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## Otoliths Then and Now: A Study of Ancient and Modern Fish Populations in Louisiana's Coastal Waters

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OTOLITHS THEN AND NOW:  
A STUDY OF ANCIENT AND MODERN FISH  
POPULATIONS IN LOUISIANA'S  
COASTAL WATERS

A Thesis

Submitted to the Graduate Faculty of the  
Louisiana State University and  
Agricultural and Mechanical College  
in partial fulfillment of the  
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Master of Science

in

The Department of Oceanography and Coastal Science

by  
Marshall James Kormanec  
B.S., University of North Carolina at Wilmington, 2005  
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“As many truths as men. Occasionally, I glimpse a truer Truth, hiding in imperfect simulacrum of itself, but as I approach, it bestirs itself & moves deeper into the thorny swamp of dissent.”

— David Mitchell, *Cloud Atlas*

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## ABSTRACT

Fish otoliths are composed of inorganic calcium carbonate that aid in gravity and auditory reception. Substances permanently accrete to otolith surfaces in distinct temporal patterns of alternating opaque and translucent rings; these rings are direct proxies for a fish's age. The objective of my research is to demonstrate how otoliths can be used through time and space to estimate both age and growth of fish. I investigated the spatial differences in age distributions and growth models for red snapper, *Lutjanus campechanus*, at four natural shelf-edge reefs in the northwestern Gulf of Mexico. Red snapper cohorts ranged 1987-2010 cohorts, with the majority (91.69%) of individuals between 4 to 9 years (2001-2009 cohorts) of age. The mean age across all sites was 7.2 years, and the modal age was 6 years. The 2006-year class dominated the distribution (22.98%) and the modal cohort was 2005. Differences in the von Bertalanffy growth parameter  $k$  were not detected despite significant differences in mean-size-at age in older age classes. Results suggest that habitat quality may be paramount in investigating red snapper demographics at shelf reefs. In addition, I investigated the temporal differences in freshwater drum *Aplodinotus grunniens*, age and growth estimates between ancient and modern freshwater drum populations. Ancient otoliths were recovered from shell middens associated with the Tchefuncte culture and the modern otoliths were collected from the commercial fishery in southeastern Louisiana between 1987-1989. Ancient otoliths were radiocarbon dated to 650 BCE, separating the two populations by ~2,600 years. Both populations exhibited a truncated age structure but significantly differed in age frequency distributions and mean age estimates. Mean otolith weight-at-age estimates were similar when plotted against biological age.

Estimates of growth rates were difficult to obtain due to low sample sizes in young and older freshwater drum age-classes and the interment of ancient otoliths. Results suggest that mean otolith weight-at-age may be the most appropriate method for modeling growth. Furthermore, fishery exploitation and fisher gear selectivity may have been similar between the Tchefuncte and modern commercial fishers, despite the common assumption that ancient fish populations reached greater sizes-at-age and exhibited faster growth rates.



## CHAPTER 1: INTRODUCTION

Teleost fishes have three pairs of otoliths within paired membranous labyrinths and they act, in concert with sensory maculae, as both gravity and auditory receptors (Campana 1999). Otoliths are composed of inorganic calcium carbonate that crystalizes in three forms, aragonite, vaterite and calcite. Bound within the crystal lattice is a chemical record of the exposure to the waters in which the fish lived. Unlike other calcified structures otoliths are not re-absorbed or re-precipitated, except under times of extreme stress (Mugiya and Uchimura 1989, Murayama et al. 2002). Therefore elements or compounds accreted onto it's surface are permanently retained and the continued growth through out the fish's lifetime is recorded (Campana and Neilson 1985).

In many subtropical fish species, the dominant features in transverse otolith sections are alternating opaque and translucent zones, which together comprise an annual increment. The quantification and measurement of annuli is a major source of information on the age and growth of fishes (Campana 1999).

Otolith growth is dependent upon the metabolism of the fish. Calcification and deposition of annuli within the otolith is dependent on the inorganic make up of the endolymphatic fluid surrounding the otolith. The basic pathway of inorganic elements into the otolith is from the continuous flow of seawater into the intestine. Trace elements from the water column are then assimilated into the blood plasma, and deposited into the crystallizing otolith via the endolymphatic fluid (Olson et al. 1998). The most important regulating factor is the pH of the endolymph. At lower alkalinities the rate of calcification decreases (Romanek and Gauldie 1996). Temperature, salinity, and

dissolved oxygen influences calcification rates as well, but the abiotic factors are less important than the composition of the endolymphatic fluid (Wheeler et al. 1987).

Age and growth studies convey two related concepts. Age is the quantitative description of a fish's lifespan; growth is change in size over time. Accurate age estimates allow fishery managers to identify strong-year classes, conduct age-structured population models, and document population recovery (Wilson and Nieland 2001). Age and growth data used separately provide important information regarding individuals and populations, however they are most powerful when interpreted in concert. For example age and growth information can identify problems, such as overfishing and recruitment limitation, and provide information on the effectiveness of management practices (Cassoff et al. 2007).

Otoliths will be used here to compare age structure and growth rates within and between and among sites, habitats and eras. Chapter two focuses on red snapper caught on four natural shelf-edge reefs in the northwestern Gulf of Mexico (GOM). Age structure, growth rate, relative cohort strength, and mean size-at-age are examined. Chapter three compares freshwater drum otolith weights and edge conditions between a modern population and otoliths recovered from an archaeological midden associated with the Tchefuncte tribe *circa* 650 BCE. Modern otoliths are used to determine the seasonal use of fishing grounds and to compare age and growth rates between the two populations.

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## CHAPTER 2: AGE AND GROWTH PARAMETERS OF RED SNAPPER AMONG THE SHELF-EDGE REEFS IN THE NORTHWESTERN GULF OF MEXICO

### 2.1 Introduction

Red snapper is an economically and ecologically important reef-associated fish in the Gulf of Mexico (GOM). The red snapper fishery is a complex mixture of competing sectors in the northern GOM where profits from commercial harvests and recreational charters support local communities, and stimulates the economy through tourism and jobs.

The 2012 benchmark red snapper stock assessment recommends an increase in small-scale, fishery-independent studies. These studies should target sub-regional and localized habitats, be designed-based, random, and representative of temporal red snapper demographics (SEDAR 31). Recent red snapper studies have investigated the biological parameters of red snapper at and among artificial and natural shelf-edge reefs with a wide range of analyses: age and growth, diet analysis, stable isotopes, hydroacoustics, and reproduction studies (Saari 2011, Kulaw 2012, SEDAR 2013, Schwartzkopf 2014, Simonsen et al. 2014a). This study, among others done in the Cowan laboratory at Louisiana State University, School of Energy, Coast and Environment beginning in 2008, are apparently the only studies that have been done on the shelf-edge reefs since 1975 (Bradley and Bryan 1975, Davis 1975), other than couple of summaries of video (Gledhill 1996), that data that remains unpublished. This became evident when members of the Cowan laboratory participated in a review done for the Bureau of Ocean Energy Management (VERSAR 2009) that revealed that more than 95% of the available information on red snapper up until the review was completed was based upon studies on artificial reefs.

This project compares age and growth estimates for red snapper at four natural shelf-edge reefs as part of a larger study to address voids in red snapper data at these habitats. Accurate age and growth information will contribute to the understanding of the role and function of natural shelf-edge reefs in the life history of red snapper in the northwestern GOM.

More than a hundred carbonate reefs are known to exist on the continental shelf and the upper continental slope in the GOM from the Mississippi River Delta to Port Isabel, Texas. Most of the reefs are associated with salt diapirs and is thought to contribute approximately 2800 km<sup>2</sup> of habitat in the northwestern GOM (Parker et al. 1983, Rezak et al. 1985). These rocky outcroppings are more common in the northwestern GOM than the northeastern GOM, in which substrates are largely composed of mud, sand, and artificial reef habitats (Szedlmayer, 1994). In general there are three types of habitat in the GOM: soft bottom composed of mud/sand/silt, natural hard bottom consisting of shell/rubble/rocky outcrops, and artificial hard substrate (oil platforms, shipwrecks, and constructed reefs) (Gallaway, 1998).

The four natural shelf-edge reefs (shelf-edge reefs) sampled in this study were selected because of their differences in location on the continental shelf, proximity to the mouth of the Mississippi River, and the diversity of biotic and biological assemblages (Figures 2.1 and 2.2). The eastern shelf-edge reefs mostly consist of sand and soft coral as opposed to the western shelf-edge reefs that are dominated by rocky carbonate outcrops and coralline algae (Gardner and Beaudoin 2005). Therefore, in this study, our results will reflect an empirical three-year ‘snapshot’ of both the similarities and

differences in age and growth estimates of red snapper among reefs in proximity to the Mississippi River moving westward along the continental shelf-edge.

Bright reef (Bright) is located on the outer-shelf, approximately 19km east of the Flower Gardens Bank Nation Marine Sanctuary (FGBNMS) and is the most western reef in this study. Bright is a living coral cap covering multiple subsurface salt domes. The community structure consists of coralline algae, drowned reef formations, and is diverse in coral and reef fish assemblages. Recently, bathymetric data has revealed the presence of a mud volcano (geo-exuded slurries or pelovolcano) and also, near an isolated reef spire, pock marks have been identified, that may be formed by hydrocarbon sinks (Moretzsohn et al. 2014).

McGrail reef (McGrail) formerly called 18-fathom reef, is located 215 km southwest of Port Fourchon, Louisiana (LA). McGrail is a horse-shoe shaped pair of northeast-southwest trending ridges separated by a valley (Hickerson and Schmahl 2002). The presence of underlying salt domes is uncertain, as is the role of salt dome tectonics at the reef (Schmahl and Hickerson 2006). The reef has an irregular surface relief ranging from 90 m (largest section) to shallower reliefs at 65 m (Gardner and Beaudoin 2005). McGrail is highly diverse in reef fish assemblages and 78 reef species have been observed (Hickerson and Schmahl 2002), but is rare in the northern GOM for its extensive reef-building corals (Hickerson and Schmahl 2002, Gardner and Beaudoin 2005). Schmal and Hickerson (2006) used a remotely operated vehicle to explore the reef and reported the presence of a deeper, richer tropical reef community, covering approximately 28% of the surrounding seafloor. Schmal and Hickerson (2002) reported the greatest species richness of reef fish taxa at McGrail.



Figure. 2.1. Geographical locations of four shelf-edge reef sites along Louisiana continental shelf break in the northwestern GOM (Google 2013).

