch fecundity estimate; L=total length; W=eviscerated body weight; A=age

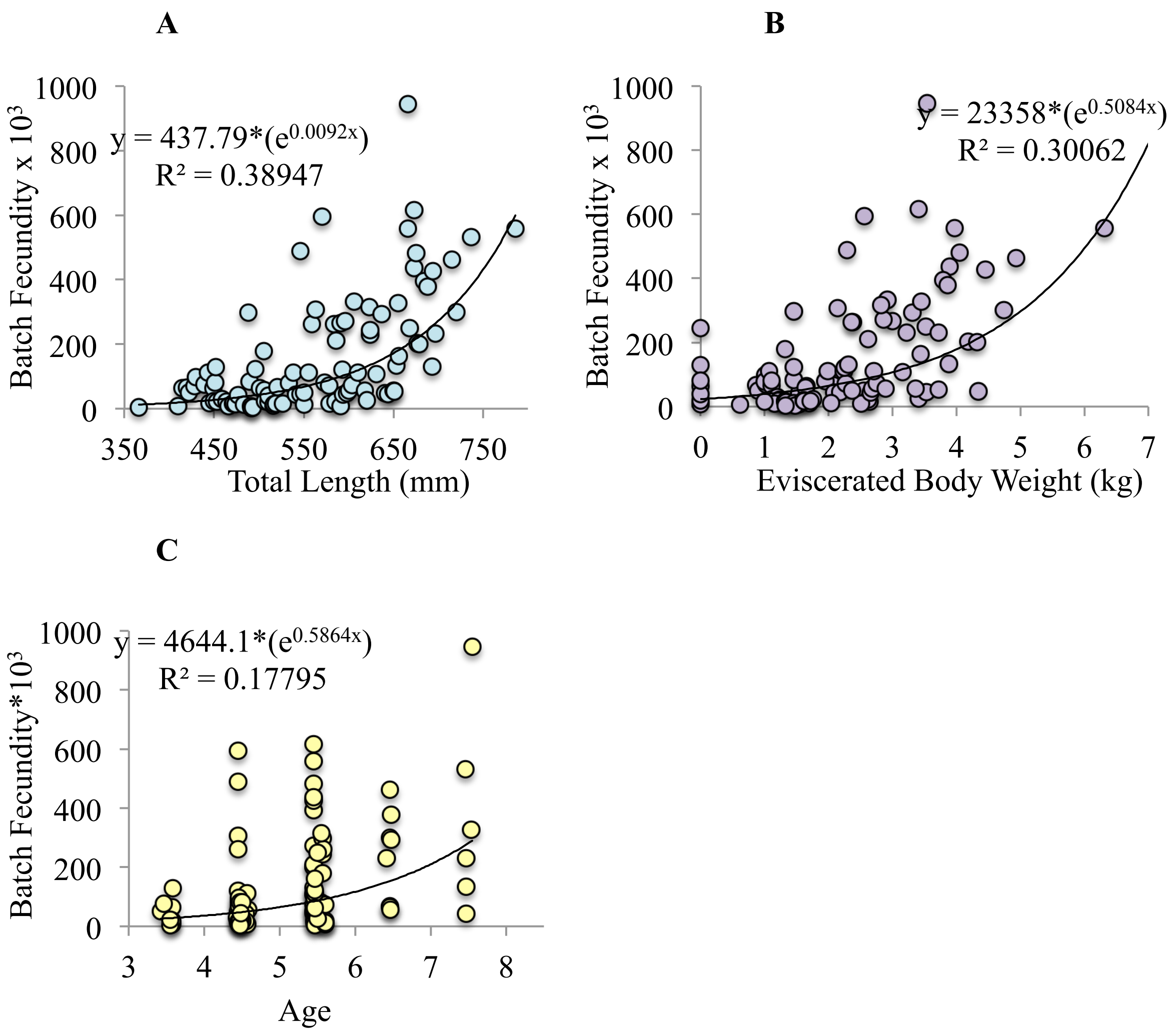


Figure 3.7 Exponential relationships between batch fecundity and A) total length, B) eviscerated body weight and C) age for female red snapper, *Lutjanus campechanus*, collected from the recreational fishery in the northern Gulf of Mexico.

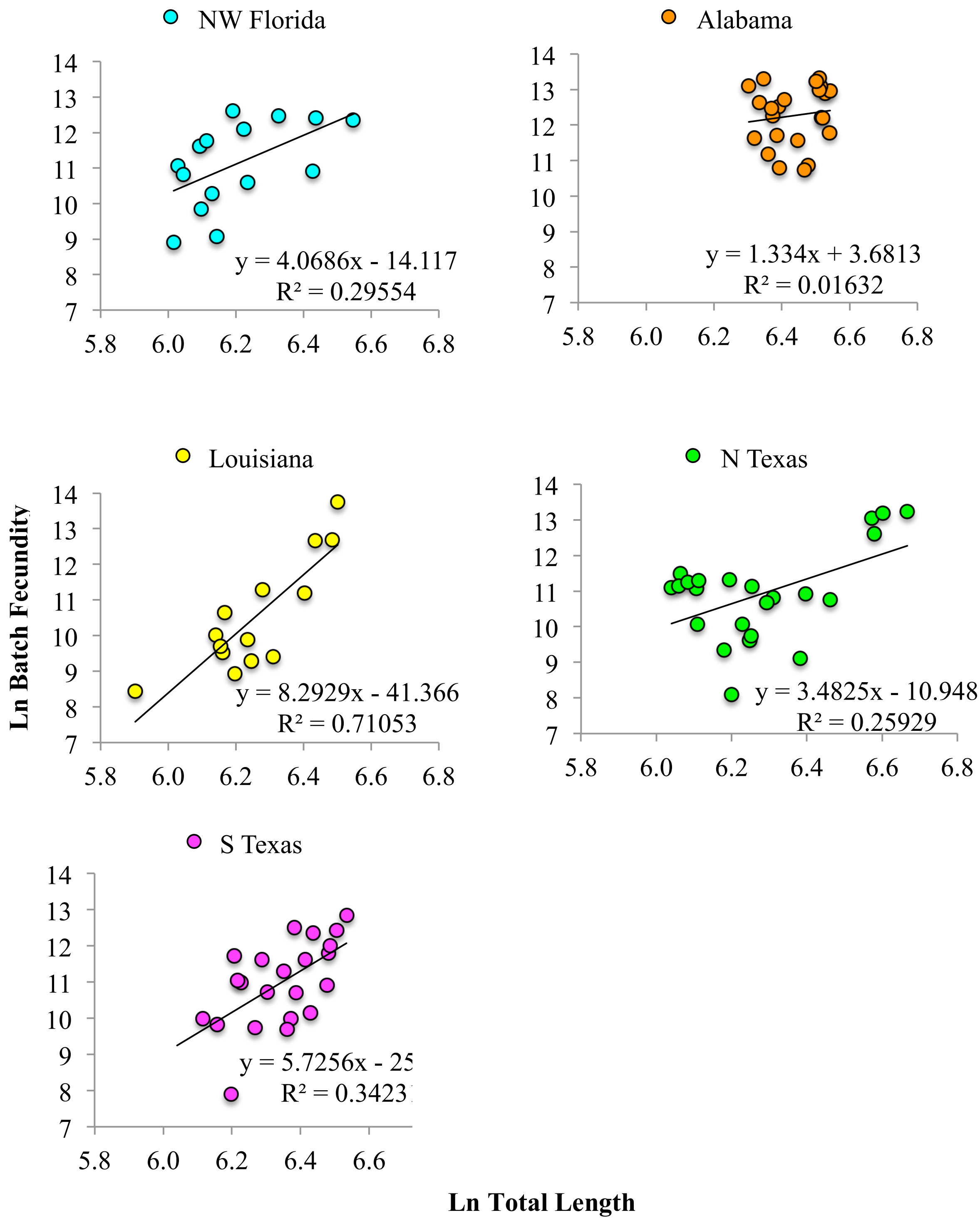


Figure 3.8 Regression relationships between natural log-transformed batch fecundity and natural log-transformed total length for female red snapper sampled from the recreational fishing sector at 5 major fishing regions in the northern Gulf of Mexico.

Table 3.11 Spawning frequency estimates (SFE) for female red snapper, *Lutjanus campechanus,* collected from the recreational fishery at six regions in the Gulf of Mexico. SFE are based on the hydrated oocyte method, the post-ovulatory follicle method and the time-calibrated method.

Region	n	n day-0	n day-1	SFE_H	SFE_{POF}	SFE_{TC}
Central Florida	83	16	1	5.2	83.0	9.8
Northwest Florida	174	41	4	4.2	43.5	7.7
Alabama	105	34	3	3.1	35.0	5.7
Louisiana	96	18	11	5.3	8.7	6.6
North Texas	60	32	3	1.9	20.0	3.4
South Texas	182	37	17	4.9	10.7	6.7
All	700	178	39	3.9	17.9	6.5

n=sample size; day-0=late vitellogenic or hydrated oocytes present; day-1=POF present; SFE_H=spawning frequency estimate based on the hydrated oocyte method; SFE_{POF}= spawning frequency estimate based on the POF method; SFE_{TC}=spawning frequency estimate based on the time-calibrated method

Table 3.12 Spawning events per season (spawns*season^{-1}) for female red snapper, *Lutjanus campechanus,* collected from the recreational fishery at six regions in the Gulf of Mexico. Spawning frequency estimates are based on the hydrated oocyte method (H method), the time-calibrated method (TC method) and a 150-day spawning season (Woods 2003).

Region	Spawns*season^{-1} (SFE_H)	Spawns*season^{-1} (SFE_{TC})
Central Florida	29	15
Northwest Florida	35	19
Alabama	49	26
Louisiana	28	23
North Texas	80	44
South Texas	30	22
All	38	23

SFE_H=spawning frequency estimate based on the H method; SFE_{TC}=spawning frequency estimate based on the TC method

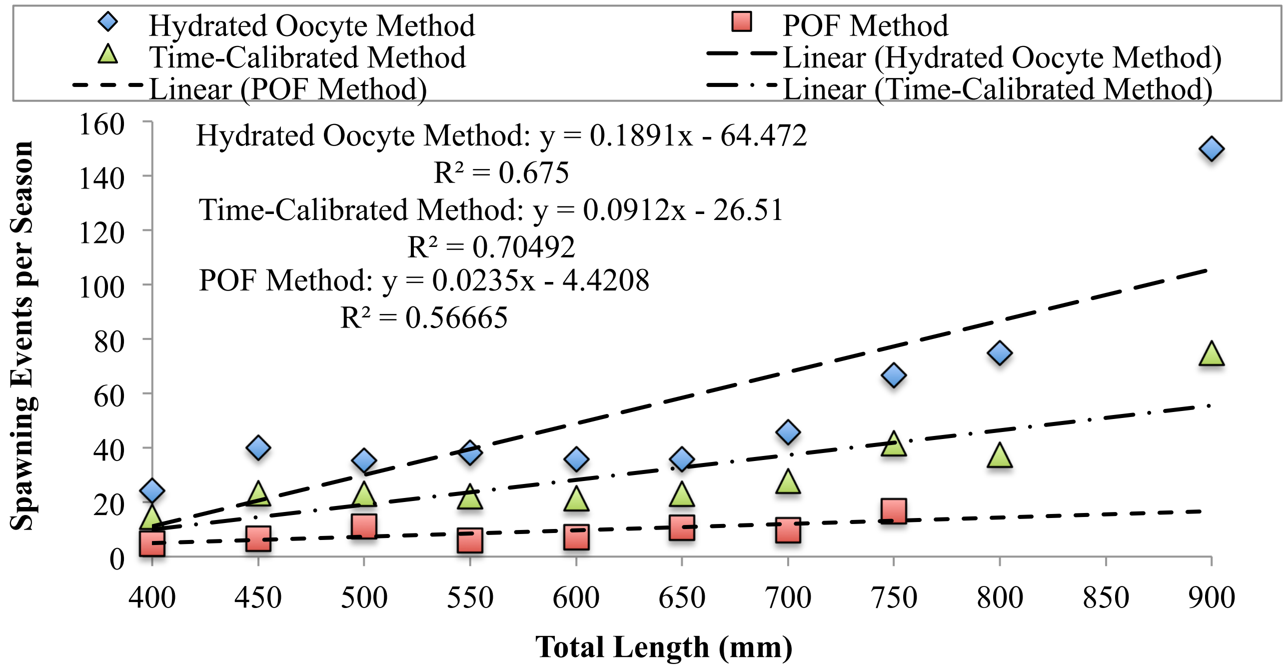
correlated less well with age (R^2=0.12, R^2=0.13 and R^2=0.34). Estimates based upon the time-calibrated method yielded the highest correlation coefficients with both size (R^2=0.70) and age (R^2=0.34).

Results for chi-square analyses indicated that red snapper in North Texas spawned significantly more often than conspecifics from the other regions. Specifically, spawning frequency estimated by using the hydrated oocyte method was significantly greater for North Texas compared to all other regions (Appendix A, Table 22A). Chi-square results for spawning frequency estimated using the time-calibrated method indicated females spawned significantly more often in North Texas than in Central Florida, Northwest Florida and Louisiana, but spawning frequency in North Texas was not different from Alabama or South Texas (Appendix A, Table 22B). Spawning frequency estimated by using the H method was significantly lower than that in North Texas, significantly greater compared to Louisiana, South Texas and Central Florida, and did not differ from Northwest Florida.

Chi-square analyses indicated that spawning generally occurred more often among females in the ≥750 mm total length size class when compared to smaller size classes. Specifically, spawning frequency estimated by using the hydrated oocyte method was significantly greater for the ≥750 mm total length size group compared to the 400 and 500 mm total length size classes ($p=0.0224$ and $p=0.0442$, respectively) (Appendix A, Table 23A). Chi-square results for spawning frequency estimated by using the time-calibrated method indicated no significant differences among any of the size groups (Appendix A, Table 23B).

