Comparing reproductive capacity of nearshore and offshore red snapper, *Lutjanus campechanus*, on artificial reefs in the western Gulf of Mexico

Ricky J. Alexander

SEDAR74-RD80

April 2021

COMPARING REPRODUCTIVE CAPACITY OF NEARSHORE AND OFFSHORE RED SNAPPER, *LUTJANUS CAMPECHANUS*, ON ARTIFICIAL REEFS IN THE WESTERN GULF OF MEXICO

A Thesis

by

RICKY J. ALEXANDER

Submitted to the Graduate College of
The University of Texas Rio Grande Valley
In partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

December 2015

Major Subject: Biology

COMPARING REPRODUCTIVE CAPACITY OF NEARSHORE AND OFFSHORE RED SNAPPER, *LUTJANUS CAMPECHANUS*, ON ARTIFICIAL REEFS IN THE WESTERN GULF OF MEXICO

A Thesis
by
RICKY J. ALEXANDER

COMMITTEE MEMBERS

Dr. Carlos E. Cintra-Buenrostro
Chair of Committee

Dr. David Hicks
Committee Member

Dr. Richard Kline
Committee Member

Mr. Dale Shively
Committee Member

December 2015

ABSTRACT

Alexander, Ricky J., Comparing Reproductive Capacity of Nearshore and Offshore Red Snapper, Lutjanus campechanus, on Artificial Reefs in the Western Gulf of Mexico. Master of Science (MS), December, 2015, 84 pp., 12 figures, references, 59 titles.

Red snapper collected quarterly from four artificial reefs in south Texas were examined to compare total length, total weight, age, and the proportion of male to female red snapper, calculate gonadosomatic index values, batch fecundity, annual spawning frequency, and annual fecundity, and estimate size and age at maturity. Spawning occurred from April to September, with most active spawning observed in June (58%). Despite larger red snapper producing more eggs, and fish being larger offshore, most active spawning (68%) and egg production (74%) was observed nearshore. Female red snapper reached 50% maturity (L_{50}) between 350-550 mm, and L_{75} by 600 mm. Males reached L_{50} between 350-450 mm, reaching L_{100} by 550 mm. Although younger, smaller fish carried the burden of reproduction, fish matured at relatively later in life.

ACKNOWLEDGEMENTS

I would like to recognize those who made this thesis a reality. First, I would like to thank the Texas Parks and Wildlife Department for funding this project and providing guidance along the way. I extend full gratitude to Carlos E. Cintra-Buenrostro, for advising me on my research and writing, and, perhaps most importantly, for helping me learn to navigate a university system undergoing major changes. I would also like to thank the University of Texas at Rio Grande Valley (UTRGV; formerly University of Texas at Brownsville) for providing the tools and space required to perform this research. Special thanks are extended to the UTRGV dive team, our vessel captain, Andres Garcia, and all the volunteers who helped me in the field and in the laboratory. Special thanks are extended to Danny Cuevas, who acted as my third hand in the field, and Ashley Moreno, for helping me enumerate otolith annuli and calibrating the Hydrolab. I am thankful to Dannielle Kulaw, James Patterson, and the Louisiana State University Fisheries Laboratory for educating me on ovarian histology and especially to Dannielle Kulaw for mentoring me throughout this process; I could not have completed this project without her assistance. I would also like to thank David Hicks, Richard Kline, and Dale Shively, my committee members, for providing advice, guidance, and editorial feedback on many articles and presentations surrounding this project. Finally, I would like to show my gratitude to Janell Brown and Jillian DiMaio for their unending love and support throughout this process.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Why Red Snapper?

Massive losses of fish stock biomass have spurred fisheries managers into action, implementing major fisheries management plans in an attempt to restore fisheries and marine ecosystems to healthy, sustainable levels. For red snapper (*Lutjanus campechanus*; Poey 1860), the most important of these plans include the Magnuson-Stevens Fishery Conservation and Management Act of 1976, which identified the need for a national program to prevent overfishing, expedite the sustainability of essential fish habitats, and realize the full potential of US fishery resources, in combination with the Reef Fish Fishery Management Plan (RFFMP), created in 1984. The RFFMP established size limits, implemented regulations on various fishing methods and gear types, limited fishing seasons for recreational fishing, and decreased total allowable catches in an attempt to reduce harvest pressure and increase stock biomass (Hood and Steele 2004, SEDAR 2013). Now in the 12th year of a 35-year recovery plan set forth by the Gulf of Mexico Fisheries Management Council, the National Marine Fisheries Service (NMFS) has revoked the overfishing status for Gulf Of Mexico (GOM) red snapper. The NMFS (2012) defines exploited fish stocks in terms of “overfishing occurring” and “overfished” as follows: “overfishing occurring” harvesting at a rate that is too high to produce the maximum sustainable yield for the fishery; while, an “overfished” stock is characterized by a biomass level so low that the stock’s ability to produce the maximum sustainable yield is at-risk. Although the rate of fishing is no longer considered to be too high, GOM *L. campechanus* stock is still classified as overfished (NMFS 2012, SEDAR 2013).

Red snapper is a historically important food fish in both the commercial and recreational sectors (Camber 1955, Carpenter 1965, Rios 2013). A significant commercial *L. campechanus* fishery has existed since at least the mid-1800s (Camber 1955, Hood et al. 2007), and recreational angler efforts on red snapper have been increasing since before 1950 (Rios 2013). From 2002-2011, the GOM commercial *L. campechanus* industry landed 16.9 x 10^6 kg, netting an average of $10.5 million/year (National Marine Fisheries Service, Fisheries Statistics Division, 1315 East-West Highway – Rm. 12441, Silver Spring, Md., 20910-3282, personal communication, April 2014), making red snapper the fourth most profitable fishery in the GOM (Brown et al. 1989, NMFS op. cit. personal communication).

Additionally, the GOM recreational *L. campechanus* industry landed 15.8 x 10^6 kg in the same time period (NMFS, op. cit. personal communication), making it the fourth largest recreational harvest in the Gulf (Voorhees 2012). While a numeric value cannot be placed on the recreational sector landings, it is important to consider the amount of time, money, and effort exerted by fishers; permits, tackle, fuel, docking fees, travel costs, ice, electronics, maintenance, and safety equipment are just some of the potential economic gains resulting from the fishery. As an integral contributor to the GOM economy, red snapper deserves the most efficient management strategies possible to ensure maximum benefit to all stakeholders.

L. campechanus are a predatory demersal fish found throughout the GOM, the Caribbean Sea, and from the U.S. Atlantic coast from South America to Massachusetts (Camber 1955, SEDAR 2005). Most commonly observed at depths of 15-30 m (Patterson et al. 2001), *L. campechanus* abundance is highest in the northern GOM and off the Campeche Banks of Mexico (SEDAR

2013). Typically associated with limestone outcroppings, natural embankments, live-bottom habitat, or artificial reefs (Camber 1955, Patterson et al. 2001), adult *L. campechanus* prefer structure with high vertical relief and opportunity for refuge (Wells and Cowan 2007). Red snapper are a moderately long-lived species, occasionally living past 55 years, but most (> 90%) individuals caught in the fisheries are 2-6 years of age (Render 1995, Wilson and Nieland 2001, SEDAR 2013).

Juveniles (ages 0-1) primarily feed on zooplankton, mysid shrimp, and squid, shifting to an adult (ages 2+) diet dominated by crustaceans, fishes, and pelagic zooplankton as maturity is reached (255 ± 65 mm; Bradley and Bryan 1975, Szedlmayer and Lee 2004, McCawley et al. 2006, Wells et al. 2008). While some studies have shown that other snappers (family Lutjanidae) primarily forage at night (e.g., Hobson 1965), Ouzts and Szedlmayer (2003) observed red snapper feeding throughout all periods of day and night with a lull in gut fullness around dusk. A review of *L. campechanus* life history by Gallaway et al. (2009) concludes that red snapper are opportunistic feeders that obtain a significant portion of their diet from reef species, independent of time of day.

Spawning in the GOM varies by region (Kulaw 2012) but generally occurs from April to October, peaking in late June-mid July (Szedlmayer and Conti 1999, Fitzhugh et al. 2012, SEDAR 2013). The eggs are approximately 0.8 mm in diameter, pelagic, spherical, and transparent (Rabalais et al. 1980). Larvae are about 2.2 mm in length when hatched (Rabalais et al. 1980), and remain in the plankton for about four weeks before metamorphosis and recruitment to benthic habitats, including sand, mud, and shell rubble, sometime between mid-June and mid-September (Szedlmayer and Conti 1999, Rooker et al. 2004). In the fall, the juvenile fish leave their nursery habitat for more structured areas, such as shell ridges, rock outcroppings, sand banks, and artificial reefs (Syc and Szedlmayer 2012, SEDAR 2013). The NMFS longline surveys and data from recreational landings indicate that large adults may be more independent of structured habitat, spending more time on the open continental shelf (SEDAR 2013; for a summary of red snapper habitat use see Figure 1).

Sexual maturity may be reached by two years of age, with 50% of *L. campechanus* reaching maturity by four years, and 100% by 5-8 years (Schirripa and Legault 1999, White and Palmer 2004, Jackson, Cowan, and Neiland 2007). Females generally reach maturity at greater total lengths than males (White and Palmer 2004, Brulé et al. 2010); 50% of females reach maturity at approximately 310-390 mm, but drops to approximately 145-260 mm in males.

Red snapper have a periodic reproductive strategy that favors delayed maturation until the fish is large enough to sustain a large clutch and is characterized by a rapid larval and juvenile growth rate (Winemiller and Rose 1992). Although age and size at maturity vary across studies and regions (Woods et al. 2003, White and Palmer 2004, Brulé et al. 2010), Woods et al. (op. cit.) suggest that size-and age-at-maturity may vary as a population responds to changes in environmental conditions and mortality. That is, when a population is stressed, the size and age at maturity decreases so that younger, fast-growing individuals have an opportunity to reproduce. Presumably, populations resume their periodic reproductive strategy in the absence of stress.

As *L. campechanus* grow, they must use most of their nutrients for growth and survival (Bohnsack 1990), but as they attain a size-refuge from predators, they can afford to spend more energy on egg production and less on growth. To illustrate the disproportionate egg contribution of large individuals to a population, consider that a single 61 cm female (~12.5 kg) produces as many eggs (9,300,000) as 212 females measuring 42 cm (~1.1 kg) (Bohnsack op. cit.). Furthermore, size-selective harvest places evolutionary pressures on fishes to grow slower and reproduce at smaller sizes and younger ages (Trippel 1995; Jørgensen et al. 2008), which has occurred in red snapper (Cowan et al. 2011). Altering phenotypic characteristics of fish populations (i.e., growth rate, size, and age) reduces the spawning biomass and likely alters the timing and duration of reproductive events, which carries negative consequences for recruitment (Anderson et al. 2008; Wright and Trippel 2009).

The observed sex ratio in the GOM is approximately 1:1 (Collins et al. 1996, White and Palmer 2004, Brulé et al. 2010, Fitzhugh et al. 2012, SEDAR 2013). Red snappers are indeterminate batch spawners (Collins et al. 1996), meaning that oocytes are present in nearly all stages of development throughout the breeding season, during which females release multiple batches of eggs (Brulé et al. 2010, Brown-Peterson et al. 2011). They are also highly fecund, often ranging from hundreds to millions of eggs per batch (Render 1995, Collins et al. 2001). Despite this high output, less than 0.1% of a brood may survive to adulthood (Fuiman 2002). Spawning occurs in asynchronous cycles throughout the breeding season with large individuals (> 575 mm total length (TL)) spawning 25-60 times in a given season (Cowan et al. 2012), facilitating the establishment of multiple year-classes (Winemiller and Rose 1992). Batch fecundity, the average number of ova produced by an individual during a spawning event, and spawning frequency increase with snapper weight, length, age, and water depth (Collins et al. 1996, Kulaw 2006, Cowan et al. 2012), and batch fecundity is best correlated with maternal length (Kulaw 2006).

Why Artificial Reefs?

The NMFS defines “essential fish habitat” as the waters and substrates necessary for spawning, breeding, feeding, or growth to maturity (NMFS 2012). In the GOM, there are approximately 349,090 km^2 of essential fish habitat, of which approximately 8% is natural rocky areas, less than one-hundredth of a percent is artificial structures (these occur within the essential fish habitat area surrounding the GOM shoreline), and the rest is sand, mud, and gravel habitat unsuitable for adult red snapper (Mueller 2012). In south Texas, the bottom habitat primarily consists of relatively open flat sand, mud, and shell substrates with occasional occurrences of rocky reef habitat (Dennis and Bright 1988).

Because *L. campechanus* are highly associated with vertical structure (Wells and Cowan 2007), including high-rise artificial structure, so-called artificial reefs may serve to mitigate, replace, or, in some cases, even create valuable hard-bottom habitats (Bombace et al. 1994). These habitats provide essential refuge, substrate for encrusting species, nutrients, and food for many benthic/pelagic fishes and invertebrate communities (Jenkins et al. 2008). In addition to any ecological benefits artificial reefs may offer, many are also utilized as valuable recreational SCUBA diving or snorkeling opportunities (Wilhelmsson et al. 1998).

Generally, reef fishes require habitat that is structurally complex, spatially diverse, and dynamic (Camber 1955, Morton and Shima 2013). As such, settlement success is largely dependent on habitat availability and structural configuration. It follows, then, that creating appropriate habitat would promote the settlement of more individuals and the adult population would grow. It is long known that reef fishes aggregate around artificial reefs (Bohnsack and Sutherland 1985, Dennis and Bright 1988, Alevizon and Gorham 1989), but Bohnsack (1989) questioned the productive benefits of artificial reefs, spurring a debate that has lasted decades (for reviews see Shipp 1999, Miller 2002, Gallaway et al. 2009, Cowan et al. 2010, Syc and Szedlmayer 2012). Bohnsack (op. cit.) says that while rapid colonization rates, high fish densities, and high catch rates on artificial reefs have been used as evidence of habitat limitation and production, it is possible that artificial reefs are simply attracting these organisms from nearby natural habitat. If true, reef construction could have problematic effects, such as increasing fishing effort and catch rate by artificially concentrating stocks to a known area (Bohnsack 1989, Grossman et al. 1997).

The scientific community first attempted to resolve the so-called production-attraction debate through gut content analyses, hypothesizing that if production is occurring, *L. campechanus* would be feeding on reef species. These studies showed that red snapper feed both on and off the reef, somewhat opportunistically (Ouzts and Szedlmayer 2003, Szeldmayer and Lee 2004, McCawley et al. 2006, Wells et al. 2008, as well as Why Red Snapper section above).

Syc and Szedlmayer (2012) contributed some evidence to the production-attraction discussion by showing that *L. campechanus* abundance increases with reef age and that fish age is positively correlated with reef age. That is, young reefs were typically occupied by fish of a similar age and this relationship continued as reefs aged so that older reefs have a full suite of year-classes present. The presence of fish older than the reefs indicated that some attraction was occurring, as well. These data suggest that reefs may require a certain amount of time (at least 10 yrs.) to reach maximum productivity.

Many recent studies have utilized radio telemetry and acoustic monitoring techniques to assess site fidelity, the tendency to return to a previously occupied location, and residence time, the amount of time spent in a given location (Szedlmayer and Schroepfer 2005, Garcia 2013). It follows that if *L. campechanus* spend large quantities of time on an artificial reef, they have at least incorporated the reef into their life history (Grossman et al. 1997). The alternative to this would be low site fidelity, indicating, that red snapper are highly transient (Patterson et al. 2001). These studies yielded mixed results (Patterson et al. 2001, Peabody 2001, Szedlmayer and

Schroepfer 2005, Topping and Szedlmayer 2011a, 2011b, Syc and Szedlmayer 2012). A recent study in south Texas utilizing two of the four proposed study sites observed relatively high site fidelity of *L. campechanus* for at least one (27% at PS-1122 and 58% at PS-1047; site description below and in Table 1) of the two sites investigated (Garcia 2013). This was despite a relatively low sample size (n = 12 at PS-1122; n = 19 at PS-1047), and an inability to account for mortality (i.e., predation).

This study builds on the Garcia (2013) study in an attempt to compare how nearshore and offshore artificial reefs function in terms of local *L. campechanus* production. In Texas state waters (within 14.5 km of the Texas coast), the *L. campechanus* fishery is open year round. However, the federal red snapper season is quota-based and generally less than one month in duration (SEDAR 2013). This means inshore sites (PS-1169L and PS-1047) (Figure 2) experience much higher levels of fishing pressure than offshore sites (PS-1070 and PS-1122; 365 days in Texas waters vs. 3-30 days offshore) (Figure 2). As such, mean length, weight, age, and reproductive capacity was expected to be suppressed at nearshore compared to offshore sites. Specific objectives for this study include: 1) Compare the proportion of male to female red snapper on four artificial reefs 2) compare TL, total weight, and age between sites and quarters, 3) calculate gonadosomatic index (GSI) values, batch fecundity, annual spawning frequency, and annual fecundity, and 4) determine size- and age-at-maturity for local male and female red snapper.

CHAPTER II

METHODS AND MATERIALS

Field Collection

Red snapper were collected quarterly for a year in accordance with SEAMAP (2012) vertical longline protocol modified to utilize two, rather than three commercial Bandit rigs, one starboard and portside amidships, aboard the vessel used in this study (RV Vollert), a 13.7 m survey launch vessel. Approximately 122 m of 181 kg test monofilament was spooled onto each rig, and a 7.3 m backbone consisting of 181 kg test monofilament attached to the terminal end. A weight (~4.5 kg) was attached to the other end of the backbone while fishing. Each backbone was rigged with ten 46 cm gangions at 61 cm intervals. Each gangion contained one of three sizes of Mustad 39960D circle hooks (8/0, 11/0, 15/0) and was made of 45 kg test monofilament with a snap swivel on the end, enabling the gangion to be connected to one of the ten swivel sleeves on the backbone. Each backbone contained ten gangions of the same hook size. Each hook was baited with Atlantic mackerel (*Scomber scombrus,* Linnaeus 1758) cut to an appropriate size relative to the hook size used. Each backbone was deployed randomly between stern and starboard sides and was fished for five minutes, one immediately after the other. Hook size was also randomized. Fishing start time began when the weight was reeled back ~2 m from the bottom. Fishing time ended when gear retrieval was initiated. This was repeated at three stations within each site, starting with a different hook size each time, for a total of nine drops per site (three of each hook size).

Study Sites

Four artificial reefs sites were sampled; Port Mansfield Liberty Ship Reef (PS-1070), Port Isabel Reef (PS-1169L), South Padre Island Reef (PS-1047), and Texas Clipper Artificial Reef (PS-1122) (Figure 2, Table 1). For the purposes of this study, PS-1169L and PS-1047 were considered inshore reefs, while PS-1070 and PS-1122 were considered offshore (see Table 1 for site description). The sites are composed of a combination of sunken ships, concrete culverts (61-183 cm diameter), decommissioned offshore oil rig jackets, and various structures specifically designed for artificial reefs (TPWD 2008). The oldest reef in this study was initially deployed in November 1975, making it ~40 yrs old for the duration of this study (PS-1070), and the youngest reef (PS-1169L) was deployed in July 2011, making it ~3 yrs old for the duration of this study.

For vertical line surveys, a target catch of 15 individuals was set for each sampling event. If the minimum was not achieved during SEAMAP sampling, supplemental hook and line fishing was conducted. In an effort to increase sample size, sampling occurred during each month throughout the summer, when spawning was expected to occur. To minimize impact on these communities, the northern sites (PS-1047 and PS-1070) were sampled twice as frequently during this period, as these sites have more robust populations of red snapper compared to PS-1169L and PS-1122 (pers. obs.). Unfortunately, due to weather-based safety concerns, no sampling was accomplished during September. Additionally, during some sampling events, few red snapper were on site (confirmed with GoPro videos and diver observations) and the minimum number was not achieved. Because 50% of mature females reached maturity between 310 – 390 mm TL, the minimum target size in this study was set at 350 mm to increase the odds of capturing a mature individual. However, smaller red snapper were randomly subsampled to obtain a complete maturity schedule. A zip-tie, marked with an identification number, was attached to each fish through the gills before placing the individuals on ice. Fish were held on ice overnight and processed the following day. Fish that were not retained for internal analysis were released with pressure-activated lip-grips (SeaQualizer) after venting to minimize release mortality (Drumhiller et al. 2014).

Laboratory

In the laboratory, total and eviscerated weight (± 0.0001 kg), standard, total, and fork length (± 1.0 mm), gonad weight (± 0.0001 g), liver weight (± 0.0001 g), and sex (male or female) were recorded. Otoliths were removed, dried, placed in an appropriately labeled air-tight container, and stored for later processing. Gonads were removed and placed in Prefer (a glycol fixative) within 24 h, where they remained for at least two weeks prior to histological processing. Oocyte distribution is homogeneous in red snapper ovarian tissue (Wilson et al. 1994; Collins et al. 1996), so a cross section (approximately 3 mm) was taken from one random location (using a random number generator) of six conceptual subsections comprising each pair of gonads. The fixed gonadal tissue was then placed into histology cassettes and processed using a KD-TS3D tissue processing system. Once the tissue was embedded in wax, 4 μm cross-sections were cut using a Reichert-Jung 2030 rotary microtome. The best cross sections (examined by eye) were then placed in a hot water bath, captured on a slide, and allowed to dry before being stripped of wax, stained with double-strength gill hemotoxylin (Gill's 2 hemotoxylin), counterstained with EOSIN-Y, and, finally, cover slipped to preserve the slide (Brown-Peterson et al. 2009, Kulaw et al. 2012). All staining was performed manually using a Tissue-Tek II slide staining set. This process was applied to all females and a random selection of five males per sampling event. If five males were not captured, all males from that date were selected for processing.

Male *L. campechanus* undergo four stages of spermatogenesis: i. spermatogia, ii. primary and secondary spermatocytes, iii. spermatid, and iv. spermatozoid (Brulé et al. 2010, Brown-Peterson et al. 2011; Tables 2 and 3). For females, microscopic features were used to assign six descriptive stages for oogenesis: i. chromatin nucleolar oocyte (CO), ii. perinucleolar oocyte (PO), iii. yolk vesicle ooctye (YVO), iv. yolk globule oocyte (YGO), v. final oocyte maturation (FOM), and vi. hydrated oocyte (HO) (Tables 2 and 3). Each slide was assigned a spawning phase code as per Brulé et al. (2010; see Tables 2 and 3): I (immature), D (developing), SC (spawning capable), AS (actively spawning), R (regressing), or X (regenerating). For this study, the presence of vitellogenic oocytes was considered the benchmark for maturity in females, and the presence of continuous germinal epithelium the benchmark in males. To calculate size- and age-at-maturity, red snapper were placed into 50 mm size classes and one year age classes.

Gonadosomatic index (GSI) values, size-and age-at-maturity, batch fecundity estimates, spawning frequency estimates, and annual fecundity estimates were used to assess *L. campechanus* reproductive biology on artificial reefs in south Texas. GSI values (gonad weight/eviscerated body weight x 100; Barber and Blake 2006), greater than one indicate spawning readiness in a fish population during the annual spawning cycle. Because oocytes are homogenously distributed throughout the ovary (Wilson et al. 1994, Collins et al. 1996), three subsamples were taken from randomly assigned ovary regions, weighed (0.03-0.05 g/sample), and placed in a petri dish containing a 3:7 glycerin to water solution. Under a microscope, (10X magnification) subsamples were gently separated with a probe and hydrated oocytes (Figure 3) enumerated. Batch fecundity estimates (number of hydrated oocytes divided by subsample weight times the total weight of the ovary) were determined for three subsamples per ovary and averaged to determine an overall estimate for each fish.

Spawning frequency estimate (SFE), the average number of days between consecutive spawning events (Kulaw 2012), determines how often a fish, in this case red snapper, releases ova in a season. Females may be classified, based on histological observations as either “day-0,” with fully hydrated oocytes or beginning signs of hydration, or “day-1,” with fresh post-ovulatory follicles (POF) present. Day-0 females are expected to spawn within 24 h and day-1 females have spawned in the past 24 h. However, very few (3) samples displayed clear signs of POF, so SFE estimates are only presented for hydrated individuals. Spawning frequency for this study was estimated using the standard equation for the hydrated oocyte method:

SFE = (total # mature females) / (total # day-0) (Hunter and Macewitz 1985)

Annual fecundity is the number of ova mature females release over the course of a season (Kulaw 2012). To calculate this, annual fecundity estimates were calculated as:

((# days in the reproductive season) / (SFE)) * (BFE) (Wilson et al. 1994)

Spawning was observed from April to September in this study, so 180 (thirty days X six months) was used as the number of days in the reproductive season.

Otoliths were collected for all retained individuals (n = 445). For all females and a random selection of five males/sampling event (if less than five males were captured, all were analyzed; altogether, n = 367 otoliths processed), the left sagittal otolith was weighed (± 0.0001 g) and sectioned by hand along the transverse plane adjacent to the core using an MTI Corp 150 low speed diamond saw. The portion of otolith containing the core was affixed to a slide using clear two-part epoxy, and, once set, the slide was mounted in a chuck and the otolith was thin sectioned using the low speed wafering saw. A drop of oil was added to the thin section to clarify annuli. Two independent readers assessed the age for each fish based on number of rings, margin status, and time of year captured. If the readers could not agree on the age of a sample, that sample would have been excluded from the analyses; however, the readers were able to agree on all age assignments.

Data Analyses

As previously mentioned, the observed sex ratio for *L. campechanus* in the GOM is approximately 1:1 (Collins et al. 1996, White and Palmer 2004, Brulé et al. 2010, Fitzhugh et al. 2012, SEDAR 2013). The sex ratio of red snapper was tested for each site and all sites combined with a Chi-square (χ^2) test (Sokal and Röhlf 1995). Assumptions of categorical data and independence were met prior to running the analyses.