Jakkula reef (Jakkula) is located 251km east of Bright. Dennis and Bright (1988) used cluster analysis and described Jakkula as belonging to the same family of shelf-edge reefs as Bright based on reef fish assemblages and coral diversity. Characterized by underlying salt domes Jakkula has a surface relief range of 120 to 140m. The surface of Jakkula is approximately 66 m below sea level and has the smallest surface area (3.68

km<sup>2</sup>), but has the largest amount of vertical relief (~ 92 m) (Dennis and Bright 1988, Gardner and Beaudoin 2005).

Table 2.2. Geological, biological and geographical summary of the four shelf-edge reefs sampled on Louisiana's continental shelf. Values obtained from Rezak et al. (1985), Dennis and Bright (1988), Gardner and Beaudoin (2005), and Cowan et al. (2007).

Shelf-Edge Reef	Bright	Jakkula	McGrail	Midnight Lumps
Latitude	27°53'N	27°59'N	27°58'N	28°37'N
Longitude	93°18'W	91°39'W	92°36'W	89°33'W
Surrounding Depth (m)	130-150	120-140	110-130	65-110
Subsurface Depth (m)	50	66	45	63
Vertical Relief (m)	75	50	65	37
Surface Area (km <sup>2</sup> )	16.67	3.68	7.19	7.14
Biotic Zones				
<i>Stephanocoenia</i>	37 (m)	Absent	Absent	Absent
Algal Sponge	52-74 (m)	59-90 (m)	45-47 (m)	67-82 (m)
Antipatharian	>74 (m)	90-98 (m)	45-82 (m)	65-85 (m)
Nepheloid	>80 (m)	>98 (m)	Present	>85 (m)
Soft Bottom	>110 (m)	120-140 (m)	110-130 (m)	>100 (m)
Habitat Complexity	Medium	Low	High	Low

Midnight Lumps reef (Midnight Lumps) consists of two protruding carbonate reefs located approximately 19km east of the Mississippi canyon (Moretzsohn et al. 2014). The northern reef (also known as Sackett reef) is well described in detail by Rezak et al. (1985). The northern reef due to its proximity to fishing ports has become a 'hot spot' for recreational fishers and much information may be found on angler websites. Structurally the reef is a symmetrical diapir with two gas seeps inside the reef's core located at the northern lump. The nepheloid layer was explored with a submersible vehicle and is consistent with the break of the continental shelf with the mud substrate increased with increasing depth (Rezak et al. 1985).



### 2.1.1 Life History

Red snapper (*Lutjanus campechanus*, family Lutjanidae) is a long-lived demersal teleost strongly associated with reef habitats (Allen 1985). Red snapper in the western Atlantic Ocean occur from Cape Hatteras, North Carolina, throughout the GOM to the Campeche Banks, Mexico (Nelson and Manooch 1982). Red snappers are periodic life history strategists distinguished by delayed maturity, high longevity, high fecundity, asynchronous spawning, and small egg size (Winemiller and Rose 1992).

A periodic life-history strategy maximizes age-specific fecundity at the expense of delayed maturation. Strong age-classes are produced when optimal oceanographic conditions favor larval and juvenile survival (Winemiller and Rose 1992). Red snapper larvae are pelagic and subsequently transported inshore by oceanographic currents. Juvenile red snapper settle over low-relief areas consisting of sand, mud, and shell deposits (Gallaway et al. 2009). At maturity, red snapper undergo an ontological shift in habitat preference to natural and artificial reefs (Szedlmayer and Lee 2004, Gallaway et al. 2009).

Maximum red snapper spawning potential is reached between 12-15 years of age (Render 1995). Red snapper have a protracted spawning season and a 'bet-hedging' reproductive strategy, which is hypothesized to produce a strong year class every 5-10 years and has the ability to produce consecutive strong year classes (Allman and Fitzhugh 2007). Producing consecutive strong year classes adds biomass that helps maintain a stable population under moderate harvest (Cowan et al. 2011). Red snapper have life spans greater than 50 years (Render 1995, Wilson and Nieland 2001) and because of their periodic reproductive strategy, prolonged overfishing lengthens the time of stock recovery attributable to the infrequency of strong year classes (Winemiller and Rose

1992, Secor 2000, Cowan et al. 2011). Red snapper studies have shown moderate site fidelity to the reefs recruited to at young ages; however, long-term site fidelity decreases with both size and age (Patterson et al. 2001b, Patterson and Cowan 2003, Strelcheck et al. 2005, Szedlmayer and Schroepfer 2005, Peabody and Wilson 2006, McDonough 2009). Therefore, identifying habitats, to which, strong year classes are recruiting is paramount to maintaining a healthy biomass and the potential for red snapper to reach maximum spawning potential (Berkely et al. 2004, Palumbi 2004, Walsh et al. 2006).

#### 2.1.2 Age Estimation

Age estimation is an important biological parameter that forms the basis of growth, mortality and productivity estimates of fish species (Campana 2001, Fischer 2007). The largest otolith (sagittal) was first used by Nelson and Manooch (1982) to age red snapper; subsequently, age estimates from otolith annulus counts were verified by bomb radiocarbon dating to life spans upwards of 50 years (Baker et al. 2001, Fischer 2007).

Age estimation in red snapper is subjective and quality control is mandatory to ensure standardization and increased accuracy of red snapper age-estimates that could lead to better stock assessments (Campana 2001, Allman et al. 2005, VanderKooy 2009). In 2003, the National Marine Fisheries Service (NMFS) laboratory in Panama City, Florida and the Gulf States Marine Fisheries Commission (GSMFC) assembled a red snapper otolith reference collection. The collection identifies sources of ageing errors and calculates an Average Percent Error (APE) between readers and laboratories. The collection acts as an important quality control tool to insure accuracy in the age estimation of red snapper GOM wide (Allman et al. 2005).

Validation of the time of first annulus formation in red snapper otoliths is important and has been a huge source of debate. The identification of the first annulus and the interpretation thereof leads to ambiguity among readers, laboratories, and regions (Campana 2001, Wilson and Nieland 2001, VanderKooy 2009). Fischer et al. (2010) used alizarin complexone to document the formation of the first opaque annulus in juvenile red snapper. Formation of the first annulus occurs during the first winter after hatching; they also determined that translucent marginal edges indicate that the first annual opaque deposition reaches completion by mid-July, consistent with the age estimation used in marginal increment analysis (Patterson et al. 2001a, Wilson and Nieland 2001, Allman et al. 2005). A recent study by Szedlmayer and Beyer (2011) reported first annulus opaque deposition to occur in late summer to early winter in oxytetracycline dehydrate (OTC) marked marked-recaptured red snapper. The most recent stock assessment SEDAR 31 proposes additional research into the timing of first annulus deposition.

Red snapper growth and size-at-age is traditionally estimated with linear regressions and nonlinear von Bertalanffy growth models. Nelson and Manooch (1982) first reported GOM wide red snapper estimates of  $L_{\infty}$  (theoretical maximum length) and the growth parameter  $k$ . Improvements in accuracy among readers and laboratories continues to refine estimates of von Bertalanffy growth parameters GOM-wide (Fischer 2007). Wilson and Nieland (2001) and Patterson et al. (2001) reported similar estimates of  $L_{\infty}$  and  $k$  from the commercial and recreational red snapper fisheries in the northern GOM off the coasts of LA and AL ( $L_{\infty}$ =941,  $k$ =0.18;  $L_{\infty}$ =969,  $k$ =0.19; respectively). Fischer (2004) reported significant differences in von Bertalanffy parameters of red

snapper from the recreation fisheries by region (AL, LA, and TX). Red snapper from Texas waters were significantly smaller than Alabama and Louisiana at age, but the growth parameter  $k$  was significantly larger than red snapper collected in Alabama and Louisiana waters. Furthermore, Saari (2011) found similar results and concluded, that in the recreational red snapper fishery small, fast growing individuals populated south Texas, northwest Florida and central Florida landings, while larger, slower growing individuals dominated Alabama and Louisiana landings. Red snapper sub-regional fishery-independent comparisons at toppled and standing gas and oil platforms differed significantly from growth comparisons on the shelf-edge reefs (Saari 2011, SEDAR 2013).

There is a lack of data comparing age and growth parameters of red snapper between natural shelf-edge reefs of varying complexity. This study addresses the need for fishery-independent, small-scale, sub-regional age and growth studies and expands the knowledge of red snapper demographics among the shelf-edge reefs off the LA continental shelf in the northern GOM, specifically age distributions and growth rates.

## 2.2 Methods

On board the research vessel Blazing Seven, red snapper were sampled twice per quarter from four natural shelf-edge reefs in the northwestern GOM that provided a range of habitat types and complexity, however Midnight Lumps was sampled once during the fall of 2011. Collections occurred at a range of depths on each reef, the minimum and maximum being approximately 20 m to 300 m. Fish were collected using both vertical long lines (10 to 30 hooks) and by rod and reel, the duration of which was dictated by weather and/or a 50 fish limit per site as prescribed by our Letter of Agreement with the National Marine Fisheries Service. Bait used included squid and chub mackerel.

### 2.2.1 Otolith Processing and Aging

Red snapper morphometrics, including total length (TL), total weight (TW), and sex (if possible), were recorded. Red snapper sagittal otoliths were removed through the gills by chipping away the otic capsule with a stainless steel chisel (VanderKooy 2009). Otoliths were washed with deionized water, stored in a manila envelope, and frozen.

Otoliths were further processed in the laboratory. The right otolith from each specimen was cleaned with a hard-bristle toothbrush and dried in a ventilation hood in preparation for age determination. Each otolith was sectioned transversely anterior to the core as described in Cowan et al. (1995). Otolith sections were cut with a Hillquist 800 thin-sectioning machine equipped with a diamond embedded wafering blade and precision grinder (Cowan et al. 1995). Otolith sections were then polished, mounted on a microscope slide, and recut to produce a 200  $\mu\text{m}$  section of the otolith's core showing the opaque annuli along the ventral margin of the sulcus groove (Figure 2.1). The number of opaque annuli and the edge condition were determined with a dissecting microscope under transmitted light and a polarized light filter at 20x to 64x magnifications. Edge conditions were recorded (Beckman et al. 1988, Wilson and Nieland 2001).

Two readers determined annulus counts and edge conditions without referencing morphometric data. Annulus counts and edge conditions were compared between the two readers and conflicts were resolved in favor of the more experienced reader. Precision of annulus counts was evaluated with the Coefficient of Variation (CV) and Average Percent Error (APE) (Beamish and McFarlane 1983). Additionally, Cohen's Kappa coefficient was used to measure the inter-rater agreement and reader agreement due to chance (Viera and Garrett 2005).