Spawning frequency was also tested among age classes. Results indicated that spawning may occur less frequently for among age-3 females compared to older age groups. Chi-square results for spawning frequency estimated using the hydrated oocyte method indicated that spawning occurred significantly less frequently for age-3 fish when compared to age-5 individuals (Appendix A, Table 24A). Results for chi-square analyses of spawning frequency

A



B

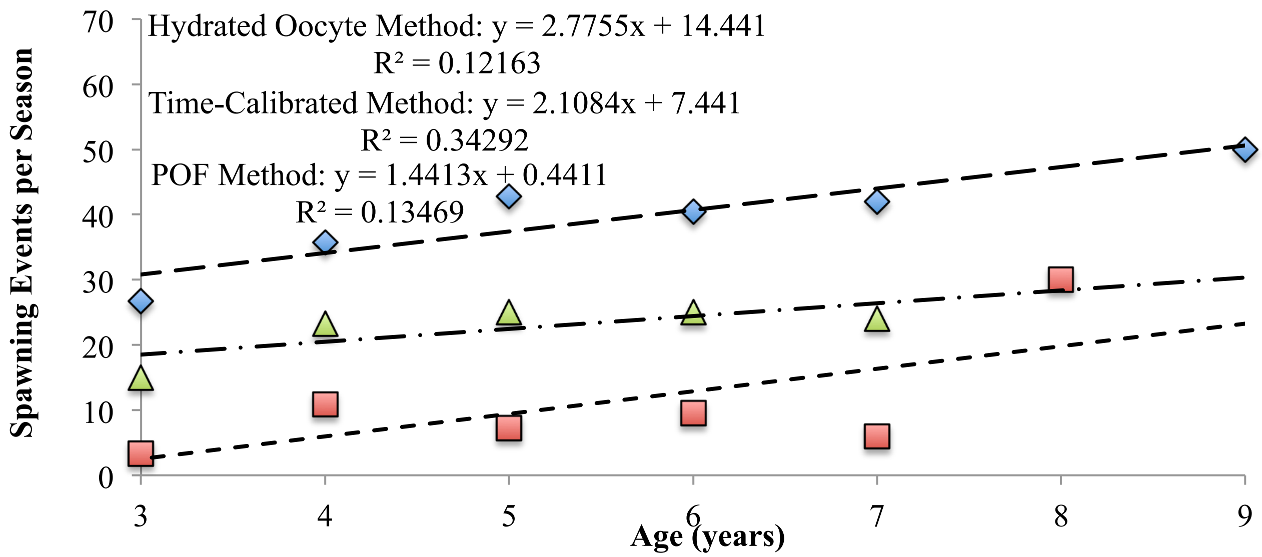


Figure 3.9 Spawning events per season at A) total length and B) age for female red snapper, *Lutjanus campechanus,* sampled from the Gulf recreational fishery. Spawning events per season are based on the inverse of spawning frequency, estimated by using the time-calibrated method, and a best-estimated 150-day spawning season (Woods 2003).

estimated by using the TC method indicated no significant differences in among age groups (Appendix A, Table 24B).

3.3.2.5 Annual Fecundity

Across all regions, mean annual fecundity was 3,660,781 ova per fish (range: 59,704 to 24,390,713 ova per female) (Table 3.13). Among regions, females from Alabama produced the largest mean annual fecundity estimate (AFE) of 7,480,633 ova per fish (range: 1,210,878 ova for an age-5 female of 644 mm TL to 16,272,124 ova for an age-5 female of 673 mm TL). North Texas produced the second largest average AFE of 5,195,144 ova per fish (range: 143,456 ova for an age-5 female of 493 mm TL to 24,390,713 ova for an age-6 female of 786 mm TL). Louisiana specimens produced the third largest mean AFE of 3,271,242 ova per fish (range: 104,921 ova for a 3-year-old female of 366 mm TL to 21,412,739 ova for a 7-year-old female of 666 mm TL). South Texas produced a lower mean AFE of 2,397,629 (range: 59,704 ova for an age-4 female of 492 mm TL to 8,413,408 ova for an age-6 female of 688 mm TL), followed by Northwest Florida (mean AFE=2,237,755 ova per female; range: 142,351 for 3-year-old female of 410 mm TL to 5,776,080 ova for a 5-year-old female of 488 mm TL). The one hydrated female from Central Florida produced an AFE of 228,658 ova per year (age-4; 517 mm TL).

Mean annual fecundity was estimated by size and age for all regions combined (Appendix A, Tables 25 and 26, respectively). Considering size, AFE ranged from 683,370 ova for individuals in the 400 mm TL size class to 23,825,994 ova for individuals in the ≥750 mm TL size group. Concerning age, AFE ranged from 467,753 ova for 3 year old red snapper to 2,303,016 ova for 7 year olds. No information was available regarding AFE for specimens older than age-7.

3.3.2.6 Index of Reproductive Importance

An Index of Reproductive Importance (IRI) was developed by combining spawning frequency, annual fecundity and maturity estimates from this study with age-based population size projections for Gulf red snapper (Shirripa and Legault 1999). The IRI indicated that the most valuable contributors to the spawning stock were age-9 and older (IRI=0.7954) (Table 3.14). Eight-year-olds were the second-most significant contributors (IRI=0.1323). Age-3, 4 and -5 fish (IRI=0.0131, 0.0218 and 0.0158, respectively) each seemed to contribute more to the spawning stock than 6 and 7 year olds (IRI=0.0079 and 0.0050, respectively). Age-2 females were the least significant contributors to the stock (IRI=0.0087). Age-0 and age-1 red snapper were not found in this study.

Table 3.13 Annual fecundity of female red snapper sampled from the Gulf recreational fishery at six primary fishing regions. An asterisk by Central Florida denotes the small number of hydrated individuals from that region (n=1).

Region	n	SFE_{TC}	Mean BFE	Mean AFE	Min AFE	Max AFE
Central Florida*	1	9.8	14939	228658	-	-
Northwest Florida	15	7.7	115369	2237755	142351	5776080
Alabama	25	5.7	283051	7480633	1210878	16272124
Louisiana	13	6.6	144386	3271242	104921	21412739
North Texas	24	3.4	118746	5195144	143456	24390713
South Texas	24	6.7	107745	2397629	59704	8413408
All	102	6.5	158182	3660781	59704	24390713

n = sample size; SFE_{TC} =spawning frequency estimate based on the time-calibrated method; BFE=batch fecundity estimate; AFE=annual fecundity estimate; Min=minimum; Max=maximum

Table 3.14 Index of reproductive importance (IRI) for female red snapper, *Lutjanus campechanus,* sampled from six primary recreational fishing regions in the Gulf of Mexico. Age-specific proportions of the red snapper population in the Gulf (% n) were based on estimates from Schirripa and Legault (1999). An asterisk marks estimates for red snapper by Woods (2003) for Louisiana and Alabama combined. One 9-year-old female was not in spawning condition and was not included.

Age	n	Spawns/ season	BFE	AFE	% n	% Mature	IRI
0	16526770	-	-	-	0.5684	0.0000	0.0000
1	9469581	-	-	-	0.3257	0.0000	0.0000
2	218530	-	-	1004250*	0.0075	0.8810*	0.0087
3	803275	15.00	46775	467753	0.0276	0.7692	0.0131
4	1125239	23.30	95446	614512	0.0387	0.6973	0.0218
5	452510	25.00	166046	996278	0.0156	0.7747	0.0158
6	152838	25.00	267779	1606673	0.0053	0.7079	0.0079
7	55392	24.00	368483	2303016	0.0019	0.8621	0.0050
8	52581	15.00	-	55609114*	0.0018	1.0000	0.1323
9+	217151	9.38	-	80938769*	0.0075	1.0000	0.7954

n=sample size; AFE=annual fecundity estimate

3.4 Discussion

3.4.1 Regional Differences in the Reproductive Biology of Female Gulf Red Snapper

Characteristics of Reproduction

Female red snapper were actively spawning during all sampling months (June, July and August). All developmental stages of oocytes were present in the ovaries of actively spawning females, indicating that red snapper are heterochronal spawners that produce multiple batches of eggs per spawning season (Wallace and Selman 1981). This is consistent with previous reports (Wilson et al. 1994; Woods et al. 2003; Brown-Peterson et al. 2009; Brulé et al. 2010).

Among regions, the highest incidence (≥90%) of reproductively active females was observed in Alabama and south Texas. The largest percentage of hydrated females (32%) was found in north Texas. The lowest spawning effort was observed among females from central

Florida, where only 41% of all female red snapper showed signs of spawning; <1% of these fish were hydrated and <1% had POF.

Gonadosomatic Index

Gulf wide, mean monthly GSI estimates from this study were similar to those reported in other Gulf wide studies for red snapper (Fitzhugh et al. 2004; Collins et al. 2001). Mean GSI unmistakably increased at higher latitudes (Figure 3.5). A similar observation was recently reported for Gulf red snapper (Brulé et al. 2010). Regional differences in GSI could be attributed to varied sizes and ages. However, water temperatures may better explain these differences.

Alabama females produced the highest average GSI estimate in this study, and this may in part be explained by the fact that significantly larger females were sampled in Alabama compared to all other regions. Females from northwest Florida had the second largest average GSI estimate despite the fact that these individuals were significantly smaller compared to conspecifics from all other regions and were significantly younger than females from all other regions except central Florida. North Texas females produced the 3rd largest GSI and comprised the only group in the western Gulf that was notably small despite their relatively older ages. Greater reproductive effort per body size in north Texas could indicate an important life history trade-off between somatic growth and reproductive output (Stearns 1989). Females from central Florida produced the 4th largest GSI; a relatively low GSI in central Florida was not surprising because these females were young and relatively small.

Louisiana females produced the 5th largest mean GSI. This is much lower than expected given that Louisiana fish were older and relatively large. The relatively low GSI estimate for Louisiana found in this study may be a result of a fairly large proportion (22%) of females

sampled from that region in early August, by which time the greatest peak in spawning may have already passed (Woods 2003). Thus, sampling month represents a potential significant source of variation in reproductive biology estimates among regions. When females sampled during the month of August were excluded from GSI analyses, Louisiana still produced a relatively low mean GSI value. A distinction in GSI values was especially notable between Alabama and Louisiana females, despite similar latitudes. This trend has been noted before (Woods 2003) and in the past was attributed to overfishing. This may, at least in part, be true. However, distinct differences in GSI between Alabama and Louisiana may also reflect a 'depth-for-latitude substitution' phenomenon, whereby red snapper captured off Louisiana, which are typically caught at deeper depths possibly more heavily influenced by warm water currents from the south and south west (Merrell 1983), may experience warmer temperatures year-round compared to counterparts caught off Alabama, which are typically fished at much shallower depths where water temperatures can get much colder (Patterson et al. 2001; SEDAR 7 2005).

Female red snapper from south Texas produced the lowest GSI of all the regions. This was unforeseen because female red snapper from south Texas were longer, heavier and older compared to conspecifics from all other regions except Louisiana and Alabama. Lower mean GSI in south Texas may be evidence of a latitudinal gradient in reproductive seasonality for red snapper (Grimes 1987; Robertson 1991; Brulé et al. 2010).

An extended spawning season at lower latitudes is prevalent among North American fishes (Conover 1992). Coincident with warmer temperatures at lower latitudes, Brulé et al. (2010) found that red snapper in the southern Gulf (Campeche Banks) remained in spawning condition essentially year-round (February-November), displaying a more protracted spawning season compared to conspecifics in the northern Gulf. Brulé et al. (2010) also reported that

maximum mean GSI values decreased with decreasing latitude in the Gulf of Mexico and speculated that red snapper populations in the northern Gulf may have elevated batch fecundities due to shorter, temperature-constrained breeding seasons. GSI estimates from this study agree. Non-hydrated female red snapper sampled from lower latitude regions (central Florida and south Texas) exhibited the lowest GSI values in June and July compared to conspecifics from all other regions (Figure 3.5). Furthermore, GSI estimates for non-hydrated female red snapper in south Florida and Mexico during June and July are needed to determine whether or not those two regions fit the trend observed in this study.

Extended spawning efforts at lower latitudes are also known to limit growth capacity due to increased energetic demands (Neal and Noble 2006); therefore, maximum sizes should decrease at lower latitudes. Similarly, Brulé et al. (2010) found that maximum sizes for red snapper declined with decreasing latitude. This agrees with findings from a companion study that reported red snapper from south Texas were significantly smaller at age and reached a smaller maximum length compared to conspecifics from the other regions (Saari 2011). However, it should be noted that Saari (2011) also found that red snapper in south Texas grew at a significantly faster rate when young compared conspecifics in more northern regions in the Gulf, a result also reported by Fischer et al. (2004). This contrasts with Neal and Noble (2006) who reported that slower growth rates are typical in fishes at lower latitudes.

Maturation

In this study, sizes- and ages-at-50%-maturity could not be determined due to a 16” (406 mm TL) minimum size limit for the recreational fishery during both sampling years. However, numerous others have reported that 50% maturity generally occurs at age-2 and between 300 and 400 mm TL for female red snapper (Nelson 1988; Render 1995; Woods 2003; White and Palmer

2004; Brown-Peterson et al. 2009; Brulé et al. 2010) (Appendix A, Table 27). In this study, all regions had already reached 50% maturity by age-3.

Only one other study to date has reported a Gulf-wide maturity schedule to 75% maturation. Fitzhugh et al. (2004) analyzed female red snapper (n=1,956) mainly from the recreational fishery and found that 75% maturation was reached by age-6 and 321 mm TL in the eastern Gulf and by age-8 and >374 mm TL in the west (Appendix A, Table 27). Contrary to Fitzhugh et al. (2004), it appears that females are currently maturing at a much earlier age (age-3), yet a similar size (≤375 mm TL) in the Gulf, and 75% maturity is reached at a similar age and size in both the eastern and western Gulf. In agreement, results from Woods (2003) indicated that female red snapper in Louisiana reached 75% maturity at age-3 and by 374 mm TL. However, 75% maturity occurred much earlier in Alabama, by age-2 and 268 mm TL (Woods 2003).

Across the Gulf of Mexico and on the U.S. Atlantic east coast, previous reports indicate that 100% maturity occurs within a wide range of sizes (435-820 mm TL) and ages (4.5-8 years) for female red snapper (Render 1995; Collins et al. 1996; Woods 2003; White and Palmer 2004; Fitzhugh et al. 2004; Brulé et al. 2010) (Appendix A, Table 27). Overall, my estimates fell within these ranges. Females generally reached 100% maturity by age-8; this estimate is in agreement with Fitzhugh et al. (2004)'s Gulf-wide study. However, 100% maturation was observed slightly earlier in the western Gulf (age-7; 725 mm TL) compared to the east (age-8; ≥775) in this study.

Females reached 100% maturation fastest in north Texas (age-6; 625 mm TL) and slowest in the Florida regions. No prior studies have reported a maturity schedule for red snapper in north Texas. Females in Alabama also reached 100% maturity by age-6, but at a

slightly larger size (675 mm TL) compared to north Texas. In contrast, Woods (2003) found that female red snapper in Alabama reached 100% maturity much earlier (age-4.5; 613 mm TL). In Louisiana and south Texas, 100% maturation was reached at 700 mm TL and by age-7. Woods (2003) also found that females from Louisiana progressed to maturity more slowly compared to conspecifics in Alabama. However, Woods (2003) estimated that 100% maturity occurred much earlier in Louisiana (age-5.5; 613 mm TL) compared to this study. Slower progressions to maturity in Alabama and Louisiana compared to earlier estimates illustrate the malleable nature of maturity rates, which often fluctuate with changes in the environment or fishing mortality rates (Law 2007; Brown-Peterson et al. 2009).

Off the Florida west coast, females progressed to 100% maturation much more slowly compared to regions farther west. Florida red snapper were predominantly young, small at age and fast-growing (Saari 2011). In northwest Florida, females reached 100% maturation by 775 mm TL and by age-9, although no data were available for 8-year-olds. Similarly, Collins et al. (1996) reported that 100% maturity was attained by 820 mm TL in Panama City, Florida.