A two-way analysis of variance (ANOVA) was utilized to compare TL, total weight, and age between sites (random) and quarters (fixed; beginning June 2014). A Tukey's HSD homogeneous subsets post-hoc test was used to identify sites/quarters which were statistically similar to one another. Assumptions of normality were visually assessed with Q-Q plots prior to running the analyses and all TL, weight, and age data were determined to be normally distributed. Levene's test was used to determine homoscedasticity (Sokal and Röhlf 1995) but was violated in all cases. Natural log and square-root transformations were attempted but the data failed to become homoscedastic in both cases (Sokal and Röhlf op. cit.). However, ANOVA is robust to these violations (Underwood 1997), so analyses were carried out using the untransformed data. Additionally, for only mature females, which were only observed during the first and fourth quarter of sampling (June-August 2014, March-May 2015), quarter could not be utilized as a factor; thus, a one-way ANOVA utilizing site was performed to detect differences in TL, total weight, and age due to site. Again, assumptions of normality were determined to be satisfactory by examining a Q-Q plot and, although variance was heteroscedastic, ANOVA is robust to this violation (Underwood op. cit.).

General linear model regression analyses were used to determine whether TL was a good predictor of eviscerated weight and/or age. Assumptions of relationship linearity, residual independence, residual variance homoscedasticity (evaluated with residual plot), and residual normality (assessed visually) (Sokal and Röhlf 1995) were satisfied. Total length (mm) and eviscerated weight (g) were ln-transformed prior to running length-weight or length-age regression analyses. Eviscerated weight was used in these analyses because it is a more consistent measure of body weight. All statistical analyses were performed using IBM SPSS statistics data editor, v22 (IBM Corp). All tests were considered significant at $\alpha = 0.05$. Means are presented with standard errors ($\bar{x} \pm SE$).

CHAPTER III

RESULTS

Size and Age Analyses

A total of 445 red snapper were sampled between June 2014 and May 2015 at four artificial reef sites in south Texas (Figure 2). Fish were captured from 19.7 to 40.0 m (65-132 ft) water depth (Table 1). Of the fish sampled, 367 (~82%) were retained for gonadal histological examination, while the others were discarded due to small size (<350 mm) or target catch number being achieved, in which case those fish kept were randomly selected. Some small fish (<350 mm total length) were retained to estimate the lower end of age-and size-at-maturity (n = 8). Of all the fish retained, 204 were male and 163 were female. Across all sites and quarters, χ^2 analyses revealed a sex ratio that differed significantly from 1:1 ($\chi^2_{(0.05,\ 1)} = 4.14$, $p = 0.042$; Figure 4, Table 4); ~25.2% more males were captured than females. Individual χ^2 tests for each site were only significantly different from 1:1 at PS-1070 ($\chi^2_{(0.05,\ 1)} = 9.50$, $p = 0.002$; Figure 5), indicating the disparity in sex ratio at PS-1070 was unique among all sampled sites and contributed heavily to the significance of the overall sex ratio (Figure 4). At PS-1070, ~66.7% more males were captured than females. A trend of more females than males at nearshore sites was not significant (Figure 5).

Across all sites and quarters, *L. campechanus* from this study were 451.20 ± 4.05 mm TL (Figure 6). Note that the number of individuals in this case was 445 instead of the 367 fish kept for the histological approach because additional fish (78) were measured and released in situ. A two-way ANOVA found significant differences in TL due to site ($F_{(3, 429)} = 18.832$, $p < 0.001$) (Figure 7) but not quarter ($F_{(3, 429)} = 0.725$, $p = 0.538$). A Tukey's HSD homogenous subsets test grouped offshore sites (PS-1070 and PS-1122) together, while inshore sites (PS-1047 and PS-1169L) were significantly different from offshore sites and from one another (Figure 7). Red snapper were shortest at PS-1169L (370.64 ± 6.775 mm), ~20.8% longer at PS-1047 (447.82 ± 5.742 mm), and longest offshore, about 28.7% and 6.5% longer than at PS-1169L and PS-1047, respectively (476.88 ± 5.240 mm for both sites combined; Figure 8A).

On average, *L. campechanus* in this study weighed 1.42 ± 0.39 kg (Figure 9). Results from a two-way ANOVA yielded significant differences in total weight due to site ($F_{(3, 429)} = 13.452$, $p < 0.001$) (Figure 10), but not quarter ($F_{(3, 429)} = 0.195$, $p = 0.900$). A Tukey's HSD post-hoc test revealed the same pattern as TL data; fish weight was significantly different from all other sites at PS-1169L and PS-1047, and similar for PS-1070 and PS-1122. Individuals were lightest at the most nearshore, southern site (PS-1169L; 0.78 ± 0.06 kg), ~70.8% heavier at PS-1047 (1.33 ± 0.05 kg), and heaviest offshore, where fish were ~112.1% and 24.2% heavier than at PS-1169L and PS-1047, respectively (1.65 ± 0.05 kg for both sites combined; Figure 8B).

For the remaining measurements, values are only reported for those fish retained for histological examination (n = 367), thus the difference in number of fish for TL/total weight. Regression analyses were significant for all sites combined ($r^2 = 0.965$ $F_{(1, 363)} = 9{,}857.56$ $p < 0.001$), as well as for each site (Table 5, Figure 11), supporting the strong relationship between TL and weight.

Fish in this study were, on average, 3.8 ± 0.8 years old (n = 256; Figure 12). A two-way ANOVA revealed significant differences due to site ($F_{(3, 240)} = 28.865$, $p < 0.001$) and quarter (F

$_{(3, 240)}$ = 3.122, p = 0.027) (Figures 13 and 14). Tukey's HSD multiple comparisons test revealed that fish ages separated into the same site categories as with TL and eviscerated weight. Age at PS-1169L was significantly different from all sites, as were fish from PS-1047, while PS-1070 and PS-1122 comprised a third and statistically similar group. Closer examination revealed that mean age followed the same pattern as TL and eviscerated weight; that is, fish were youngest at PS-1169L, older at PS-1047, and oldest at offshore sites (Figure 13). Red snapper were youngest at PS-1169L (2.43 ± 0.09 years) and ~45.7% older at PS-1047 (3.54 ± 0.10 years). Offshore fish were oldest; ~71.2% and ~24.4% older than fish at PS-1169L and PS-1047, respectively (4.45 ± 0.13 years for both sites combined; Figure 8C). Although quarter was a significant factor in the ANOVA, Tukey's HSD homogeneous subsets test grouped all quarters into one group (Figure 14).

Reproductive Biology

Total length, total weight, and age were reassessed for mature female *L. campechanus* using one-way ANOVAs (for TL, F $_{(3, 39)}$ = 5.945, p = 0.002; for total weight, F $_{(3, 39)}$ = 5.380, p = 0.003; for age, F $_{(3, 39)}$ = 5.553, p = 0.003) and Tukey's post-hoc tests. The patterns for TL and age were similar to those observed above; PS-1169L was significantly different from all other sites ($p < 0.025$ in all pairwise comparisons), while PS-1047, PS-1070, and PS-1122 were similar to one another ($p > 0.119$ in all pairwise comparison). However, the pattern for total weight was slightly different; a post-hoc test found significant differences between PS-1169L and PS-1047/PS-1070 (p = 0.027 and p = 0.007, respectively), but not PS-1122 (p = 0.075). No other pairwise comparisons were significantly different from one another. Despite these groupings, the pattern is the same as for the general population; fish were smallest and youngest at PS-1169L, larger and older at PS-1047, and largest and oldest offshore (Figure 15).

Only the most common ages (2, 3, 4, and 5 years) were used in length-age analysis due to low sample size at younger (< 2 years) and older (> 5 years) age groups resulting from the SEAMAP sampling protocol. Again, the results were significant overall ($r^2 = 0.432$, $F_{(1, 76)} = 57.867$; $p < 0.001$); however, an r^2 value of < 0.5 indicated that length was not a very good predictor of age (Figure 16).

Histological examination of gonads occurred for 163 females and 83 males collected from June 2014 to May 2015 in south Texas. Based on histological observations, the spawning season occurs from April to September in the area of study, with peak reproduction occurring in June for 2014 (Figure 17A). Of the 246 red snapper collected for histological examination, 91 females and 41 males occurred during the spawning season (June-August 2014 + April 2015; no samples were collected in September 2014 due to unsafe weather conditions and only males were captured in May 2015). Overall, 48.4% of females possessed vitellogenic cells (Figure 18) see Table 3 for characteristics), the benchmark for maturity, and 24.2% showed signs of imminent spawning (late vitellogenic, hydrated, or postovulatory follicles; for examples see Figures 19 and 20). Postovulatory follicles were only identifiable in two individuals, and, thus, not a reliable source of information for this study. In 58.3% of the males, continuous germinal epithelium (CGE) was observed during the spawning season determined in this study (Figure 21).

The smallest mature female was 347 mm long (PS-1070) and the smallest mature male was 348 mm long (PS-1169L). The length at which 50% of the population was mature (L_{50}) occurred at the 350 mm size class for females (n = 4), but varied from ~33-46% maturity from the 400 mm size class to the 550 mm size class (Figure 22). At 600 mm, 75% of the female population was mature, but 100% maturity-at-length could not be determined for females in this study. For males, L_{50} occurred at the 350 mm size class (n = 2) and averaged 52% maturity between 350-500 mm, before abruptly shifting to 100% maturity by 550 mm (Figure 23).

Age was, in general, a better predictor of maturity than size. The youngest mature female was 2.9 years old, and the youngest male to reach maturity was 2.0 years old. The age at which 50% of the individuals in this study were capable of reproduction (A_{50}) occurred at age 5 in females (Figure 22) and age 3 in males (Figure 23). Female and male *L. campechanus* reached 100% maturity by ages 8 and 6, respectively.

Spawning readiness in mature females was measured with GSI values, where values greater than one coincide with peak reproductive readiness during the spawning cycle (Hunter and Macewitz 1985). Overall, mean GSI value was 0.81 ± 0.12. Mean GSI was highest in April 2015, at the onset of the spawning season, and lowest in July 2014 (Figure 17A). Individuals collected from PS-1169L, the southernmost nearshore site, displayed the highest mean GSI, followed by PS-1122 (the southernmost offshore site), then PS-1047 (the northernmost nearshore site), with the lowest values observed at PS-1070, the northernmost offshore site (Figure 24). GSI values greater than 1.0 were observed in April (Figure 17A). However, lower GSI values and no evidence of spawning was observed in March 2015.

Batch fecundity (BFE) was calculated for each fully hydrated red snapper (n = 19). Fully hydrated oocytes, indicative of imminent spawning (within 24 h) were observed at all sites, but were observed more frequently at nearshore sites (n = 13) vs. offshore sites (n = 6). The smallest female with hydrated oocytes was 366 mm long and 2.9 years old, while the longest, oldest hydrated individual was 658 mm long and 6.0 years old. Mean BFE was 16,995 ± 4,549 ova per spawning event. Due to low sample size of hydrated individuals, BFE could not be statistically compared among sites, TL, weight, or age; however, general trends are presented here. It is important to note that BFE generally increased with size and age (Figure 25), but generally decreased with distance from shore (19,215 ± 12,548, 17,122 ± 7,084, 16,727 ± 3,387, and 10,904 ± 2,692 ova/spawning event at PS-1169L, PS-1047, PS-1070, and PS-1122, respectively) (Figure 26A) despite observing larger females offshore (Figure 15). One extremely fecund individual (producing ~78,890 ova/batch) at PS-1169L was an outlier (Figure 26A). When removed, BFE from PS-1169L most closely resembled that site's offshore counterpart, PS-1122 (Figure 26B). Batch fecundity, for the most part, also increased with age (15,044 ± 9,582, 18,401 ± 9,558, 17,765 ± 6,027, and 20,539 ± 5,342 ova/spawning event for ages 3, 4, 5, and 6, respectively). Mean BFE without the outlier changes to 5,924 ± 3,390 ova/spawning event for age 3 fish, reinforcing this general trend.

It total, 43 mature female *L. campechanus* were used to estimate spawning frequency. Of these, ~44.2% (n = 19) showed signs of yolk coalescence and/or hydration, indicative of an imminent spawning event (Figures 19 and 20). No females with the simultaneous presence of yolk coalescence/hydration and post ovulatory follicles were observed in this study. On average, spawning was estimated to occur every 2.2 d and ~84 times/spawning season (Table 6). SFE generally increased with age among 3-5 year old females (Table 6), with age 6 females producing eggs more frequently, excluding the age 3 outlier. A lack of imminent spawners above this age made it impossible to estimate SFE at older age classes (6+ years). Additionally, SFE generally increased with distance from shore (Table 6).

Across all sites, mature *L. campechanus* from this study produced an estimated 1,815,805 ± 653,966 ova/year (range: 99,464-12,137,052). When considering annual fecundity estimate (AFE), the results vary, depending on whether or not the exceptionally fecund outlier was removed from the sample. When removed, AFE generally increased with size and age (Figure 27) and decreased with increasing distance from shore (Figure 28A). However, when the extremely fecund outlier was removed, these patterns were less evident (Figure 28B). For the sake of brevity, the following discussion focuses on the data with this outlier included.

CHAPTER IV

DISCUSSION

The goal of this study was to provide the Texas Parks and Wildlife Department with important information regarding the reproductive biology of red snapper, *L. campechanus*, on artificial reefs in the Gulf of Mexico, and contribute to the ongoing debate concerning the attraction of red snapper to artificial reef structures. In addition, this study helps to fill a data gap in red snapper reproductive status between the Campeche Banks in Mexico and the Northern Gulf of Mexico, including northern Texas, Louisiana, Mississippi, Alabama, and Florida. To this end, red snapper were collected from four artificial reefs in south Texas and biologically examined to gain a deeper understanding of their reproductive habits.

Size and Age

Red snapper were shortest, lightest, and youngest at PS-1169L, the southernmost nearshore site in this study (e.g., Figure 8). PS-1169L is the most frequented by anglers (recreational/charter boats; pers. obs.). At offshore sites, where fishing is only permitted 3-30 days/year, mean length, weight, and age were significantly higher. These results may reflect fisheries-induced size and age truncation (Trippel 1995) at nearshore sites, or could simply be an effect of ontogenetic shifts from nearshore to more offshore habitat as individuals grow larger and older (Bradley and Bryan 1975, Gallaway et al. 2009, Cowan et al. 2010). Sizes and ages observed in this study suggest a truncated size/age distribution due to a lack of older, larger individuals (no individuals > 10 yrs, 5,250 g, or 714 mm compared to maximum observed values; Wilson and Nieland 2001), which is a sign of a stressed fishery (Cowan et al. 2010, Saari 2012). However, sampling sites are relatively nearshore (< 32 km from shore), so these exceptionally large individuals simply may not occur in these shallow waters (<40 m water depth). No other fishery-independent data set exists for this area, so these data should be considered a baseline.

In terms of size, female *L. campechanus* in this study were 464.07 mm long (range: 286-705 mm) and weighed 1,421 g (range: 370-4,990 g). Comparatively, Kulaw (2012) observed a mean length of 500 mm (range: 235-864 mm) and mean weight of 1,915 g (range: 176-9,527 g) off the coast of Louisiana, while Brulé et. al. (2011) observed a median length of ~474 cm (range: 272-833 mm), with weights ranging from 450-8,850 g off the Campeche Banks. These differences, while not major, particularly for TL, could be attributed to distance from shore (and corresponding water depth). Red snapper in this study were caught in 19.7-40.0 m depth (< 32 km from shore) (Table 1) while Kulaw (2012) captured *L. campechanus* at 70.1-85.3 m water depths (129-161 km from shore), and Brulé et al. (2011) sampled fish from 43-130 m water depth. Saari (2012), who also performed fishery-independent analyses, and in the same area as Kulaw (op. cit.) (Louisiana's continental shelf), observed values only marginally larger fish than those observed in this study (~486 mm long and ~1,760 g). The fact that red snapper generally move offshore as they grow (Szedlmayer and Shipp 1994, Wells and Cowan 2007) may explain why heavier fish were not captured in this study compared to these others.

It is noteworthy that studies which rely on fisheries data are inherently skewed to larger sized fish. Indeed, White and Palmer (2004) found significantly larger fish in fishery-dependent samples. As such, most studies do not report these general statistics. In fact, the lower end of the juvenile spectrum could not be observed in this study due to the size of hooks used. Both Saari (2012) and Kulaw (2012) deployed chevron traps to obtain fish which would generally be too small to capture on a hook and line, while this study was limited to vertical line survey. Despite this, similar minimum sizes and similar mean TL between red snapper observed in this study compared to others (see above) indicate that fish in south Texas are at least similar in size structure to surrounding populations.

In terms of age, the results of this study are similar to others (Nieland et al. 2007, Kulaw 2012, Saari 2012) where age two to five red snapper dominate the frequency distribution (Figure 12). Overall, there was a significant effect of quarter on age in this study (Figure 14); however, a post-hoc analysis did not reveal any significant groupings of quarters. However, by examining Figure 14, it seems mean age may have been higher in the first quarter (June-August 2014) of this study, but it was highly variable. It is possible that older, more experienced individuals congregate near artificial reefs in the summer to spawn, then venture away from the reefs outside of the spawning season (perhaps to forage), leaving primarily young red snapper which require more protection than these more experienced individuals. Interestingly, *L. campechanus* size is not a very good predictor of age (Nieland et al. 2007, Saari 2012, Figure 16), which is reinforced by similar lengths and weights among quarters. This is unfortunate for fishery managers, as age seems to be a much better indicator of maturity compared to length.

Reproductive Biology

Of the 91 female red snapper collected during the spawning season, approximately 48% were capable of spawning, and 24% within 24 h of a spawning event. Kulaw (2012) observed a similar albeit smaller percentage of imminent spawners (19%) but observed a much higher proportion of vitellogenic females (91%). These discrepancies are likely an effect of fishery-dependent vs. fishery-independent data. Mean total length of females (560 ± 5 mm; Kulaw op. cit.) vs. 464 ± 6 mm (this study) and associated mean age were lower in this study, likely due to smaller fish being retained. Similarly, a higher percentage of mature females can be attributed to larger *L. campechanus* being more likely to have reached maturity compared to smaller individuals.

On average, the youngest, shortest mature females (2.43 ± 0.09 years, and 368.67 ± 6.33 mm) were captured at PS-1169L while the oldest mature females were captured at PS-1122 (4.73 ± 0.27 years), and the longest at PS-1070 (466.98 ± 5.60 mm) (Figure 15). Despite this, mean GSI values were generally higher at nearshore sites compared to their offshore counterparts (Figure 24). This result suggests a life history strategy that involves *L. campechanus* moving inshore to spawn as observed by Bradley and Bryan (1975), and is further supported by one extremely fecund female captured at PS-1169L (3 years old, 416 mm TL, 1,024 g eviscerated weight, producing ~78,890 ova/batch). However, if true, one would expect that mean size and age would be similar between mature females at nearshore and offshore sites in the summer, indicating that offshore fish had migrated inshore to spawn. The results did not reflect this; mature females were, on average, significantly heavier and older at offshore sites, regardless of quarter. Bradley and Bryan (1975) observed a partial inshore migration pattern during spring and summer months among red snapper along the Texas coast (based on catch rates and mean sizes at various depth ranges). However, studies focused on red snapper movement detected relatively high site fidelity with no back-and-forth movement between reefs or patterns consistent with seasonal migration (Szedlmayer and Schroepfer 2011, Garcia 2013). Specifically for PS-1047 and PS-1022, Garcia (op. cit.) observed maximum residencies of 180 and 208 d, respectively. Thus, it is possible that smaller, nearshore spawners remain closer to the reef to spawn, affording more protection for the mother but a higher risk of predation for the eggs, while larger, more fecund offshore females, which are not as vulnerable to predation, may venture farther from the reef to spawn, minimizing the initial risk of predation from other reef-dwelling species.

If true, it is also possible that mean GSI offshore is actually higher among spawning females, but capturing these females is less likely, given that fishing efforts took place adjacent to artificial reefs. This idea is further supported by a smaller percentage of females captured at offshore sites, especially at PS-1070 where males were 67% more common (Figure 5) and the largest mature individuals were observed, of which only four (of ten) displayed hydrated oocytes. Additionally, slightly more females than males were observed at nearshore sites, although not significantly so (Figure 5). If *L. campechanus* reproduce away from the reef, sampling with large fish traps or trawling nearby the reef may permit better estimation of spawning characteristics for fish at these sites. However, in either case, nearshore spawners seem to be an essential portion of the spawning population in south Texas contributing 2,198,033 ± 933,930 ova/individual/year (or 1,353,892 ± 458,871 ova/individual/year excluding the outlier), ~175% more than offshore fish (799,946 ± 183,679 ova/individual/year). Given the affinity of these red snapper to reproduce adjacent to artificial reefs, one may conclude that a lack of physical structure in the nearshore environment could limit the reproductive success of this community. Unexpectedly, AFE was highest nearshore, where most fishing occurs, with the most heavily fished site (PS-1169L) producing ~92.3% than the next most productive (and second most fished) site, PS-1047 (~2,964,628 vs. ~1,540,952 ova/individual/year).

Evidence exists for a latitudinal gradient of GSI; that is, individuals captured at southern sites were more ready to spawn than their northern counterparts, respective to shore locality (Figure 24; see Figure 2 for site reference). However, this latitudinal gradient is in reverse of the gradient observed by Brulé (2010) and Kulaw (2012), where the highest GSI values occurred in the northernmost portion of the GOM and lowest in the southernmost portion. Importantly, the distance among sites in this study (< 32 km) was much smaller than those studied by either Brulé et al. (op. cit) Kulaw (op. cit.) (< 80 km compared to the entire width of the GOM, ~1500 km), and could thus be a local phenomenon, attributable to differences in associated biomass or site composition. For example, PS-1047 and PS-1070 enjoy much higher densities of pelagic fish biomass compared to their southern conspecifics (33.5 ± 15.3 and 1,445.8 ± 525.2 g/m^2 at PS-1047 and PS-1070 vs. 2.7 ± 0.6 and 2.4 ± 1.1 g/m^2 at PS-1169L and PS-1122, respectively; Bollinger 2015). Thus, locally, GSI could depend more on stocking density than latitude. That is, *L. campechanus* in areas with lower biomass likely experience less competition for food resources, and, thus, have more energy available for egg production. Further, Nikolsky (1963) reported that when food is limited males predominate the community. A biomass per area of red snapper and its niche competitors that is high enough to limit food availability could also explain the disproportionate amount of males observed at PS-1070.

To provide context, consider that the observed mean GSI was most similar to south Texas samples taken by Kulaw (2012; GSI = 0.81 ± 0.12 in this study vs. 1.08 ± 0.05), compared to all ports sampled (six sites from the Florida Keys to south Texas). This minor discrepancy could be an effect of smaller sample size (n = 42 mature females in the present study compared to n = 182 mature individuals in Kulaw (op. cit.)), annual variability in environmental conditions/prey availability, or collection methods. Larger, and presumably older, fish are also better represented by samples from the recreational fishery (as in Kulaw (op. cit.)). Additionally, results from Kulaw (op. cit.) included twice as many June samples as July/August samples. GSI values from June in the present study were 59.6% greater than those observed in July/August (July/August GSI = 0.52 ± 0.11, and June GSI = 0.83 ± 0.19; Figure 17A); thus, the overall mean observed in both studies could be heavily influenced by unequal sample sizes among months. GSI values from this study are very similar to those observed on the Campeche Banks by Brulé et al. (2010), who observed GSI values ranging from 0.82 ± 0.54 to 1.02 ± 0.88 from July to September (compared to 0.49 ± 0.05 to 0.89 ± 0.22 in this study). Thus, in context, these results are consistent with the latitudinal gradient of GSI described by Kulaw (2012) and Brulé et al. (2010).

On average, spawning was predicted to occur every 2.2 days, and 80 times per spawning season in this study, which is similar to findings from other studies (Collins et al. 2001, Fitzhugh et al. 2004, Brown-Peterson et al. 2008). In general, SFE was estimated to increase with distance from shore, ranging from 1.5 d at nearshore sites to 3.5 d at offshore sites. Additionally, SFE was estimated to increase with age, from 1.3 d at 3 years (n = 10) to 2.4 d at 5 years (n = 12). This is almost twice as often as reported by Kulaw (2012), who observed a spawning frequency of 3.6 d at age 4 increasing to 5.4 d at age 5 and 5.2 d at age 6 in south Texas. However, sample size (in relation to mature females) was relatively low in this study, and, thus, not as reliable (n = 43 mature females during the spawning season vs. n = 182 females in Kulaw op. cit.). Additionally, Collins et al. (2001) observed a 50% increase in spawning frequency in fish older than 6 compared to age 3, 4, and 5 year red snapper. In this study, spawning frequency generally decreased with age to age 5, after which spawning was most frequent (1.5 d for age-6 fish; n = 2), indicating that the phenomenon of marked SFE increase in older fish observed by Collins (op.

cit.) and Kulaw (2012) may exist in south Texas, but a relatively small sample size at-age calls for additional efforts to either support or refute this.

Similarly, BFE generally decreased with distance from shore (Figure 26). Put simply, nearshore *L. campechanus* produce more eggs per batch compared to their offshore conspecifics. However, for PS-1169L, PS-1047, and PS-1070, the difference in batch fecundity was minimal (mean ranges from ~16,268 to ~19,215 ova/spawning event/fish), and when the extremely fecund outlier was removed, BFE at PS-1169L drops from ~19,215 to just ~7,280 ova/spawning event/fish. This result is most similar to PS-1122 (~10,904 ova/spawning event/fish) and suggests a latitudinal gradient of BFE, with northern sites contributing more than twice the number of ova/batch than southern sites (16,978 vs. 8,316 ova/spawning event/fish, respectively), which is consistent with a higher BFE in north Texas compared to south Texas (118,746 vs. 107,745 ova/spawning event/fish, respectively) observed by Kulaw (2012).