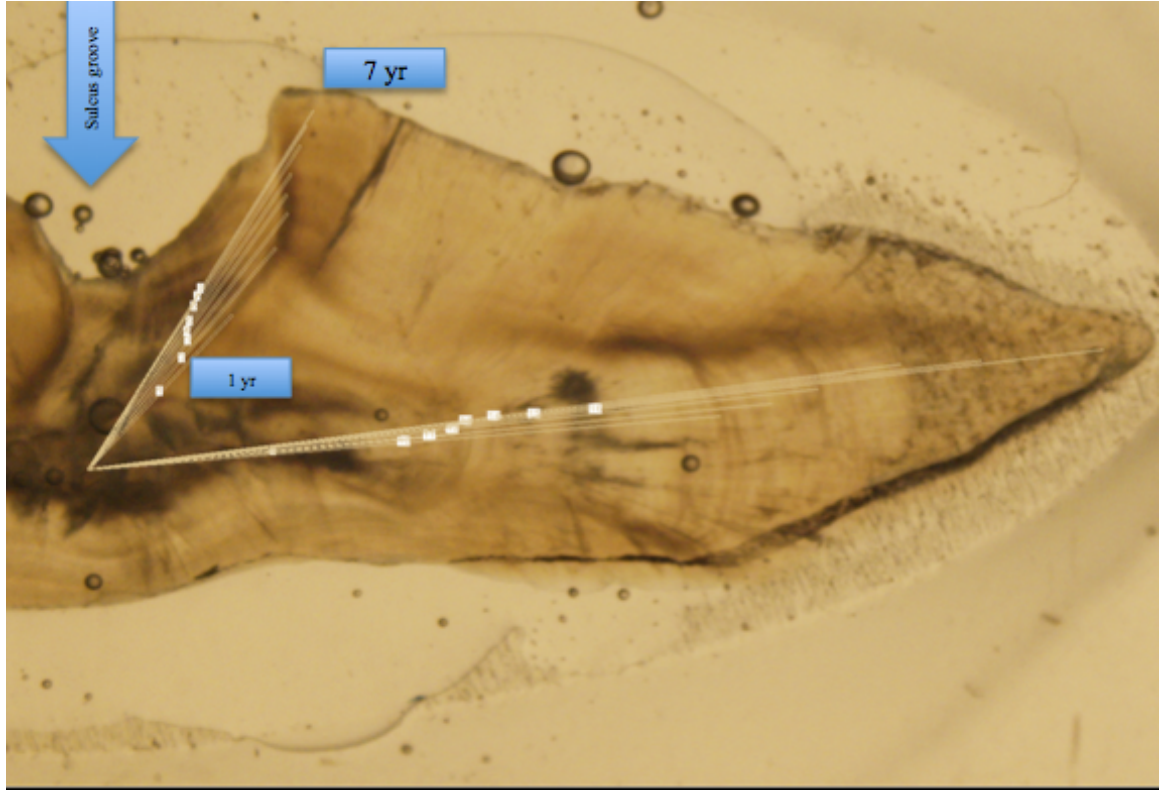


Figure 2.1. Red snapper transverse otolith section showing opaque annuli counts and the sulcus groove, collected from Jakkula reef.

### 2.2.2 Age Calculation

Red snapper in the northern GOM have been assigned a hatching date of July 1<sup>st</sup> and opaque deposition has been shown to begin in January (Wilson and Nieland 2001). Age estimations were made according Wilson and Nieland (2001). Age in days was calculated as

$$Age = -182 + (annulus\ count * 365) + ((m - 1) * 30) + d \quad \{1\}$$

where  $m$  is the ordinal number of the month of capture, and  $d$  is the day within the month captured. To correct for a uniform hatching day of July 1<sup>st</sup>, 182 days was subtracted from

each estimate. To calculate the age in years, the ordinal number of days was divided by 365. To assign red snappers to the correct cohort, fish captured in September, October, and November that had evidence of early opaque formation had their ages adjusted by subtracting 365 days from their age estimates. Conversely, red snappers captured in January, February, and March that had otoliths with translucent margins and evidence of delayed opaque deposition were adjusted by the addition of 365 days.

### 2.2.3 Growth, Size-at-Age, and Age Distribution

Mean TL, TW, and age between habitats were each tested with a one-way ANOVA. Tukey-Kramer pairwise analyses were used to identify significant differences. All statistical analyses for this study were done using SAS 9.4 with a significance level of 0.05.

An exponential growth function was used to describe a TW-TL relationship.

$$TW = aTL^b \quad \{2\}$$

TW=total weight

TL=total length

$b$ =is the exponential growth parameter

$a$ =the correction factor

An ANCOVA compared differences in TW and TL relationships among habitats. Linearized intercepts and slopes correspond to the multiplier  $a$ , and the exponent  $b$  {Eq. 2}.

Von Bertalanffy growth models for TL and TW were fitted with nonlinear regression by iteratively reweighted least squares (von Bertalanffy 1957).

$$TL_t = L_{\infty}(1 - e^{-k(t-t_0)}) \quad \{3\}$$

$TL_t$ =TL at age t

$L_{\infty}$ = average length of oldest age class

k= rate at which the asymptotic  $L_{\infty}$  is reached

t= age in years

$t_0$ = TL at time 0

$$TL_t = L_{\infty}(1 - e^{-k(t)}) \quad \{4\}$$

$$TW_t = W_{\infty}(1 - e^{-k(t)})^b \quad \{5\}$$

$TW_t$ = TW at age t

$W_{\infty}$ = average weight of oldest age class

k= rate at which the asymptotic  $L_{\infty}$  is reached

t=age in years

b=exponent derived from the TW-TL regressions

Red snapper von Bertalanffy growth models by site were fitted to TL and TW with biological age as the explanatory variable for each study site {Eq. 3}. However, one disadvantage of the von Bertalanffy method is the requirement of a large sample size across all age classes in the population. Therefore, due to low sample sizes in age classes less than 3 years of age,  $t_0$  was forced through zero to better estimate the TL and TW at age for young individuals not present {Eq. 4 and 5}.

Red snapper von Bertalanffy growth functions were compared using an asymptotic Chi-square approximation used by Kimura (1980) and Khattree and Naik (2003), calculated as

$$X^2_{df} = -n * \ln \left( \frac{SSE_{unrestricted}}{SSE_{restricted(i)}} \right)$$

$$df = (\# \text{ of restrictions in model (i)}) * (\# \text{ of sites} - 1) \quad \{6\}$$



$\chi^2_{df}$  = Chi-square

n = sample size

SSE = the sum of the squares error

$SSE_{unrestricted}$  = SSE for the model without restrictions (all parameters free)

$SSE_i$  = is the SSE for the restricted model (one or more parameters among sites constrained to be equal)

df = chi-square degrees of freedom

This test compares the chi-square estimation to a one-sided critical value of Chi-square<sub>df, alpha</sub>; p-values less than alpha imply rejection of the model ( $\alpha < 0.05$ ) {Eq. 6} (Kimura 1980, Khattree and Naik 2003). If von Bertalanffy convergence criterion was not met, then a linear ANCOVA was used to model TL, TW-at-age.

### 2.3 Results

During the years 2011, 2012, and 2013, red snapper from Bright, Jakkula, and McGrail shelf-edge reef habitats were collected twice per quarter for morphometric data and to extract sagittal otoliths for further analysis. Midnight Lumps was sampled once during the fall of 2011. A total number of 365 red snappers were collected (Table 2.1). Males disproportionately populated Bright, while all other sites were dominated by females (Table 2.2). Unidentified red snapper was a result of the difficulty in distinguishing immature sex organs at young ages. An ANCOVA fit to a binomial distribution showed that the total ratio of males to females did not differ ( $\chi^2=0.73$ ,  $p=0.3937$ ) and sex ratios by site differed significantly ( $\chi^2=26.66$ ,  $p<0.0001$ ). Patterson et al. (2001) reported a ratio of 1:1 (n=1755) for all red snapper sampled from an artificial reef area off Alabama and reported no significant difference between von Bertalanffy growth functions and log-transformed TW-TL relationships. In the western GOM, Fischer et al. (2004) reported no significant difference (n=5197) in the male to female

ratios between regions (AL, LA, and TX) and analyses were modeled with pooled data.

Therefore, males and females red snapper were combined for all analyses.

Table 2.1. Numbers of red snapper, *Lutjanus campechanus*, male, female, and unidentified sexes sampled from the shelf-edge reefs on Louisiana's continental shelf.

Shelf-Edge Reef	n	Female	Male	Unidentified
Bright	215	78	132	5
Jakkula	81	51	28	2
McGrail	27	15	12	0
Midnight Lumps	42	27	3	12
Total	365	171	175	19

Table 2.2. Red snapper, *Lutjanus campechanus*, sex ratios sampled from the shelf-edge reefs on Louisiana's continental shelf.

Shelf-Edge Reef	n	Female	Male	Unidentified	Total
Bright	215	0.36	0.61	0.02	0.99
Jakkula	81	0.63	0.35	0.02	0.98
McGrail	27	0.56	0.44	1.00	1.00
Midnight Lumps	42	0.64	0.13	0.23	1.00

Red snapper otoliths were returned to the laboratory for processing. The initial reading, the two readers (Dannielle Kulaw and the author) agreed on 59.85% of the otoliths, an Average Percent Error (APE) of 9.08%, a Coefficient of Variation (CV) of 0.19, and a Kappa statistic of 0.36 (Table 2.3). Second readings produced better values for all tests. A third reading significantly improved the estimates between readers. The two readers agreed on 91.55% of annulus counts, with an APE of 0.175%, a CV of 0.039, and a Kappa statistic of 0.7142.

Table 2.3. Differences between two readers in average percent error (APE), coefficient of variation (CV), Kappa statistic, percentages of agreement (O) for opaque annuli counts, and percentages of differences in age estimates ( $\pm 1$ , 2, and 3 or more years) in red snapper, *Lutjanus campechanus*, otoliths after the first, second and third reading.

	1st	2nd	3rd
APE	9.082	2.143	0.175
CV	0.192	0.102	0.039
Kappa	0.3635	0.5136	0.7142
O	59.85%	86.43%	91.55%
$\pm 1$	35.66%	13.45%	6.54%
$\pm 2$	7.31%	3.89%	1.56%
$>\pm 3$	2.88%	1.12%	0.78%

### 2.3.1 Age Structure

Ages for red snappers from all sites ranged from 2 to 26 years of age with the majority (92.2%) of individuals between the ages of 4-11 years, modal age was 6 years (Table 2.4)(Figures 2.1 and 2.2). Mean biological age for red snappers at all reef sites was  $7.05 \pm 0.16$  years and the largest age range occurred at McGrail reef. Red snapper cohorts ranged from 1987 to 2010, while the modal cohort was 2005. The majority of red snapper cohorts were dominated by the 2004, 2005, 2006, and 2007 year-classes: Bright (66.03%), Jakkula (52.56%), McGrail (81.49%) and Midnight Lumps (95.24%)(Figures 2.3 and 2.4).