In central Florida, 50% of females were sexually mature (i.e. vitellogenic) by age-3. However, very low proportions of older and larger fish were in spawning condition. For instance, only 40% of females between 3 and 7 years old, and 26% between 525 and 775 mm TL, were reproductively active. Thus, it may be that females in central Florida initially reach sexual maturity at sizes and ages similar to conspecifics from other regions, but for some reason choose to spawn less often or not at all when older.

No other studies to date have reported red snapper maturation schedules in central Florida. However, Brown-Peterson et al. (2009) found that while some spawning did occur during May, July and August in the Dry Tortugas, large percentages of female red snapper did not

demonstrate spawning activity during those months. This prompted speculation that some females in the Dry Tortugas may not reproduce or may participate in a spawning season more similar to the extended reproductive season that occurs off the Yucatan Peninsula (Brulé et al. 2010).

It may also be that skipped spawning plays a larger role in red snapper reproductive biology in central Florida compared to the other regions. For instance, during the peak of spawning season, 56% of age-3 females sampled in central Florida were actively spawning, while only 34% of fish in the 4, 5, 6 and 7 age classes combined were reproductively active. This may imply that a larger proportion of females in these older age classes were actually capable of spawning but were not investing their energy into reproduction when sampled (i.e., skipped spawning). Skipped spawning is a relatively common phenomenon among iteroparous fishes, and is most commonly associated with poor feeding conditions but may also be associated with energy allocation (Rideout and Tomkiewicz 2011). For fish with indeterminate fecundity, skipping batches until favorable conditions for reproduction occur is more common than skipping an entire reproductive season (Rideout and Tomkiewicz 2011).

Maturity is a plastic life history trait designed to adapt to and evolve with variable environmental conditions (Ricklefs and Wikelski 2002). Maturation schedules naturally fluctuate over time and may be influenced by a host of biotic and abiotic factors including nutrient availability, growth, habitat type, latitude, predation rates or stock composition (Trippel et al. 1997; Woods 2003; Brulé et al. 2010; Nash et al. 2010). Anthropogenic stressors such as overfishing may also induce changes in maturation schedules, and abrupt declines in age at maturity may signify a compensatory response to significant decreases in population size and/or genetic selection (Trippel 1995). Evidence of early maturity has been well documented among

numerous exploited fish stocks, including red snapper (Beacham 1983; Jørgensen 1990; Hunter et al. 1992; Olsen 2004; Jackson et al. 2007).

The discovery that Gulf red snapper are reaching 75% maturity at a much younger age but similar size compared to findings by Fitzhugh et al. (2004) could indicate a Gulf-wide density-dependent compensatory response to reduced stock size and may be attributed to heavy fishing pressures Gulf-wide (Schirripa and Legault 1999). Density-dependent compensatory responses are phenotypic reactions to reduced intraspecific competition. In the absence of larger fish, surplus energy consumption permits young members of the stock to grow faster and to reach sexual maturity earlier. This adaptive response to reduced stock size increases stock resilience by allowing quicker expansion of the population than if the reproductive age had stayed the same (Trippel 1995). However, if physiological limits exist for growth and age at maturity, then decreases in size and age at maturation may not occur at the same time (Jackson et al. 2007).

In Alabama, female red snapper may be undergoing a density-dependent compensatory response to overfishing similar to that seen in Arctic cod (Jørgensen 1990). In the late 20th century, Arctic cod exhibited early maturity, while fish sizes remained unchanged. Similarly, females in Alabama reached 100% maturity faster (with the exception of north Texas) compared to the other regions, but were significantly larger at age and attained a significantly larger asymptotic length compared to conspecifics from all other regions. These observations are similar to those of Jackson et al. (2007), who reported that maturity was reached at an earlier size and age in Alabama and speculated that this could indicate that late-maturing fish have been selected out of that population.

Off north Texas, early maturity coupled with significantly slower growth (Saari 2011) may be a function of genetic selection (Trippel 1995). Fishers of highly exploited stocks often develop an increasing reliance upon smaller, younger fish because older, larger conspecifics have been removed. Heavy harvest of small, young fish may select for early maturing genotypes as fish that mature sooner may have more opportunities to reproduce before removal compared to late-maturing conspecifics. Therefore over time, size-selective fishing may cultivate a stock genetically predisposed to early maturity. Similarly, earlier maturation rates simultaneous with decreased growth over time have been observed in vermilion snapper in the South Atlantic Bight and is attributed to losses in stock biomass greater than the biomass gained through somatic growth (Zhao and McGovern 1997; Jackson et al. 2007).

On a final note, it is important to recognize that once sexual maturity is reached, immaturity will not occur again. However, it can be difficult to distinguish an immature fish from one that has reproduced in the past but chooses not to spawn later in life. Mature females that are reproductively inactive during a spawning cycle are either "regressing" or "regenerating" (Brown-Peterson et al. 2011). The regressing phase is distinguishable through the presence of large blood vessels, atresia, POF, cortical alveoli and/or some vitellogenic oocytes. However, the regenerating phase appears more similar to the immature phase in that the ovary is small and only primary growth cells are present (regenerating females may have distinguishable thicker ovarian walls or some atresia as opposed to immature females). Thus, unless a spawning phase is accurately assigned to each reproductively inactive female, reporting spawning capability as a "% maturity schedule" can be misleading. This is especially true for areas such as central Florida, where large proportions of small, young females demonstrate spawning capability, while the majority of older, larger females are reproductively inactive. These older, reproductively

inactive females have likely reached sexual maturity already. Therefore, using % maturity to describe reproductive activity among sizes and ages may more accurately be referred to as "% spawning capable" or "% reproductively active."

Batch Fecundity

Generally, batch fecundity increases exponentially with size and asymptotically with age (Bagenal 1978; Collins et al. 2001; Porch et al. 2007). In this study, batch fecundity was most closely correlated with total length, followed by weight. Age correlated less well with batch size. This is consistent with Porch et al. (2007), who found that age had a less significant effect on red snapper egg production and that the age effect was greatest among fish of extremely small or large sizes, which constitute a small percentage of the population.

Among all regions, female red snapper produced a mean batch fecundity estimate (BFE) of 158,182 ± 17,540 ova per spawning episode. This estimate is extremely low considering the potential fecundity of female red snapper, which at optimal size and age can produce several million ova in a single spawning episode (Nelson 1988; Render 1995; Collins et al. 2001; Woods 2003). However, the oldest hydrated female in this study was just 7 years old, and the maximum observed BFE was 945,114 ova. These estimates agree with Collins et al. (2001), who found that in the Gulf of Mexico, BFEs were generally <1 million ova for female red snapper up to 8 years of age.

Mean batch fecundity was similar among northwest Florida, Louisiana, north Texas and south Texas, but a significantly higher mean BFE was evident for females in Alabama (mean BFE= 283,051 ± 35,761 ova). In comparison, Woods (2003) reported a similar but slightly higher BFE off Alabama (mean=304,996 ± 32,005 ova); this is probably due to much wider size

and age ranges in her study. Greater BFE off Alabama is likely attributable to the collection of significantly larger specimens in that region.

In northwest Florida, females produced comparable batch sizes to those in Louisiana and Texas despite that they were significantly smaller and younger. Recall, northwest Florida females also produced a greater mean GSI estimate. This may imply that reproductive effort is greater per capita in northwest Florida and may be evidence of an energetic trade-off between growth and reproduction (Stearns 1989). Further supporting this notion, there is evidence that red snapper in northwest Florida are smaller-at-age compared to conspecifics in central Florida, Alabama, Louisiana and north Texas (Saari 2011). Smaller sizes-at-age and increased reproductive output by younger fish are each symptoms of a compensatory response to population decline (Trippel 1995; Nieland et al. 2007a).

Off Louisiana, batch fecundity was approximately ½ of that observed off Alabama, despite broader size and age ranges among Louisiana samples. This may be explained by the fact that on average, females in Louisiana were significantly smaller compared to fish in Alabama. Similarly, Woods (2003) reported that females in Alabama up to 772 mm TL consistently yielded larger batch sizes compared to fish in Louisiana; yet, when larger females were included, overall batch fecundity was higher off Louisiana (Woods 2003). However, in this study, a high proportion of females in Louisiana were collected in July and August (48% and 22%, respectively), while in Alabama 100% of the females were collected in June. Spawning effort may be greater during the month of June in those two regions than in July and/or August (Woods 2003). Thus, sampling month may be the dominant source of variation in batch fecundity estimates between regions.

In south Texas, female red snapper produced ~2/3 fewer ova per batch compared to fish off Alabama. It is important to also recall that in south Texas, females also exhibited a lower mean GSI compared to all other regions in this study and that while fish off south Texas are comparable in age to the other regions in the western Gulf, they reach significantly smaller maximum sizes (Saari 2011; this study). Smaller sizes-at-age may indicate overfishing in south Texas (Nieland et al. 2007b). However decreased reproductive effort in this region could also reflect a more insular spawning pattern similar to that seen in fish in Mexico (Brulé et al. 2010).

An extremely low number of hydrated females was found in central Florida (n=1). The one female found with hydrated oocytes was 4 years old and had a batch fecundity of 14,939 ova. No previous studies have reported batch fecundity specifically for central Florida. However, Brown-Peterson et al. (2009) reported that relative fecundity was extraordinarily low in the Dry Tortugas and may reflect a different spawning season than that typical of more northern regions in the Gulf.

Reasons for larger, more fecund females off Alabama compared to the other regions are unclear. Alabama red snapper had the greatest mean GSI and exhibited significantly higher batch fecundity compared to all other regions (this study) and were also significantly longer and heavier at ages 4 and 5 compared to conspecifics from all other regions (Saari 2011). Larger sizes at age and increased fecundity may be associated with countergradient variation in growth and reproduction, phenomena that occur at higher latitudes among a wide range of fish species as a compensation mechanism for shorter breeding and growing seasons (see Conover and Present 1990; Conover 1992). Water temperatures experienced by red snapper harvested off Alabama may be colder compared to other recreational fishing regions in the Gulf due to shallower depths of capture (SEDAR 7 2005), and this could be affecting growth and spawning in that region.

Further research is warranted to better understand the dynamics of reproductive seasonality for Gulf red snapper. More insular breeding patterns may exist in south Texas and central Florida compared to regions at higher latitudes, while colder water temperatures off Alabama may be positively influencing batch fecundity. If water temperature and latitude is not causing these demographic differences, other factors may be involved. These factors may be related to local differences in resource availability or may signify compensatory responses to reductions in population size (Fischer et al. 2004; Berkeley et al. 2004; Saari 2011; Nieland et al. 2007a).

Spawning Frequency

Estimation of spawning frequency using the post-ovulatory follicle method and the time-calibrated method was difficult because fresh post-ovulatory follicles (POF) were infrequently observed compared to hydrated or late vitellogenic oocytes. This is likely attributed to the time of day when most of the red snapper in this study were caught. Females from all regions were sampled from recreational fishing boats, which most commonly caught red snapper in the morning and docked in the afternoon. For red snapper, hydration usually occurs in the morning and ovulation takes place in the early afternoon (Jackson et al. 2006). Fresh POF occur in the ovary post-ovulation and degrade within 24 hours of spawning, but warmer water temperatures may accelerate the degradation process (Jackson et al. 2006). In this study, old POF were commonly observed but were not considered. Therefore, the best estimates of spawning frequency in this study are those determined using the hydrated oocyte and the time-calibrated methods. Those estimates are discussed here.

In this study, spawning frequency was positively correlated with both total length and age, although a greater correlation with total length was evident. These observations agree with other

reports that spawning frequency may be correlated with size and age for iteroparous fishes including red snapper (Chesney and San Fillipo 1994; Ganias et al. 2003; Claramunt et al. 2007; Porch et al. 2007). Generally, females ≥725 mm TL spawned significantly more often than smaller conspecifics, and age-3 females spawned significantly less often than older conspecifics. Similarly, Collins et al. (2001) reported that SFE were approximately 50% greater for females between the ages of 6 to 35 years compared to 3 to 5 year old fish.

In general, female red snapper in the Gulf of Mexico spawned once every 3.9 to 6.5 days and 23-38 times during a 150-day reproductive season. This estimate differs from previous studies. In contrast, Fitzhugh et al. (2004) reported that females reproduce once every 3.0 days in the eastern Gulf and once every 2.9 days in the west. More similar to this study, Woods (2003) found that in Louisiana and Alabama combined, spawning occurred once every 3.6 days. Less frequent spawning observed in this study may be a result of more restricted size and age distributions in this study compared to the other reports.

Among regions, females from north Texas spawned the most frequently (once every 1.9-3.4 days), followed by specimens in Alabama (SFE=3.1-5.7 days). Woods (2003) reported that female red snapper spawn more often in Alabama (once every 3.2 to 3.6 days). In northwest Florida, spawning occurred slightly less often (SFE=4.2-7.7 days). These results are similar to Collins et al. (1996), who reported a spawning frequency of 4.0 to 6.0 days for female red snapper in northwest Florida. SFEs were lower but comparable between south Texas and Louisiana (SFE=4.9-6.7 and 5.3-6.6 days, respectively). Similarly, Woods (2003) found that spawning occurred less frequently in Louisiana compared to Alabama. However, Woods (2003) reported that spawning occurred more frequently (SFE=3.8-4.5 days) in Louisiana than was found in this study. Less frequent spawning in Louisiana may reflect the recent reduction in size

at age, which could be attributed to recovery from overfishing or to the fishery-induced selection of slower-growing fish in that region (Nieland et al. 2007a; Saari 2011).

Reduced spawning frequency observed in Louisiana could also reflect a potential depth-related effect on spawning. Among females sampled in Louisiana, 42% were collected by hook-and-line on the continental shelf-edge at ≤85 m depths. The shelf-edge in the western Gulf is influenced by warm water currents from the southwest and west, and waters up to ~100 m depths at the shelf-edge stay warmer year-round compared to more inshore areas (Merrell 1983). Thus, spawning on Louisiana's outer shelf may actually reflect a more tropical pattern compared to that observed in females further inshore.

In central Florida, female red snapper spawned less frequently compared to all other regions (SFE=5.2-9.8 days). Conversely, Brown-Peterson et al. (2009) reported a spawning frequency of 4.3 days for red snapper in the Dry Tortugas, which is more similar to Collins et al. (1996)'s estimate for northwest Florida. While reasons for less frequent spawning in central Florida remain unclear, females in central and northwest Florida were similar in age and shared similar length-weight regression relationships (Saari 2011), thus indicating that fish condition may be similar between those two regions. Therefore, varying fishing pressures or seasonal water temperatures may be causing these reproductive differences between central and northwest Florida.

Annual Fecundity

Female red snapper produced 3.7 million ova per year on average (range= <1 million-24.4 million ova). Compared to previous reports, these estimates are relatively low. Woods (2003) found that females in the northern Gulf produced an average 16.2 million eggs each year with older and larger fish producing up to 63.1 to 76.6 million ova annually. Similar to Woods

(2003), Collins et al. (1996) reported a maximum annual fecundity estimate (AFE) of 60.0 million ova in northwest Florida. The lower AFEs in this study probably reflect the smaller sizes and younger ages of the specimens sampled.