These results contradict the hypothesis that larger offshore fish would contribute more eggs to the population than smaller nearshore fish. It is true that, in general, larger (older) fish produced more ova than smaller fish (Figure 27), but most active reproduction was observed nearshore (13 hydrated individuals nearshore vs. just 6 offshore) and the highest productivity was observed nearshore (Figures 26 and 28) where individuals were significantly smaller (Figure 15). There are some uncertainties, then, which must be assessed for this population before further conclusions may be drawn. First is the possibility that offshore females are, in fact, producing more offspring than nearshore fish, but for some reason the study design was not able to detect this, as discussed above. A second uncertainty in these results is egg quality, which was not assessed for these sites. Evolutionary pressures of fisheries-inducted size selection may burden younger, smaller fish to produce more eggs than they would naturally (Trippel 1995). Red snapper utilize their energetic resources differentially at different stages in their lives. Young fish utilize the bulk of their resources for growth, using almost none for reproduction (Bohnsack 1990). As the fish attains a size refuge, growth dramatically slows and a much larger portion of their resources become dedicated to reproduction. Without sufficient developmental time, it is likely that the young fish observed reproducing in this study produce lower quality eggs than their larger, offshore counterparts. Further, Woods et al. (2003) suggest that fish experiencing sub-optimal environmental conditions may reproduce as younger age and smaller sizes, which may be the case in the present study (discussed in more detail later). Additionally, Trippel (1995) notes that fish which start reproducing at young ages tend to be less productive over the course of a lifetime.

Given that young fish move offshore as they get older and larger, it is likely that offshore fish represent a former nearshore cohort. If so, another possible explanation of these unexpected results could entail nearshore fish being pressured into reproducing at an earlier age, while fish at offshore sites, which experience much lower levels of fishing pressure, can energetically afford to minimize reproductive efforts due to sub-optimal spawning conditions, or opt out of reproduction completely. This line of thought is also in agreement with an observation put forth in other studies (e.g. Rideout and Tomkiewicz 2011, Kulaw 2012, Glenn 2014) which suggests that not all mature females are reproductively active at all times during a given spawning season (discussed in more detail later), and the idea put forth by Trippel (1995) that early spawners produce fewer eggs over a lifetime.

Length- and Age-at-Maturity

Female *L. campechanus* in this study matured at the upper end of the length-and age-at-maturity spectrum presented in other studies throughout the GOM. For example, the shortest female red snapper to reach maturity in this study had a TL of 347 mm. This is longer than those observed in other studies (286 mm in Alabama (Woods et al. 2003), 312-320 mm in Louisiana (Kulaw 2012)), but only two females were captured below this length (299 and 320 mm long). Thus, maturation may occur below 347 mm in south Texas. Similarly, L_{100} (≥ 700 mm) fell within the range of values observed in other studies (435-820 mm; Render 1995, Collins et al. 1996, Fitzhugh et al. 2004, White and Palmer 2004, Brulé et al. 2010, Kulaw 2012). The only other study which has examined length-and age-at-maturity in south Texas (Kulaw op. cit.) found an L_{100} of 700 mm and an A_{100} of 7 years which is very similar to the one observed in this study (L_{75} = 700 mm, A_{100} = 8 years) and other studies outside this region (Schirripa and Legault 1999, White and Palmer 2004, Jackson et al. 2007), and validates the results of this study (despite a somewhat smaller sample size than reported in other studies). The minimum observed age at maturity in this study was 2 years, which is consistent with other studies (Futch and Bruger 1976, Woods et al. 2003, Fitzhugh et al. 2004, White and Palmer 2004, Kulaw 2012). Additionally, L_{50} was reached in the smallest size class at which mature males were observed in this study (350 mm) which is consistent with findings from other studies (White and Palmer 2004, Brown-Peterson et al. 2009, Brulé et al. 2010).

This delayed maturation schedule is interesting, given that all of the actively spawning females observed at PS-1169L were 3 yrs old and most (5 of 6) actively spawning individuals at PS-1047 were < 4 yrs old (Figure 22). Thus, although 50% of individuals are not mature until age 5, it seems that younger fish are reproducing the most. If fish reproduce at younger ages to compensate for fisheries-induced selection processes, perhaps they rest their ovaries in subsequent years, when environmental conditions are not as conducive to spawning. This is consistent with finding from Trippel (1995), who suggests that fish which breed at earlier than "natural" ages tend to produce fewer eggs over the course of a lifetime.

Additionally, Kulaw (2012) observed a pattern in maturity schedules of *L. campechanus* off the west coast of Florida that is similar to the one estimated in this study. She (op. cit.) found that females in this area reached L_{100} much more slowly than their western (and northern) conspecifics. In particular, red snapper collected at the docks in Clearwater, Fl, which is on a similar latitude to south Texas (27.9736° N in Clearwater, Fl vs. 26.5556° N in Port Mansfield, Texas), reached 50% maturity in females by age 3, with only 26% of females between 525 and 775 mm displaying signs of reproductive activity. Similarly, *L. campechanus* from this study reached 50% maturity at 350 mm (n = 4), although percent maturity from 350-550 mm averaged 42% (Figure 23).

Kulaw (2012) suggested that these fish reached maturity, but, for some reason, were not reproductively active. This has also been postulated for red snapper by Glenn (2014) and has been documented for other species (Morgan and Lily 2006, Rideout and Tomkiewicz 2011). This could be the case in south Texas, as well. For example, mean GSI in April 2015 was the highest observed in any month. Previous studies consistently show June and July to be the peak months for reproduction throughout the northern GOM (Woods et al. 2003), while one study in the Dry Tortugas, Fl, observed two spawning peaks, in July and September, within a season (Brown-Peterson et al. 2008). Although only one GSI peak was evident in 2014 (June; Figure 17), a GSI value greater than one indicated another peak in reproduction in April of 2015.

This result presents three scenarios. In one, there is a spawning peak in April and June. However, if two spawning peaks were present, one would expect an early peak (suggested by April) and later peak (July-September), as observed by Brown-Peterson et al. (2008).

Additionally, only one peak can be observed in the studies surrounding this area (Collins et al. 2001, Brulé et al. 2010, Kulaw 2012). In another scenario, spawning peaks in April and gradually declines until October. This is possible, but has been previously unreported, and is thus less likely. In the final scenario, which seems most likely to this author, spawning conditions may be better in 2015 compared to 2014, and, thus, females were more reproductively active. Support for this scenario comes from Porch (2004), who observed significant differences in maturity schedules through consecutive spawning seasons, with no clear trend between years. One possible explanation for this difference could be prey availability between years. Studies have demonstrated the link between nutrient availability and fecundity in red snapper (Bohnsack 1990, Glenn 2014) and other species (Rideout and Tomkiewicz 2011); thus, if 2015 yields higher levels of available prey, reproductive output would increase accordingly. If true, this would reinforce the idea that some mature individuals rested their ovaries in 2014 (as discussed above).

Further, *L. campechanus* spawn when temperature and photoperiod conditions are adequate. Mean sea surface temperature was 3.2°C cooler in April of 2014 (20.4°C) compared to April of 2015 (23.6°C), which was more similar to May 2014 (23.7°C) (temperature data for Port Isabel waters obtained from National Weather Service, National Data Buoy Center, Bldg. 3205, Stennis Space Center, Missouri 39529, personal communication, November 2015). Thus, spawning conditions may have been favorable earlier into 2015, allowing red snapper a jump start on the spawning season. Unfortunately, no red snapper were collected prior to June, so it was not possible to validate this.

Artificial Reefs as Supplemental Habitat

One of the primary purposes of this study was to determine whether artificial reefs play an important role in red snapper reproduction in south Texas. While the concept of attraction or production carries substantial theoretical weight, it inherently pins artificial reefs against natural reefs. In this study, however, the role of natural reefs is likely to be minimal, given the relative proportion of these reefs to artificial structure nearshore in south Texas. Given that *L. campechanus* are highly associated with vertical structure (Wells and Cowan 2011), removing all artificial reefs from the system would leave very little habitat that meets the structural requirements for survival and growth of not just red snapper, but the entire GOM reef fish complex.

In the Pleistocene Era, algal reefs dominated the nearshore Texas coast (Dennis and Bright 1988). In fact, although sea level rise has moved the Texas coast westward, these areas are still known as bountiful offshore *L. campechanus* fishing grounds (Bright and Rezak 1975). One might infer that, historically, red snapper used these areas for refuge and food as they made their eventual journey offshore. This inference is substantiated somewhat by annual historical *L. campechanus* landings of more than 5.4 million kg (12 million pounds) in the early 1900s (Porch et al. 2004), although, admittedly, little is known concerning the evolutionary origins of *L. campechanus*.

Further, the dietary, refuge, and nutrient contributions of artificial reefs are well-documented (Szedlmayer and Lee 2004, McCawley et al. 2006, Jenkins et al. 2008). In light of the observations above, combined with the simple act of capturing actively spawning individuals adjacent to artificial reefs, and reported site fidelities of 208 and 180 d on PS-1122 and PS-1070, respectively (Garcia 2013), this author feels comfortable saying that red snapper utilize artificial reefs to their advantage. Unfortunately, this characteristic makes *L. campechanus* very easy to target, and, as a result, is somewhat of a double-edged sword. Thus, the inherent problem with the attraction/production debate is neither attraction nor production, but, rather, fisheries management. Perhaps some artificial reefs should be created or declared as marine reserves. Alternatively, artificial reefs could be treated as essential spawning areas during certain times of the year (mid-summer). Independent of whether red snapper are attracted to structure or fisheries are enhanced by structure is irrelevant to this discussion; at this point, artificial reefs are an essential component to *L. campechanus* recovery. The next step should be to determine the best configurations (structures) to achieve specific management goals, and to encourage connectivity between natural reefs and other artificial reef areas.

Further support for the idea that artificial reefs are an important component of the GOM ecosystem is rooted in the fact the mean age increases with artificial reef age until a climax community is observed (mean age levels off around 4.5 yrs in red snapper when reefs have been deployed 8+ yrs; Figure 29). This lends support to Syc and Szedlmayer (2012), who observed a significant positive correlation in mean age of red snapper compared to resident reef age and argued compellingly that this correlation, in combination with long-term residence (Szedlmayer and Schroepfer 2011, Garcia 2013), is evidence that artificial reefs actually enhance fisheries production in the Northern GOM.

Conclusions and Recommendations

Minimum size restrictions on red snapper, originally intended to protect the reproductive potential of a population (Donaldson and Donaldson 1992), are too low to provide a substantial probability that sub-legal fish even have a shot at reproduction. For example, mean size for age-

2 *L. campechanus* was 378.78 ± 5.73 mm, which is a similar length to the minimum legal size for red snapper, which ranges from 330.2 mm (13 in) to 406 mm (16 in), depending on the fishery. However, females did not reach 50% maturity until age 5 in this study, which averaged ~515 mm TL. Based on these results, if *L. campechanus* size restrictions are intended to protect the reproductive potential of red snapper populations, minimum size restrictions must be increased dramatically in south Texas. That said, a possibility exists that alternative management strategies may be more efficient. For example, based on batch fecundity at size and age, *L. campechanus* produce more eggs at larger sizes and ages (Figure 25). This is supported and expanded upon by other studies (Bohnsack 1990, Collin et al. 2001, Kulaw 2012).

Collins et al. (op. cit.) found an exponential relationship between batch fecundity and age/length, with females 6+ years of age spawning ~50% more often than fish 5 and younger. Because the reefs in this study were relatively nearshore, very few large reproductively active fish were obtained in this study (n =3 hydrated individuals > 600 mm TL). Only two age-six spawning-imminent females (and none older) were captured in this study, the age after which Collins et al. (2001) observed a dramatic increase in reproductive output. Thus, even if the exponential relationship between batch fecundity and red snapper size/age exist at these sites, it could not be observed in this study. Furthermore, size-selective harvest places evolutionary pressures on fish to grow slower and reproduce at smaller sizes and younger ages (Trippel 1995; Jørgensen et al. 2008), which has occurred in *L. campechanus* (Cowan et al. 2011). For example, ~57.9% of hydrated individuals were captured nearshore and accounted for approximately 86.3% of total egg production (~3.5 y old and ~442.5 mm long nearshore vs. ~5.3 y old and ~552 mm long offshore). Altering phenotypic characteristics of fish populations (i.e., growth rate, size, and age through selective harvest) reduces the spawning biomass and likely alters the timing and duration of reproductive events, which carries negative consequences for recruitment (Anderson et al. 2008; Wright and Trippel 2009). Thus, implementing a maximum size restriction, or slot size restriction, may more effectively protect the reproductive potential of the population compared to current regulations.

Furthermore, in Texas, no seasonal closures exist for *L. campechanus*. A temporary moratorium in the summer, when red snapper spawning activity peaks, could enhance recruitment and expedite stock recovery. As batch fecundity, annual fecundity, and spawning frequency were highest nearshore (Table 6, Figures 26 and 28), where no moratorium exists, implementing this measure could have a profound effect on the local population, both nearshore and offshore. However, a relatively high mean GSI value at PS-1122 (Figure 24) indicates the potential for high reproductive productivity offshore, as well. The federal recreational *L. campechanus* season occurs in June each year, when red snapper reproductive efforts peak (Woods et al. 2003, Kulaw 2012, Figure 17; spawning peak may vary in south Texas depending on environmental conditions, as above). Shifting this open season to late winter or early spring, when fish are heavy from winter growth and reproductive efforts have not reached their peak, or fall, when reproductive efforts diminish, could increase recruitment and expedite recovery.

In addition to enhancing recruitment through seasonal closures and slot-limits, supplementing habitat (i.e., artificial reefs) may enhance *L. campechanus* production under the assumption that habitat availability limits population success. However, whether red snapper year classes are limited by habitat availability or number of recruits is still unclear (Cowan et al. 2011), and is most likely a function of both. Nonetheless, managing stocks for both scenarios is prudent. Artificial reef construction supplements habitat availability, whereas slot-limits and moratoriums (during the breeding season) are intended to increase recruitment. It is important to note, however, that *L. campechanus* size-at-maturity varies geographically, so determining appropriate slot-limits for each area may be critical.

Future Studies

Future studies should focus on obtaining more samples during the summer months, when spawning occurs, while minimizing sampling intensity in the late fall and winter, to reduce impact on the local fishery. Additional sampling methods should be employed offshore, either large fish traps or bottom trawls, to capture females which may not associate with artificial reefs while spawning. It is important to study this portion of the breeding stock, which may have been missed in this study, because previous studies suggest these larger offshore females contribute disproportionally more to reproduction than their nearshore counterparts (Bohnsack 1990, Cowan et al. 2012, SEDAR 2013). In addition, fishing effort should occur in the afternoon and evening, when possible, as red snapper tend to spawn in the afternoon/evening (Chesney and San Filippo 1994, Jackson, Nieland, and Cowan 2006). Alternatively, given that POF are resident for ~24 h, fishing could occur in the early morning, just after *L. campechanus* have spawned. However, POF tend to breakdown relatively fast (to the lifespan of hydrated oocytes- ~24 h) and, as such, can be difficult to identify. Thus, preference should be given to the afternoon. Additionally, Jackson, Nieland, and Cowan (2006) found no evidence of spawning association with the lunar cycle, so this need not be considered.

To further pinpoint where red snapper spawn in this region, simultaneous plankton tows could be performed to enumerate the relative frequency of *L. campechanus* larvae in the waters adjacent to artificial reefs. This would also provide valuable information on red snapper recruitment strategies. It may also be worthwhile to compare spawning on some natural reef structures in the area to concurrent spawning on artificial reefs, to quantify relative habitat value for *L. campechanus*, as studies suggest that red snapper on natural reefs spend less energy on growth and survival and more on reproduction than their artificial conspecifics (Cowan et al. 2012, Glenn 2014). Thus, an understanding of the relative contribution of natural reefs is essential to proper management. Additionally, adding reference sites that are further offshore (closer to the continental shelf) would provide some context for the results of this study, and may help to clarify and explain some of the observed patterns.

Finally, one point on streamlining the survey protocol for red snapper. Given that total length is an excellent indicator of weight (Figure 11), surveys which aim to simply collect metrics, rather than take tissue samples, could save valuable time by foregoing weight measurements, which are generally unreliable on a moving vessel, anyway. Total lengths can be converted into weights later to estimate catch per unit effort or biomass, and this affords individual red snapper a greater likelihood of survival.

REFERENCES

Alevizon, W.S., and Gorham, J.C. 1989. Effects of artificial reef deployment on nearby resident fishes. Bull. Mar. Sci. **44**(2): 646-661.

Barber, B.J., and Blake, N.J. 2006. Reproductive physiology. *In* Scallops: biology, ecology, and aquaculture. *Edited by* S.E. Shumway and G.W. Parsons. Elsevier, Boston, Mass. pp. 357-416.

Beets, J., and Hixon, M.J. 1994. Distribution, persistence, and growth of groupers (Pisces: Serranidae) on artificial and natural patch reefs in the Virgin Islands. Bull. Mar. Sci. **55**(2-3): 470-483.

Bohnsack, J.A. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? Bull. Mar. Sci. **44**(2): 631-644.

Bohnsack, J.A. 1990. The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic. NOAA Technical Memo.

Bohnsack, J.A., and Sutherland, D.L. 1985. Artificial reef research: a review with recommendations for future priorities. Bull. Mar. Sci. **37**(1): 11-49.

Bombace, G., Fabi, G., Fiorentini, L., and Speranza, S. 1994. Analysis of the efficacy of artificial reefs located in five different areas of the Adriatic Sea. Bull. Mar. Sci. **55**(2-3): 559-580.

Bradley, E., and Bryan, C.E. 1975. Life history and fishery of the red snapper (*Lutjanus campechanus*) in the northwestern Gulf of Mexico: 1970-1974. Proceedings of the Gulf and Caribbean Fisheries Institute. **27**(1975): 77-106.

Bright, T.J. and Rezak, R. 1975. Fishing banks of the Texas continental shelf. Contract 08550-CT5-4. Final Report. U.S. Department of the Interior, Bureau of Land Management, Outer Continental Shelf Office, New Orleans, La. 45 pp.

Brown-Peterson, N.J., Wyanski, D.M., Saborido-Rey, F., Macewitz, B.J., and Lowerre-Barbieri, S.K. 2011. A standardized terminology for describing reproductive development in fishes. Mar. Coast. Fish. **3**(1): 52-70.

Brown, A., Jr., Bohnsack, J.A., and Harper, D. 1989. Automated landings assessment for responsive management (ALARM): Gulf of Mexico commercial reef fish landings. National

Marine Fisheries Service, Southeast Fisheries Science Center, Miami Lab., CRD-89/90-02, Miami, Fl.

Brulé, T., Colás-Marrufo, T., Pérez-Díaz, E., and Sámano-Zapata, J.C. 2010. Red snapper reproductive biology in the southern Gulf of Mexico. Trans. Am. Fish. Soc. **139**: 957-968.

Camber, C.I. 1955. A survey of the red snapper fishery of the Gulf of Mexico, with special reference to the Campeche Banks. Florida State Board of Conservation Technical Series **12**: 1-64.

Carpenter, J.S. 1965. A review of the Gulf of Mexico red snapper fishery. U.S. Department of the Interior, Fish and Wildlife Service, Bureau of Commercial Fisheries, Circular 208.

Clarke, K.R., and Gorley, R.N. 2006. Primer v6: user manual/tutorial. PRIMER-E, Plymouth.

Chesney, E.J., and San Filippo, R. 1994. Size-dependent spawning and egg-quality of red snapper. Final report to the U.S. Dept. Comm., NMFS. Marine Fisheries Initiantive (MARFIN) Coop. Agreement. NA37FF048-01. 17 pp.

Collins, L.A., Johnson, A.G., and Keim, C.P. 1996. Spawning and annual fecundity of the red snapper (*Lutjanus campechanus*) from the northeastern Gulf of Mexico. *In* Biology, fisheries and culture of tropical groupers and snappers. *Edited by* F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly. International Center Living Aquatic Resources Management Conference Proceedings 48. Panama City, Fl. pp. 174-188.

Collins, L. A., Fitzhugh, G.R., Mourand, L., Lombardi, L.A., Walling, W.T., Jr., Fable, W.A., Jr., Burnett, M.R., and Allman, R.J. 2001. Preliminary results from a continuing study of spawning and fecundity in the red snapper (Lutjanidae: *Lutjanus campechanus*) from the Gulf of Mexico, 1998-1999. Proceedings of the Gulf and Caribbean Fisheries Institute **52**: 34-47

Cowan J.H., Jr., Grimes, C.B., Patterson W.F., III, Walters, C.J., Jones, A.C., Lindberg, W.J., Sheehy, D.J., Pine W.E., III, Powers, J.E., Campbell, M.D., Lindeman, K.C., Diamond, S.L., Hilborn, R., Gibson, H.T., and Rose, K.A. 2010. Red snapper management in the Gulf of Mexico: science- or faith-based? Rev. Fish Biol. Fish. **21**: 187-204.

Cowan, J.H., Jr., Boswell, K.M., Simonsen, K.A., Saari, C.R., and Kulaw, D. 2012. Working paper for red snapper data workshop (SEDAR 31). SouthEast Data Assessment and Review 31-Data Workshop 03. SEDAR, North Charleston, S.C.

Dennis, G.D., and Bright, T.J. 1988. Reef fish assemblages on hard banks in the northwestern Gulf of Mexico. Bull. Mar. Sci. **43**(2): 280-307.

Donaldson, W.E. and Donaldson, W.K. 1992. A review of the history and justification for size limits in Alaskan king, tanner, and snow crab fisheries. Fishery Research Bulletin. 92-02.

Drumhiller, K.L., Johnson, M.W., Diamond, S.L, Robillard, M.M., and Stuntz, G.W., 2014. Venting of rapid recompression increase survival and improve recovery of red snapper with barotrauma. Mar. Coast. Fish. **6**: 190-199.

Fitzhugh, G.R., Duncan, M.S. Collins, L.A., Walling, W.T., and Oliver, D.W. 2004. Characterization of red snapper (*Lutjanus campechanus*) reproduction: for the 2004 Gulf of Mexico SEDAR. NMFS Panama City Laboratory Contribution Series: 04-01. 29 pp.

Fitzhugh, G.R., Lang, E.T., and Lyon, H. 2012. Expanded annual stock assessment survey 2011: red snapper reproduction. SouthEast Data Assessment and Review 31-Data Workshop 07. SEDAR, North Charleston, S.C.

Futch, R.B., and Bruger, G.E. 1976. Age, growth, and reproduction of red snapper in Florida waters. *In* Proceedings of the colloquium on snapper-grouper fishery resources for the western central Atlantic Ocean. *Edited by* H.R. Bullis and A.C. Jones. Fl. Seagrant Coll. Rep. 17. St. Petersburg, Fla. pp. 165-184.

Fuiman, L. 2002. Special consideration of fish eggs and larvae. *In* Fishery science: the unique contributions of early life stages. *Edited by* L. Fuiman and R. Werner. Blackwell Science. N.Y. pp. 1–32.

Gallaway, B.J., Szeldmayer, S.T., and Gazey, W.J. 2009. A life history review for red snapper in the Gulf of Mexico with an evaluation of the importance of offshore petroleum platforms and other artificial reefs. Rev. Fish. Sci. **17**(1): 48-67.

Garcia, A. 2013. A comparison of site fidelity and habitat use of red snapper (*Lutjanus campechanus*) to evaluate the performance of two artificial reefs in South Texas utilizing acoustic telemetry. M.Sc. thesis, Department of Biological Sciences, The University of Texas at Brownsville, Brownsville, Tx.

Glenn, H.D. 2014. Does reproductive potential of red snapper in the Northern Gulf of Mexico differ among natural and artificial habitats? M.Sc. thesis, Department of Oceanography and Coastal Science. The Louisiana State University and Agricultural and Mechanical College, Baton Rouge, La.

Goodyear, C.P. 1988. Recent trends in the red snapper fishery of the Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Science Center, Miami Laboratory, CRD 87/88-16, Miami, Fl.

Goodyear, C.P. 1995. Red snapper in US waters of the Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Science Center, Miami Laboratory, MIA-95/96-05, Miami, Fl.

Goodyear, C.P., and Phares, P. 1990. Status of red snapper stocks in the Gulf of Mexico: report for 1990. National Marine Fisheries Service, Southeast Fisheries Science Center, Miami Laboratory, CRD 89/90-05, Miami, Fl.

Google Maps. 2013. South Texas coastline. Available from https://www.google.ca/maps [accessed 04 June 2014].

Grossman, G.D., Jones, G.P., and Seaman, W.J., Jr. 1997. Do artificial reefs increase regional fish production? A review of existing data. Fisheries. **22**(4): 17-23.

Hobson, E.S. 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia. **1965**: 291–302.

Hood, P., and Steele, P. 2004. History of red snapper management in federal waters of the U.S. Gulf of Mexico -1984-2004: 2004 red snapper SEDAR. SouthEast Data Assessment and Review 7-Data Workshop 40. SEDAR, St. Petersburg, Fl.

Hood, P.B., Strelcheck, A.J., and Steele, P. 2007. A history of red snapper management in the Gulf of Mexico. American Fisheries Society Symposium. **60**: 241-256.

Hunter, J.R., and Macewitz, B.J. 1985. Measurement of spawning frequency in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the Northern Anchovy, *Engraulis mordax*. *Edited by* R. Lasker. National Marine Fisheries Service, National Oceanographic and Atmospheric Administration Technical Report **36**: 79-93.

IBM Corp. 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, N.Y.

Jackson, M.W., Nieland, D.L., and Cowan, J.H., Jr. 2006. Diel spawning periodicity of red snapper, *Lutjanus campechanus,* in the northern Gulf of Mexico. J. Fish. Biol. **68**(3): 695-106.