Tests for differences in least significant difference (LSD) ages found that red snappers at Bright were not significantly different from Jakkula ( $p=0.18$ ), and McGrail ( $p=0.76$ ). Red snapper ages at Jakkula were not significantly different from those at McGrail. Red snapper ages at Midnight Lumps were significantly different from mean age at all other reefs: Bright ( $p<0.0001$ ), Jakkula ( $p<0.0001$ ), and McGrail ( $p=0.003$ ). Tukey-Kramer pairwise comparisons of mean age found that only red snapper at Midnight Lumps differed significantly from those at all other reefs (Table 2.5). A

Kolmogorov-Smirnov test for equal age frequency distributions were not significantly different among red snappers at the four shelf-edge reefs, with the exception of Midnight Lumps (Table. 2.6).

Table 2.4 Red snapper (*Lutjanus campechanus*) minimum, maximum, range and mean  $\pm$  standard error of ages, for the shelf-edge reefs sampled on Louisiana's continental shelf.

Site	Minimum (Yrs)	Maximum (Yrs)	Range (Yrs)	Mean $\pm$ Standard Error (Yrs)
Bright	2	17	15	7.31 $\pm$ 0.19
Jakkula	3	20	17	7.79 $\pm$ 0.29
McGrail	4	26	22	7.48 $\pm$ 0.84
Midnight Lumps	4	10	6	5.48 $\pm$ 0.19

Table 2.5. Pair-wise comparisons of red snapper of mean age among sites performed using a Tukey-Kramer *post hoc* adjustment, sampled from the shelf-edge reefs on Louisiana's continental shelf. Model significance:  $F_{3,322}=584.85$ ,  $p<0.0001$ .

Site	Estimate (Age Yrs)	Tukey-Kramer Grouping by Site
Bright	7.3113	A
Jakkula	7.7949	A
McGrail	7.4815	A
Midnight Lumps	5.4762	B

Table 2.6. Kolmogorov-Smirnov (Ksa) test for age frequency distributions of red snapper, *Lutjanus campechanus*, for the shelf-edge reefs on Louisiana's continental shelf.

Site	Ksa	Pr > Ksa
Bright vs. Jakkula	1.22	0.10
Bright vs. McGrail	0.46	0.99
Bright vs. Midnight Lumps	2.62	<0.0001
Jakkula vs. McGrail	1.05	0.22
Jakkula vs. Midnight Lumps	3.05	<0.0001
McGrail vs. Midnight Lumps	1.42	0.04

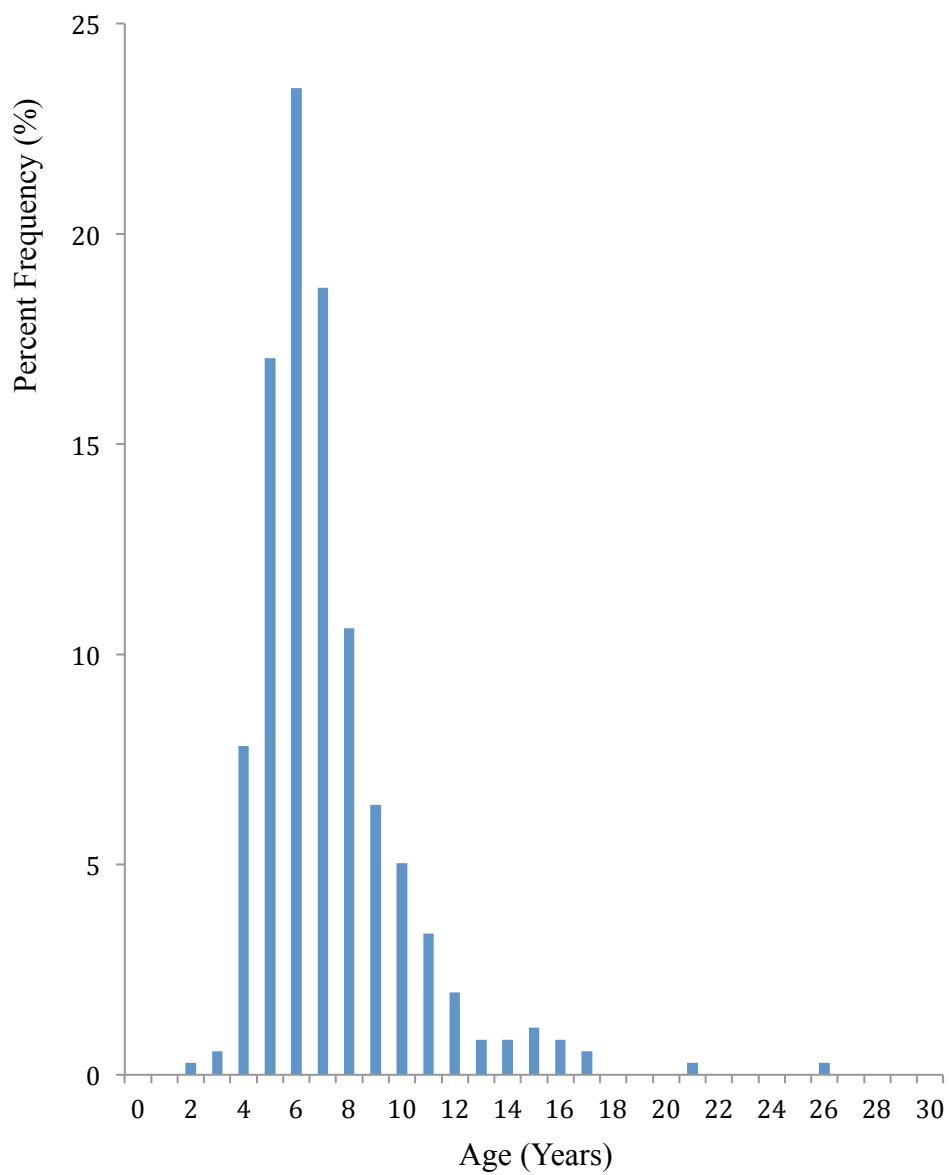


Figure 2.1. Distributions of age in years for red snapper, *Lutjanus campechanus*, sampled from four shelf-edge reefs on Louisiana's continental shelf ( $n=351$ ).

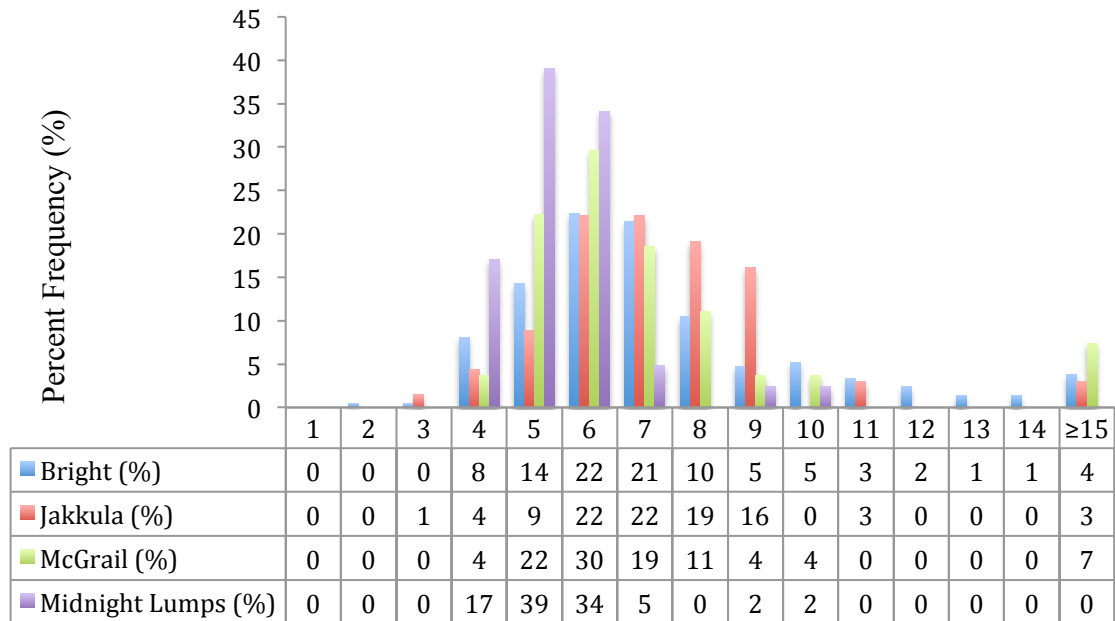


Figure 2.2. Distributions of ages in years for red snapper, *Lutjanus campechanus*, sampled from four shelf-edge reefs on Louisiana's continental shelf; Bright ( $n=215$ ), Jakkula ( $n=81$ ), McGrail ( $n=27$ ) and Midnight Lumps ( $n=42$ ).

### 2.3.2 Growth

Total lengths for all red snappers sampled ranged from 352 mm to 840 mm with mean TL  $570.03 \pm 4.56$  mm and modal length of 525 mm (Table 2.7)(Figure 2.5). Red snappers from Jakkula had the largest mean TL  $636.27 \pm 11.03$ mm, while Midnight Lumps had the smallest mean TL  $538.74 \pm 10.08$ mm. Jakkula and McGrail red snappers were not significantly different in mean TL ( $p=0.09$ ). Red snappers at Jakkula ( $p<0.0001$ ) and McGrail ( $p=0.001$ ) were significantly different from those at Midnight Lumps. Tukey-Kramer comparisons of mean TL found that red snappers at Midnight

Lumps and Bright were significantly smaller than those at Jakkula and McGrail (Table 2.8).