Females in Alabama yielded the highest mean AFE (7.5 million ova), followed by fish in north Texas (mean AFE=5.2 million ova). Females in Louisiana and south Texas yielded AFE of 3.3 million and 3.4 million ova, respectively. Florida females yielded the lowest AFE on average. In comparison, Woods (2003) reported that females up to 772 mm TL and 6.5 years old produced more eggs annually in Alabama compared to conspecifics in Louisiana. My findings agree, as females in Alabama were up to 5 years old and ≤694 mm TL, while fish in Louisiana were up to 7 years old and 666 mm TL. However, it is important to note that Woods (2003) also found that when all sizes and ages were included, annual fecundity was greater in Louisiana compared to Alabama (AFE= 19.9 million and 13.4 million ova, respectively). Differences in fecundity between Alabama and Louisiana females could highlight divergent population structures between these two regions. Larger females in Alabama may reflect a compensatory response to decreased population size (Jackson et al. 2007), or counter-gradient growth as described by Conover and Present (1990). Because red snapper in the extreme northern Gulf are at their northern limits of geographic range, and many fish in the Alabama Artificial Reef Permit Area are found in shallower waters than red snapper in most other locations (<40 m depth), it is possible that red snapper there experience colder winter temperatures than in other regions. Fish there may have adapted by growing more rapidly to reach weights that enable them to withstand longer periods of bioenergetically lowered feeding rates. In Louisiana and other locations, fish are generally found much farther offshore in deeper waters that may provide a depth refuge from colder temperatures during winter.

Index of Reproductive Importance

IRI values indicated that females older than 8 years old were the most significant contributors to the red snapper spawning stock, while 2-year-olds were the least significant contributors. These findings are consistent with other reports that reproductive importance increases with age (Schirripa and Legault 1999; Woods 2003). Schirripa and Legault (1999) reported that in the absence of fishing reproductive importance peaks at age-14, then steadily decreases as a result of progressive declines in survivorship of older age groups.

In this study a very high degree of relative importance was attributed to the 9+ age group (IRI=0.80). In contrast, Woods (2003) reported an IRI value of ~1/2 of the estimate in this study for the 9+ age group (IRI=0.41). Findings from this study also indicated that females between the ages of 3 and 5 years contributed 4 times more to egg production compared to fish ages 6 to 7 years old. Similarly, Woods (2003) results indicate that females aged 3 to 5 years contributed 2.4 times more than counterparts aged 6 to 7 years. This may be an artifact of reduced representation of 6 and 7 year olds in the Gulf (Schirripa and Legault 1999).

Some of the variation among IRI values in this research may reflect variability in maturity estimates among regions. For instance in Alabama, Woods (2003) found that 4-year-old female red snapper contributed nearly as much to egg production as conspecifics over twice their age (9+ years old); conversely in Louisiana, 4 year olds contributed approximately half as much to egg production as the 9+ age group. Such differences in IRI values among age groups likely reflect regional age frequency distributions and population sizes.

In light of results indicating that older age groups contribute significantly more to stock reproductive potential compared to younger individuals, it should be noted that a truncated age structure was clearly evident among all regions in this study. This is a product of the removal of

older age groups through overfishing (SEDAR 7 2005). Age truncation can substantially reduce reproductive potential per average recruit, resulting in a lower spawning potential ratio (SPR) (i.e. reproductive fitness) for the stock. A truncated age structure negatively impacts stock reproductive capacity because increased dependence on younger spawners becomes necessary to maintain population size (Goodyear 1993; Trippel 1995). Reductions in fishing pressure among all age groups should be considered to rebuild the age structure, increase SPR and meet management goals to rebuild the stock by 2032.

3.4.2 Potential Explanations for Regional Differences in Reproductive Biology

It is important to recognize that potential sources of bias for regional reproductive biology estimates reported in this study may exist through annual and monthly sampling variation. Naturally, maturity rates are known to gently fluctuate annually in response to changes in the environment, and spawning frequency and batch fecundity are often highly variable per capita (Trippel 1995; Woods 2003; Porch et al. 2007). Peak months in the spawning season may also vary over time or geographically. Generally, red snapper spawning peaks from June-August in the northern Gulf (Fitzhugh et al. 2004). However, more region-based reports indicate that reproduction may peak at slightly different times of the year. For example, spawning peaks in May-July off Alabama and Louisiana (Woods 2003), in August off Louisiana/Texas (Render 1995) and in June-August off northwest Florida (Collins et al. 1996). Thus, the months during which females were sampled in this study could represent a significant source of variation among regional estimates of GSI, spawning frequency or fecundity.

Life history parameters including growth and reproduction provide essential information regarding stock composition and dynamics. Consistent with numerous other reports (Fitzhugh et al. 2004; Jackson et al. 2007; Brown-Peterson et al. 2009; Brulé et al. 2010), demographic

differences in the reproductive biology of Gulf red snapper were evident in this study. Demographic differences among red snapper assemblages in the Gulf of Mexico may reflect adaptive responses to the local environment (i.e., resource availability, predator/prey abundance, habitat quality and/or temperature) and fishing (i.e., fishing practices and/or fishing mortality rates) (Conover and Present 1990; Woods et al. 2003; Fischer et al. 2004; Gold and Saillant 2007).

Local nutrient availability may cause demographic differences among red snapper subpopulations in the Gulf. In the north-central Gulf, nutrient and sediment influxes from Mobile Bay and the Mississippi-Atchafalaya River system nourish surrounding coastal regions and promote fishery production through enhanced recruitment (Grimes 2001). Increased primary and secondary productivity in this area may supply higher trophic level species such as red snapper with increased food intake and could therefore enhance fish condition (Fischer et al. 2004; Jackson et al. 2007). Improved condition for spawning females may result in greater fecundity, larger egg sizes or earlier maturity (Kennedy et al. 2008; Kjesbu et al. 1991; Morgan 2004). However, if condition is improved in Louisiana, reproductive parameters do not suggest it (Jackson et al. 2007; this study). Instead, females in Louisiana displayed modest to low fecundity and relatively late maturity in this study. These observations may instead reflect a declining size at age for red snapper in Louisiana (Nieland et al. 2007a), or higher population size in the northwestern Gulf (Gold and Saillant 2007; SEDAR 7 Update 2009).

Selecting a better habitat may also afford more chances of encounter with quality prey, hence positively influencing growth and survival (Wells 2007). Off Alabama and Louisiana, larger red snapper of similar size and growth rate have been reported (Fischer et al. 2004; Saari 2011), and similar habitat structures may in part be the reason. The majority of the recreational

catch off Alabama comes from a network of over 15,000 deployed artificial reefs (Patterson et al. 2001), while most of the recreational catch off Louisiana comes from an extensive network of over 4,000 oil and gas platforms which serve as de facto reefs (Stanley and Wilson 2003). Yet, despite the existence of numerous natural gas platforms and other suitable habitat off the Texas coast, red snapper off Texas reach considerably smaller maximum sizes at a faster rate compared to conspecifics off Alabama and Louisiana (Fischer et al. 2004; Saari 2011). While habitats do differ across the Gulf of Mexico, there is no substantial evidence that habitat quality differs between natural and artificial reefs to the extent that population size is regulated by artificial habitats (Jackson et al. 2007; Cowan et al. 2010). Therefore, habitat type alone is not the sole driver of regional differences among red snapper in these three regions.

Water temperatures may cause intraspecific variation in fishes as well. At lower latitudes, extended spawning seasons are common because progeny have a better chance of survival at warmer temperatures (Conover 1992). Additionally, growth is often slowed in tropical regions due to greater energetic investment in reproduction, higher metabolic demands and reduced assimilation efficiency (Neal and Noble 2006). At higher latitudes, colder water temperatures limit breeding seasons, and larger clutch sizes serve as a mechanism to compensate for shorter spawning seasons (Conover 1992). Evidence of insular spawning for red snapper has been reported in Mexico (Brulé et al. 2010), and similar observations have been described for females in the Dry Tortugas (Brown-Peterson et al. 2009).

Alternately, the depth at which red snapper are caught could have a potential affect on reproductive biology, at least in the western Gulf, through depth-for-latitude substitution. Across the Gulf of Mexico, recreational harvests vary with depth. In the northeastern and north-central Gulf, recreational catches are typically derived from shallower areas (20-40 m depths), while

recreational fishing efforts off Louisiana and Texas are concentrated at deeper depths (~40 m but may range up to 115 m) (Patterson et al. 2001; SEDAR 7 2005). In the western Gulf, inshore waters up to ~40 m depth often reach temperatures lower than 16˚C in the wintertime. However on the outer continental shelf, the influx of currents from the south and southwest maintains warmer water temperatures year-round, which rarely get colder than 18˚C (Merrell 1983). These differences in depth-related temperatures may produce a more tropical/sub-tropical spawning pattern (i.e., extended spawning seasons, lower batch fecundity, lower spawning frequency) for red snapper inhabiting deeper depths along the shelf-edge compared to those spawning characteristics observed for conspecifics further inshore.

3.5 General Summary and Conclusion

Findings from this study clearly demonstrate that a truncated age distribution exists for the Gulf red snapper stock. A scarce abundance of older (>age-9) red snapper in the Gulf and the South Atlantic has been widely acknowledged over the past 20 years and is attributed to long-term overfishing (Wilson et al. 1994; Render 1995; Wilson and Nieland 1998; Patterson 1999; Wilson and Nieland 2001; Woods 2003; Fischer et al. 2004; SEDAR7 2005; Nieland et al. 2007a; SEDAR 7 Update 2009; Cowan 2011; Saari 2011). Removal of older individuals is common in overfished stocks, but it makes population recovery particularly challenging for long-lived species because population biomass must be maintained by younger, smaller members of the stock. Increasing dependence on younger fish inhibits population increase and resilience and provokes slower recovery from overharvesting (Trippel 1995).

Red snapper may live to be nearly 60 years old, females do not reach full reproductive potential until 14 to 15 years of age (Cowan et al. 2010), and fecundity is correlated with size and age (Bagenal 1973). Thus, older, larger females offer several major reproductive advantages

compared to younger conspecifics. For instance, older females produce exponentially larger batches of eggs, and they spawn more frequently than first-time spawners (Bagenal 1978; Hunter et al. 1985a; Chesney and San Fillipo 1994; Ganias et al. 2003; Murua et al. 2003; Fitzhugh et al. 2004; Trippel and Neil 2004; Claramunt et al. 2007; Porch et al. 2007; Jackson et al. 2007). Older females also spawn for longer durations during the spawning season; this increases chances for larvae to encounter suitable prey patches, thus enhancing the probability of recruitment success and strong year classes (Lambert and Ware 1984; Trippel 1998). Larger females also produce more viable progeny, which are larger at hatch, are more likely to feed and exhibit faster growth, all of which are qualities more conducive to survival (Rjinsdorp 1994; Trippel 1998; Johnston and Leggett 2002; Walsh et al. 2006).

Decreased egg production due to a truncated age structure raises questions of whether young spawners are capable of maintaining a sustainable population size while high exploitation rates persist. For the Gulf red snapper stock, recent reports suggest that fish age-6 and younger comprise over 90% of the population off the coasts of Alabama, Louisiana and Texas (Fischer et al. 2004; Nieland et al. 2007a; Saari 2011). This may be the case off the west Florida coast as well (Saari 2011; this study). In the northern Gulf, population responses to overexploitation have been well documented. Gulf red snapper are exhibiting multiple signs of juvenescence including smaller sizes at age (Nieland et al. 2007a; Saari 2011), increased growth rates (Fischer et al. 2004; Nieland et al. 2007a; Saari 2011), and earlier maturity (Jackson et al. 2007). These adverse, harvest-induced changes impede stock recovery and may provoke genetic selection (i.e., fishery induced evolution) for smaller, faster growing fish, which can be very difficult to reverse. Despite these warning signs, fishing mortality rates for red snapper remain dangerously high (Cowan et al. 2010).

Gulf-wide, data from this study indicate that female red snapper are reaching 75% maturity at a much younger age (3 years) but similar size compared to a previous estimate by Fitzhugh et al. (2004). This could indicate a density-dependent compensatory response to reductions in population size wherein younger fish are now investing more energy into reproduction at an earlier age. A similar trend was reported for Arctic cod in the early 1990's, and heighted overharvest of late maturing fish was believed to be the cause (Jørgensen 1990). Early maturation is problematic in that greater energetic investment in reproduction detracts from investment in somatic growth; therefore, trade-offs in favor of early reproduction may result in decreased fitness and weakened chances of parent survival (Stearns 1989).

Data from this study also show that the spawning schedule in central Florida is drastically different from the other regions as far less emphasis is placed on egg production during the summertime, even among older and larger fish. Reasons for this are unknown. Large percentages of females may be skipping spawning in that region or may not reproduce at all. Alternatively, an extended spawning season at lower latitudes is common in fishes (Conover 1992) and may explain this phenomenon. An extended spawning season may exist in south Texas as well. Regardless of the cause, reduced spawning effort in central Florida presents a potential negative influence on spawning stock biomass (SSB) that, if not accounted for, may result in overestimation of stock egg production.

Reproductive effort per body size was highest among northwest Florida, Alabama and north Texas. In northwest Florida fish were young and relatively small. This may indicate the selective removal of faster growers in that region. Off Alabama, females were significantly larger compared to the other regions, highly fecund and reached 100% maturity relatively early. These qualities may imply a density-dependent compensatory response to overfishing in

Alabama (Jackson et al. 2007). In north Texas, fish were smaller but older and reached 100% maturity the fastest compared to all other regions. These are symptoms of juvenescence and may be attributed to overfishing in north Texas.

Improvement of stock health for Gulf red snapper is critical to population recovery. An expanded age structure would greatly enhance spawning stock biomass and rates of recovery from overfishing (Jackson et al. 2007; Cowan 2011). Older and larger broodstock improve chances of strong year-classes as well as stock resilience. In addition, given the clear regional differences in red snapper vital rates in the Gulf of Mexico (Fischer et al. 2004; Jackson et al. 2007; Nieland et al. 2007a; Saari 2011; this study), a management scheme designed to prevent regional overfishing would contribute greatly to restoration of spawning stock biomass and future population expansion.

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APPENDIX A: SUPPLEMENTARY TABLES

Table 1. Female red snapper sampled at Eugene Island and Shipp Shoal Blocks off the coast of Louisiana. Bank= natural shelf edge bank; Standing =standing platform; Toppled=toppled platform.

Site	Nov 2008	Jan 2009	Apr 2009	Jun 2009	Jul 2009	Dec 2009	Feb 2010	Mar 2010	Apr 2010	Jul 2010	Oct 2010	Total
Bank	-	-	-	132	134	-	-	-	-	45	-	311
Standing	42	32	59	92	85	61	75	-	31	23	51	551
Toppled	3	46	36	-	98	108	30	27	44	24	4	420
Total	45	78	95	224	317	169	105	27	75	92	55	1282

Table 2. Percent total at age for female red snapper collected year-round from November 2008 to October 2010 at the Louisiana shelf-edge banks.