Jackson, M.W., Cowan, J.H., Jr., and Nieland, D.L. 2007. Demographic differences in northern Gulf of Mexico red snapper reproductive maturation: Implications for the unit stock hypothesis. *In* Red snapper ecology and fisheries in the U.S. Gulf of Mexico. *Edited by* W.F., Patterson, III, J. H., Cowan, Jr., G.R., Fitzhugh, and D.L., Nieland. American Fisheries Society, Symposium 60, Bethesda, Md. pp. 217-228.

Jenkins, C., Bethel, M., Penland, S., and Mixon, D. 2008. A marine substrates geodatabase of the northern Gulf of Mexico, for benthic and fisheries habitats. Institute of Arctic and Alpine Research, University of Colorado Pontchartrain Institute for Environmental Sciences University of New Orleans. Gulf States Marine Fisheries Commission.

Kulaw, D. 2012. Habitat- and region-specific reproductive biology of female red snapper (*Lutjanus campechanus*) in the Gulf of Mexico. M.Sc. thesis, Department of Oceanography and Coastal Science. The Louisiana State University and Agricultural and Mechanical College, Baton Rouge, La.

United States of America. 1976. Magnuson-Stevens Fishery Conservation Management Act (MSA). Public Law 94-265, Washington, D.C.

McCawley, J. R., and Cowan, J.H., Jr. 2007. Seasonal and size specific diet and prey demand of red snapper on Alabama artificial reefs. *In* Red snapper ecology and fisheries in the U.S. Gulf of Mexico. *Edited by* W. F., Patterson, III, J. H., Cowan, Jr., G. R., Fitzhugh, and D. L., Nieland. American Fisheries Society Symposium 60, Bethesda, Md. pp. 77-104.

Miller, M.W. 2002. Using ecological processes to advance artificial reef goals. ICES J. Mar. Sci. **59**: S27-S31.

Morton, D.N., and Shima, J.S. 2013. Habitat configuration and availability influences the settlement of temperate reef fishes (*Tripterygiidae*). J. Exp. Mar. Biol. Ecol. **449**: 215-220.

Morgan, M., and G. Lilly. 2006. The impact of condition on reproduction in Flemish Cap cod. Journal of Northwest Atlantic Fishery Science **37**:81-86.

Mueller, M. 2012. Artificial structure and hard-bottom spatial coverage in the Gulf of Mexico. SouthEast Data Assessment and Review 31-Data Workshop 29. SEDAR, North Charleston, S.C.

National Marine Fisheries Service (NMFS). 2012. Status of Stocks 2012. Annual Report to Congress on the Status of U.S. Fisheries.

Nieland, D.L., Wilson III, C.A., and Fischer, A.J. 2007. Declining size at age among red snapper in the Gulf of Mexico off Louisiana, USA: recovery or collapse? American Fisheries Society Syposium. Eds. W.F. Patterson III, J. Cowan, G.R. Fittzhugh, and D.L. Nieland, no. 60. American Fisheries Society, 5410 Grosvernor Ln. Ste. 110 Bethesda, Md. 20814-2199 USA.

Nikolsky, G.V. 1963. The ecology of fishes. 6th ed. Academic Press. London.

Ouzts, A.C., and Szedlmayer, S.T. 2003. Diel feeding patterns of red snapper on artificial reefs in the north-central Gulf of Mexico. Trans. Am. Fish. Soc. **132**(6): 1186-1193.

Patterson, W.F., III. 1999. Aspects of the population ecology of red snapper, *Lutjanus campechanus*, in an artificial reef off Alabama. Ph.D. dissertation. Department of Marine Science. The University of South Alabama, Mobile, Ala.

Patterson, W.F., III, Watterson, C.J., Shipp, R.L., and Cowan, J.H., Jr. 2001. Movement of tagged red snapper in the northern Gulf of Mexico. Trans. Am. Fish. Soc. **130**(4): 533-545.

Peabody, M.B. 2001. The fidelity of red snapper (*Lutjanus campechanus*) to petroleum platforms and artificial reefs in the northern Gulf of Mexico. M.Sc. thesis. Department of Oceanography and Coastal Sciences. The Louisiana State University and Agricultural and Mechanical College, Baton Rouge, La.

Rabalais, N.N., Rabalais, S.C., and Arnold, C.R. 1980. Description of eggs and larvae of laboratory reared red snapper (*Lutjanus campechanus*). Copeia. **1980**(3): 704-708.

Render, J. H. 1995. The life history (age, growth, and reproduction) of red snapper (*Lutjanus campechanus*) and its affinity for oil and gas platforms. Ph.D. dissertaion. Department of Oceanography and Coastal Sciences. The Louisiana State University and Agricultural and Mechanical College, Baton Rouge, La.

Rideout, R., and Tomkiewicz, J. 2011. Skipped spawning in fishes: more common than you might think. Mar. Coast. Fish. **3**: 176-189.

Rios, A. 2013. Estimating historical recreational angler effort in the Gulf of Mexico for the private, charter, and headboat fishing modes. SouthEast Data Assessment and Review 31-Assessment Workshop 11. SEDAR, North Charleston, S.C.

Rooker, J.R., Landry, A.M., Jr., Geary, B.W., and Harper, J.A. 2004. Assessment of a shell bank and associated substrates as nursery habitat of postsettlement red snapper. Est. Coast. Shelf Sci. **59**: 653-661.

Saari, C.R. 2012. Comparison of the age and growth of red snapper (*Lutjanus campechanus*) amongst habitats and regions in the Gulf of Mexico. M.Sc. thesis, Department of Oceanography and Coastal Science. The Louisiana State University and Agricultural and Mechanical College, Baton Rouge, La.

Schirripa, M. J., and Legault, C. M. 1999. Status of the red snapper in U.S. waters of the Gulf of Mexico: updated through 1998. Southeast Fisheries Science Center, Sustainable Fisheries Division Contribution: SFD-99/00-75, 3.

Shipp, R.L. 1999. The artificial reef debate: Are we asking the wrong questions? Gulf Mex. Sci. **17**(1): 51-55.

Sokal, R.R., and Röhlf, J.F. 1995. Biometry: the principles and practice of statistics in biological research. 3rd ed. Macmillan. New York, N.Y.

SouthEast Data, Assessment, and Review (SEDAR). 2005. SouthEast Data Assessment and Review 7 – Gulf of Mexico red snapper complete stock assessment. SEDAR, North Charleston, S.C.

SouthEast Data, Assessment, and Review (SEDAR). 2013. SouthEast Data Assessment and Review 31 – Gulf of Mexico red snapper stock assessment report. SEDAR, North Charleston S.C.

Southeast Monitoring and Assessment Program (SEAMAP). 2012. Southeast Monitoring and Assessment Program vertical line survey protocol, Version 1.6. Gulf States Marine Fisheries Commission, Ocean Springs, Md.

Syc, T.S., and Szedlmayer, S.T. 2012. A comparison of size and age of red snapper (*Lutjanus campechanus*) with the age of artificial reefs in the northern Gulf of Mexico. Fish. Bull. **110**: 458-469.

Szedlmayer, S.T., and Conti, J. 1999. Nursery habitats, growth rates, and seasonality of change of age-0 red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico. Fish. Bull. **97**(3): 626-625.

Szedlmayer, S.T., and Schroepfer, R.L. 2011. Long-term residence of red snapper on artificial reefs in the northeastern Gulf of Mexico. Trans. Am. Fish. Soc. **134**(2): 315-325.

Szedlmayer, S.T., and Lee, J.D. 2004. Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size. Fish. Bull. **102**(2): 366-375.

Texas Parks and Wildlife Department Artificial Reef Program. 2008. Texas Artificial Reef Program Materials Summary.

Topping, D.T., and Szedlmayer, S.T. 2011a. Home range and movement patterns of red snapper (*Lutjanus campechanus*) on artificial reefs. Fish. Res. **112**: 77-84.
Topping, D.T., and Szedlmayer, S.T. 2011b. Site fidelity, residence time and movements of red snapper (*Lutjanus campechanus*) estimated with long-term acoustic monitoring. Mar. Ecol. Prog. Ser. **437**: 183-200.

Trippel, E.A. 1995. Age at maturity as a stress indicator in fisheries. BioScience. 45(11):759-771.

Trippel, E.A., Kjesbu, O.S. and Solemdal, P. 1997. Effects of adult age and size structure on reproductive output in marine fishes. *In:* Early Life History and Recruitment in Fish Populations. *Edited by* R.C. Chamber and E.A. Trippel. Chapman and Hall, London. pp. 31-62.

Underwood, A.J. 1997. Experiments in ecology. Cambridge University Press, United Kingdom.

Voorhees, D.V. 2012. Fisheries of the United States 2011. Natlional Marine Fisheries Service Office of Science and Technology, Fisheries Statistics Division, Silver Springs, Md.

Wells, D.R.J., and Cowan, J.H., Jr. 2007. Video estimates of red snapper and associated fish assemblages on sand, shell, and natural reef habitats in the north-central Gulf of Mexico. *In* Red snapper ecology and fisheries in the U.S. Gulf of Mexico. *Edited by* W. F., Patterson, III, J. H., Cowan, Jr., G. R., Fitzhugh, and D. L., Nieland. American Fisheries Society Symposium 60, Bethesda, Md. pp. 39-57.

Wells, D.R.J., Cowan, J.H., Jr., and Fry, B. 2008. Feeding ecology of red snapper *Lutjanus campechanus* in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. **361**: 213-225.

White, D.B., and Palmer, S.M. 2004. Age, growth, and reproduction of the red snapper, *Lutjanus campechanus*, from the Atlantic waters of the southeastern U.S. Bull. Mar. Sci. **75**(3): 335-360.

Wilhelmsson, D., Öhman, M.C., Ståhl, H., and Shlesinger, Y. 1998. Artificial reefs and dive tourism in Eilat, Israel. Ambio. **27**(8): 764-766.

Wilson, C.A., and Nieland, D.L. 2001. Age and growth of red snapper, *Lutjanus campechanus*, from the northern Gulf of Mexico off Lousiana. Fish. Bull. **99**(4): 653-664.

Wilson, C. A., Render, J.H. and Nieland, D.L. 1994. Life history gaps in red snapper (*Lutjanus campechanus*), swordfish (*Xiphias gladius*), and red drum (*Sciaenops ocellatus*) in the northern Gulf of Mexico: age distribution, growth, and some reproductive biology. Final report to the U.S. Department of Commerce, National Marine Fisheries Service, Marine Fisheries Initiative, Coop. Agreement NA17FF0383-02.

Winemiller, K.O., and Rose, K.A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Can. J. Fish Aquat. Sci. **49**: 2196-2218.

Woods, M.K., Fischer, A.J., Cowan, J.H., Jr., and Nieland, D.L. 2003. Size and age at maturity of female red snapper *Lutjanus campechanus* in the northern Gulf of Mexico. Proceedings of the Gulf and Caribbean Fisheries Institute. **54**: 526-537.

Wright, P.J. and Trippel, E.A. 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. Fish and Fisheries. **10**: 283-304.

Table 1. List of four artificial reef sites sampled for red snapper (*Lutjanus campechanus*) along the south Texas coast. Sites less than 15 km from shore are considered inshore sites.

Site	Latitude (N)	Longitude (W)	Depth (m)	Distance to Shore (km)	Reef Materials Deployed	Date of Initial Deployment
PS-1169L	25°96’48”	97°06’42”	21.8	7.96	2 three-pile jackets; 1 ultra reef ball; 15 pallet balls; 4 bay balls; 33 reef balls; 1 US YR Navy barge (~45 x 10 m); 1 tugboat (~18 m x 6 m); 1 shrimp boat (~20 x 4 m)	July 2011
PS-1047	26°52’36”	97°15’24”	19.7	10.37	1 tugboat (~30 m); ~4800 concrete culverts (61-183 cm diameter)	July 2009
PS-1070	26°42’42”	97°02’24”	30.9	20.19	3 WWII Liberty ships (~134 x 17 m); 13 four-pile jackets; 2 ½-four-pile jackets	November 1975
PS-1122	26°18’54”	96°85’54”	40.0	31.70	1 Texas Clipper Ship (~145 x 22 m)	November 2007

Table 2. Definition of each reproductive stage: immature (I), developing (D), spawning capable (SC), actively spawning (AS), regressing (R), and regenerating (X)] for male and female red snapper (*Lutjanus campechanus*). Male red snapper undergo four stages of spermatogenesis: Stage I. spermatogonia, Stage II. primary and secondary spermatocytes, Stage III. spermatid, and Stage IV. spermatozoid. The six female stages of oocyte development are defined as: Stage I. chromatin nucleolar oocyte (CO), Stage II. perinucleolar oocyte (PO), Stage III. yolk vesicle ooctye (YVO), Stage IV. yolk globule oocyte (YGO), Stage V. final oocyte maturation (FOM), and Stage VI. hydrated oocyte (HO). Modified from Brulé et al. (2010).

Reproductive Stage	**Male**	**Female**
I	Only Stage I present	Stage I and Stage II ooctyes present
D	Stages II and III predominate	Stage I to Stage III oocytes present
SC	Stages III and IV predominate and fill lobules	Stage I to Stage IV oocytes present
AS	All stages present; free spermatozoa predominate and fill lobules and sperm ducts	Stage I to Stage IV oocytes present; Stage V and/or Stage VI and/or postovulatory follicles present
R	Residual Stage IV in lobules and sperm ducts	Stage I and Stage II oocytes; residual Stage III to Stage IV and/or atresic oocytes present
X	Stage I predominate with a few residual Stage IV present in lobules and sperm ducts	Stage I and Stage II oocytes with muscle bundle remnants and connective tissue surrounding blood vessels in center of lamellae

Table 3. Description of each reproductive stage for red snapper (*Lutjanus campechanus*). Spermatogenic stages are described by: Sg1 – primary spermatogonia, Sg2 – secondary spermatogonia, Sc1 – primary spermatocytes, Sc2 – secondary spermatocytes, St – spermatids, Sz – spermatozoa, GE – germinal epithelium. Oocyte developmental stages are described by: CA – cortical alveolar, GVBD – germinal vesicle breakdown, GVM – germinal vesicle migration, OM – oocyte maturation, PG – primary growth, POF – postovulatory follicle complex, Vtg1 – primary vitellogenic, Vtg2 – secondary vitellogenic, Vtg3 – tertiary vitellogenic. Modified from Brown-Peterson et al. (2011).

Reproductive Stage	Male	Female
Immature	Testes small. Often clear and thread-like. Only Sg1 present; no lumen in lobules	Small, often clear ovaries with no atresia or muscle bundles present. Ovarian wall is thin with little space among oocytes. Only oogonia and primary growth ooctyes present
Developing	Testes small, but readily identifiable. Sg2, Sc1, Sc2, St, and Sz can be present in spermatocysts. Sz not present in sperm ducts/lumen of lobules. GE continuous throughout. Early developing subphase in Sg1, Sg2, and Sc1 only	Ovaries enlarging, blood vessels becoming distinct. PG, CA, Vtg1, and Vtg2 ooctyes present. No POFs present. Early developing subphase may be present in PG and CA only
Spawning Capable	Testes large and firm, Sz present in sperm ducts/lumen of lobule. All stages of spermatogenesis may be present. GE can be continuous or discontinuous, depending on subphase. In the actively spawning subphase, milt can be released by applying gentle pressure to the abdomen	Ovaries large, blood vessels prominent. Individual oocytes are macroscopically observable. POFs present. Atresia of vitellogenic and/or hydrated ooctyes may be present. Early stages of OM may be observed. Oocytes may be undergoing late GVM, GVBD, or hydration
Regressing	Small, limp testes, no milt release with gentle pressure, residual Sz present in sperm ducts/lumen of lobules, widely scattered spermatocysts near periphery containing Sz, St, and Sc2. Little to no active spermatogenesis. Spermatogonial proliferation and regeneration of GE common in periphery	Ovaries limp and blood vessels obvious. Atresia and POFs present. Some CA and Vtg1/Vtg2 present
Regenerating	Testes small, often threadlike. No spermatocysts, lumen of lobule often nonexistent. Proliferation of spermatogonia throughout. GE continuous throughout. Some residual Sz may be present in sperm ducts/lumen of lobules	Ovaries small, blood vessels reduced, but observable. Only oogonia and PG oocytes present. Muscle bundles, enlarged blood vessels, thick ovarian wall, or old, degenerating POFs may be present

Table 4. Female to male sex ratios for red snapper (*Lutjanus campechanus*) captured between June 2014 and May 2015 at four artificial reef sites in south Texas. Values in bold represent ratios significantly different from 1:1 as per χ^2 (see text for details).

Location	**Site**	**Female (F)**	**Male (M)**	**F:M Ratio**
Nearshore	PS-1169L	27	25	1 : 0.93
	PS-1047	49	48	1 : 0.98
Offshore	PS-1070	57	95	**1 : 1.67**
	PS-1122	30	36	1 : 1.20
	Total	163	204	**1:1.25**

Table 5. Transformed (ln) total length-eviscerated weight regression analyses for red snapper (*Lutjanus campechanus*) sampled from June 2014 to May 2015 at four artificial reef sites off the coast of south Texas. Eviscerated weight (g) = EW; total length (mm) = TL. P-values, in bold, represent significant relationships (see text for details).

Site	r^2	P-value	F-value	Regression Equation
PS-1169L	0.980	**0.001**	2393.96	EW = 3.767 + 0.76 (TL)
PS-1047	0.917	**0.001**	1053.47	EW = 3.748 + 0.77 (TL)
PS-1070	0.952	**0.001**	2926.27	EW = 3.808 + 0.75 (TL)
PS-1122	0.988	**0.001**	5132.61	EW = 3.849 + 0.73 (TL)
All Sites Combined	0.965	**0.001**	9872.56	EW = 3.766 + 0.76 (TL)

Table 6. Spawning frequency estimate (SFE), spawns per season, and annual fecundity estimate (AFE) ± 1 standard error (SE) for hydrated female red snapper (*Lutjanus campechanus*) captured between June 2014 and May 2015 for four artificial reef sites in south Texas (shown) and the most prevalent age classes (3-6 years; n = 37). Sites are listed in order of distance from shore. An asterisk indicates a repeated line of data with one outlier removed. Total includes the outlier. Number of hydrated females = n (day-0); number of mature females = n (mature).

Site	n (day-0)	n (mature)	SFE	Spawns per Season	AFE ± SE
PS-1169L	6	7	1.2	150	2,964,628 ± 1,936,043
PS-1169L*	5	6	1.2	150	1,092,008 ± 711,883
PS-1047	7	14	2.0	90	1,761,087 ± 728,611
PS-1070	4	12	3.0	60	1,003,644 ± 203,192
PS-1122	2	10	5.0	36	392,550 ± 96,906
Total	**19**	**43**	**2.2**	**84**	**1,756,532 ± 651,367**

Age	n (day-0)	n (mature)	SFE	Spawns per Season	AFE ± SE
3	8	12	1.5	120	1,805,331 ± 1,129,814
3*	7	11	1.6	113	678,511 ± 388,319
4	4	10	2.5	72	1,656,082 ± 869,217
5	5	12	2.4	75	1,332,365 ± 452,046
6	2	3	1.5	120	2,464,647 ± 640,939

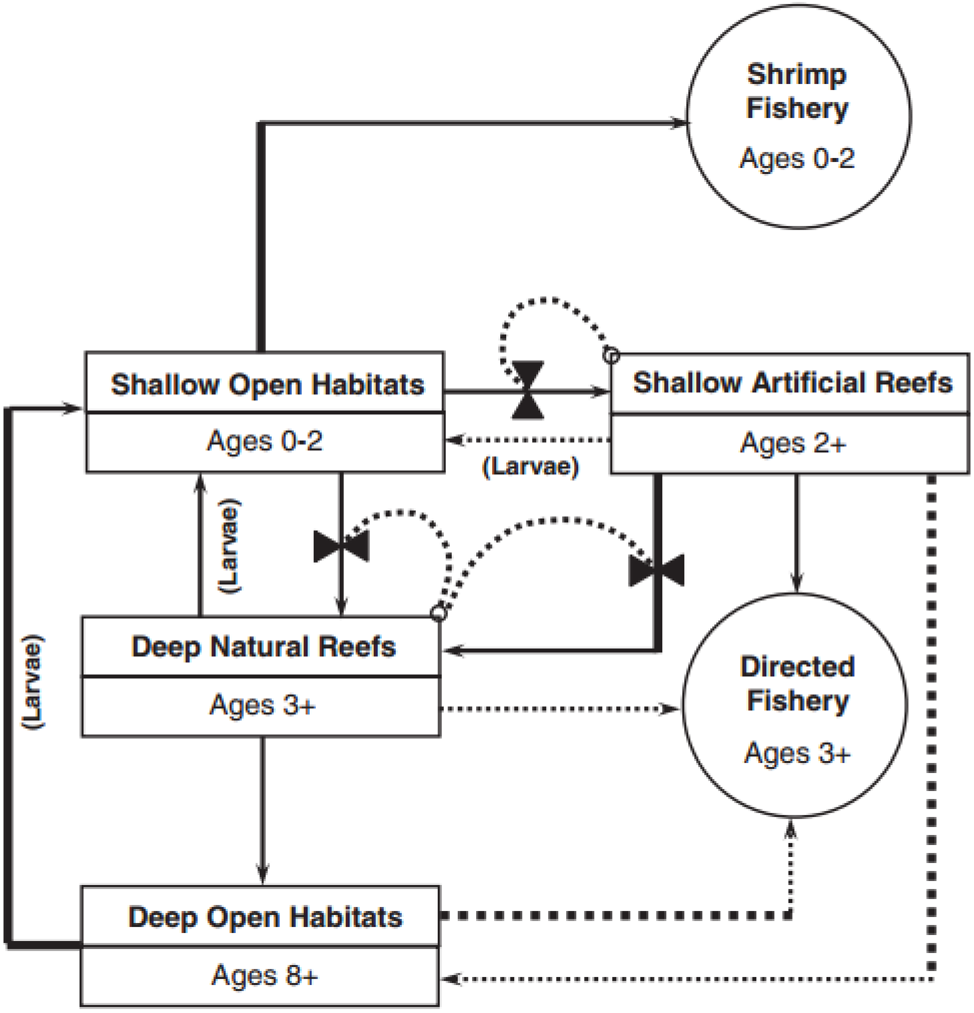

Figure 1. A conceptual model of red snapper (*Lutjanus campechanus*, Poey 1860) habitat preference throughout its lifecycle (from Gallaway et al. 2009).

Figure 2. Satellite image from 2013 of the four artificial reef study sites (stars) along the coast of south Texas (Google Maps 2013).

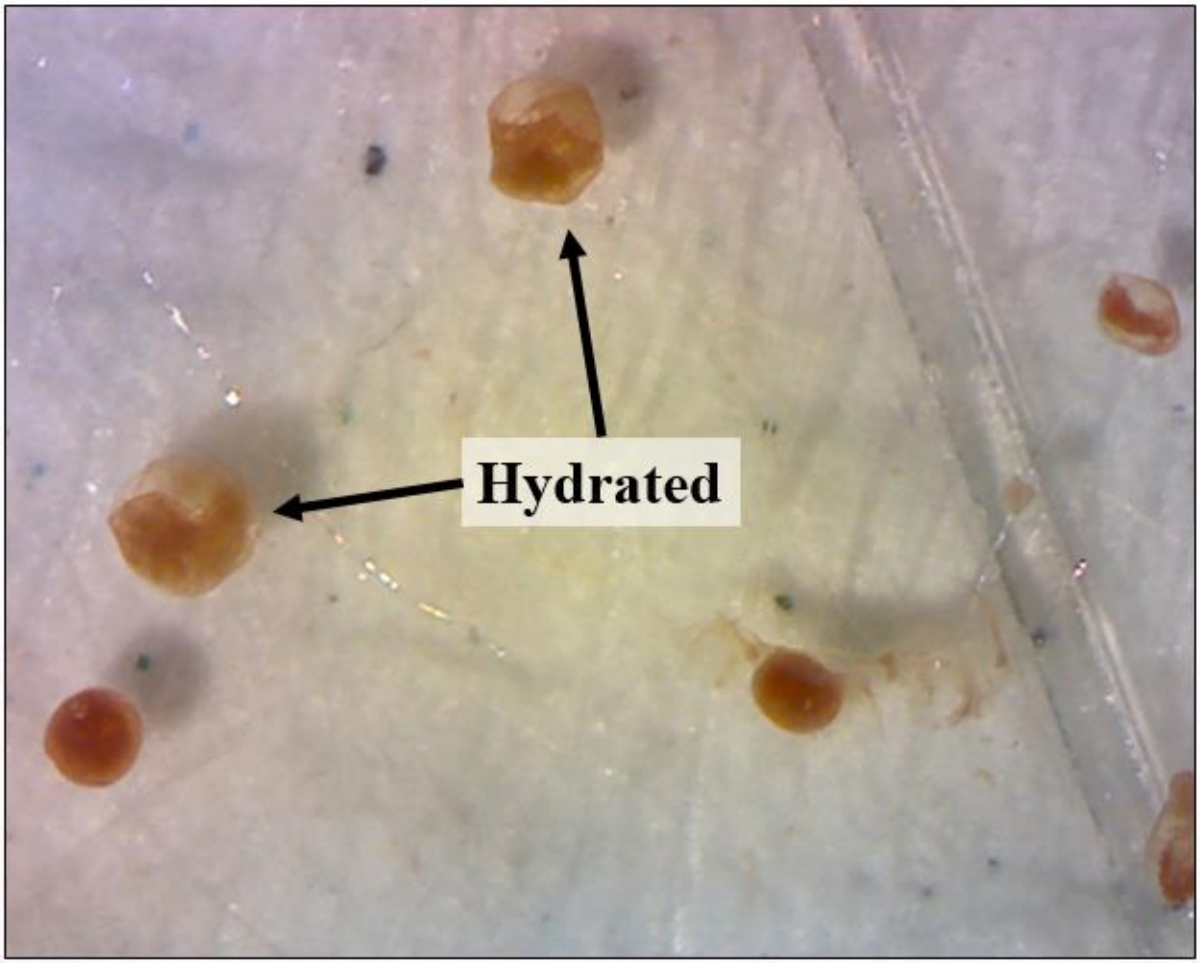

Figure 3. Hydrated red snapper (*Lutjanus campechanus*) oocytes were enumerated in a glycerin spread to calculate batch fecundity. Oocytes were ~1 mm diameter.