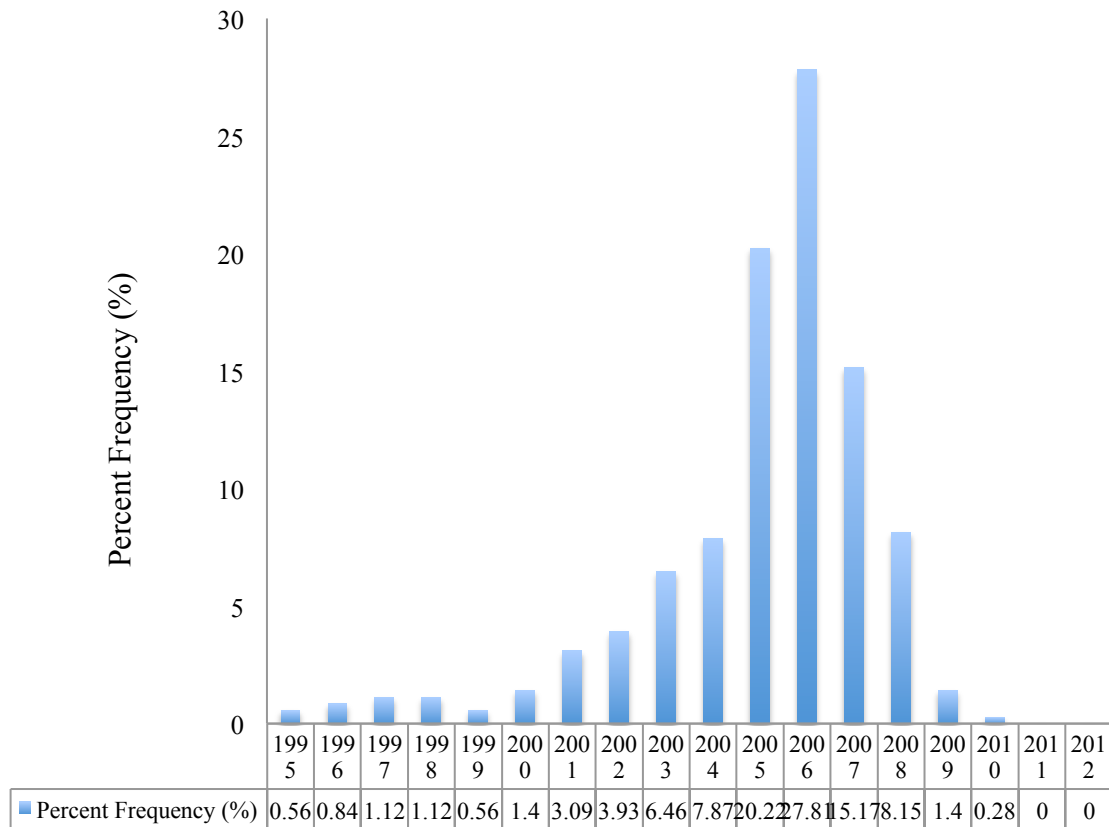


Figure 2.3. Distributions of red snapper cohorts sampled from the shelf-edge reefs on Louisiana's continental shelf.

Jakkula had the largest proportion of red snapper longer than 550mm (83.53%), McGrail (69.57%), Bright (63.67%), and Midnight Lumps (45.24%)(Figure 2.6).

Kolmogorov-Smirnov tests for red snapper TL frequency distributions were significantly different among reefs, with the exception of Bright vs. Midnight Lumps and Jakkula vs. McGrail (Table 2.9).

Total weights for all red snappers sampled ranged from 0.66 kg to 9.08 kg with mean TW of  $2.56 \pm 0.07$  kg with a modal weight of 1.53 kg (Table 2.10)(Figure 2.7).

Total weight differences in LSD found that red snapper at Bright were significantly smaller than those at Jakkula ( $p<0.0001$ ) and McGrail ( $p<0.0001$ ), but not at Midnight Lumps. Jakkula and McGrail red snapper TW did not differ significantly from each other ( $p=0.17$ ). Red snapper at Midnight Lumps were significantly smaller than at both Jakkula and McGrail reefs ( $p<0.0001$ ).

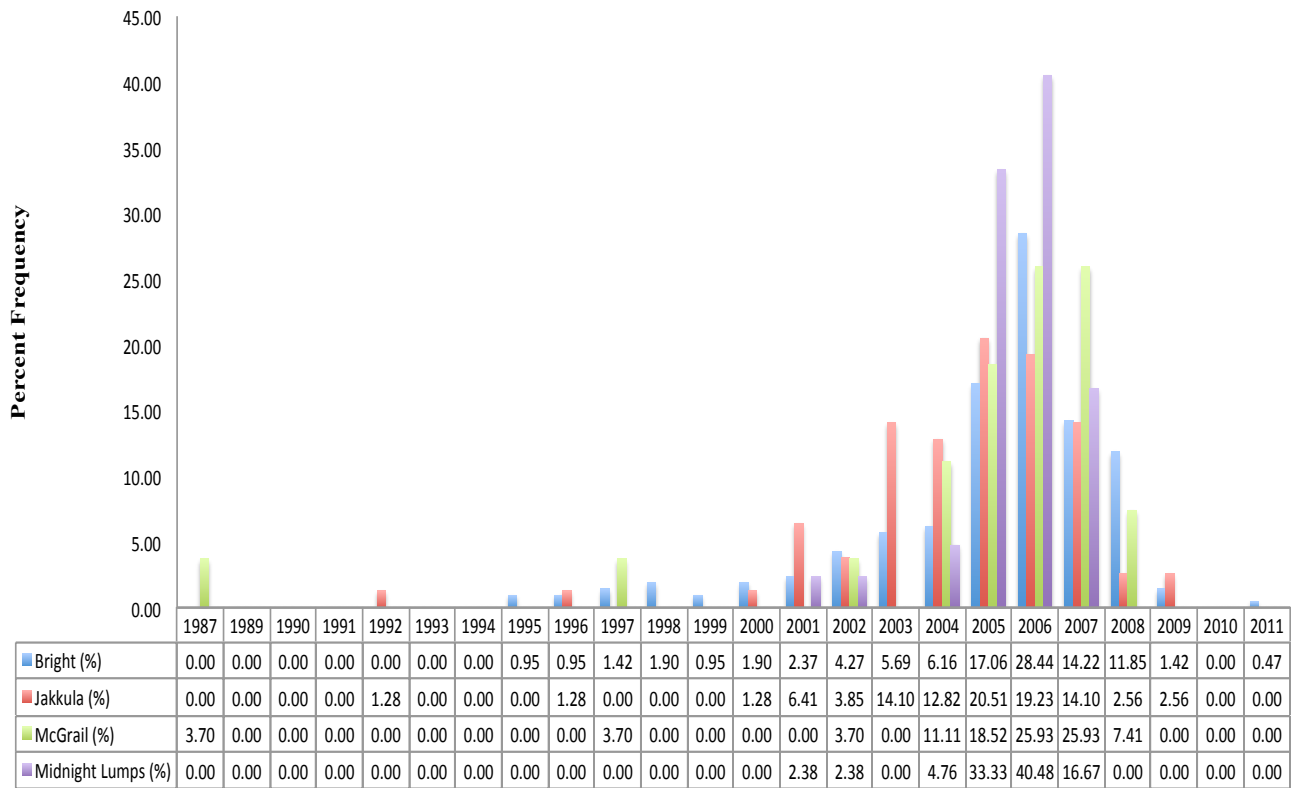


Figure 2.4. Distributions of year-classes for red snapper, *Lutjanus campechanus*, sampled from four shelf-edge reefs: Bright ( $n=215$ ), Jakkula ( $n=81$ ), McGrail ( $n=27$ ) and Midnight Lumps ( $n=42$ ).



Table 2.7. Descriptive statistics for red snapper, *Lutjanus campechanus*, total length (mm), sampled from four shelf-edge reefs on Louisiana's continental shelf.

Shelf-Edge Reef	Minimum TL (mm)	Maximum TL (mm)	Mean TL (mm) $\pm$ Standard Error
Bright	352	742	547.72 $\pm$ 4.71
Jakkula	368	840	636.28 $\pm$ 11.03
McGrail	481	816	604.86 $\pm$ 18.82
Midnight Lumps	397	668	538.74 $\pm$ 10.08

Table 2.8. Red snapper, *Lutjanus campechanus*, mean total length (mm) pair-wise comparison of means with a Tukey-Kramer *post hoc* adjustment, sampled from four shelf-edge reefs off of Louisiana's continental shelf. Model significance:  $F_{3,353}=29.26$ ,  $p<0.0001$ .

Site	Mean TL (mm)	Tukey-Kramer Grouping by Site
Bright	547.72	B
Jakkula	636.28	A
McGrail	604.86	A
Midnight Lumps	538.74	B

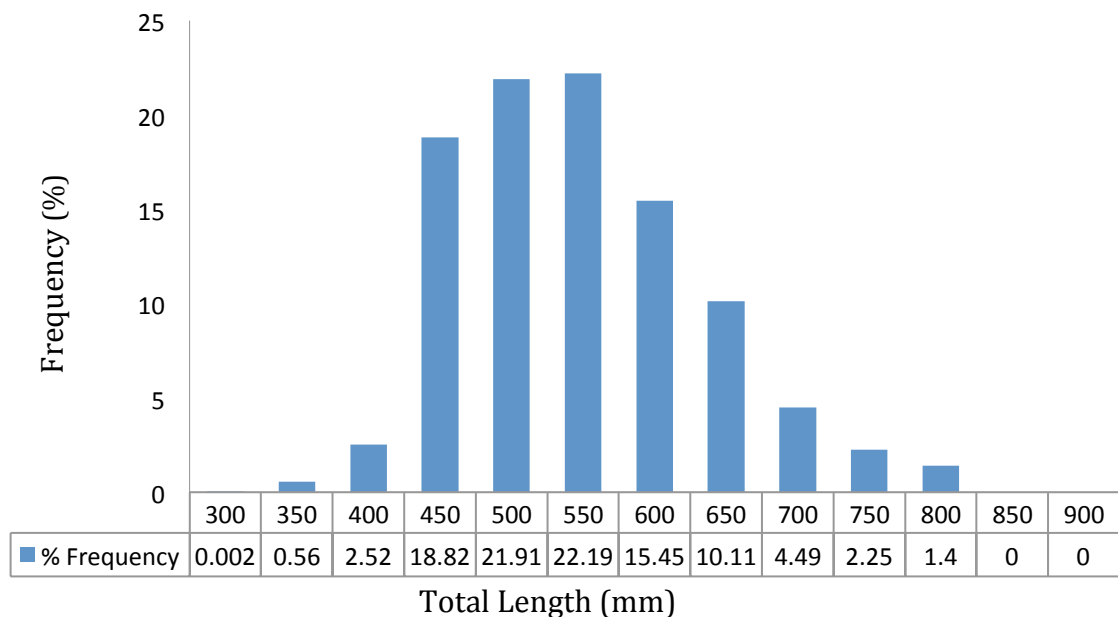


Figure 2.5. Distribution of total length of red snapper, *Lutjanus campechanus*, for all shelf-edge reefs sampled off of Louisiana's continental shelf (n=365).