Age	n	% Total
0	0	0.0000
1	1	0.0016
2	20	0.0326
3	197	0.3208
4	199	0.3241
5	126	0.2052
6	31	0.0505
7	21	0.0342
8	10	0.0163
9	5	0.0081
10	2	0.0033
11	1	0.0016
12	1	0.0016
Total	614	1.0000

Table 3. Results for comparing mean age, total length and total weight of female red snapper, *Lutjanus campechanus*, at natural bank, standing platform and toppled platform sites (Mann-Whitney-Wilcoxon). Fish were sampled November 2008 through October 2010 on the Louisiana continental shelf.

A		Bank vs Standing		
	n	Wilcoxon	Z	p-value
Age	405	36235.5	3.8048	<0.0001
TL	422	33444.5	-2.2126	0.0269
TW	421	31353.5	-3.6866	0.0002
B		**Bank vs Toppled**		
	n	Wilcoxon	Z	p-value
Age	364	30072.0	1.4282	0.1532
TL	378	27413.0	-4.7204	<0.0001
TW	377	26688.0	-5.1684	<0.0001
C		**Standing vs Toppled**		
	n	Wilcoxon	Z	p-value
Age	455	51721.5	3.2417	0.0012
TL	458	51543.0	2.8630	0.0042
TW	458	50185.5	1.9000	0.0574

TL=total length; TW=total weight; n=sample size; Wilcoxon=Wilcoxon Statistic; Z=Z-statistic

Table 4. Analysis of covariance results for comparing log_{10}-log_{10} transformed length-weight regression slopes between habitats for female red snapper (*Lutjanus campechanus*). Total length (L) was used as the independent variable, and eviscerated body weight (W) was the dependent variable.

	Parameter	df	Type III SS	MS	F	p-value
Bank and Standing	Log TL	1	29.49	29.49	17831.1	<0.0001
	Site	1	0.02	0.02	12.59	0.0004
	Log TL x site	1	0.02	0.02	10.35	0.0014
Bank and Toppled	Log TL	1	20.24	20.24	8859.85	<0.0001
	Site	1	0.02	0.02	7.09	0.0081
	Log TL x site	1	0.02	0.02	6.6	0.0106
Standing and Toppled	Log TL	1	23.3	23.3	11385.5	<0.0001
	Site	1	0	0	0.04	0.8460
	LogTL x site	1	0	0	0.12	0.7331

df=degrees of freedom; SS=sum of squares; ms=mean square; F=f-statistic

Table 5. Tests for habitat-specific effects on mean age, total length and total weight of female red snapper, *Lutjanus campechanus*. Fish were sampled at A) natural shelf edge banks and standing platforms, B) natural banks and standing platforms and C) standing platforms and toppled platforms on the Louisiana continental shelf.

A	Bank vs Standing			
	n	Wilcoxon	Z	p-value
Age	300	20361.5	-1.5475	0.1217
TL	315	24944.5	2.5246	0.0116
TW	315	26138.5	4.0066	<0.0001

B	Bank vs Toppled			
	n	Wilcoxon	Z	p-value
Age	230	8685.0	0.2922	0.7701
TL	240	10234.5	3.3302	0.0009
TW	240	10510.5	3.8896	0.0001

C	Standing vs Toppled			
	n	Wilcoxon	Z	p-value
Age	217	8814.0	1.7097	0.0873
TL	215	8123.5	0.9723	0.3309
TW	215	7906.0	0.4682	0.6397

TL=total length; TW=total weight; n=sample size; Wilcoxon=Wilcoxon Statistic; Z=Z-statistic

Table 6. Tests for annual effects on mean age, total length and total weight of female red snapper, *Lutjanus campechanus*, sampled from A) natural shelf edge banks, B) standing platforms, C) toppled platforms and D) all sites combined in 2009 versus 2010. All fish were collected on the Louisiana continental shelf.

A	Bank			
	N	Wilcoxon	Z	Pr>|Z|
Age	157	3114	3.7364	0.0002
TL	170	3539	4.3872	<0.0001
TW	170	3593	4.6109	<0.0001

B	Standing			
	N	Wilcoxon	Z	Pr>|Z|
Age	143	4574	3.1777	0.0015
TL	145	4273	1.6546	0.0980
TW	145	4254	1.5786	0.1144

C	Toppled			
	N	Wilcoxon	Z	Pr>|Z|
Age	74	1223	1.5196	0.1286
TL	71	1089	2.2696	0.0232
TW	71	1150	3.0036	0.0027

D	All			
	N	Wilcoxon	Z	Pr>|Z|
Age	374	25055.5	4.4469	<0.0001
TL	386	25789	5.1799	<0.0001
TW	386	26374	5.7776	<0.0001

TL=total length; TW=total weight

Table 7. Percent maturity at total length for female red snapper, *Lutjanus campechanus,* sampled during spawning season from three habitat types on the Louisiana continental shelf. Bold font marks the size at which 50% maturity was reached for a given size class. Asterisk indicates n<5.

Total Length (mm)	Bank (n=169)	Standing (n=101)	Toppled (n=56)
<274	-	-	-
275-324	50*	-	-
325-374	19	38	50*
375-424	31	10	**50**
425-474	**62**	**75**	71
475-524	59	45	77
525-574	69	40	75
575-624	86	50	40
625-674	78	90	-
675-724	100	100*	100*
725-774	100*	100*	100*
>775	100*	-	-

n=sample size

Table 8. Percent maturity at age for female red snapper, *Lutjanus campechanus,* collected during spawning season from three habitat types on the Louisiana continental shelf. Bold font marks the size at which 50% maturity was reached for a given size-class. Asterisk indicates n<5.

Age (year)	Bank (n=152)	Standing (n=101)	Toppled (n=56)
2	50*	25*	-
3	26	35	**58**
4	39	**50**	68
5	**66**	53	80
6	81	100*	-
7	91	100	-
8	100	100*	100*
9	100*	100*	-
10	100*	-	-
11	100*	-	-

n=sample size

Table 9. Batch fecundity estimates, age, total length, total weight and eviscerated body weight for each hydrated female red snapper sampled from natural banks, standing platforms, toppled platforms and from all sites combined on Louisiana's continental shelf.

Site	BFE	Age	TL (mm)	TW (g)	EBW (g)
Bank	326734	7.04	655	3944	3446
Standing	945114	7.05	666	3878	3544
Standing	22388	3.05	464	1306	1234
Standing	16363	4.05	471	1384	1312
Toppled	4631	3.05	366	650	620
Toppled	42221	4.05	477	1638	1542
Toppled	316514	5.05	623	3024	2814
Toppled	80101	5.05	533	2048	1944
Overall Mean	219258	4.80	532	2234	2057

BFE=batch fecundity estimate; TL=total length; TW=total weight; EBW=eviscerated body weight

Table 10. Chi-Square tests comparing spawning frequency estimates of sexually mature female red snapper, *Lutjanus campechanus*, sampled from A) natural banks and standing platforms B) standing platforms and toppled platforms and C) natural banks and toppled platforms on the Louisiana continental shelf.

A	Bank vs Standing		
	df	χ^2	p
SFE_{TC}	1	0.1954	0.6585
SFE_{POF}	1	0.2880	0.5915

B	Standing vs Toppled		
	df	χ^2	p
SFE_{TC}	1	0.5386	0.4630
SFE_{POF}	1	0.0042	0.9481

C	Bank vs Toppled		
	df	χ^2	p
SFE_{TC}	1	1.6071	0.2049
SFE_{POF}	1	0.3196	0.5719

SFE_{TC}=spawning frequency estimate based on the time-calibrated method; SFE_{POF}= spawning frequency estimate based on the post-ovulatory follicle method

Table 11. Mean spawning frequency estimates at age for female red snapper sampled at A) natural banks, B) standing platforms and C) toppled platforms on the Louisiana continental shelf.

	A Bank		**B** Standing		**C** Toppled	
Age	SFE_{POF}	SFE_{TC}	SFE_{POF}	SFE_{TC}	SFE_{POF}	SFE_{TC}
2	-	-	-	-	-	-
3	11.0	11.0	-	26.0	11.0	7.3
4	-	-	2.1	3.8	5.7	6.8
5	6.7	8.0	-	18.0	4.0	2.7
6	3.0	6.0	3.0	6.0	-	-
7	3.3	3.3	5.0	3.3	-	-
8	5.0	10.0	-	-	1.0	2.0
≥9	-	6.0	-	-	-	-

SFE_{TC}=spawning frequency estimate based on the time-calibrated method; SFE_{POF}= spawning frequency estimate based on the post-ovulatory follicle method

Table 12. Spawning frequency estimates (SFE) at total length for female red snapper sampled from Louisiana's continental shelf. SFE are based on the post-ovulatory follicle method (POF) and the time-calibrated method (TC). ** indicates no POF found for a designated age group.

	A Bank		**B** Standing		**C** Toppled	
TL (mm)	SFE_{POF}	SFE_{TC}	SFE_{POF}	SFE_{TC}	SFE_{POF}	SFE_{TC}
425-474	8.5	6.8	11.0	7.3	-	-
475-524	6.3	9.5	4.5	6.0	5.7	5.7
525-574	-	**22.0	-	-	6.0	6.0
575-624	4.0	6.0	2.5	5.0	2.0	2.0
625-674	3.5	4.7	4.5	6.0	-	-
675-724	3.5	7.0	-	-	1.0	1.0
725-774	2.0	2.0	-	4.0	1.0	2.0
>775	-	-	-	-	-	-

Bank=natural banks, Standing=standing platforms; Toppled=toppled platforms; TL=total length

Table 13. Annual fecundity estimates (± standard error) for individual hydrated red snapper (n=8) collected at natural bank, standing platform and toppled platform sites on the Louisiana continental shelf.

Site	Age	BFE	SFE	AFE ± SE
Bank	7.04	326734	8.5	5765894
Standing	7.05	945114	7.0	20252443 ± 6612523
Standing	3.05	22388	7.0	479743 ± 6612523
Standing	4.05	16363	7.0	350636 ± 6612523
Toppled	3.05	4631	4.9	141765 ± 2150780
Toppled	4.05	42221	4.9	1292480 ± 2150780
Toppled	5.05	316514	4.9	9689204 ± 2150780
Toppled	5.05	80101	4.9	2452071 ± 2150780
Overall Mean	4.80	219258	7.1	4632217 ± 2467934

Bank=natural bank; Standing=standing platform; Toppled=toppled platform; BFE=batch fecundity estimate; SFE=spawning frequency estimate based on the time-calibrated method; AFE=annual fecundity estimate; SE=standard error.

Table 14. Size- and age-at-maturity estimates for female red snapper (*Lutjanus campechanus*) sampled off the Louisiana coast in the northern Gulf of Mexico. Asterisks indicate fork length was converted to total length using a conversion method developed by Allman et al. (2002)).

Age_{min} (yr)	Age_{50} (yr)	Age_{100} (yr)	L_{min} (mm)	L_{50} (mm)	L_{75} (mm)	L_{100} (mm)	Sampling Location	Source
-	-	-	* 306	*401	-	-	FGB	Nelson 1988
2	-	-	* 268	* 310	-	* 448	LA	Wilson et al. 1994
2	2	5.5	* 312	*321	-	* 613	LA	Woods 2003
2	2	6	*312	* 321	-	* 692	LA	Woods et al. 2003
2	-	-	-	-	*374	*692	LA, TX	SEDAR7-DW35
2	< 2.5	6.5	*312	*< 347	-	* 666	LA	Jackson et al. 2007
2	4	8	*320	450	650	700	LA	This study

Age_{min}=minimum size at maturity; Age_{50}=age at 50% maturity; Age_{100}=age at 100% maturity; L_{min}=total length of smallest mature female; L_{50}=total length at 50% maturity; L_{100}=total length at 100% maturity; FGB=Flower Garden Banks, located directly south of the Louisiana/Texas border

Table 15. Male-to-female ratio for red snapper, *Lutjanus campechanus,* sampled from six recreational fishing regions in the Gulf of Mexico. Bold font indicates a significant difference between proportions of males and females.

Location	M:F	χ^2	p-value
Central Florida	1 : 1.943	31.7184	**<0.0001**
Northwest Florida	1 : 1.183	2.8473	0.0915
Alabama	1 : 1.258	2.7429	0.0977
Louisiana	1 : 1.099	0.5193	0.4711
North Texas	1 : 0.838	1.5882	0.2076
South Texas	1 : 1.493	13.0419	**0.0003**
All	1 : 1.292	27.5094	**<0.0001**

M:F=male-to-female ratio; χ^2 = chi-square value

Table 16. Percent frequency at A) total length and B) age for female red snapper (*Lutjanus campechanus*) sampled from six regions of the Gulf recreational fishery.

A

Size Class (mm)	Central Florida (%)	Northwest Florida (%)	Alabama (%)	Louisiana (%)	North Texas (%)	South Texas (%)	All Regions (%)
400	7.98	13.51	0.00	4.03	3.23	1.02	6.11
450	21.47	32.82	5.26	4.84	34.41	16.24	20.63
500	22.09	23.55	5.26	18.55	29.03	17.77	19.79
550	15.95	11.97	24.56	16.94	15.05	19.80	16.74
600	14.11	8.49	28.95	22.58	6.45	21.83	16.32
650	11.04	5.02	20.18	19.35	3.23	17.26	12.11
700	4.91	2.70	13.16	10.48	5.38	6.09	6.32
≥750	2.45	1.54	2.63	2.42	3.23	0.00	1.79

B

Age Class	Central Florida (%)	Northwest Florida (%)	Alabama (%)	Louisiana (%)	North Texas (%)	South Texas (%)	All Regions (%)
2	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	25.47	29.92	0.88	4.92	3.23	6.15	14.82
4	47.20	38.19	39.82	31.15	55.91	25.64	38.17
5	18.01	22.44	53.98	41.80	19.35	46.67	32.73
6	8.07	7.09	1.77	13.11	12.90	14.87	9.59
7	1.24	1.97	1.77	5.74	6.45	4.10	3.20
8	0.00	0.00	0.88	2.46	0.00	0.51	0.53
9+	0.00	0.39	0.88	0.82	2.15	2.05	0.96

Table 17. Mean monthly gonadosomatic index (GSI) values for vitellogenic female red snapper, *Lutjanus campechanus,* sampled from the Gulf of Mexico recreational fishery. An asterisk indicates one extremely fecund female from Alabama (GSI = 15.03) was excluded from this analysis.

Month	n	Mean GSI	StDev	SE	Min GSI	Max GSI	95% CI
June	333	1.66	1.44	0.08	0.23	15.03	(1.51, 1.81)
July	156	1.48	1.30	0.10	0.28	7.92	(1.28, 1.68)
August	19	0.82	0.68	0.16	0.33	2.65	(0.51, 1.13)

n=sample size; StDev=standard deviation; CI=confidence interval; SE=standard error

Table 18. Percent maturity at A) age and B) total length for female red snapper (*Lutjanus campechanus*) sampled from the recreational fishery in the eastern and western Gulf of Mexico. Note: one non-vitellogenic 9-year-old female from the western Gulf was excluded.