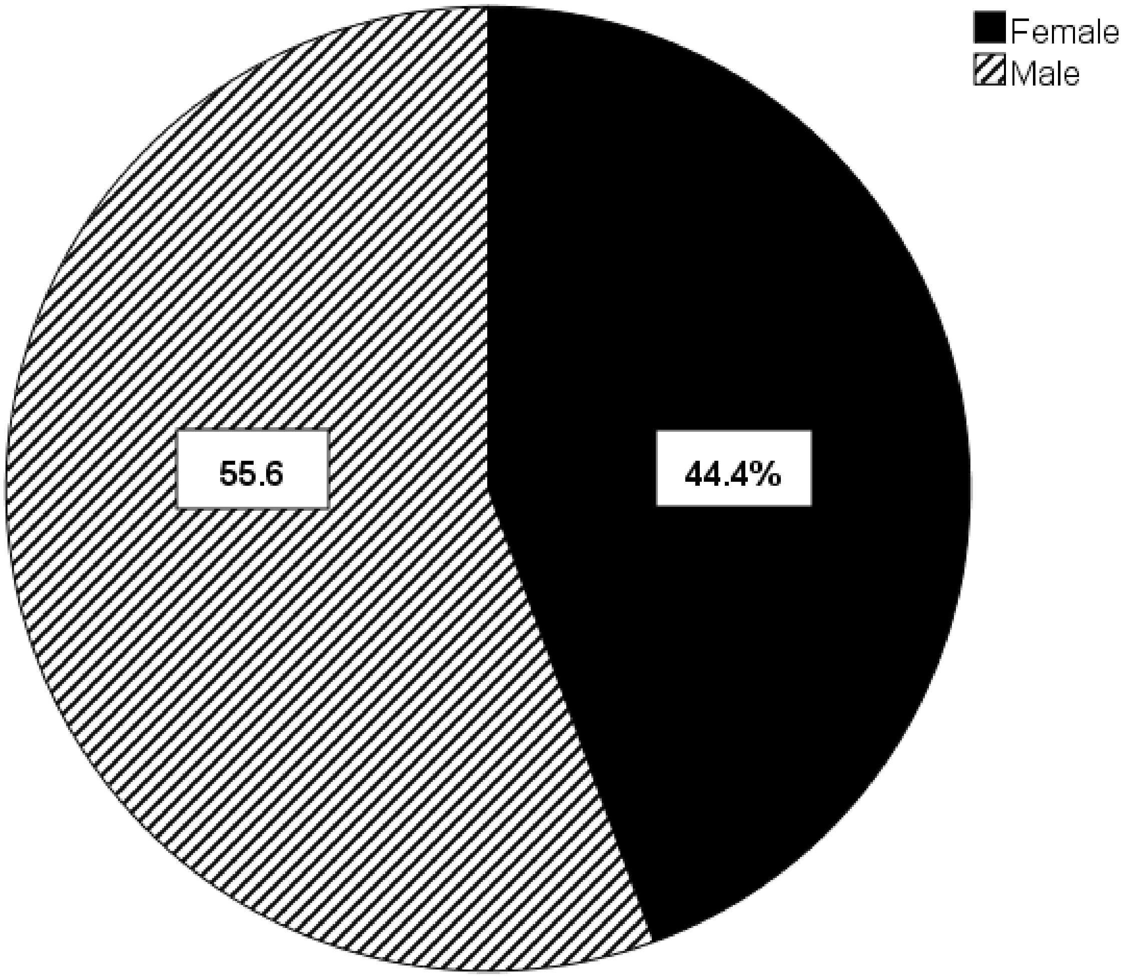

Figure 4. Pie chart displaying the ratio of male (n = 204) to female (n = 163) in percentage of red snapper (*Lutjanus campechanus*) collected from June 2014 to May 2015 at four artificial reef sites in south Texas.

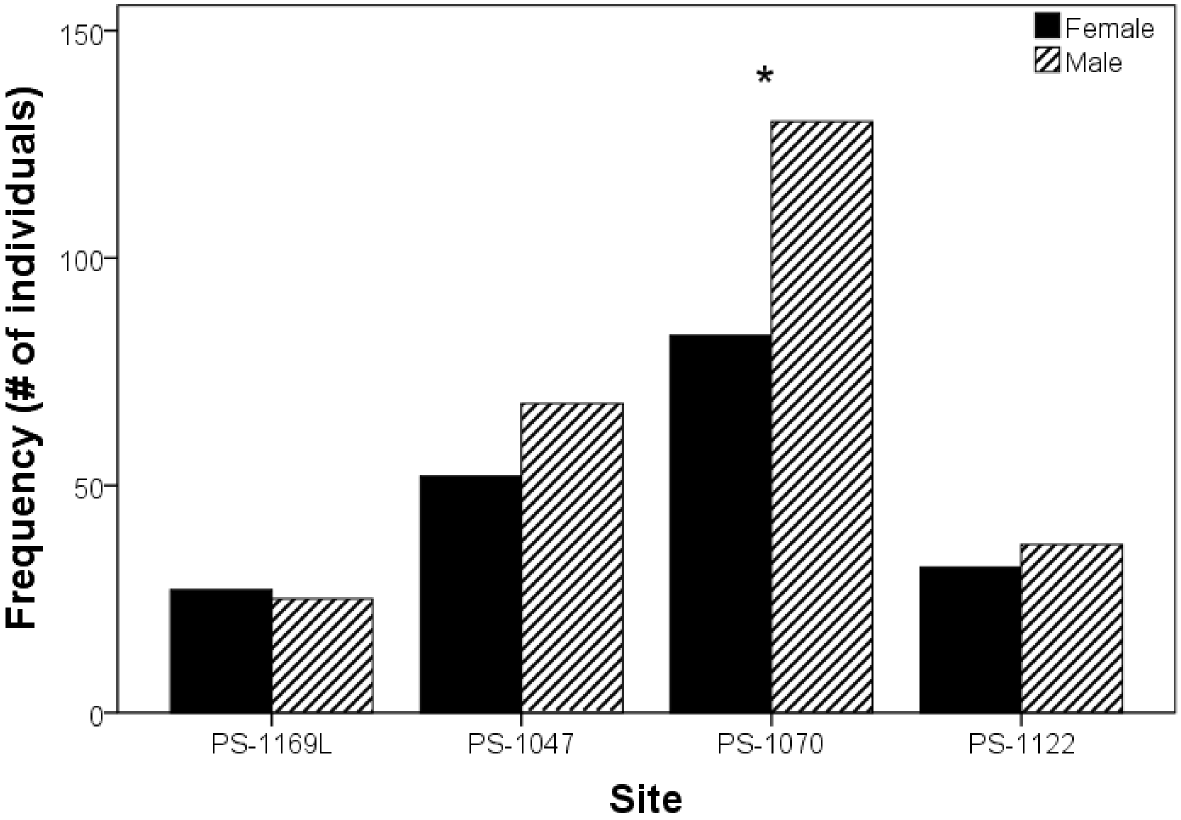

Figure 5. Frequency distribution (number of individuals; n = 367) of female and male red snapper (*Lutjanus campechanus*) collected from June 2014 to May 2015 at four artificial reef sites in south Texas (labeled from left to right with increasing distance from shore; for gender n see Figure 4). PS-1169L and PS-1047 are considered nearshore sites, while PS-1070 and PS-1122 are considered offshore sites. An asterisk indicates a significant deviation from a 1:1 sex ratio (see text for details).

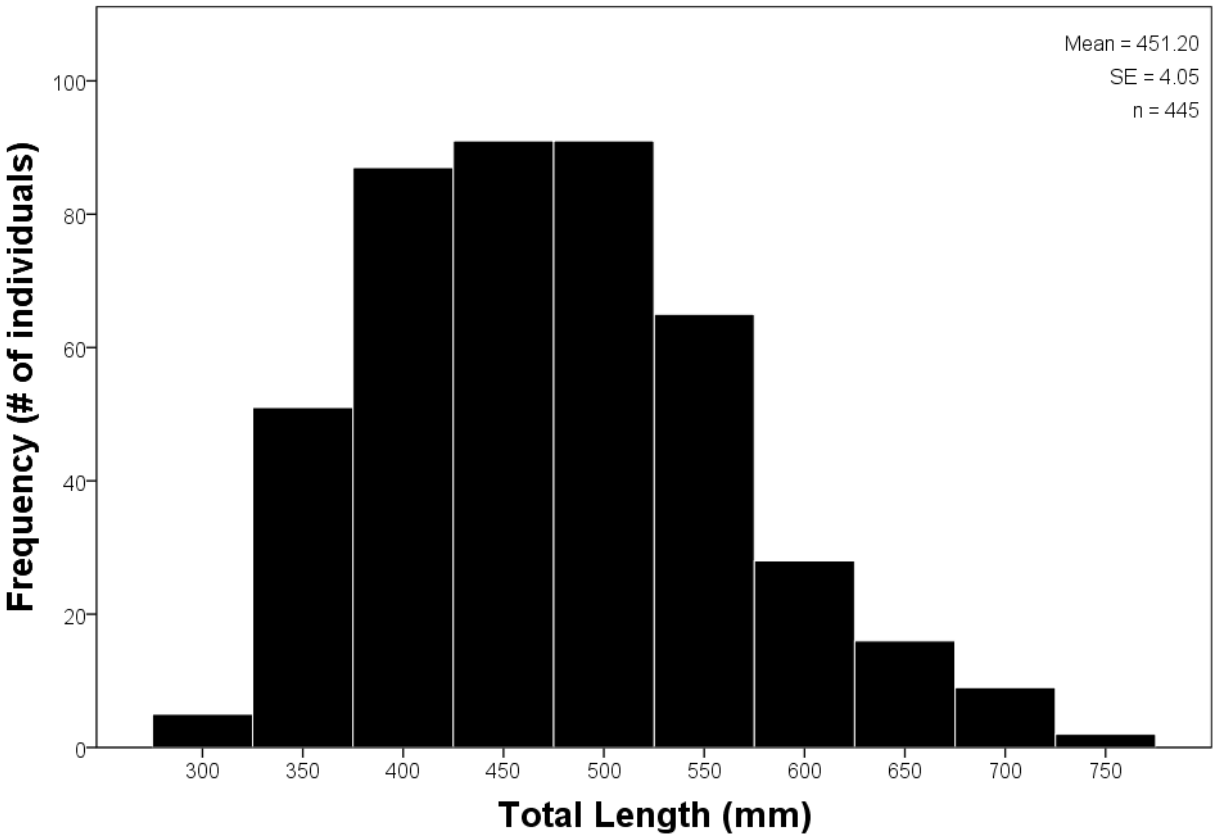

Figure 6. Total length (mm) frequency distribution (number of individuals; n = 445) for red snapper (*Lutjanus campechanus*) collected from June 2014 to May 2015 on four artificial reefs in south Texas. Mean and standard error (SE) not plotted but included.

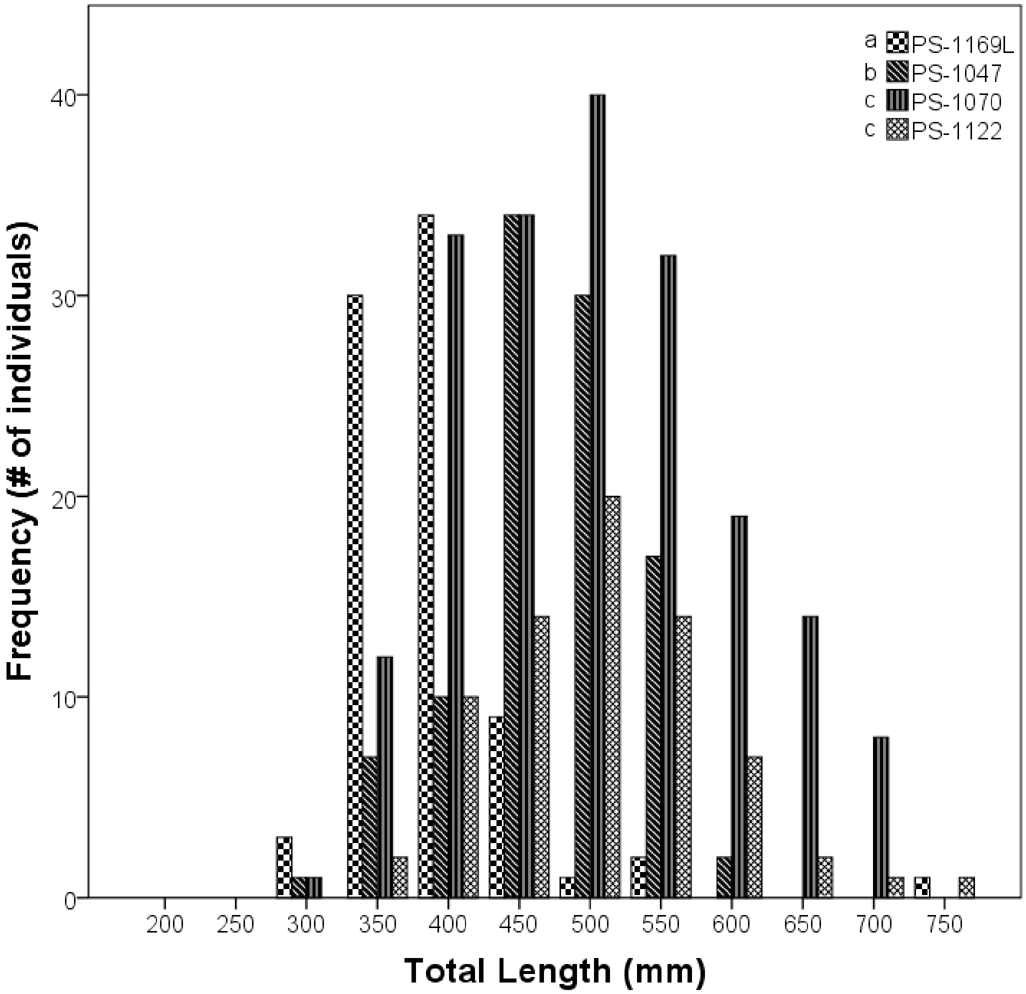

Figure 7. Total length (mm) frequency distribution (number of individuals; n = 445) for red snapper (*Lutjanus campechanus*) collected between June 2014 and May 2015 at four artificial reefs in south Texas. Site groups with different letter assignments (a-c) are significantly different (see text for details).

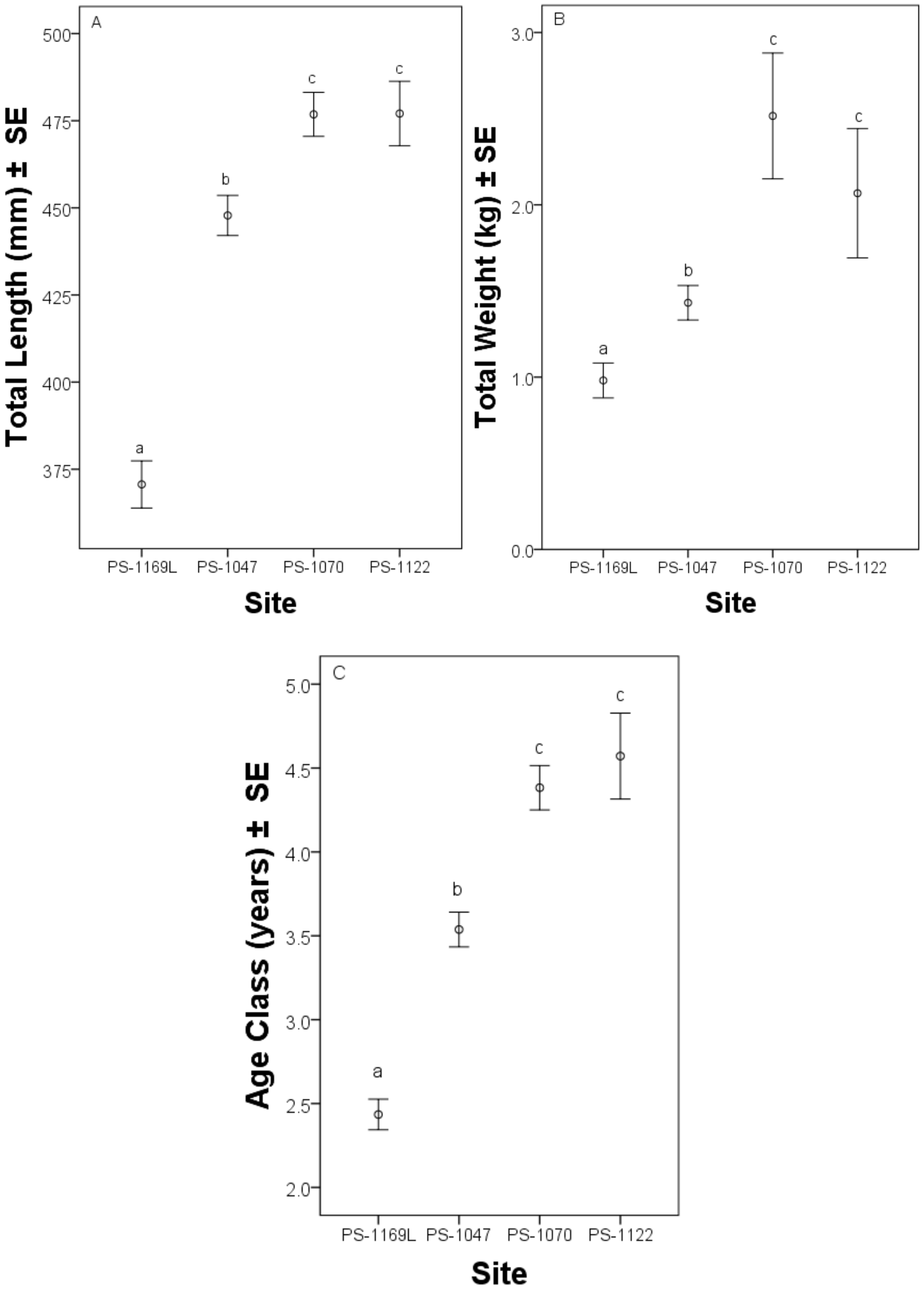

Figure 8. Mean (A) total length (mm), (B) total weight (kg) and (C) age class (years) ± 1 standard error (SE) of red snapper (*Lutjanus campechanus*) collected from June 2014 to May 2015 at four artificial reef sites in south Texas (labeled as in Figure 5). Note changes in scale on axes. Sample size for (A) and (B) as in Figure 6. For (C), n = 256.

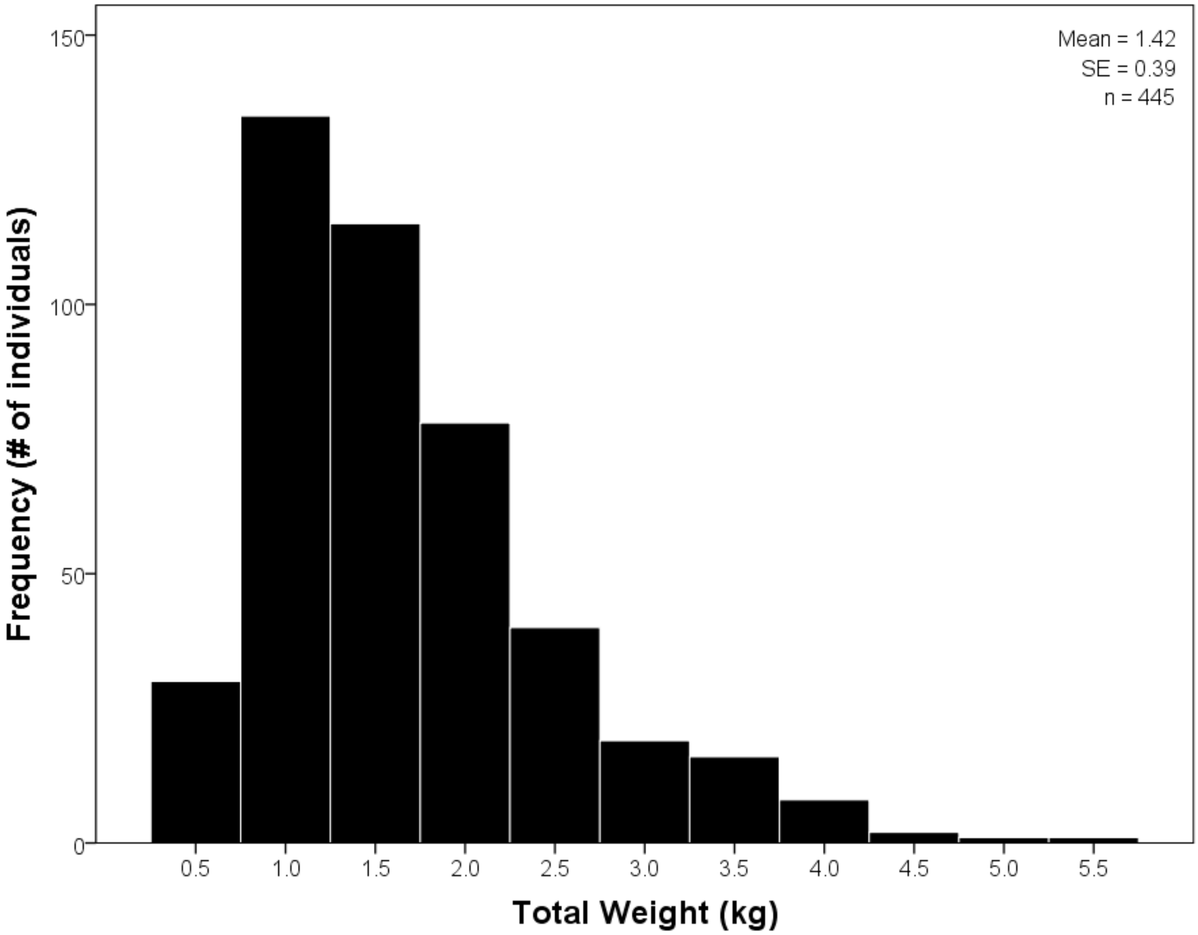

Figure 9. Total weight (kg) frequency distribution (number of individuals) of red snapper (*Lutjanus campechanus*) collected from June 2014 to May 2015 at four artificial reef sites in south Texas. Sample size as in Figure 6. Mean and standard error (SE) not plotted but included.

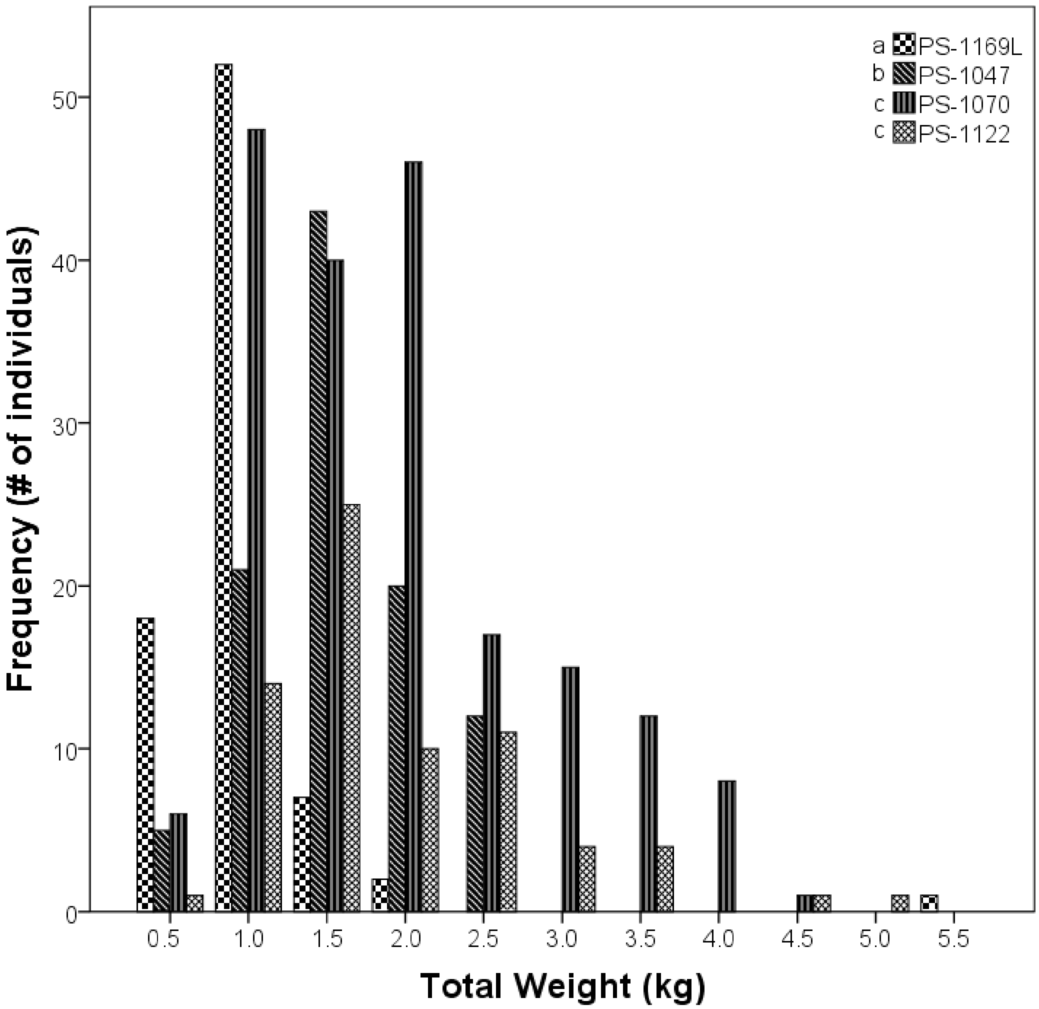

Figure 10. Total weight (kg) frequency distribution (number of individuals) for red snapper (*Lutjanus campechanus*), collected between June 2014 and May 2015 at four artificial reefs in south Texas. Sample size as in Figure 6. Site groups with different letter assignments (a-c) are significantly different (see text for details).