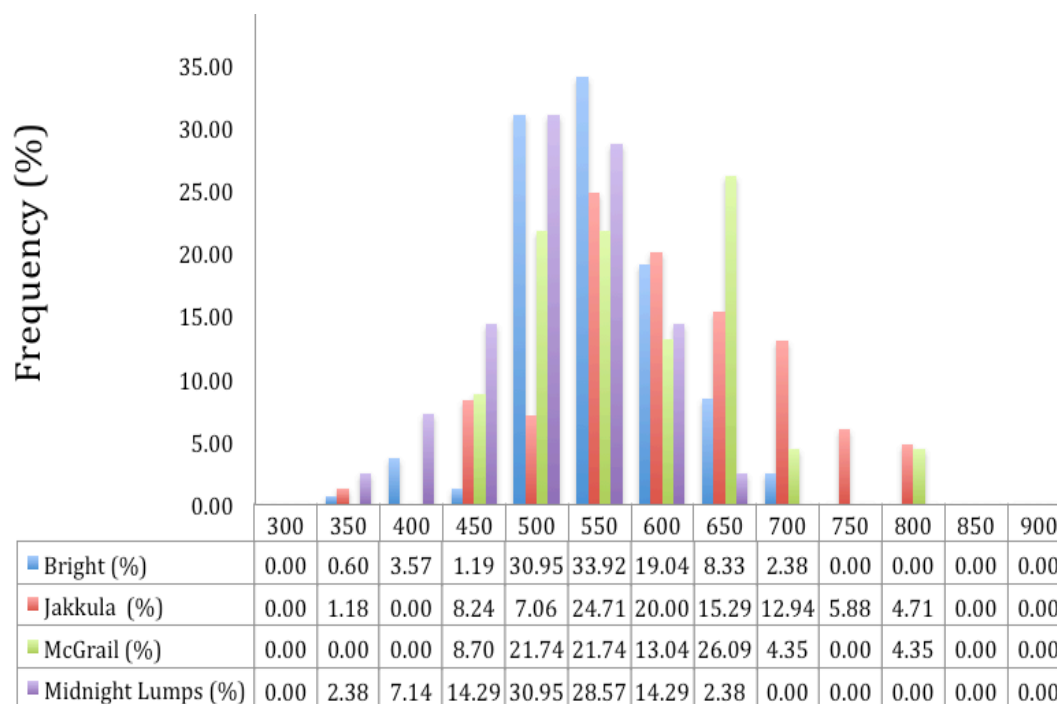


Figure. 2.6. Red snapper, *Lujantus campechanus*, total length (mm) distributions for each shelf-edge reef sampled on Louisiana's continental shelf; Bright (n=215), Jakkula (n=81), McGrail (n=27) and Midnight Lumps (n=42).

Table 2.9. Kolmogorov-Smirnov (KSa) tests for red snapper, *Lujantus campechanus*, comparison of total length frequency distributions sampled from four shelf-edge reefs on Louisiana's continental shelf.

Shelf-Edge Reefs	Ksa	Pr > Ksa
Bright vs. Jakkula	3.33	<0.0001
Bright vs. McGrail	1.47	0.03
Bright vs. Midnight Lumps	0.51	0.96
Jakkula vs. McGrail	0.88	0.43
Jakkula vs. Midnight Lumps	2.57	<0.0001
McGrail vs. Midnight Lumps	1.43	0.03

Total weights for all red snappers sampled ranged from 0.66 kg to 9.08 kg with mean TW of  $2.56 \pm 0.07$  kg with a modal weight of 1.53 kg (Table 2.10)(Figure 2.7).

Total weight differences in LSD found that red snapper at Bright were significantly smaller than those at Jakkula ( $p < 0.0001$ ) and McGrail ( $p < 0.0001$ ), but not at Midnight

Lumps. Jakkula and McGrail red snapper TW did not differ significantly from each other ( $p=0.17$ ). Red snapper at Midnight Lumps were significantly smaller than at both Jakkula and McGrail reefs ( $p<0.0001$ ).

Tukey-Kramer comparisons of mean TW found that red snapper between Bright and Midnight Lumps were not significantly different; TW between Jakkula and McGrail were also not significantly different (Table 2.11). Jakkula had the largest proportion of red snapper heavier than 3 kg (56.97%), McGrail (50.01%), Bright (19.53%) and Midnight Lumps (11.09%)(Figure 2.10). Kolmogorov-Smirnov tests for TW frequency distributions were significantly different for red snapper among reefs, with the exception between Bright and Midnight Lumps, and between Jakkula and McGrail (Table 2.12).

Table 2.10. Red snapper, *Lutjanus campechanus*, total weight (TW) descriptive statistics for each shelf-edge reef off of Louisiana's continental shelf.

Site	N	Minimum TW (kg)	Maximum TW (kg)	Mean TW (kg) $\pm$ Standard Error
Bright	210	242	5.12	$2.17 \pm 0.86$
Jakkula	79	0.66	9.08	$3.63 \pm 0.19$
McGrail	22	1.53	7.22	$3.28 \pm 1.41$
Midnight Lumps	42	2.14	3.73	$2.14 \pm 0.71$

Table 2.11. Red snapper, *Lutjanus campechanus*, mean total weight (TW) pair-wise comparison of means with a Tukey-Kramer *post hoc* adjustment, sampled from four shelf-edge reefs off Louisiana's continental shelf. Model significance:  $F_{3,353}=469.27$ ,  $p<0.0001$ .

Site	Mean TW (kgs)	Tukey-Kramer Grouping by Site
Bright	2.17	B
Jakkula	3.64	A
McGrail	3.28	A
Midnight Lumps	2.15	B

Table. 2.12. Red snapper, *Lutjanus campechanus*, Kolmogorov-Smirnov tests for total weight frequency distributions by shelf-edge reef on Louisiana's continental shelf.

Shelf-Edge Reefs	KSa	Pr > KSa
Bright vs. Jakkula	3.28	<0.0001
Bright vs. McGrail	1.81	0.03
Bright vs. Midnight Lumps	0.90	0.96
Jakkula vs. McGrail	0.09	0.43
Jakkula vs. Midnight Lumps	2.5	<0.0001
McGrail vs. Midnight Lumps	1.43	0.03

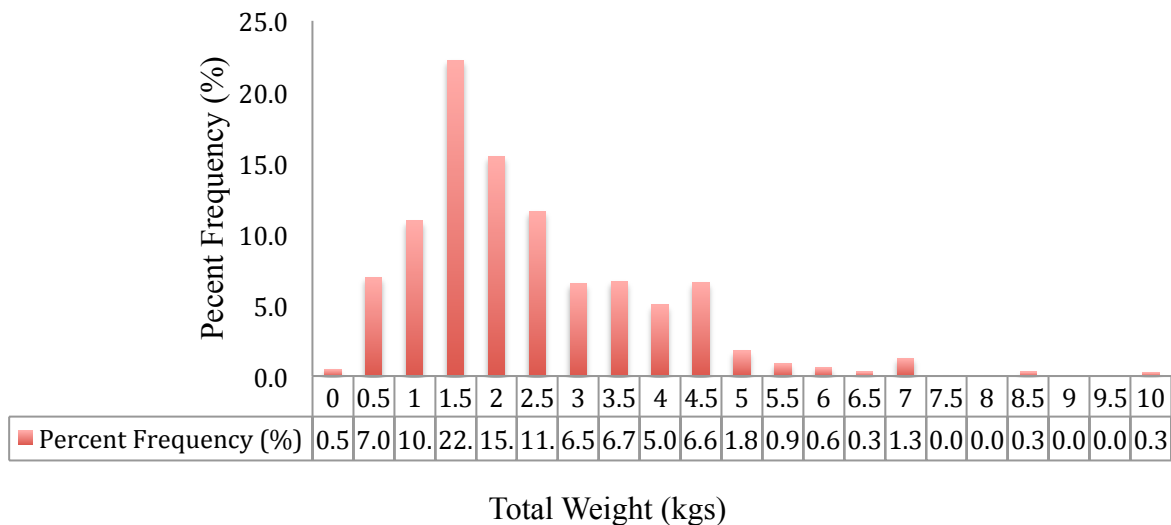


Figure 2.7. Red snapper, *Lutjanus campechanus*, total weight (kg) percent frequency for four shelf-edge reefs off of Louisiana's continental shelf.

Significant differences in red snapper TW-TL regression models were detected among reefs for combined tests for equality of slopes and intercepts ( $F_{3, 351}=2.64$ ;  $p=0.0492$ ;  $r^2=0.969$ )( $F_{3, 351}=2.72$ ;  $p=0.0445$ ;  $r^2=0.969$ ). Therefore, one model was not appropriate for specimens from all habitats (Table 2.13). The TW-TL equation for red

snapper from Jakkula had a larger growth coefficient ( $b$ ) and a smaller intercept ( $a$ ) and differed significantly from all other shelf-edge reefs (Table 2.14)(Figure 2.8).

Table 2.13. Red snapper, *Lutjanus campechanus*, total length-total weight regression models at four reefs sampled on Louisiana's continental shelf. Model significance  $F_{3,351}=1529.76$ ,  $p<0.0001$ ,  $r^2=0.9688$ .

Site	TW-TL Equation
Bright	$TW = 1.60 \times 10^{-8} (TL^{2.96})$
Jakkula	$TW = 4.96 \times 10^{-9} (TL^{3.15})$
McGrail	$TW = 1.72 \times 10^{-8} (TL^{2.95})$
Midnight Lumps	$TW = 2.40 \times 10^{-8} (TL^{2.90})$

Table 2.14. Red snapper, *Lutjanus campechanus*, parameter comparisons for alpha ( $a$ ) and beta ( $b$ ) for red snapper, *Lutjanus campechanus*, sampled from four shelf-edge reefs on Louisiana's continental shelf.

Site	<i>a</i>	Lower 95% CI	Parameter Estimate	Upper 95% CI	t-value	p-value
Bright		$3.79 \times 10^{-9}$	$1.60 \times 10^{-8}$	$6.77 \times 10^{-8}$	-0.55	0.5845
Jakkula		$1.09 \times 10^{-9}$	$4.96 \times 10^{-9}$	$2.25 \times 10^{-8}$	-2.04	0.0423
McGrail		$2.25 \times 10^{-9}$	$1.72 \times 10^{-8}$	$1.31 \times 10^{-7}$	-0.32	0.7491
Midnight Lumps		$6.34 \times 10^{-9}$	$2.40 \times 10^{-8}$	$9.04 \times 10^{-8}$	.	.