A

Age Class (yr)	East (n=480)	West (n=399)
3	76	84
4	68	72
5	72	82
6	41	88
7	50	100
8	100	100
9+	100	100

B

Total Length (mm)	East (n=483)	West (n=402)
375-424	78	75
425-474	79	76
475-524	74	80
525-574	66	68
575-624	59	85
625-674	56	89
675-724	68	97
725-774	50	100
≥775	100	100

Table 19. Analysis of covariance results testing for regional differences in regression relationships between natural log-transformed batch fecundity (BFE) and natural log transformed total length (L), natural log-transformed eviscerated body weight (W), and natural log-transformed age. Equality of A) slopes and B) y-intercepts was tested among 5 regions in the northern Gulf of Mexico: Northwest Florida, Alabama, Louisiana, North Texas and South Texas.

A. ANCOVA Results for Equal Slopes

Model	n	df	F-value	Pr>F	R^2
Ln(BFE)*Ln(L)	97	4	1.87	0.1236	0.4912
Ln(BFE)*Ln(W)	92	4	2.17	0.0796	0.5097
Ln(BFE)*Ln(Age)	92	4	1.76	0.1458	0.4524

B. ANCOVA Results for Equal y-intercepts

Model	n	df	F-value	Pr>F	R^2
Ln(BFE)*Ln(L)	97	4	1.93	0.1126	0.4912
Ln(BFE)*Ln(W)	92	4	2.34	0.0620	0.5097
Ln(BFE)*Ln(Age)	92	4	2.14	0.0832	0.4524

Ln=natural logarithm; n=sample size; df=degrees of freedom

Table 20. Spawning frequency estimates (SFE) at age for female red snapper, *Lutjanus campechanus*, sampled from the Gulf recreational fishery. Spawning frequency was estimated with (A) the hydrated oocyte method, (B) the post-ovulatory follicle method and (C) the time-calibrated method. Asterisks indicate n<10; n=sample size.

A.

Age	Central Florida	Northwest Florida	Alabama	Louisiana	North Texas	South Texas	All
3	7.7	4.2	-	-	**2.0	-	5.6
4	12.0	5.5	3.7	4.5	2.3	3.6	4.2
5	4.0	3.7	2.6	4.3	1.4	5.4	3.5
6	**4.0	**7.0	-	6.0	1.5	5.2	3.7
7	-	**2.0	-	**7.0	**2.0	**4.0	3.6
8	-	-	-	-	-	-	-
≥9	-	**1.0	-	-	-	-	**8.0

B.

Age	Central Florida	Northwest Florida	Alabama	Louisiana	North Texas	South Texas	All
3	-	25.0	-	-	-	-	45.0
4	24.0	71.0	-	5.4	25.0	5.2	13.8
5	-	-	17.3	-	6.5	12.5	20.7
6	-	-	-	6.0	-	13.0	15.8
7	-	-	-	**7.0	-	-	25.0
8	-	-	-	**3.0	-	-	**5.0
≥9	-	-	-	-	-	-	-

C.

Age	Central Florida	Northwest Florida	Alabama	Louisiana	North Texas	South Texas	All
3	15.3	7.1	-	-	**4.0	-	10.0
4	16.0	10.1	7.5	4.9	4.2	4.3	6.4
5	8.0	7.4	4.5	8.7	2.4	7.5	6.0
6	**8.0	**14.0	-	6.0	3.0	7.4	6.0
7	-	**4.0	-	**7.0	**4.0	**8.0	6.3
8	-	-	-	**6.0	-	-	**10.0
≥9	-	**1.0	-	-	-	-	**16.0

Table 21. Spawning frequency estimates (SFE) for female red snapper, *Lutjanus campechanus*, sampled from the Gulf recreational fishery. Spawning frequency was estimated with (A) the hydrated oocyte method, (B) the post-ovulatory follicle method and (C) the time-calibrated method. Asterisks indicate n<10; n=sample size.

A.

Total Length (mm)	Central Florida	Northwest Florida	Alabama	Louisiana	North Texas	South Texas	All
400	**7.0	6.0	-	-	**2.0	-	6.2
450	4.8	3.0	-	-	2.5	6.5	3.8
500	8.5	5.8	-	3.2	1.6	4.9	4.3
550	**7.0	7.0	2.8	**9.0	**2.0	3.8	3.9
600	-	3.7	3.7	7.7	**1.7	3.7	4.2
650	-	-	2.3	6.7	**1.5	5.2	4.2
700	-	**1.5	2.4	4.3	**1.7	11.0	3.3
≥750	**1.0	**3.0	-	**1.5	**1.5	-	2.0

B.

Total Length (mm)	Central Florida	Northwest Florida	Alabama	Louisiana	North Texas	South Texas	All
400	-	18.0	-	-	-	-	31.0
450	-	60.0	-	-	20.0	6.5	22.5
500	-	46.0	-	6.3	7.0	8.5	13.6
550	**7.0	-	-	-	-	11.3	25.5
600	-	-	-	23.0	-	8.3	21.0
650	-	-	10.5	6.7	-	31.0	14.0
700	-	-	12.0	13.0	-	11.0	15.3
≥750	-	-	-	**3.0	-	-	12.0

C.

Total Length (mm)	Central Florida	Northwest Florida	Alabama	Louisiana	North Texas	South Texas	All
400	**14.0	9.0	-	-	**4.0	-	10.3
450	9.5	5.7	-	-	4.4	6.5	6.4
500	17.0	10.2	-	4.2	2.5	6.2	6.5
550	7.0	14.0	5.6	**18.0	**4.0	5.7	6.8
600	-	7.3	7.4	11.5	**3.3	5.1	7.0
650	-	-	3.8	6.7	**3.0	8.9	6.5
700	-	**3.0	4.0	6.5	**3.3	11.0	5.4
≥750	**2.0	**6.0	-	**2.0	**3.0	-	3.4

Table 22. Chi-Square test results for differences in spawning frequency among female red snapper, *Lutjanus campechanus*, sampled from six fishing regions of the Gulf recreational fishery. Spawning frequency was estimated by using A) the hydrated oocyte method and B) the time-calibrated method. Bold font denotes significant differences between regions.

A

Region	Central Florida	Northwest Florida	Alabama	Louisiana	North Texas
Northwest Florida	0.4393	-	-	-	-
Alabama	**0.0435**	0.1075	-	-	-
Louisiana	0.9286	0.3596	**0.0275**	-	-
North Texas	**<0.0001**	**<0.0001**	**0.0082**	**<0.0001**	-
South Texas	0.8425	0.4609	**0.0027**	0.7532	**<0.0001**

B

Region	Central Florida	Northwest Florida	Alabama	Louisiana	North Texas
Northwest Florida	0.5358	-	-	-	-
Alabama	0.1520	0.2840	-	-	-
Louisiana	0.3322	0.6192	0.6307	-	-
North Texas	**0.0038**	**0.0040**	0.0840	**0.0343**	-
South Texas	0.3085	0.6037	0.5340	0.9523	0.0652

Table 23. Chi-square test results for differences in spawning frequency among size groups of female red snapper, *Lutjanus campechanus*, sampled from six regions of the Gulf recreational fishery. Spawning frequency was estimated by using A) the hydrated oocyte method and B) the time-calibrated method. Bold font denotes significant differences between size groups.

A

Total Length (mm)	400	450	500	550	600	650	700
450	0.2199	-	-	-	-	-	-
500	0.3706	0.5514	-	-	-	-	-
550	0.2803	0.8383	0.7273	-	-	-	-
600	0.3648	0.6140	0.9595	0.7791	-	-	-
650	0.3756	0.6374	0.9621	0.7915	1.0000	-	-
700	0.1533	0.6261	0.3516	0.5307	0.3919	0.4111	-
≥750	**0.0224**	0.0864	**0.0442**	0.0739	0.0515	0.0562	0.2041

B

Total Length (mm)	400	450	500	550	600	650	700
450	0.4013	-	-	-	-	-	-
500	0.4091	0.9792	-	-	-	-	-
550	0.4735	0.8568	0.8755	-	-	-	-
600	0.5059	0.7846	0.8030	0.9316	-	-	-
650	0.4253	0.9874	0.9944	0.8838	0.8189	-	-
700	0.2566	0.5674	0.5539	0.4930	0.4473	0.5896	-
≥750	0.0810	0.1620	0.1577	0.1419	0.1272	0.1771	0.3681

Table 24. Chi-square test results for differences in spawning frequency among age groups for female red snapper, *Lutjanus campechanus*, sampled from six regions of the Gulf recreational fishery. Spawning frequency was estimated by using A) the hydrated oocyte method and B) the time-calibrated method. Bold font denotes significant differences between size groups.

A

Age	3	4	5	6	7
4	0.2397	-	-	-	-
5	**0.0479**	0.2520	-	-	-
6	0.1730	0.6052	0.8118	-	-
7	0.2583	0.6436	0.9573	0.9231	-
8+	0.3958	0.1782	0.1016	0.1363	0.1452

B

Age	3	4	5	6	7
4	0.1880	-	-	-	-
5	0.1313	0.7724	-	-	-
6	0.1910	0.7702	0.9215	-	-
7	0.4019	0.9664	0.9322	0.8930	-
8+	0.7928	0.4357	0.3928	0.3895	0.4723

Table 25. Annual fecundity at total length for female red snapper sampled from six primary recreational fishing regions in the Gulf of Mexico.

Size Class (mm TL)	n	SFE_{TC}	Mean BFE	Mean AFE
400	4	10.3	47077	683370
450	16	6.4	50168	1170576
500	17	6.5	60368	1398232
550	13	6.8	169605	3741297
600	20	7.0	139421	2987603
650	14	6.5	287715	6679106
700	10	5.4	321026	8898010
≥750	2	3.4	544594	23825994

TL=total length; n = sample size; SFE_{TC} =spawning frequency estimate based on the time-calibrated method; BFE=batch fecundity estimate; AFE=annual fecundity estimate

Table 26. Annual fecundity estimates at age for female red snapper sampled from six primary recreational fishing regions in the Gulf of Mexico.

Age	n	SFE_{TC}	Spawns* $season^{-1}$	Mean BFE	Mean AFE
2	-	-	-	-	-
3	8	15.00	10.0	46775	467753
4	29	23.30	6.4	95446	614512
5	42	25.00	6.0	166046	996278
6	9	25.00	6.0	267779	1606673
7	6	24.00	6.3	368483	2303016
8	-	15.00	10.0	-	-
≥9	-	9.38	16.0	-	-

n = sample size; SFE_{TC} =spawning frequency estimate based on the time-calibrated method; BFE=batch fecundity estimate; AFE=annual fecundity estimate

Table 27. Regional estimates for maturity-at-age (years) and -size (total length, mm) for female red snapper (*Lutjanus campechanus)* sampled from the directed fishery and independently off the southeastern U.S., across the Gulf of Mexico and at the Yucatan Peninsula. Exceptions: one female from South Texas (524 mm TL; age-6) and one female from North Texas (610 mm TL; age-9) were not in spawning condition. An asterisk indicates length was converted from fork length to total length using the equation developed by Allman et al. (2002).

Region	n	A_{min}	A_{50}	A_{75}	A_{100}	L_{min}	L_{50}	L_{75}	L_{100}	Citation
Atlantic Coast	996	2	2	-	5	287	378	-	435	White & Palmer 2004
Florida, Atlantic Coast	<66	-	-	-	-	312	-	-	-	Brown-Peterson et al. 2009
Florida, Central	108	2	-	-	-	-	-	-	-	Futch & Bruger 1976
Florida, Central	158	-	-	-	-	-	-	-	-	This study
Florida, Northwest	923	-	-	-	-	349	-	-	820	Collins et al. 1996
Florida, Northwest	214	-	-	3	8 or 9	-	-	≤375	775	This study
Alabama	1020	2	2	-	4.5	286*	294*	-	613*	Woods 2003
Alabama	113	-	-	-	6	-	-	≤425	675	This study
Louisiana	916	2	2	-	5.5	312*	321*	-	613*	Woods 2003
Louisiana/Texas	1849	-	-	-	-	268*	310*	-	448*	Render 1995
Louisiana	120	-	-	4	7	-	-	475	675	This study
Texas, North	153	-	-	-	-	306*	401*	-	-	Nelson 1988
Texas, North	91	-	-	5	6	-	-	575	625	This study
Texas, South	191	-	-	3	7	-	-	≤375	475	This study
Eastern Gulf	~1291	2	-	6	8	-	-	321*	692*	Fitzhugh et al. 2004
Eastern Gulf	483	-	-	3	8	-	-	≤375	≥775	This study
Western Gulf	~665	2	-	8	8	-	-	>374*	692*	Fitzhugh et al. 2004
Western Gulf	402	-	-	3	7	-	-	≤375	725	This study
Gulf-wide	783	-	-	-	-	-	-	-	-	Collins et al. 2001
Gulf-wide	1956	2	-	-	8	-	-	-	692*	Fitzhugh et al. 2004
Gulf-wide	884	-	-	3	8	-	-	375	-	This study
Yucatan Peninsula	531	-	-	-	-	283	314	-	526	Brulé et al. 2010

n=sample size; A_{min}=minimum age at maturity; A_{50}=age at 50% maturity; A_{75}=age at 75% maturity; A_{100}=age at 100% maturity; L_{min}=minimum total length at maturity; L_{50}=total length at 50% maturity; L_{75}=total length at 75% maturity; L_{100}=total length at 100% maturity

APPENDIX B: SUPPLEMENTARY FIGURES

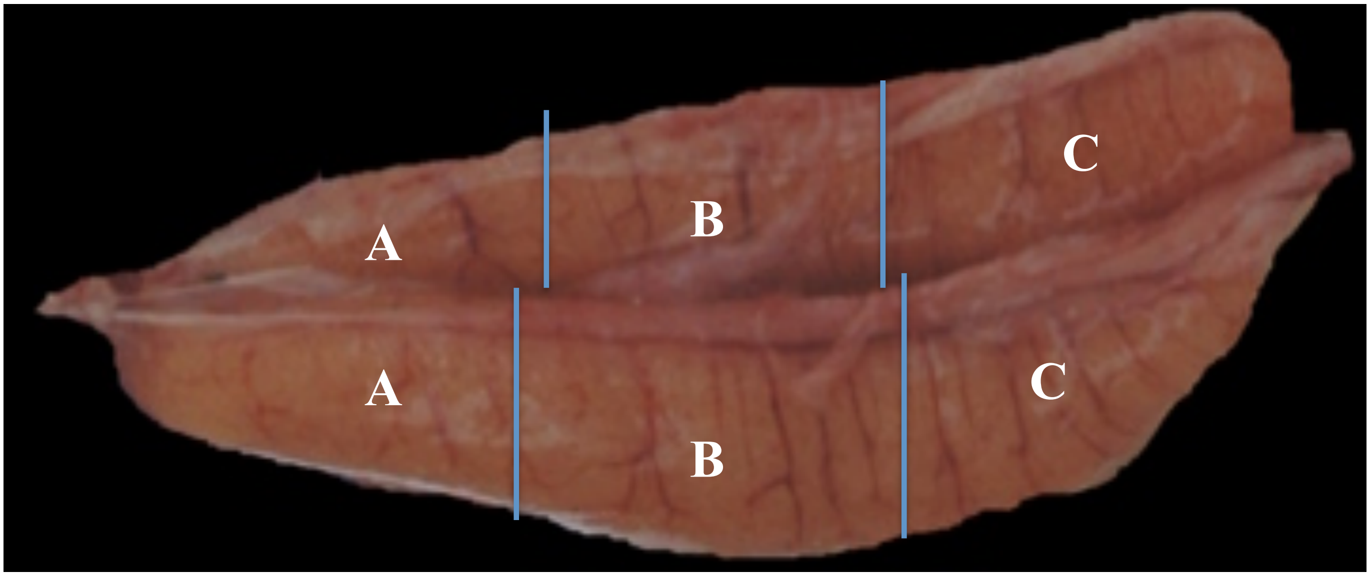

Figure 1. A red snapper ovary is comprised of two lobes. Each lobe is divided into three subsections: A) anterior, B) medial, and C) posterior, the sum of which makes six total regions per ovary. Photograph courtesy of Courtney Saari.