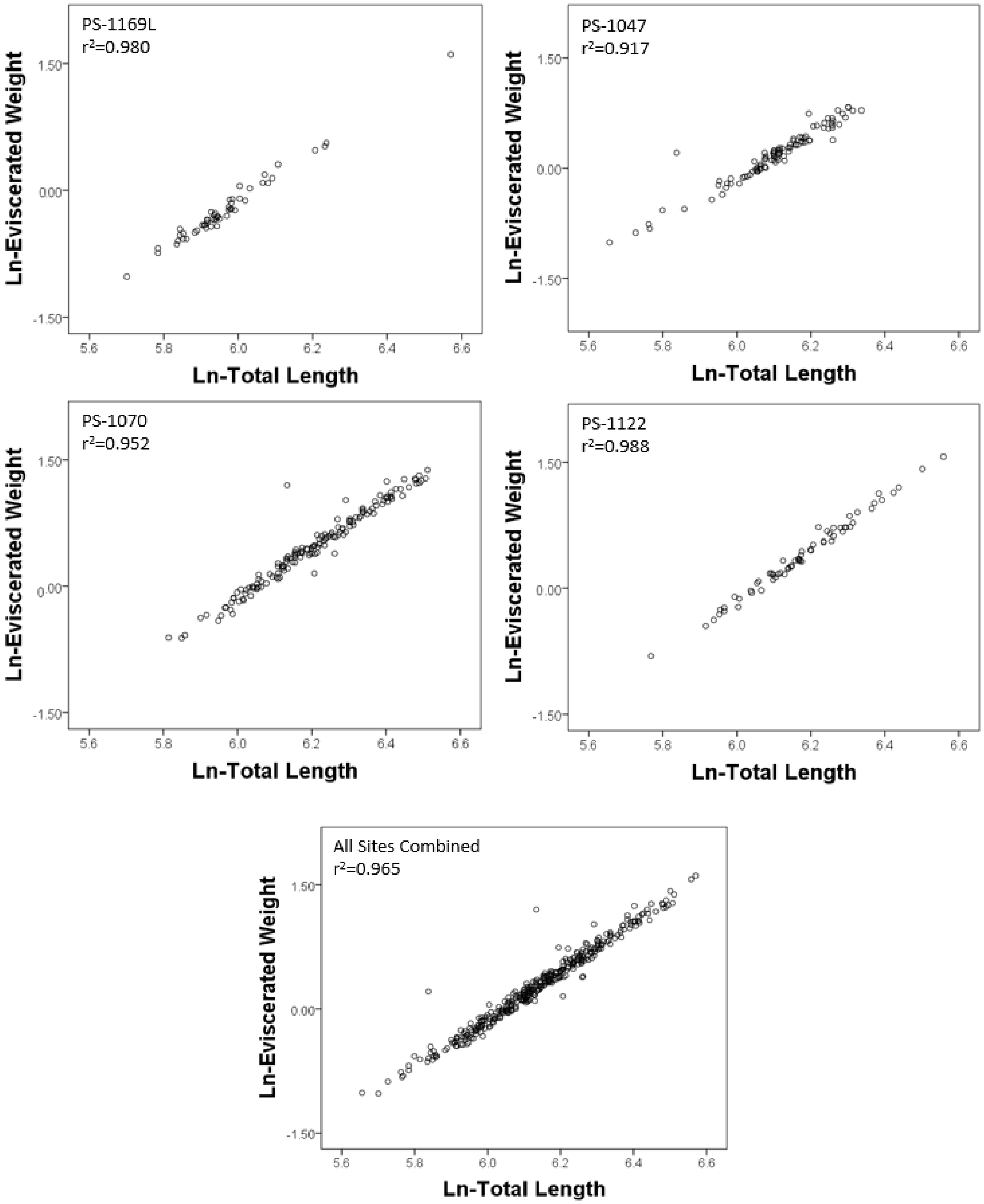

Figure 11. Transformed (ln) total length (mm)-eviscerated weight (g) regressions for red snapper (*Lutjanus campechanus*) collected from June 2014 through May 2015 at four artificial reef sites, and all sites combined, in south Texas. All relationships are significant ($p < 0.001$; see Table 5). Note changes in scale between axes.

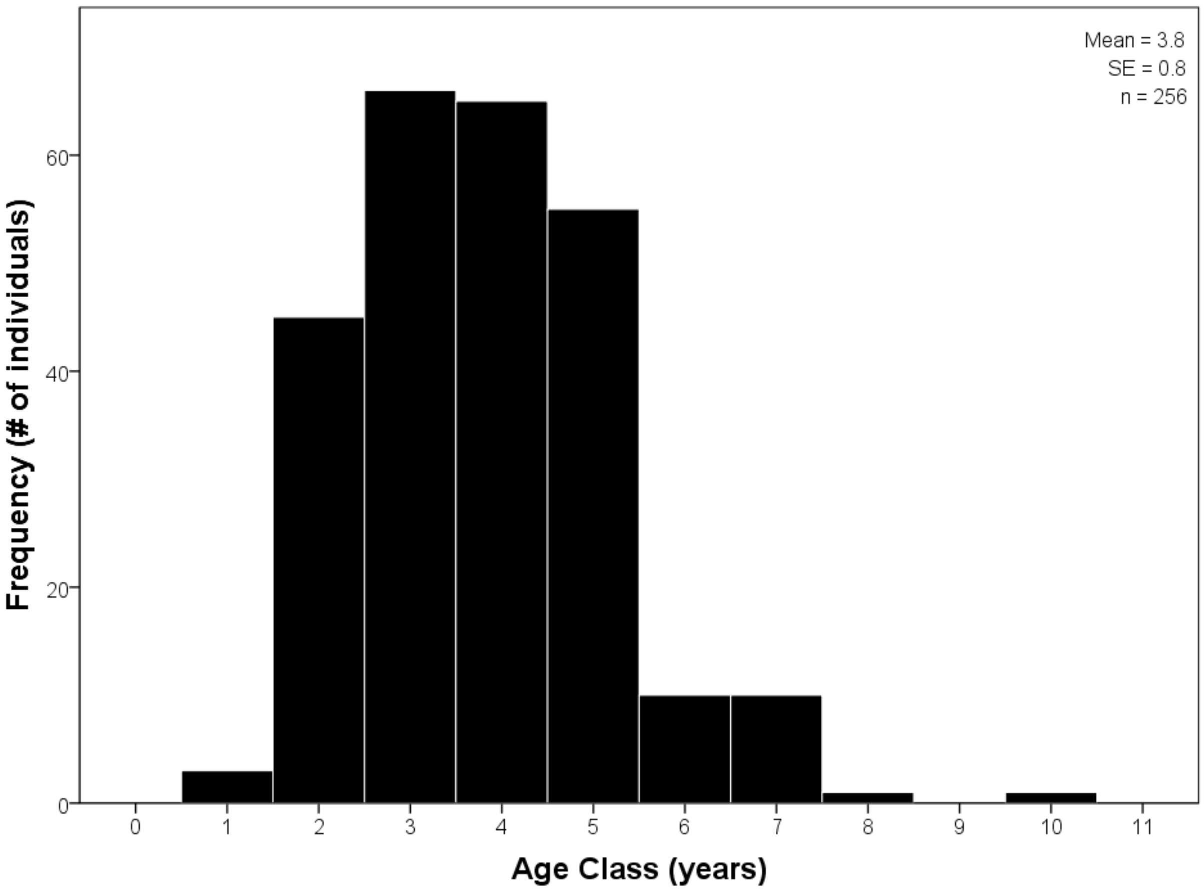

Figure 12. Frequency distribution (number of individuals; n = 256) of age classes (years) for red snapper (*Lutjanus campechanus*) collected from June 2014 to May 2015 at four artificial reef sites in south Texas. Sample size as in Figure 8C. Mean and standard error (SE) not plotted but included.

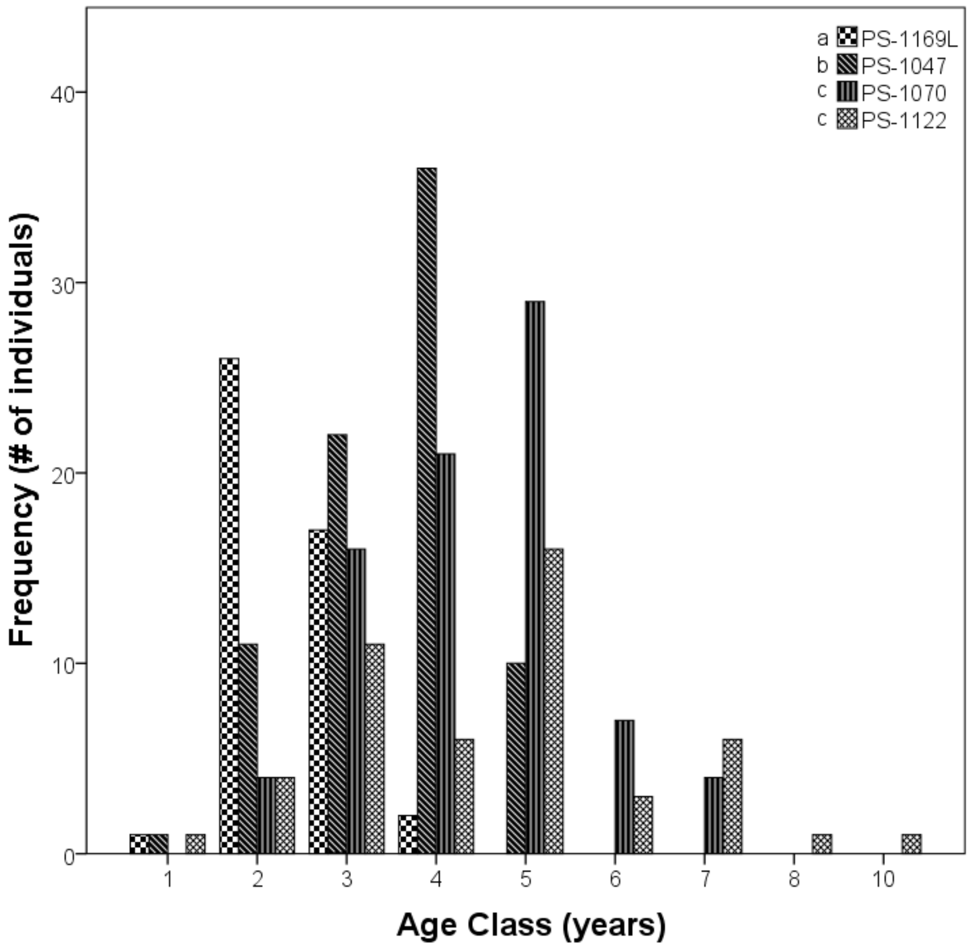

Figure 13. Frequency distribution (number of individuals) of age classes (years) for red snapper (*Lutjanus campechanus*) collected between June 2014 and May 2015 at four artificial reefs in south Texas (reference to nearshore or offshore sites and labels as in Table 4). Sample size as in Figure 8C. Site groups with different letter assignments (a-c) are significantly different (see text for details).

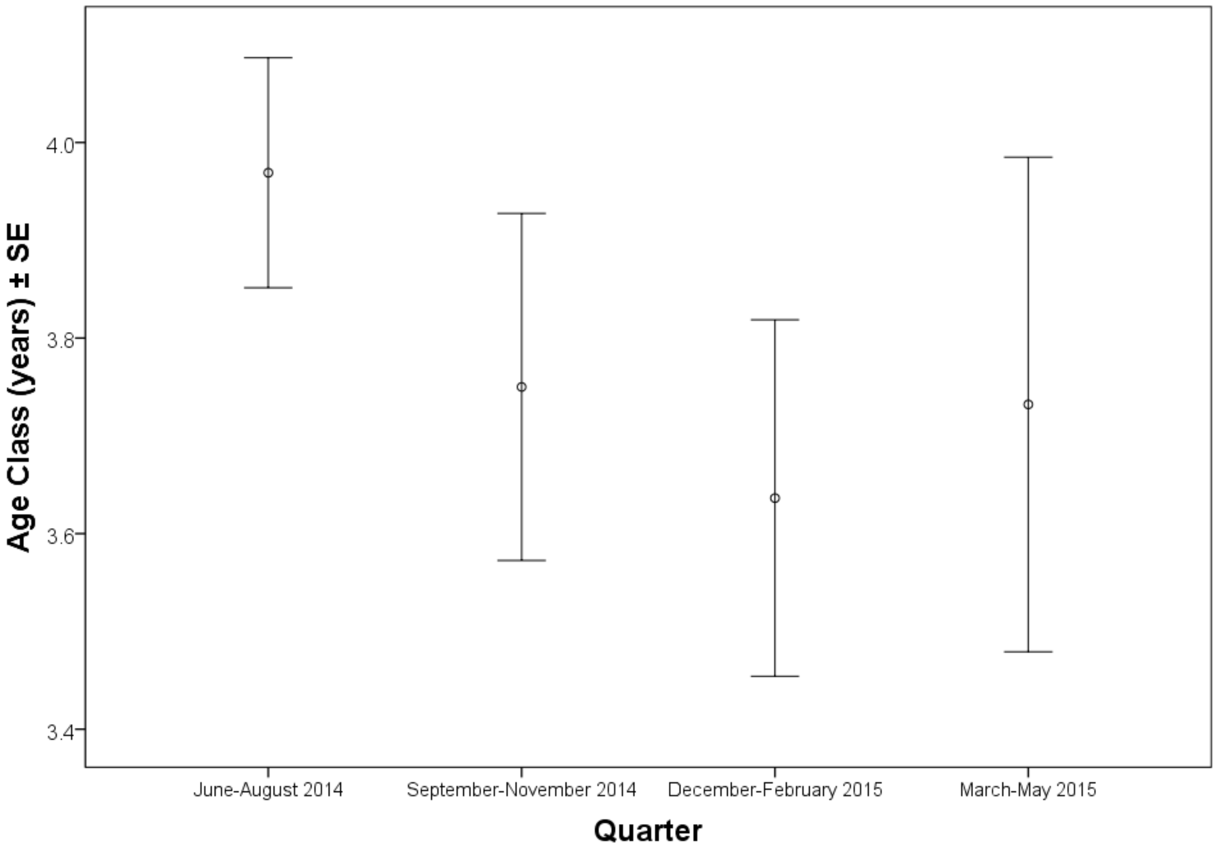

Figure 14. Mean age class (years) ± 1 standard error (SE) of red snapper (*Lutjanus campechanus*) collected from June 2014 to May 2015 by quarter at four artificial reef sites in south Texas. Sample size as in Figure 8C.

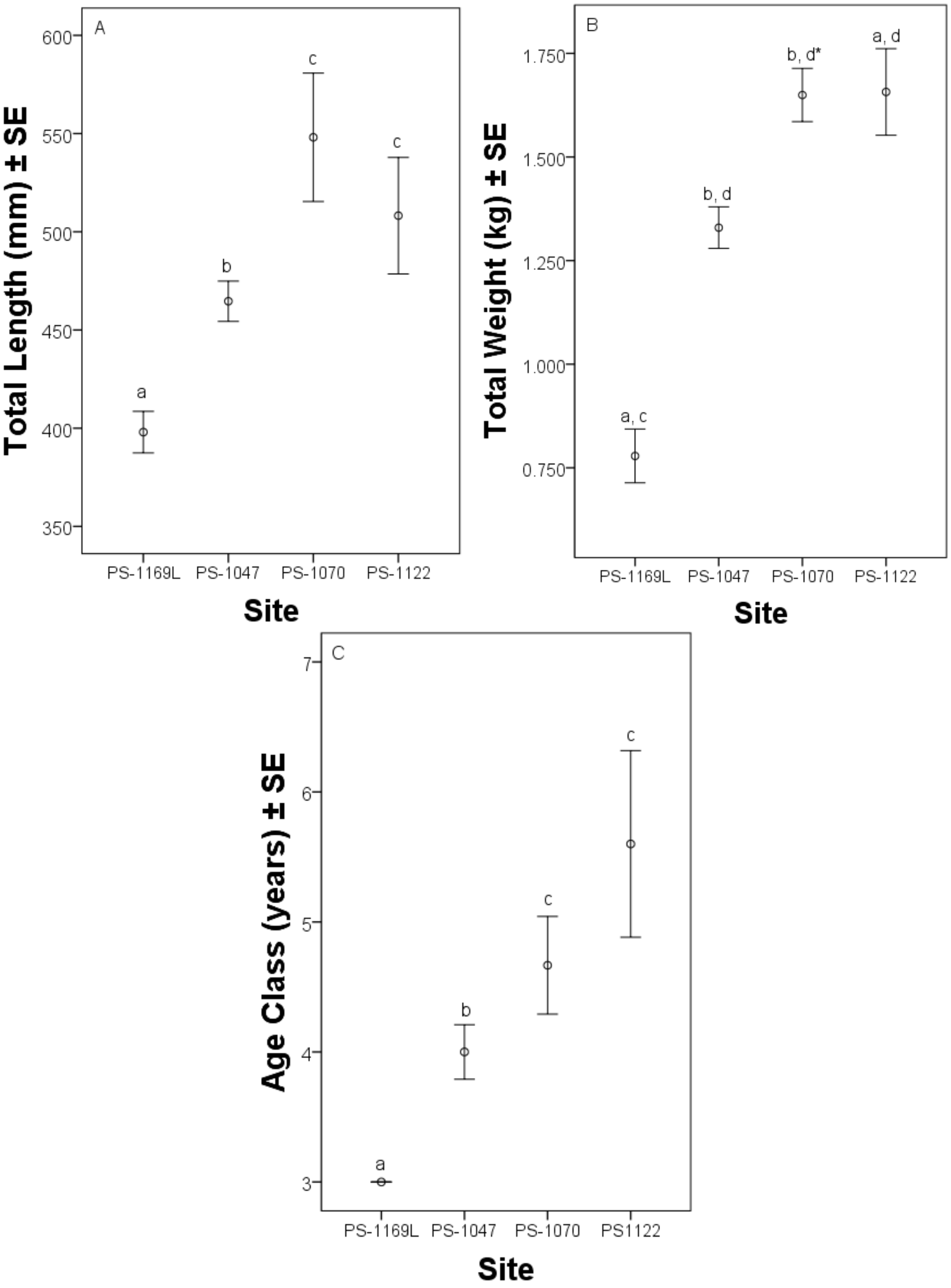

Figure 15. Mean (A) total length (mm), (B) total weight (kg), and (C) age class (years) ± standard error (SE) of mature female red snapper (*Lutjanus campechanus*) collected from June 2014 to May 2015 at four artificial reef sites in south Texas (labeled as in Figure 5). Note changes in vertical axes. Site groups with different letter assignments (a-c) are significantly different (see text for details). n = 43

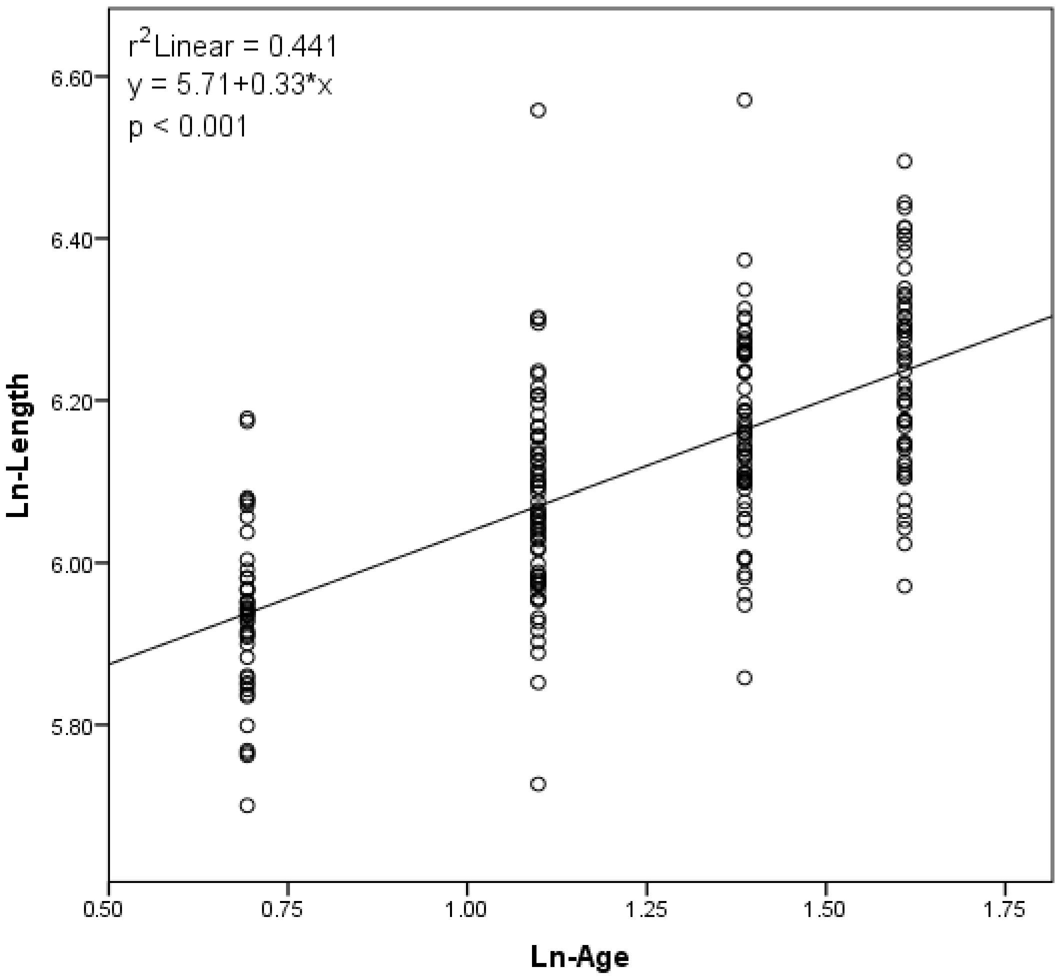

Figure 16. Linear regression of transformed (ln) total length (mm) and age class (years) for female red snapper (*Lutjanus campechanus*), collected during the spawning season (June-September 2014 + April 2015) between June 2014 and May 2015 at four artificial reef sites in south Texas (n = 78). Younger age classes (< 2 years) and older age classes (> 5 years) are omitted from the analyses due to low sample size (see text for details).

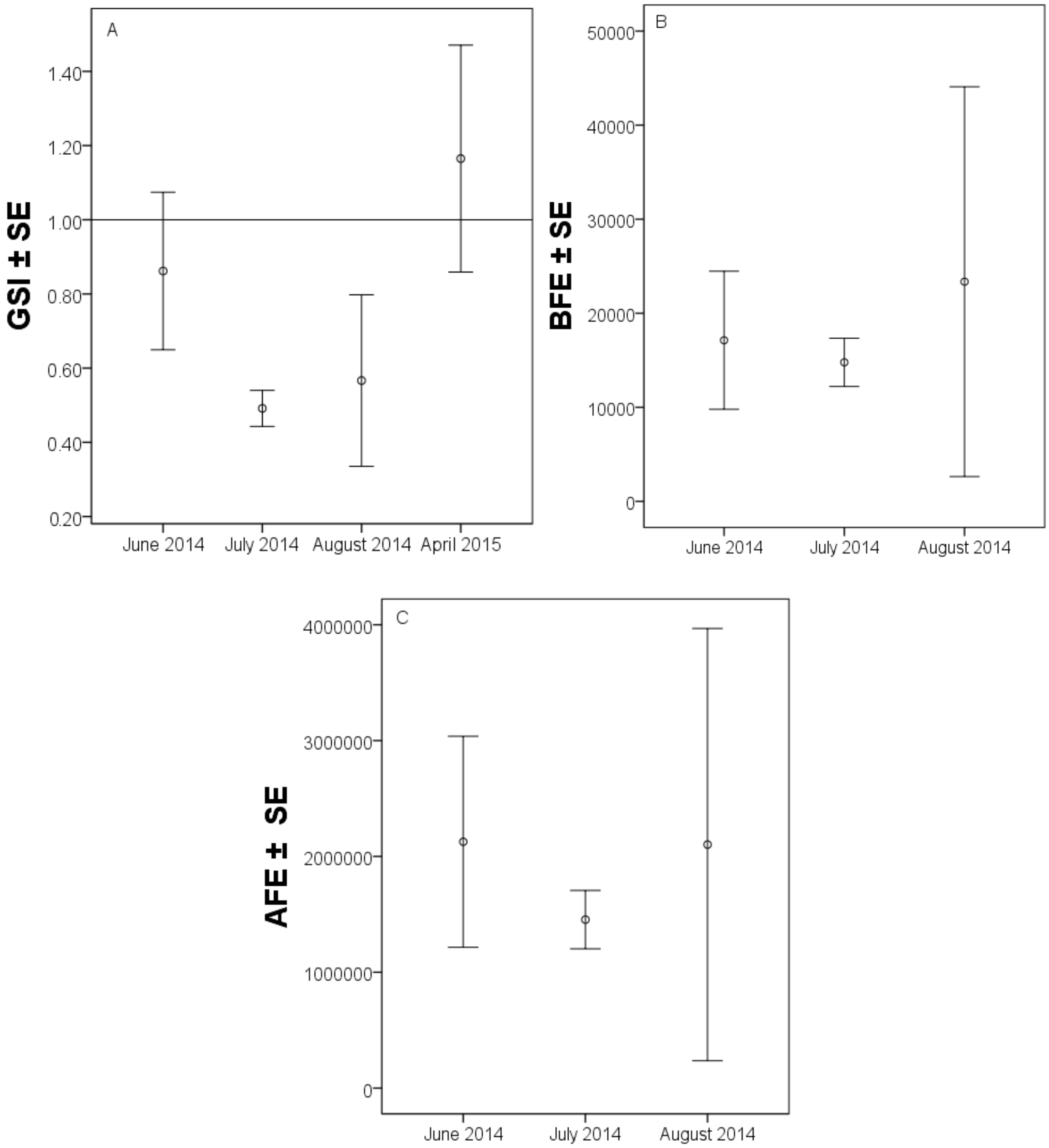

Figure 17. Seasonal variability in reproductive output as measured by mean (A) gonadosomatic index (GSI) values, (B) batch fecundity estimate (BFE), and (C) annual fecundity estimate (AFE) ± 1standard error (SE) of mature female red snapper (*Lutjanus campechanus*) collected from June 2014 to May 2015 at four artificial reef sites in south Texas (labeled as in Figure 5). Only hydrated individuals are used to measure BFE and AFE and no hydrated individuals were observed in April 2015. High variability in (B) and (C) is the result of smaller sample size; for June (n = 11), July (n = 6), and August (n = 2). Note changes in scale among axes.