Site	<i>b</i>	Lower 95% CI	Parameter Estimate	Upper 95% CI	t-value	p-value
Bright		2.73	2.96	3.19	0.5	0.6179
Jakkula		2.91	3.15	3.39	2.01	0.0449
McGrail		2.63	2.95	3.27	0.31	0.7547
Midnight Lumps		2.69	2.90	3.11	.	.

Along with differences among size and age distributions, there were significant differences in red snapper mean size-at-age among specimens from the four shelf-edge reefs (Figure 2.9). Mean size-at-age was evaluated for the most common ages (4-7 years) due to small sample sizes of red snapper < 3 years and > 7 years of age. Total length-at-age and total weight-at-age did not display the same significant differences according to the ANOVA, and the Tukey-Kramer's grouping (Tables 2.15 and 2.16).

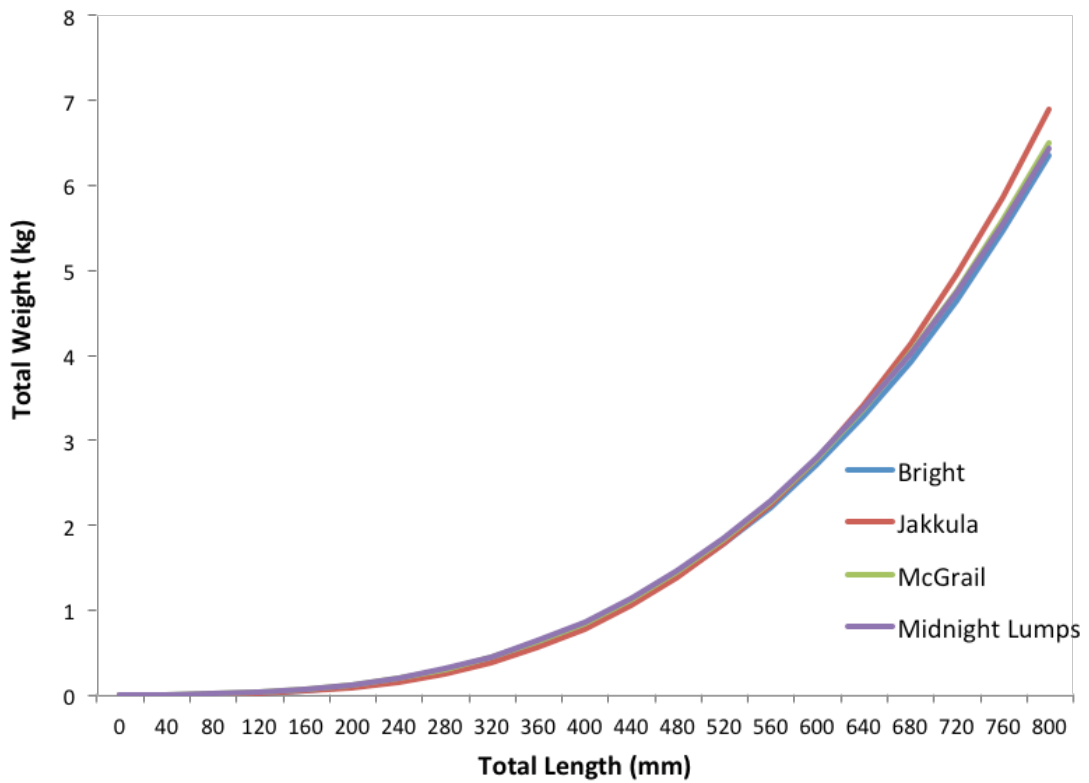


Figure 2.8. Red snapper, *Lutjanus campechanus*, observed total weight-total length relationship fitted to a power function for four shelf-edge reefs sampled, Bright (n=215), Jakkula (n=81), McGrail (n=27), and Midnight Lumps (n=42) on Louisiana's continental shelf.

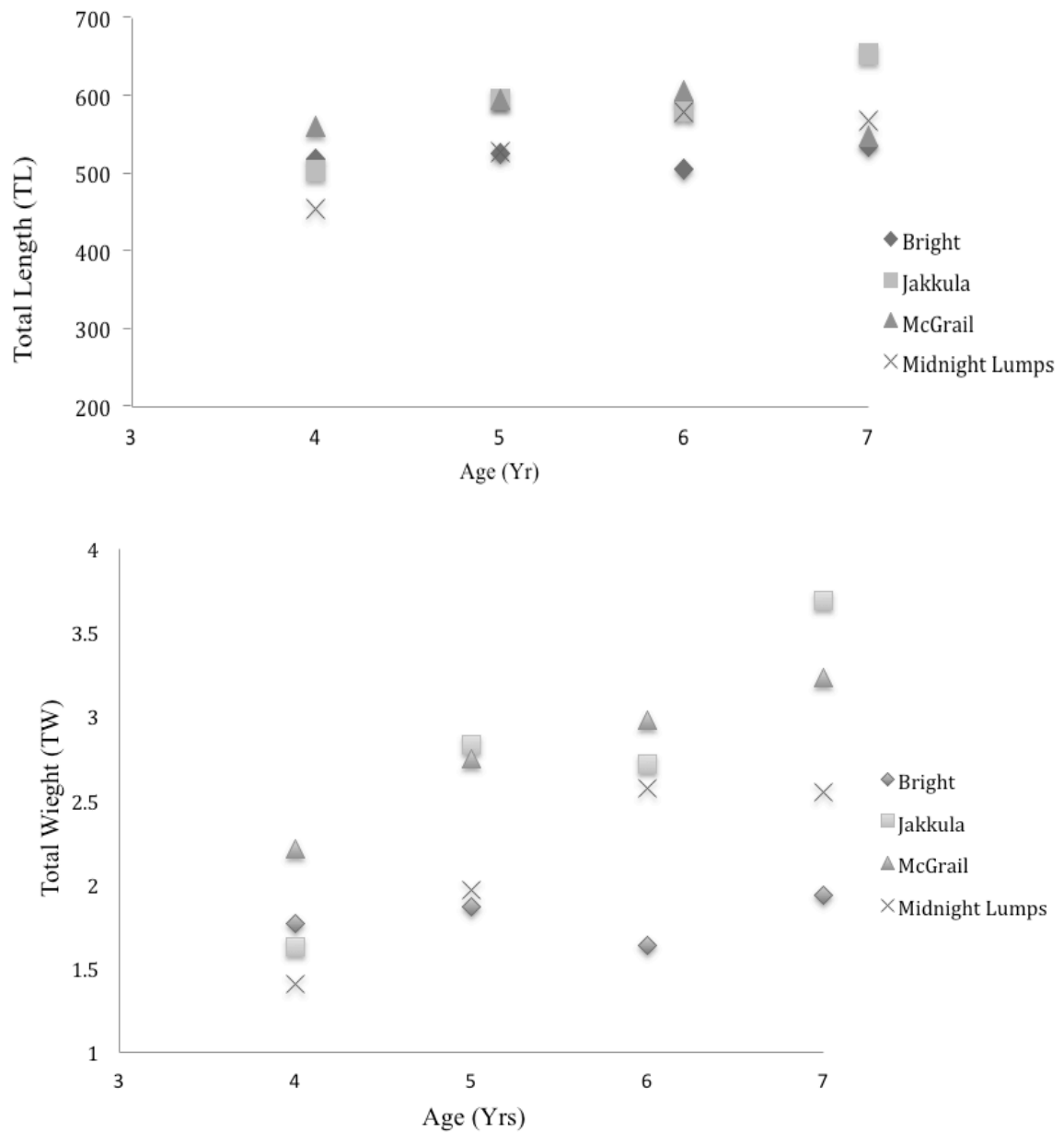


Figure 2.9. Mean (A) total length-at-age and (B) total weight-at-age for common ages of red snapper, *Lutjanus campechanus*, for four shelf-edge reefs on Louisiana's continental shelf.

Mean total length-at-age (TL-at-age) estimates for red snapper at Bright and Jakkula followed a similar pattern: TL-at-age increased between the ages 4 and 5, plateaued from 5 to 6, and increased from 6 to 7 years of age. McGrail red snapper TL-at-age increased from ages 4 to 5 years and plateaued from 5 to 7 years of age. Midnight Lumps red snapper TL-at-age increased between 4 and 6 years and from 6 to 7 years of age. Tukey-Kramer comparisons found that TL-at-age was similar at 4 years of age. At age 5, Jakkula and McGrail were longer at age then those at Bright and Midnight Lumps. At age 6, Midnight Lumps was significantly smaller at age then all other shelf-edge reefs. At age 7, Jakkula was significantly larger at age then Bright, McGrail, and Midnight Lumps.

Table 2.15. Analyses of variance and Tukey-Kramer grouping for red snapper, *Lutjanus campechanus*, mean total length at age by shelf-edge reef for the most common ages sampled (ages 4-7 years) on Louisiana's continental shelf. Within each age, similar letters indicate no difference in mean total length (alpha=0.05)

Age (Yr)	ANOVA		Tukey-Kramer Grouping			
	F	P	Bright	Jakkula	McGrail	Midnight Lumps
4	2.22	0.1118	A	A	A	A
5	2.9039	0.0484	AB	A	B	AB
6	14.2992	<0.0001	B	A	A	A
7	19.382	<0.0001	B	A	B	AB

Table 2.16. Analyses of variance and Tukey-Kramer grouping for red snapper, *Lutjanus campechanus*, mean total weight at age by shelf-edge reef for the most common ages sampled (ages 4-7 years) on Louisiana's continental shelf. Within each age, similar letters indicated no difference in mean total weight (alpha=0.05)

Age (Yr)	ANOVA		Tukey-Kramer Grouping			
	F	P	Bright	Jakkula	McGrail	Midnight Lumps
4	0.6581	0.5858	A	A	A	A
5	3.8241	0.0146	B	A	A	B
6	15.1425	<0.0001	B	A	A	A
7	18.1382	<0.0001	B	A	A	AB



A similar pattern was apparent for red snapper mean total weight-at-age (TW-at-age) estimates except for those at Midnight Lumps: growth increased between ages 4 and 5, plateaued from age 5 to 6 and increased from 6 to 7 years of age. Midnight Lumps increased from 4 to 6 years of age and plateaued from 6-7 years of age. Tukey-Kramer comparisons found that all red snapper TW-at-age estimates were similar for ages 4 and 5 but not at age 6, Midnight Lumps was significantly smaller. At age 7, Jakkula and McGrail were most similar as were Bright and Midnight Lumps; however, all shelf-edge reefs were not significantly different.