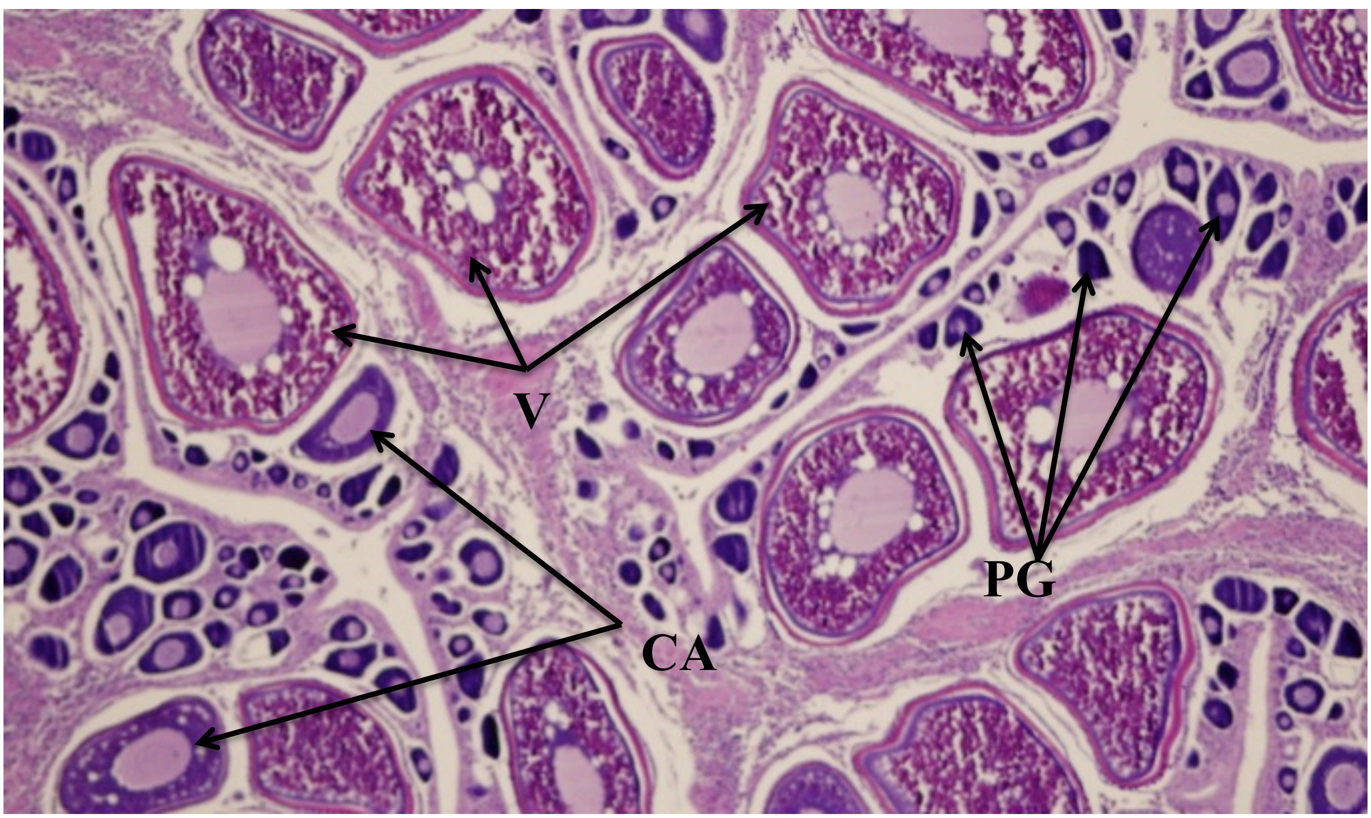

Figure 2. Three stages of red snapper oocyte maturation: PG is primary growth, CA is cortical alveoli, V is vitellogenic.

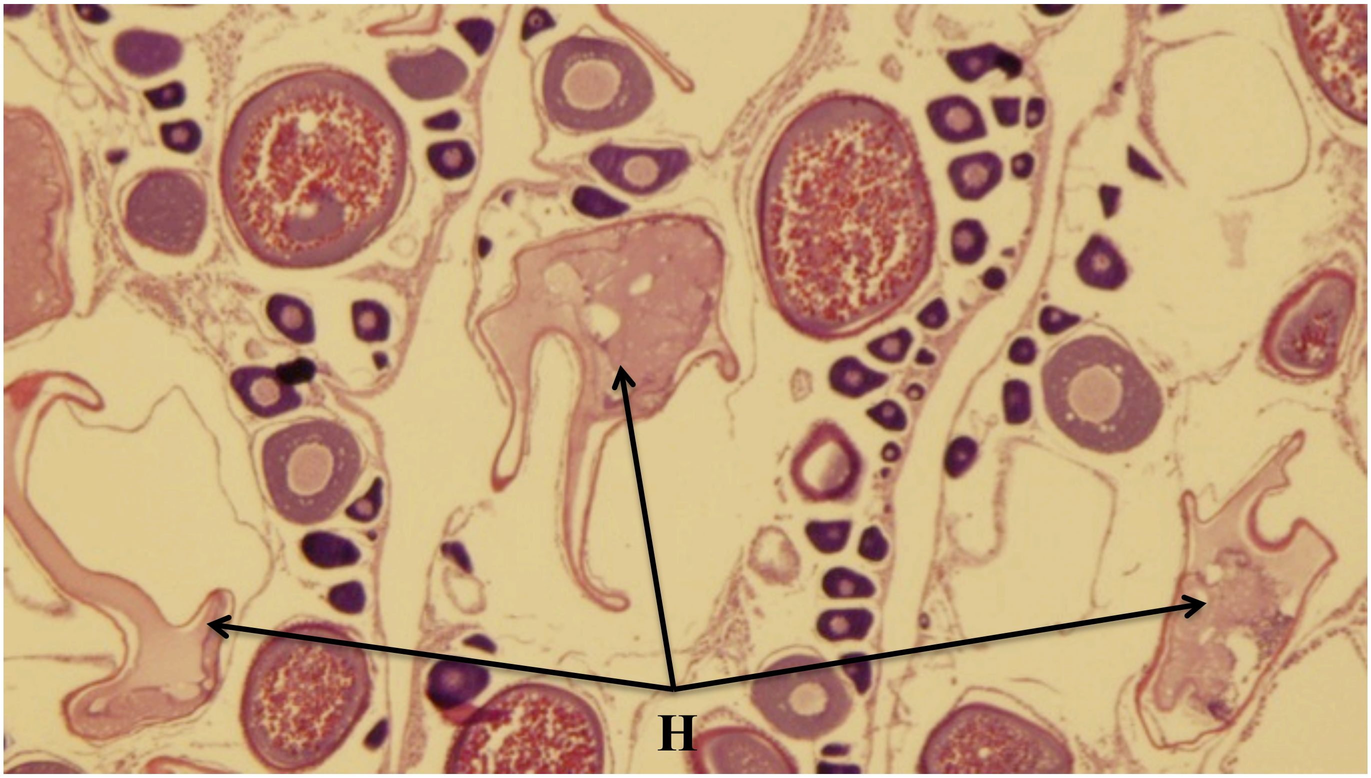

Figure 3. The final stage of oocyte maturation: hydration. H is hydrated. For red snapper, hydration of oocytes occurs after the vitellogenic stage and <24 hours prior to spawning.

Figure 4. POF is post-ovulatory follicles, which remain in the ovary for 24 hours post-spawning before degradation and resorption.

Figure 5. Atretic oocyte. Atresia is the breakdown and resorption of an oocyte prior to ovulation.

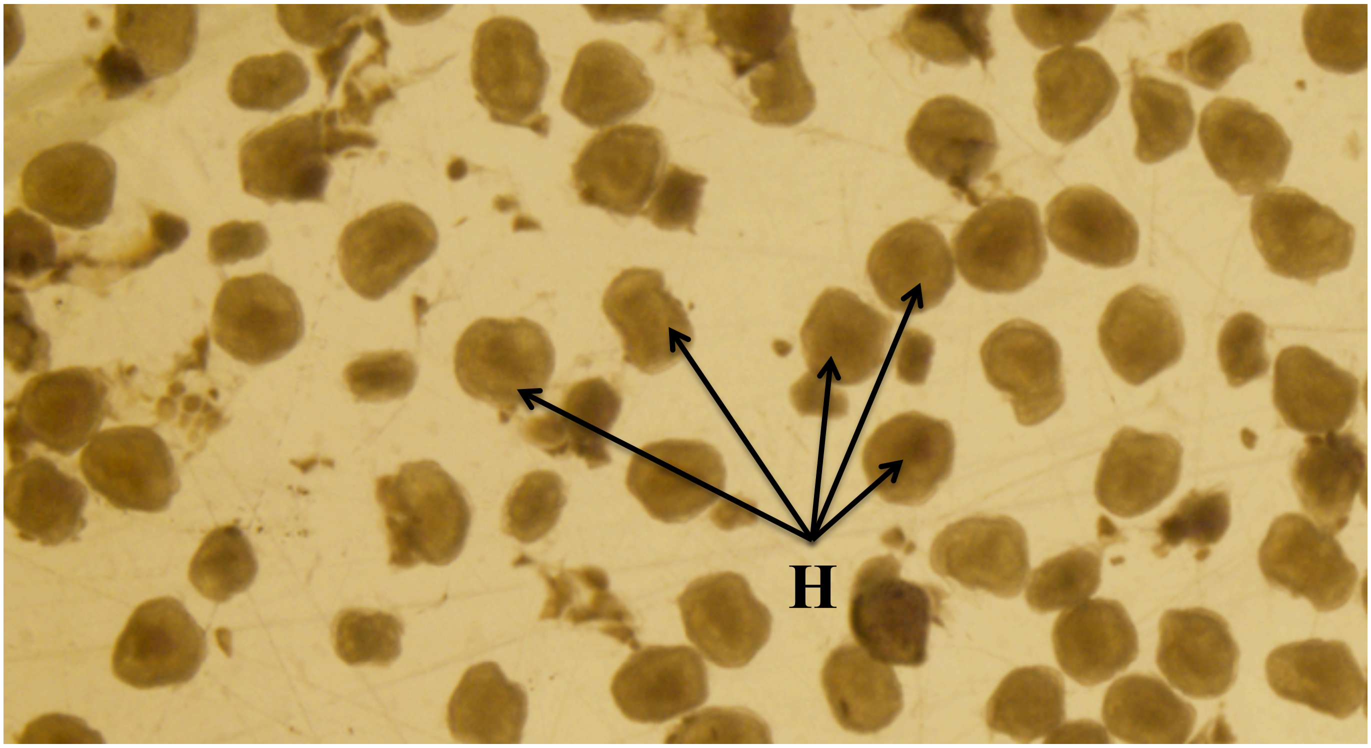

Figure 6. Glycerin spread featuring hydrated oocytes (H) observed under a compound microscope at 10x magnification.

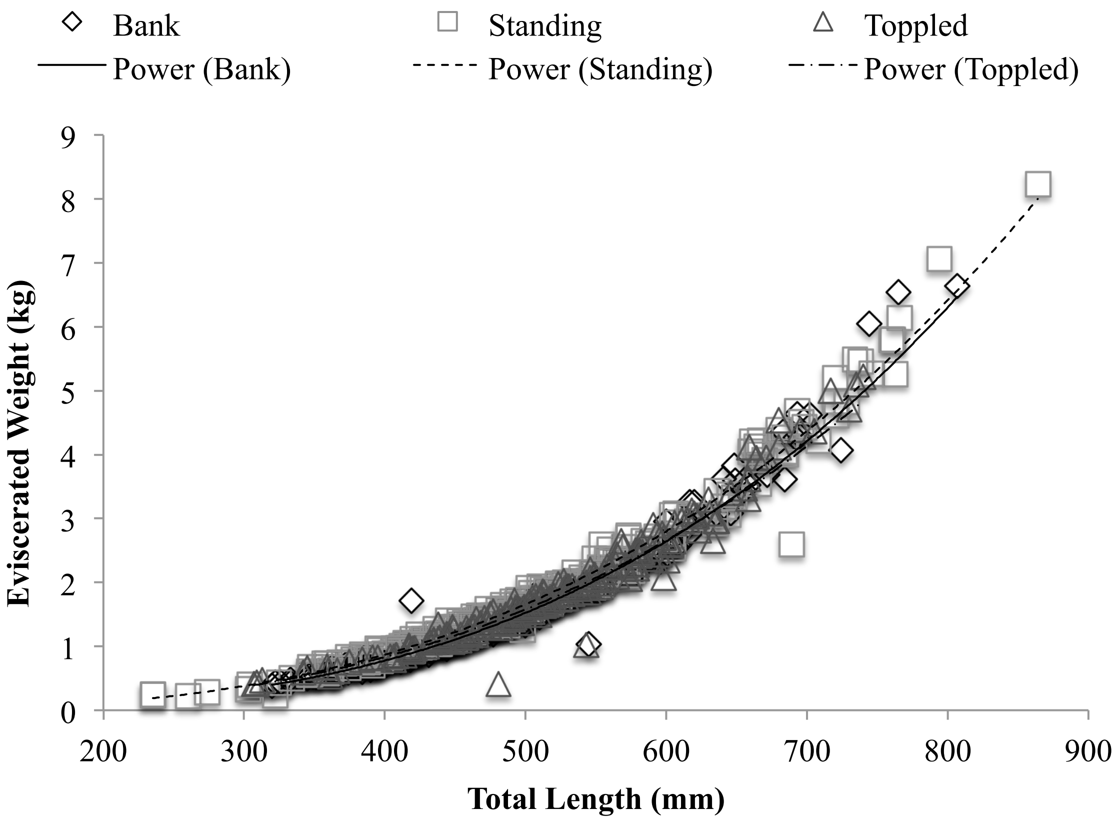

Figure 7. Eviscerated body weight (W) at total length (L) for female red snapper, *Lutjanus campechanus,* sampled at on the Louisiana continental shelf. See Table 2.3 for equation of the best-fit line.