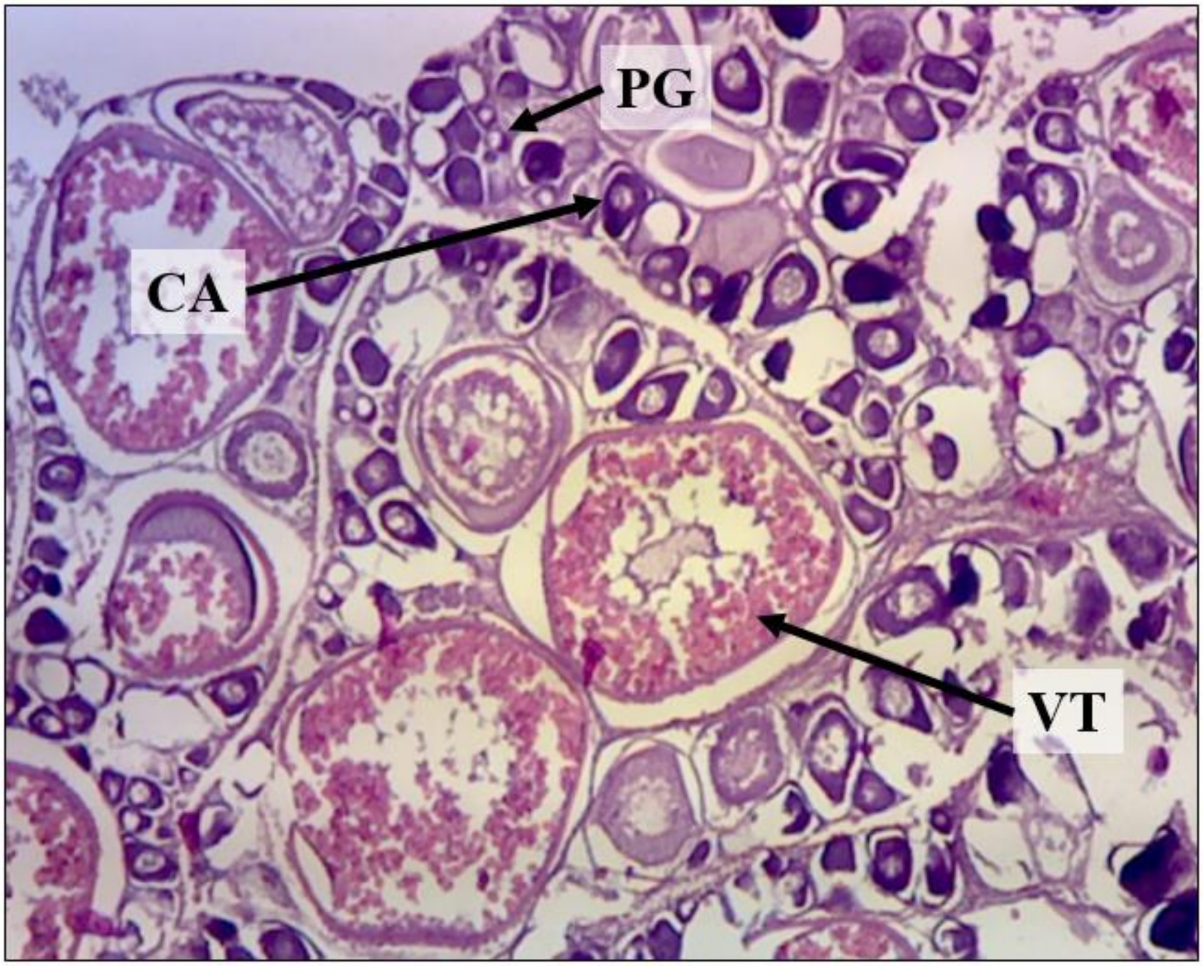

Figure 18. Primary growth (PG), cortical alveolar (CA), and vitellogenic (VT) oocytes represent the first three developmental stages in red snapper (*Lutjanus campechanus*). Vitellogenic oocytes indicate that an individual is sexually mature.

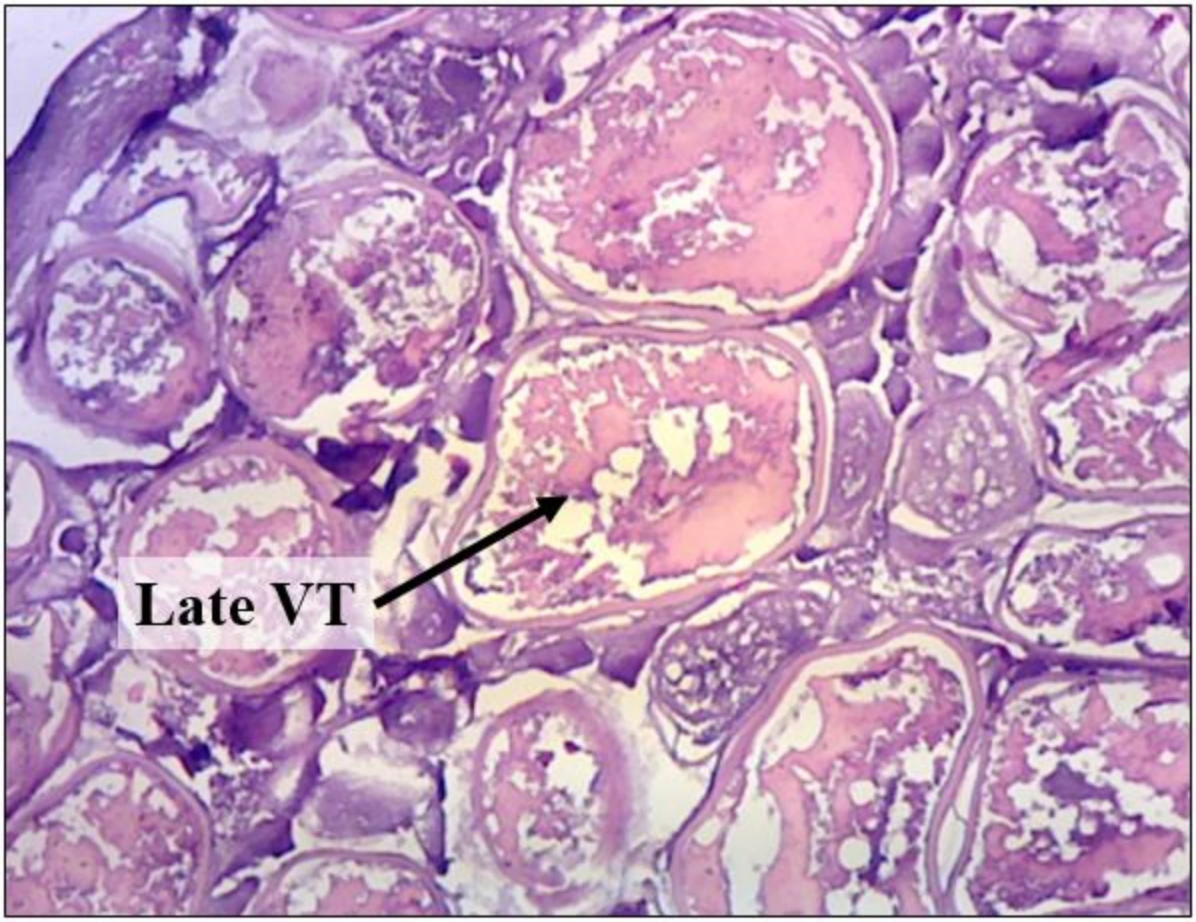

Figure 19. Late-stage vitellogenic (VT) red snapper (*Lutjanus campechanus*) oocytes indicate an imminent spawning event.

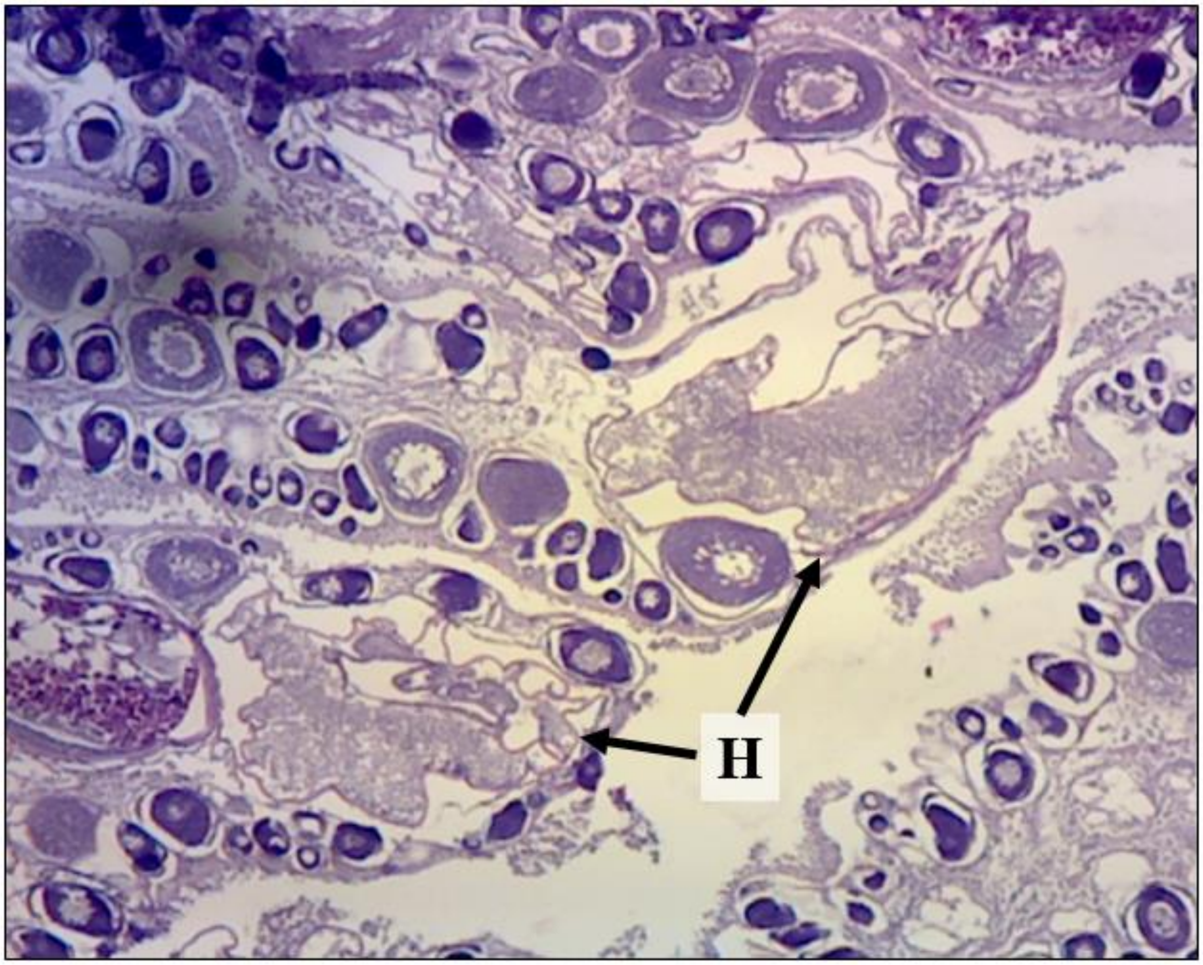

Figure 20. Hydrated (H) red snapper (*Lutjanus campechanus*) oocytes indicate an imminent spawning event.

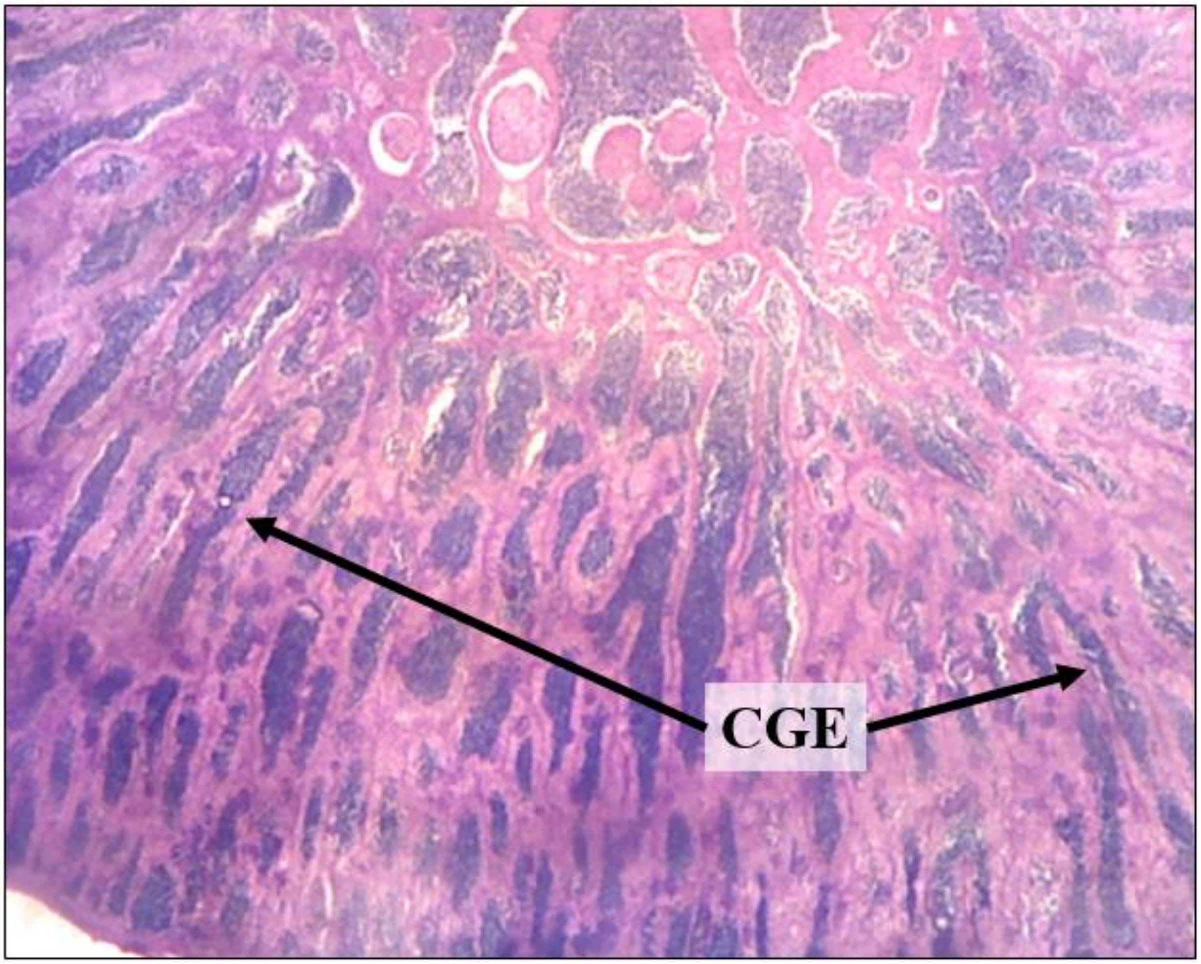

Figure 21. The presence of continuous germinal epithelium (CGE) indicates sexual maturity in male red snapper (*Lutjanus campechanus*).

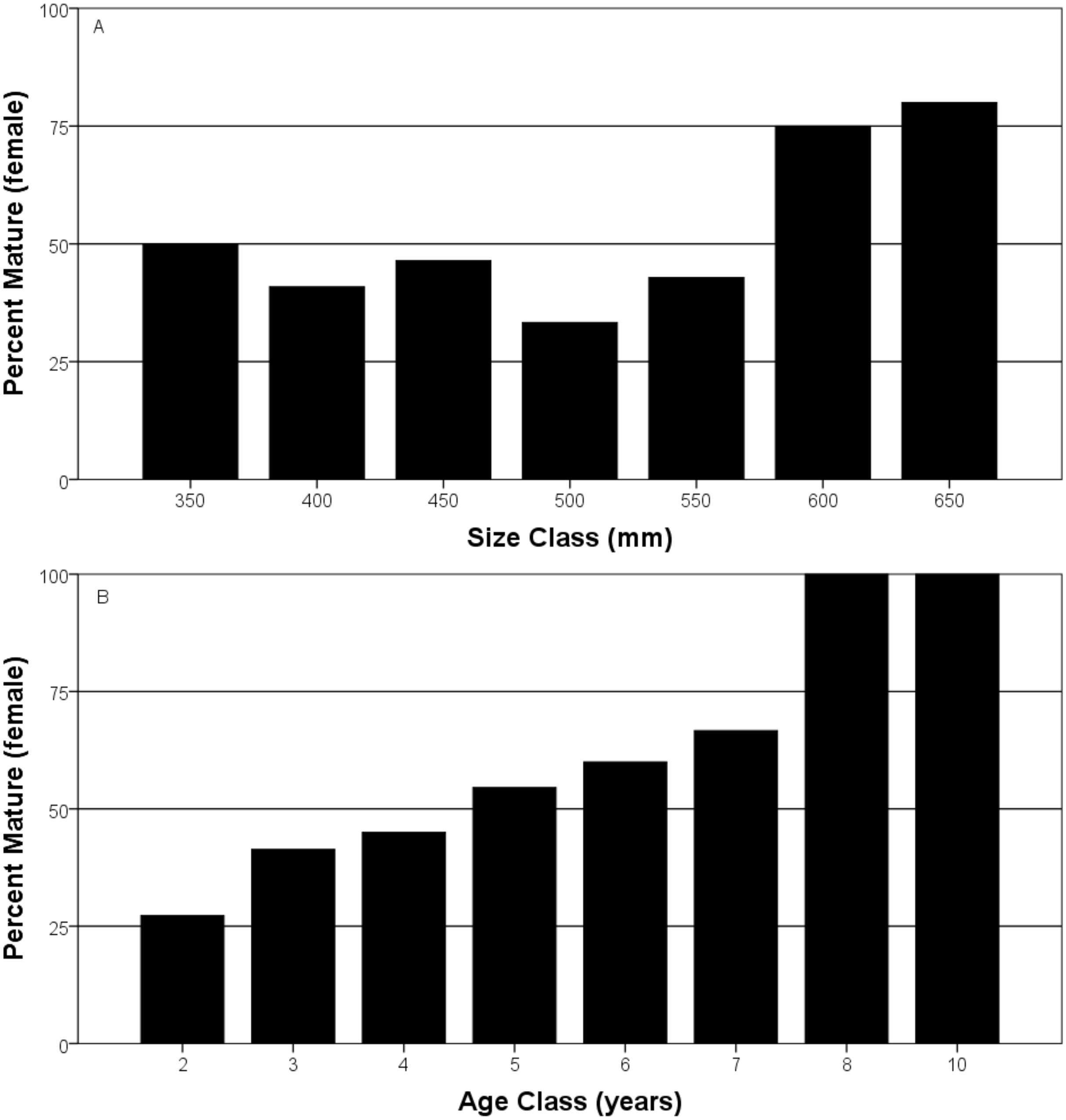

Figure 22. (A) Size- (B) and age-at-maturity for female red snapper (*Lutjanus campechanus*) collected from June 2014 to May 2015 at four artificial reef sites in south Texas. Samples from October to March were excluded because it is impossible to differentiate between mature and immature individuals outside of the spawning season. Reference lines occur at 25, 50, 75, and 100% maturity. n = 91

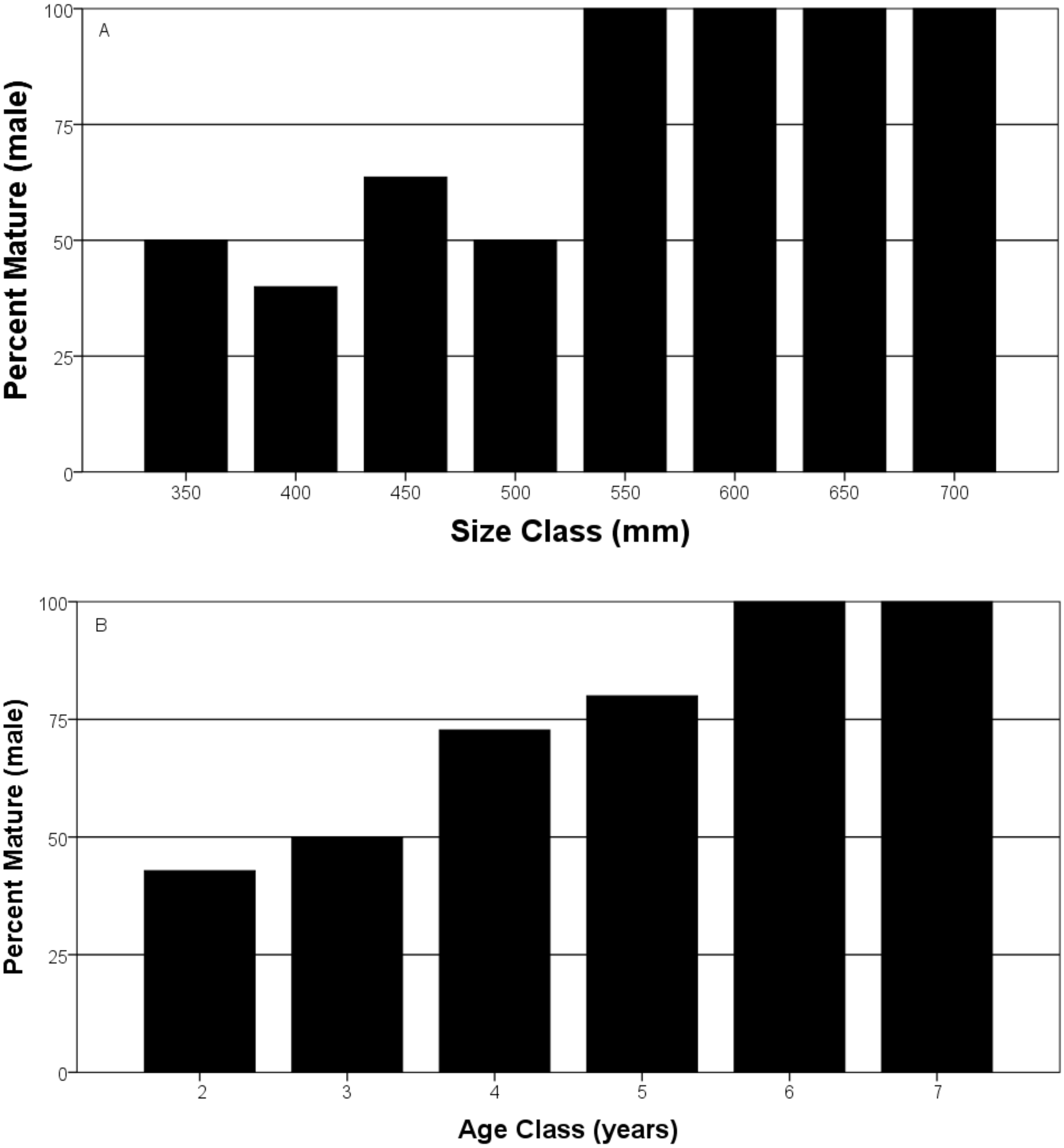

Figure 23. (A) Size- and (B) age-at-maturity for male red snapper (*Lutjanus campechanus*) sampled from June 2014 to May 2015 at four artificial reef sites in south Texas. Samples from October to March were excluded because it is impossible to differentiate between mature and immature individuals outside of the spawning season. Reference lines occur at 25, 50, 75, and 100% maturity. n = 41

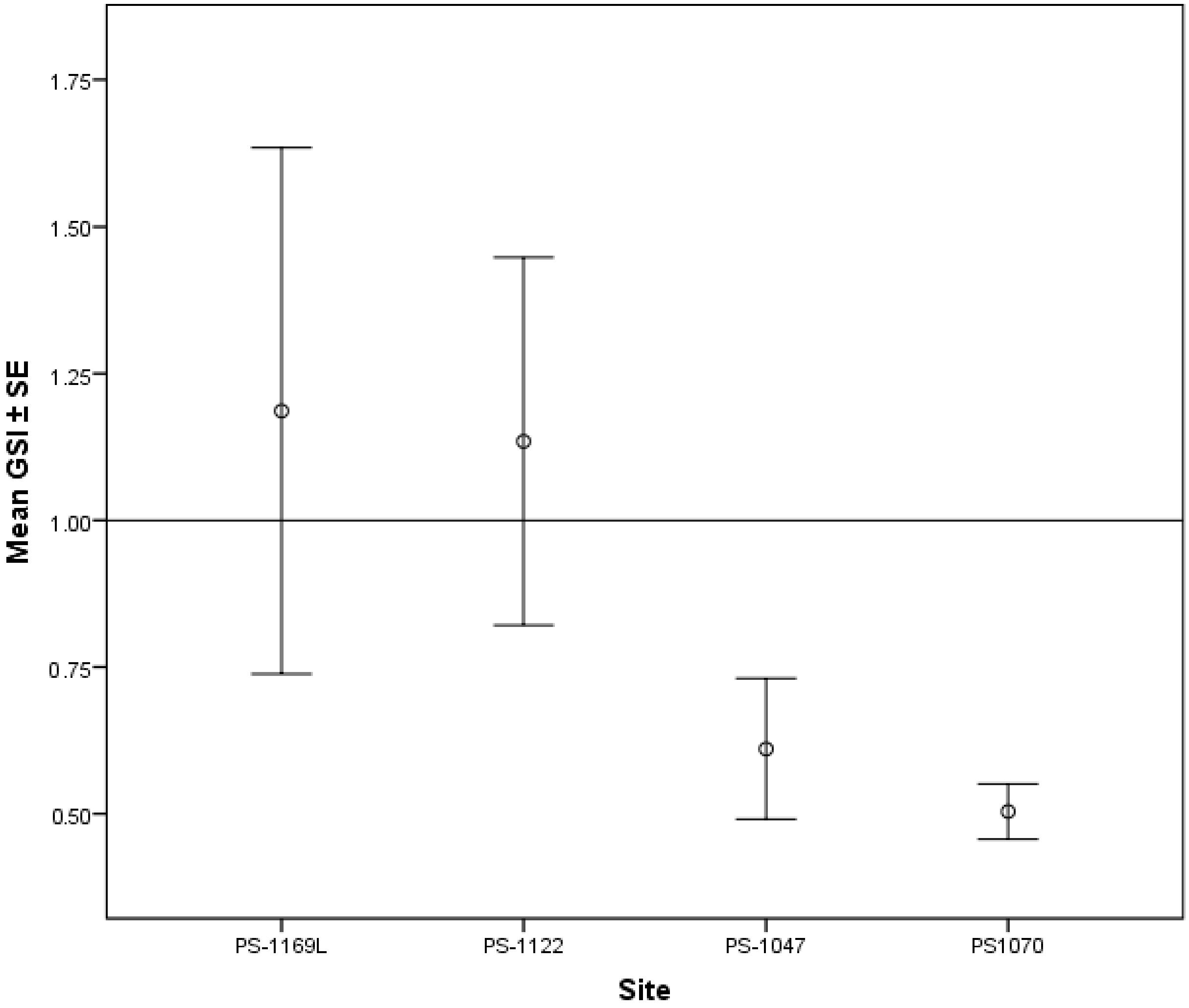

Figure 24. Mean gonadosomatic index (GSI) values ± 1 standard error (SE) of mature female red snapper (*Lutjanus campechanus*) collected during the spawning season (June, July, and August 2014 + April 2015) at four artificial reef sites in south Texas (labeled as in Figure 5). GSI values less than 1 (reference line) indicate the population is producing suboptimal batch sizes. No sampling occurred in September due to unsafe weather conditions. PS-1169L and PS-1122 are 30-70 km south of PS-1047 and PS-1070. Sample size as in Figure 22.