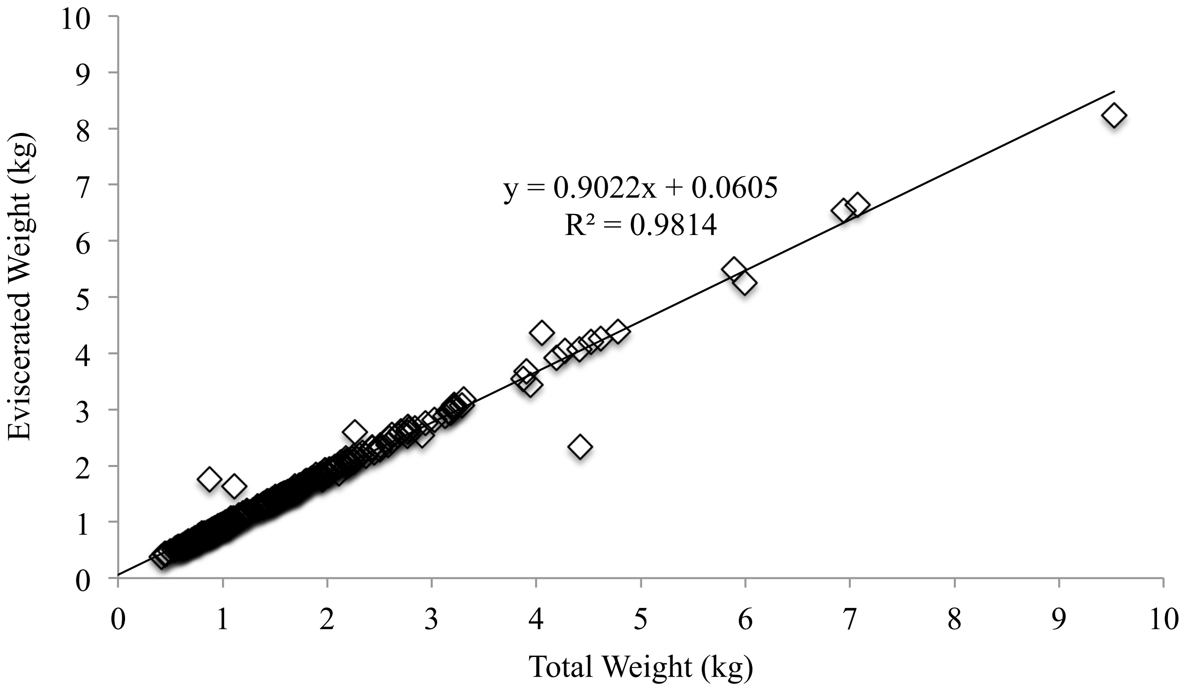

Figure 8. Predictive linear function for eviscerated body weight (EBW) at total weight (TW) for female red snapper, *Lutjanus campechanus*, collected at Eugene Island from all sites combined. Fish were collected from November 2008 through October 2010.

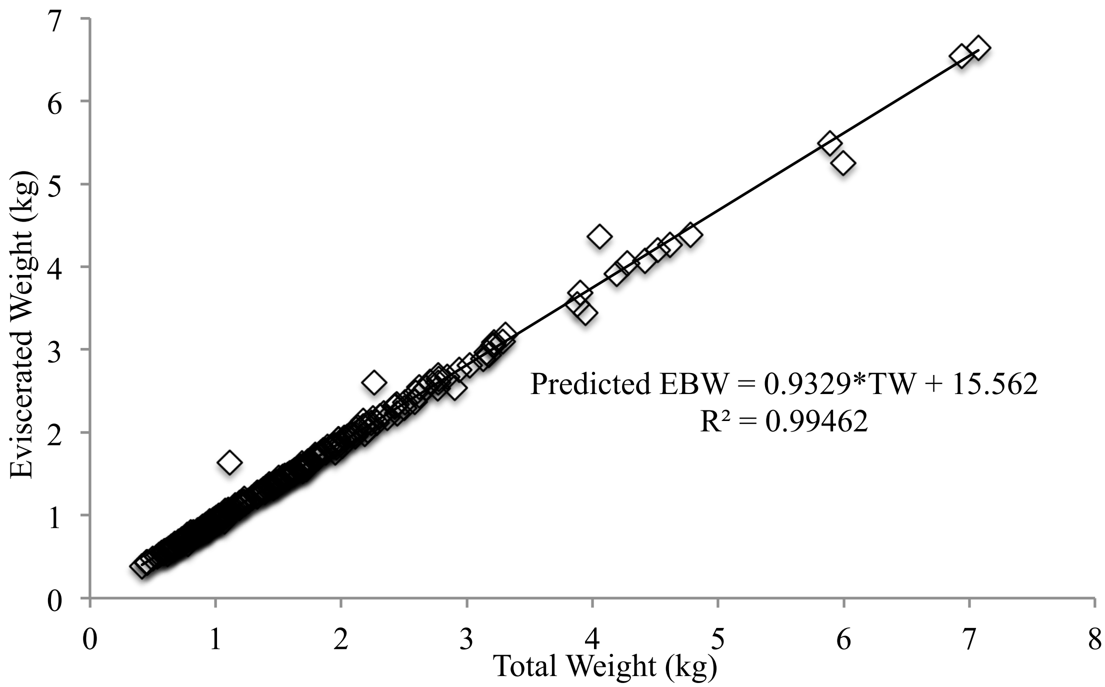

Figure 9. Predictive function for eviscerated body weight (predicted: n=136) based on given total weight (TW) values (n=386) and actual eviscerated body weight values (n=250) of female red snapper, *Lutjanus campechanus*, sampled from the Louisiana continental shelf.

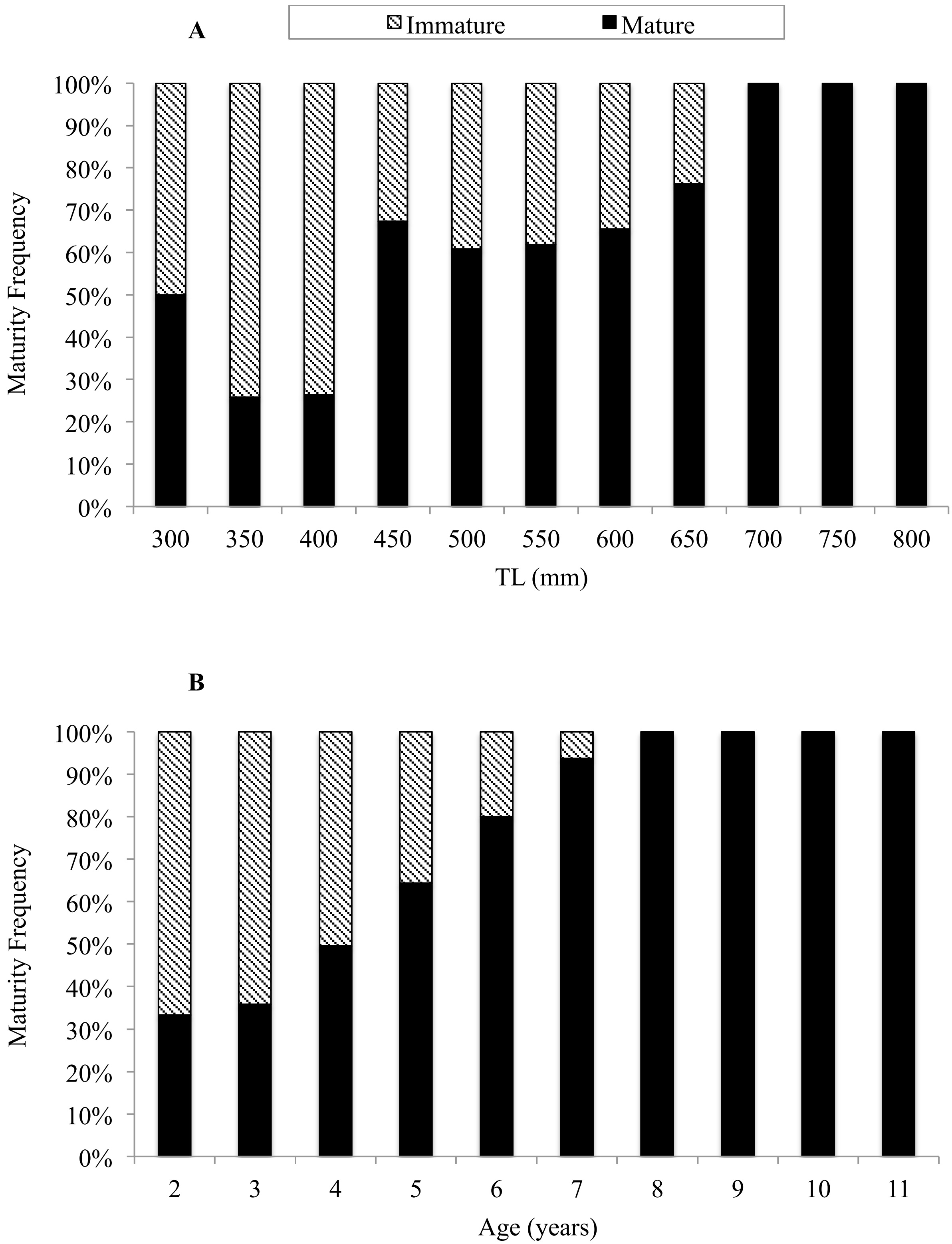

Figure 10. Maturity ogives based on A) total length (n=326) and B) age (n=309) for female red snapper, *Lutjanus campechanus,* collected during spawning season on the Louisiana continental shelf.

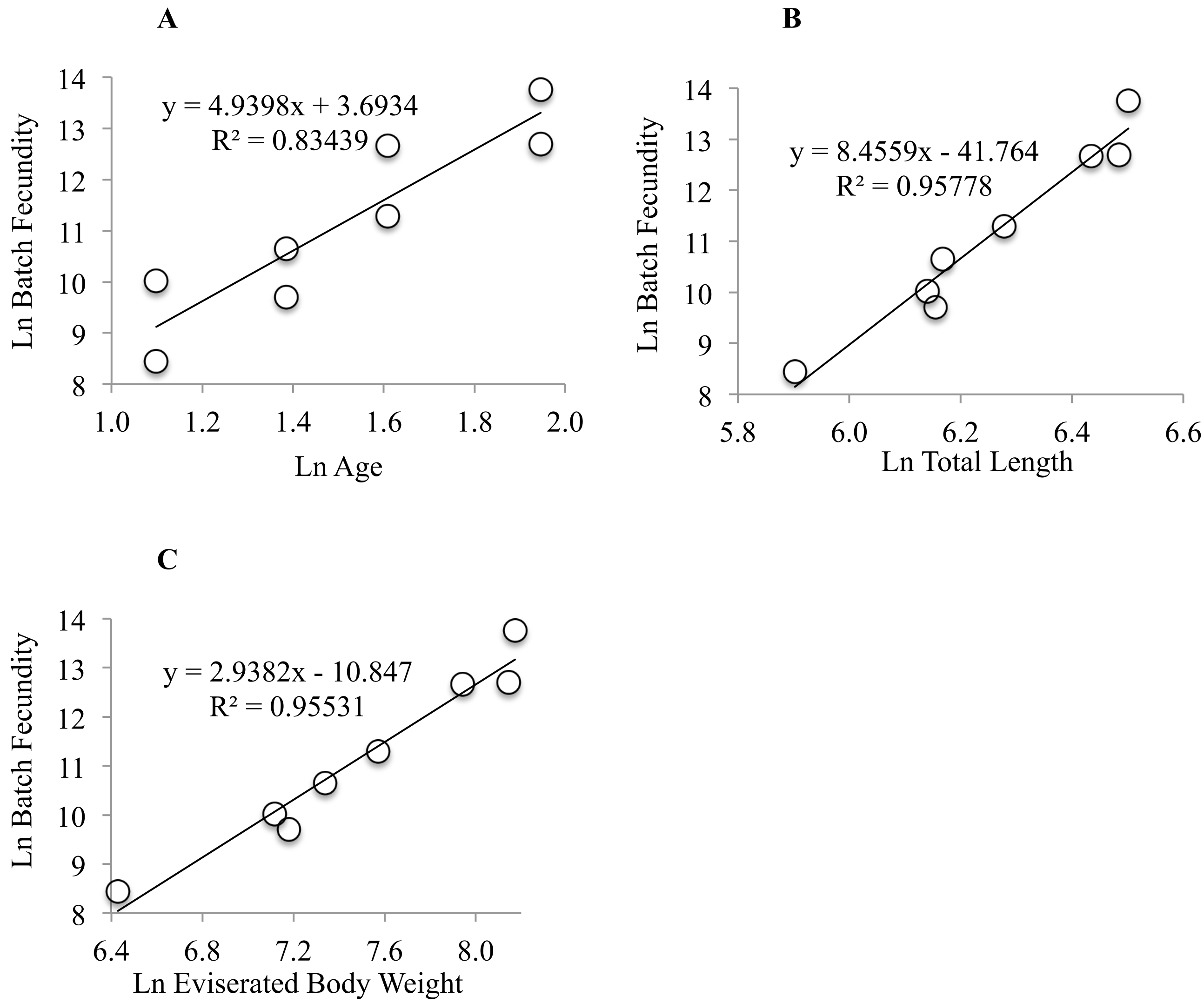

Figure 11. Natural logarithm (ln) of batch fecundity against A) ln of total length, B) ln of eviscerated body weight and C) ln of age. Female red snapper, *Lutjanus campechanus*, were collected on the Louisiana continental shelf.

VITA

Dannielle Helen Kulaw was born in Alabama in July of 1984. She grew up with her younger sister in Fort Walton Beach, Florida, and graduated with her high school diploma and Associate of Arts degree from the Collegiate High School at Okaloosa-Walton Community College with honors in May 2002. For her undergraduate work, she went to the University of West Florida and participated in the Marine Ecology Research Society (MERS) and the Fisheries Biology Club. In 2006, she graduated with a Bachelor of Science in Marine Biology and a certificate in Aquaculture and Fisheries. Upon graduation, Dannielle worked as a student services contractor with the U.S. Environmental Protection Agency Gulf Ecology Division in Pensacola, Florida, serving two years on the Ecotoxicology and Proteomics Teams. She moved to Baton Rouge, Louisiana, in the summer of 2008 to begin her work in the School of Coast and Environment at Louisiana State University. At LSU, she served as co-chair on the Education and Community Outreach Committee for the Marine Environmental Researchers (MER) for one year. She was granted the Joseph Lipsey, Sr. Memorial Scholarship Award in 2011 for excellence in the studies of marine science. She is currently a candidate for the degree of Master of Science in the Department of Oceanography and Coastal Sciences, which will be awarded in August 2012.