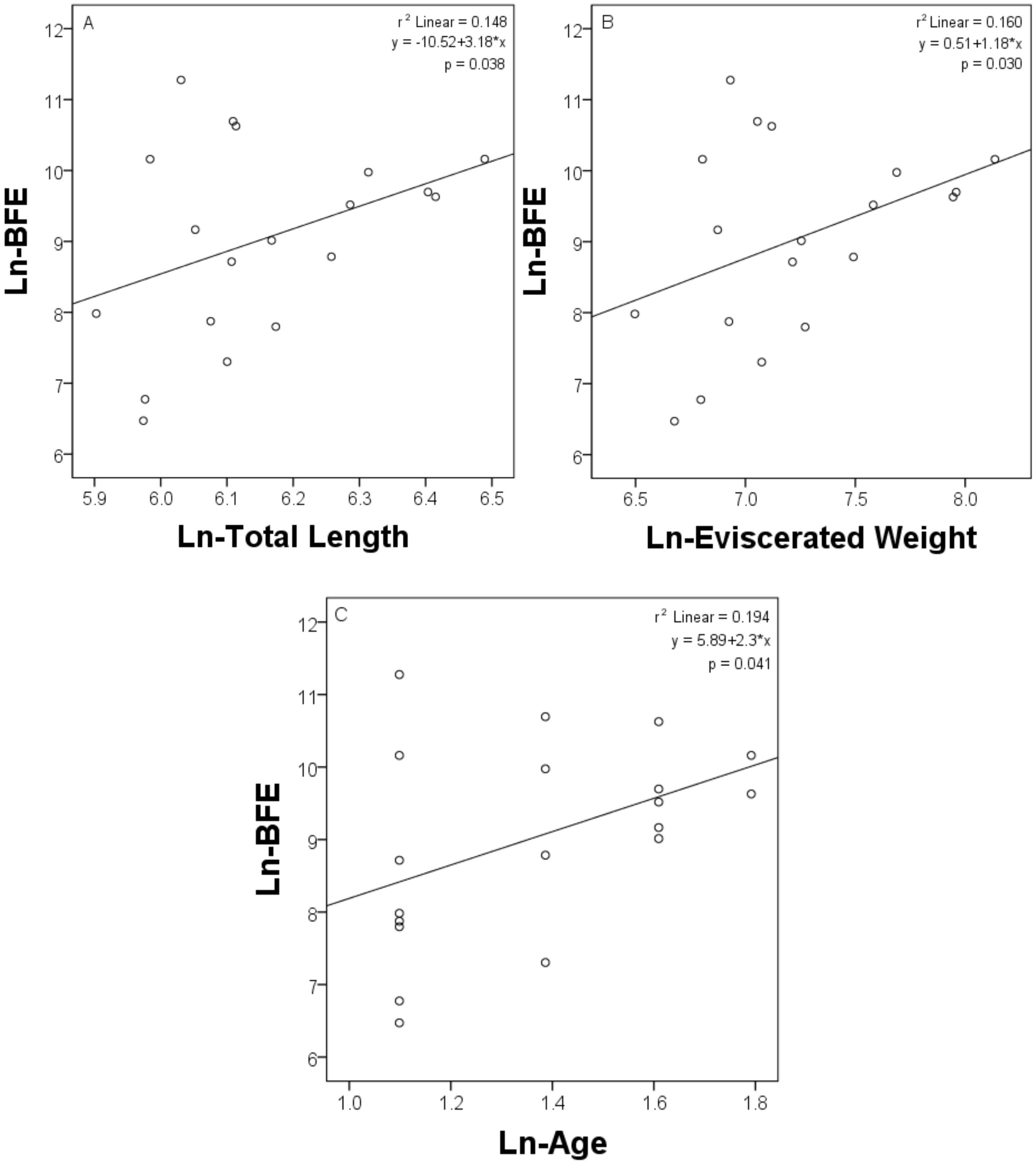

Figure 25. Scatterplots with regression lines display relationships between ln-transformed (A) length, (B) eviscerated weight, and (C) age and ln-transformed batch fecundity estimates (BFE) of hydrated female red snapper (*Lutjanus campechanus*) collected from June 2014 to May 2015 at four artificial reef sites in south Texas. Values for r^2, linear equation, and p-values are shown. Note changes in scale along axes. n = 19 hydrated individuals

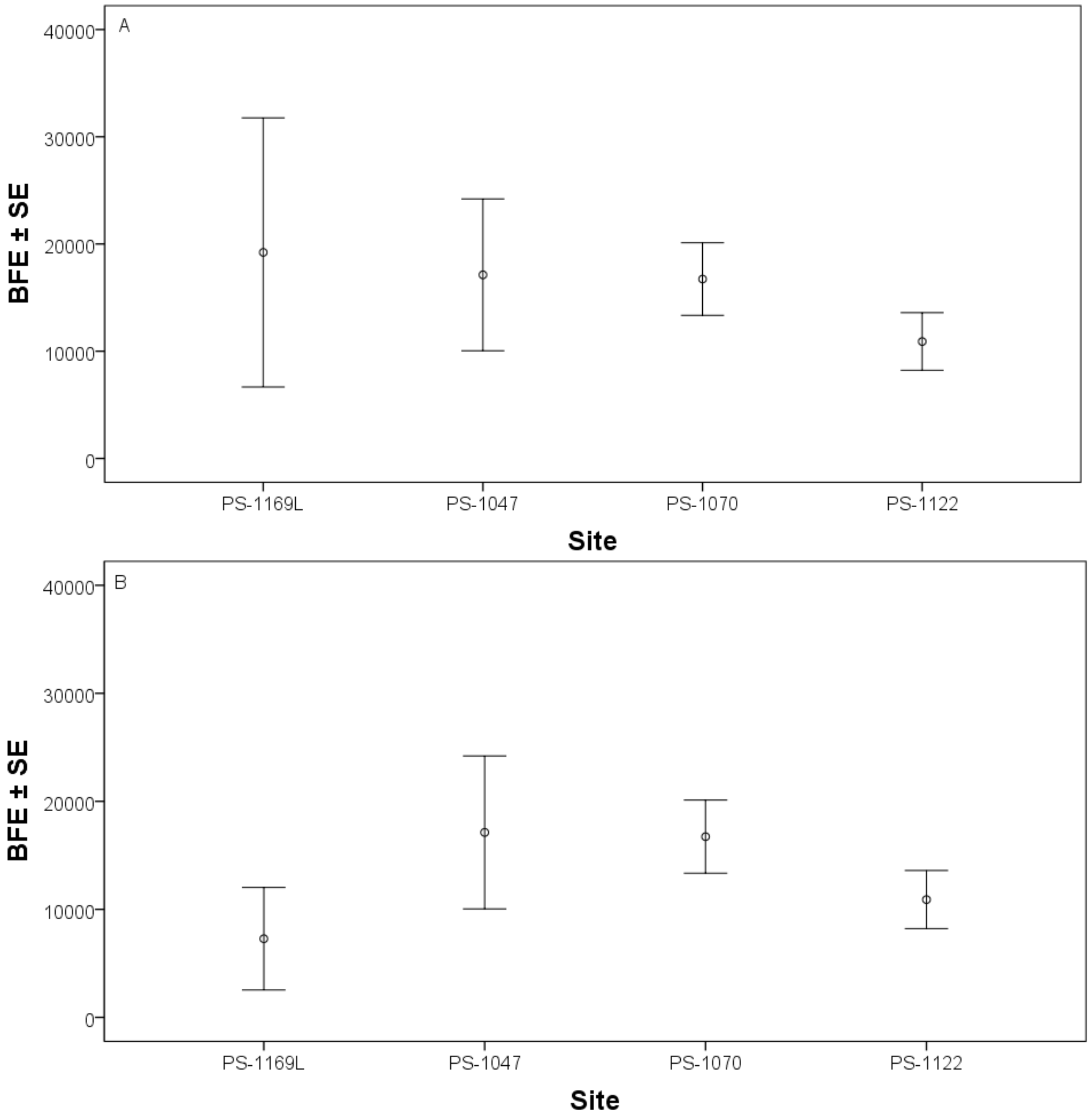

Figure 26. Mean batch fecundity estimate (BFE) ± 1 standard error (SE) for mature female red snapper (*Lutjanus campechanus*) collected between June 2014 and May 2015 at four artificial reef sites in south Texas (labeled as in Figure 5). At one site (PS-1169L), one extremely fecund female was an outlier. This outlier is included in Figure (A) and excluded in (B). Sample size as in Figure 25. Note changes in scale along the vertical-axes.

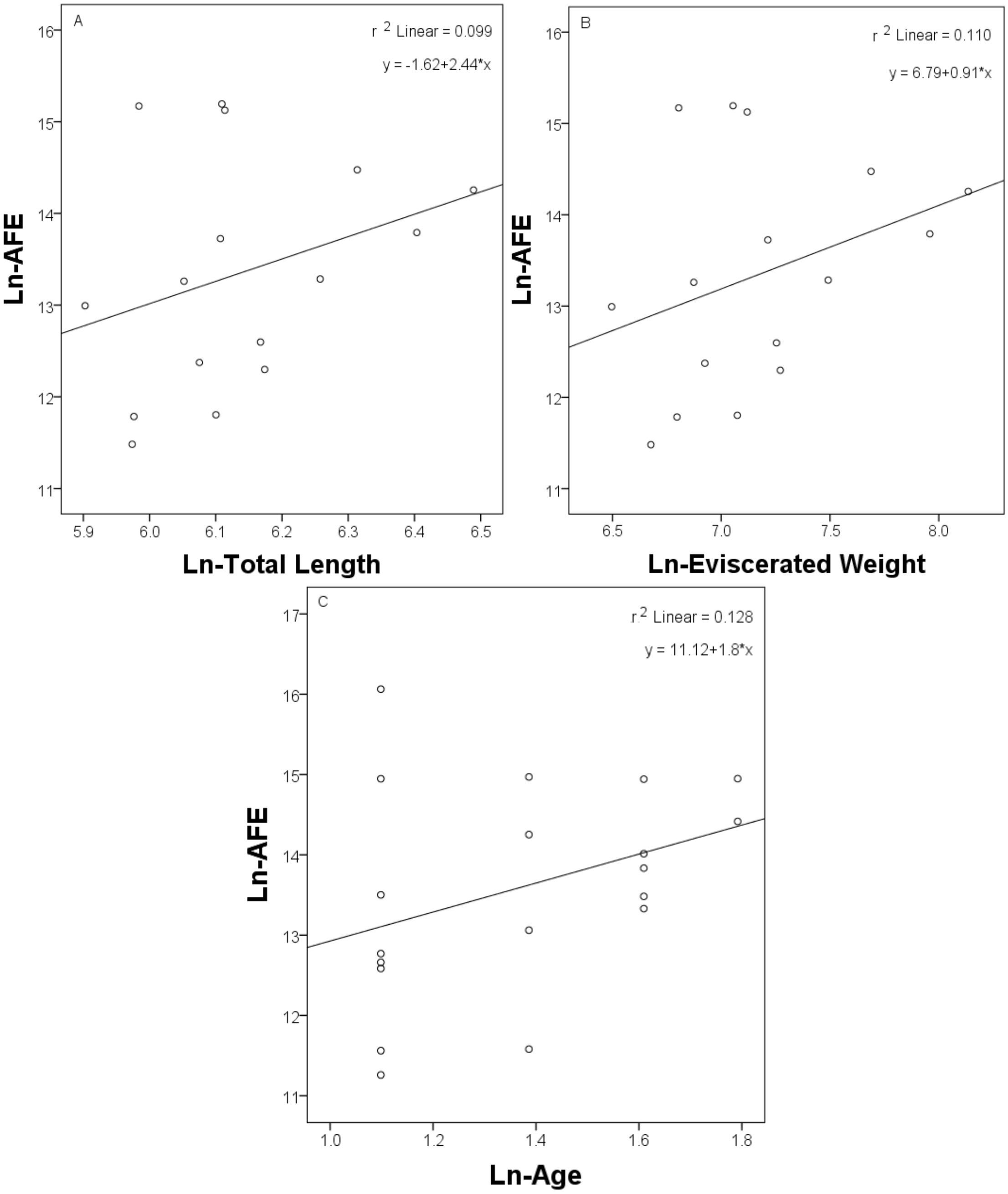

Figure 27. Scatterplots with regression lines display relationships between ln-transformed (A) total length, (B) eviscerated weight, and (C) age class and ln-transformed annual fecundity estimate (AFE) for hydrated female red snapper (*Lutjanus campechanus*) collected from June 2014 to May 2015 at four artificial reef sites in south Texas. Sample size as in Figure 25. Values for r^2 and linear equation are shown.

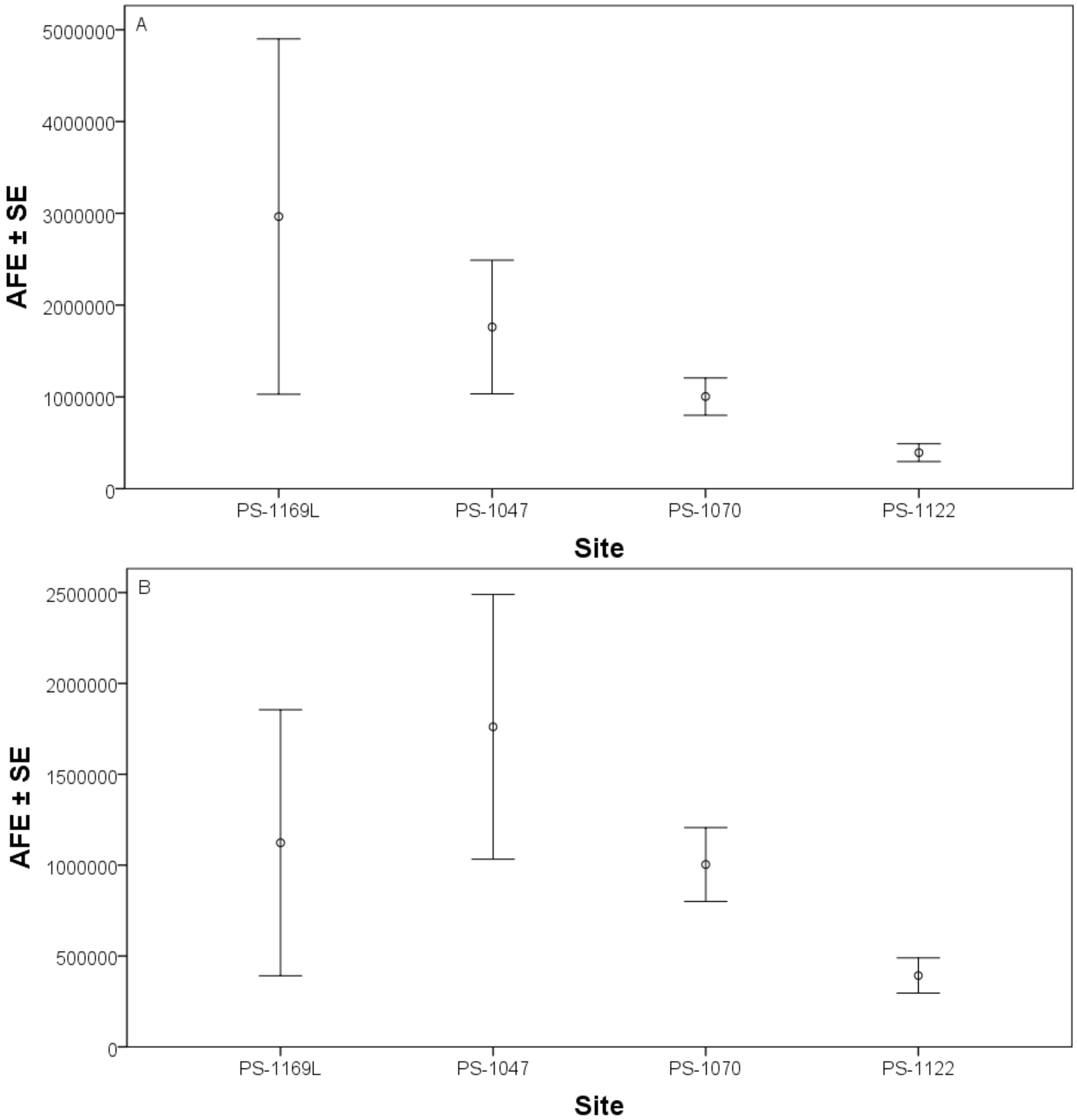

Figure 28. Mean annual fecundity estimate (AFE) ± 1 standard error (SE) for mature female red snapper (*Lutjanus campechanus*) collected between June 2014 and May 2015 at four artificial reef sites in south Texas (labeled as in Figure 5). At one site (PS-1169L), one extremely fecund female was an outlier. This outlier is included in Figure (A) and excluded in (B). Sample size as in Figure 25. Note changes in vertical axes.

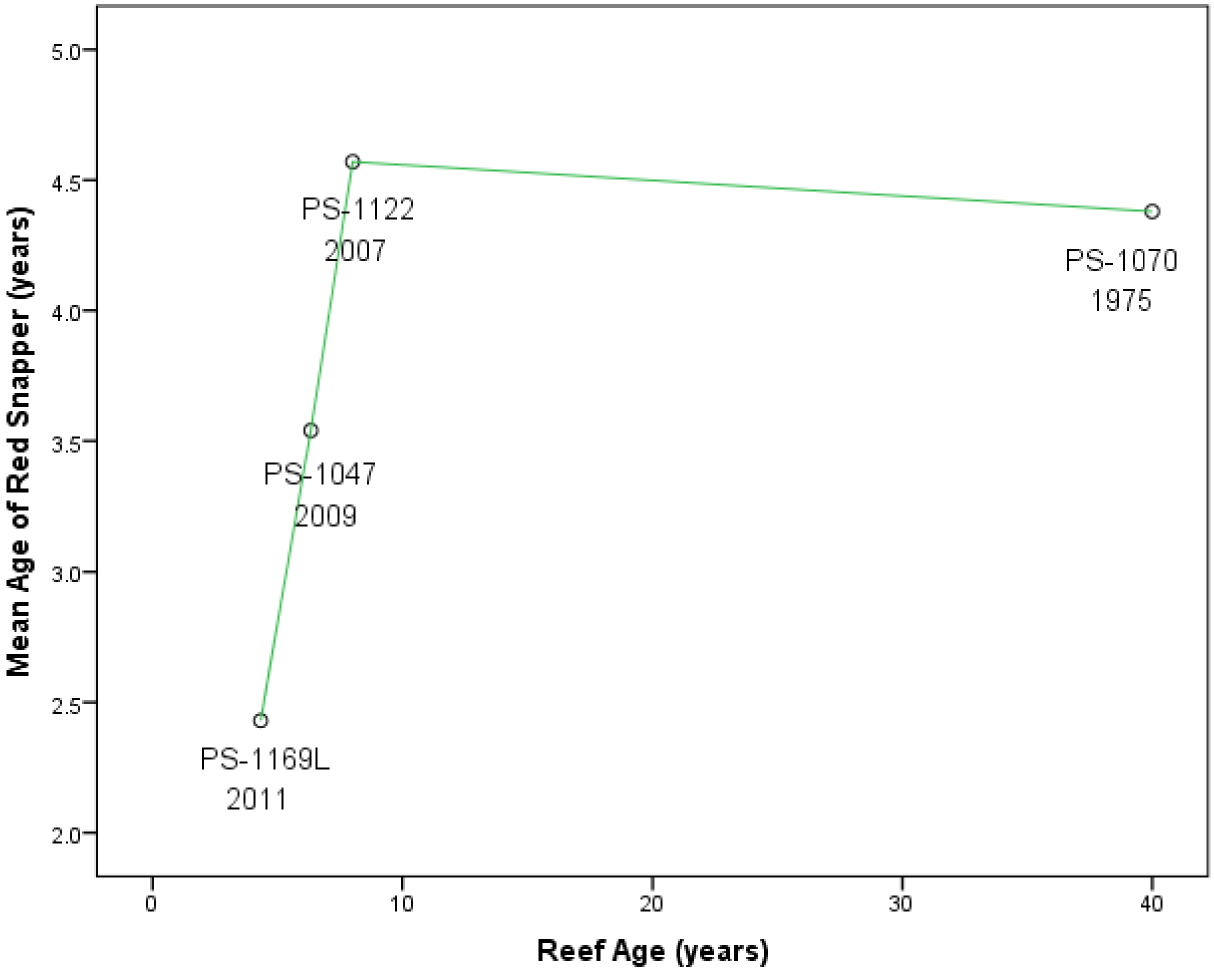

Figure 29. Mean age (years) of red snapper (*Lutjanus campechanus*) plotted against artificial reef age (years). A reference line shows the increasing pattern of age for younger artificial reefs. Sites are labelled with name and year of initial deployment. Sample size as in Figure 6.

BIOGRAPHICAL SKETCH

Ricky Jay Alexander was born and raised in Evansville, Indiana. He graduated magna cum laude and was awarded a full tuition academic scholarship to the University of Maine at Machias, where Ricky studied marine biology, with a special focus in ecology, performing research on bivalves and completing an internship at a shellfish hatchery. After graduating with a B.S., Ricky began his career as a fisheries biologist working for MRAG Americas, a NMFS contractor, based out of Falmouth, MA. Ricky served many roles for MRAG; he held titles as a dockside monitor, at-sea-monitor, Northeast fisheries observer, West Coast groundfish observer, and Inter-American Tropical Tuna Commission transshipment observer, in addition to helping on a handful of smaller projects. In May 2011, his diligence was rewarded when Ricky was named At-Sea-Monitor of the Month by the National Marine Fisheries Service.

In 2013, Ricky began working a second job with RPS Groups, a Houston-based energy consultation firm. This work, as a marine mammal observer, required monitoring offshore waters for signs of marine life and advising industry personnel on environmental compliance with the MMPA, ESA, and OCSLA. The same year, Ricky moved to Brownsville, Texas, where he began his graduate work at the University of Texas, Rio Grande Valley. In addition to his graduate studies, Ricky has volunteered with the Marine Mammal Stranding Group, Fishing’s Future, the Restoration Ecology Club, and the Port Mansfield Floating Classroom. Further, Ricky interned with Rancho Viejo Country Club, providing fish management recommendations for two ponds. Ricky was also nominated by Texas Sea Grant as a 2015 John D. Knauss Fellow and was awarded the degree of Master of Science in biology in December 2015.