Chi-square tests suggest that  $L_{\infty}$  for red snapper is significantly different among the four shelf-edge reefs, but  $k$  is not significantly different (Table 2.17). Confidence intervals suggest that  $L_{\infty}$  for red snapper at Bright is significantly smaller than Jakkula and McGrail, but not Midnight Lumps. Red snapper at Midnight Lumps were significantly smaller than at Jakkula, but not McGrail reefs. Red snapper at Jakkula and McGrail are not significantly different from each other (Table 2.18)(Figures 2.10 and 2.11).

Table 2.17. Von Bertalanffy model restrictions for red snapper, *Lujantus campechanus*, sampled from Louisiana's continental shelf. Model restrictions indicate parameter equalities under null hypothesis. Chi-square tests are against model without restrictions.

Model Restrictions	SSE	Chi-square	d.f.	p-value
None	1507782			
$L_{\infty}=L_{\infty, \text{ All}}; k=k_{\text{All}}$	195890	91.08	6	<0.0001
$k=k_{\text{all}}$	1524426	3.82	3	0.2815

Table 2.18. Von Bertalanffy parameter estimates, standard error, and lower and upper 95% confidence intervals (CI) for red snapper, *Lutjanus campechanus*, for each shelf-edge reef on Louisiana's continental shelf. Confidence intervals are asymptotic.

Parameter	Estimate	Standard Error	Lower 95% CI	Upper 95% CI
$k$	0.3331	0.019	0.2956	0.3705
$L_{\infty}$ , Bright	615.41	9.9257	595.92	634.94
$L_{\infty}$ , Jakkula	709.82	12.48	685.24	734.33
$L_{\infty}$ , McGrail	688.45	19.08	650.94	725.96
$L_{\infty}$ , Midnight Lumps	637.58	16.99	604.12	670.91

Linear ANCOVA models of mean TW-at-age for red snapper caught at the shelf-edge reefs were significantly different. Intercepts and slopes differed significantly among shelf-edge reefs among fish captured over the study's three-year sampling effort (Table 2.19) (Figure 2.12). Red snapper TW-at-age regressions all differed significantly from those at Midnight Lumps ( $p < 0.0001$ ). The steepest slope and the smallest intercept occurred at Jakkula suggesting rapid growth compared to other reef sites. The shallowest slope with a moderate intercept occurred at Bright suggesting slower growth compared to other reef sites.

Table 2.19. Analysis of covariance for red snapper, *Lutjanus campechanus*, model significance, equality of intercepts, slopes and regression models fitted to observed total weight at age.

Model (TW)	$F_{4,346}=86.51$ , $p < 0.0001$ , $r^2=0.51$	
Equality of Intercepts	$F=181.95$	$p < 0.0001$
Equality of Slopes	$F=43.95$	$p < 0.0001$
Site	Regression Model	
Bright	$TW=0.19(\text{Age}) + 0.74$	
Jakkula	$TW=0.42(\text{Age}) + 0.32$	
McGrail	$TW=0.21(\text{Age}) + 1.79$	
Midnight Lumps	$TW=0.34(\text{Age}) + 0.26$	

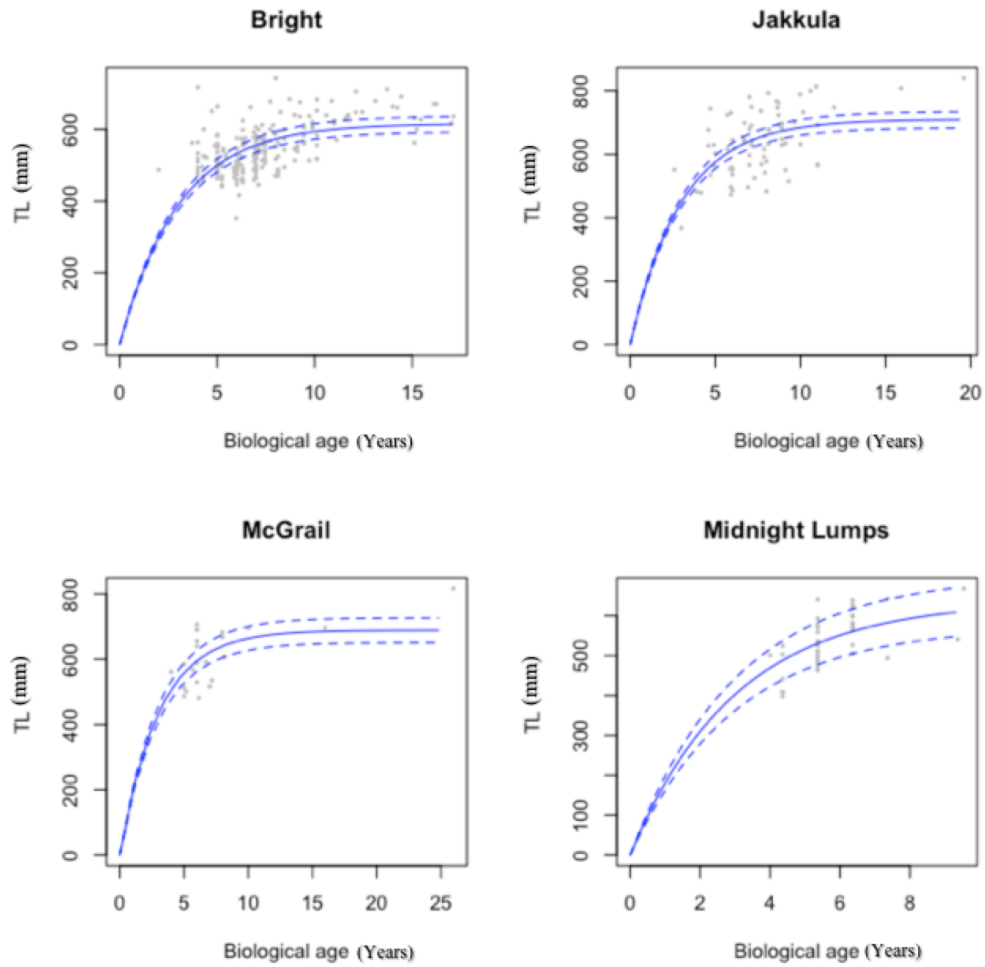


Figure 2.10. Von Bertalanffy growth model fitted for total length (TL) at biological age for equal growth coefficients ( $k$ ) and separate  $L_{\infty}$ 's for red snapper, *Lutjanus campechanus*, at four shelf-edge reefs on Louisiana's continental shelf.

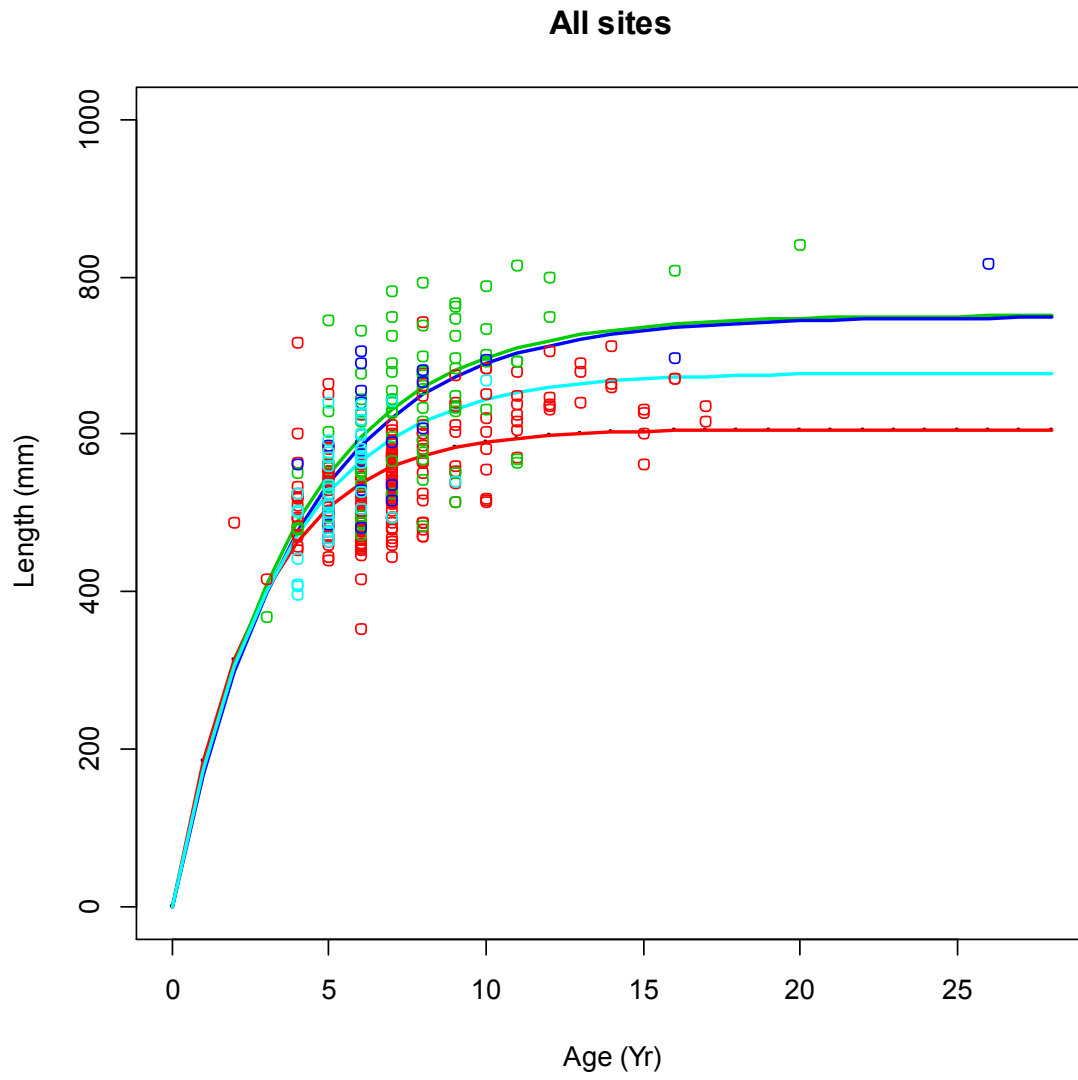


Figure 2.11. Red snapper, *Lutjanus campechanus*, von Bertalanffy growth models of total length at age, fit for equal growth coefficients ( $k$ ) and separate  $L_{\infty}$ , sampled from each shelf-edge reef off of Louisiana's continental shelf edge; Bright (red), Jakkula (green), McGrail (blue), and Midnight Lumps (teal).

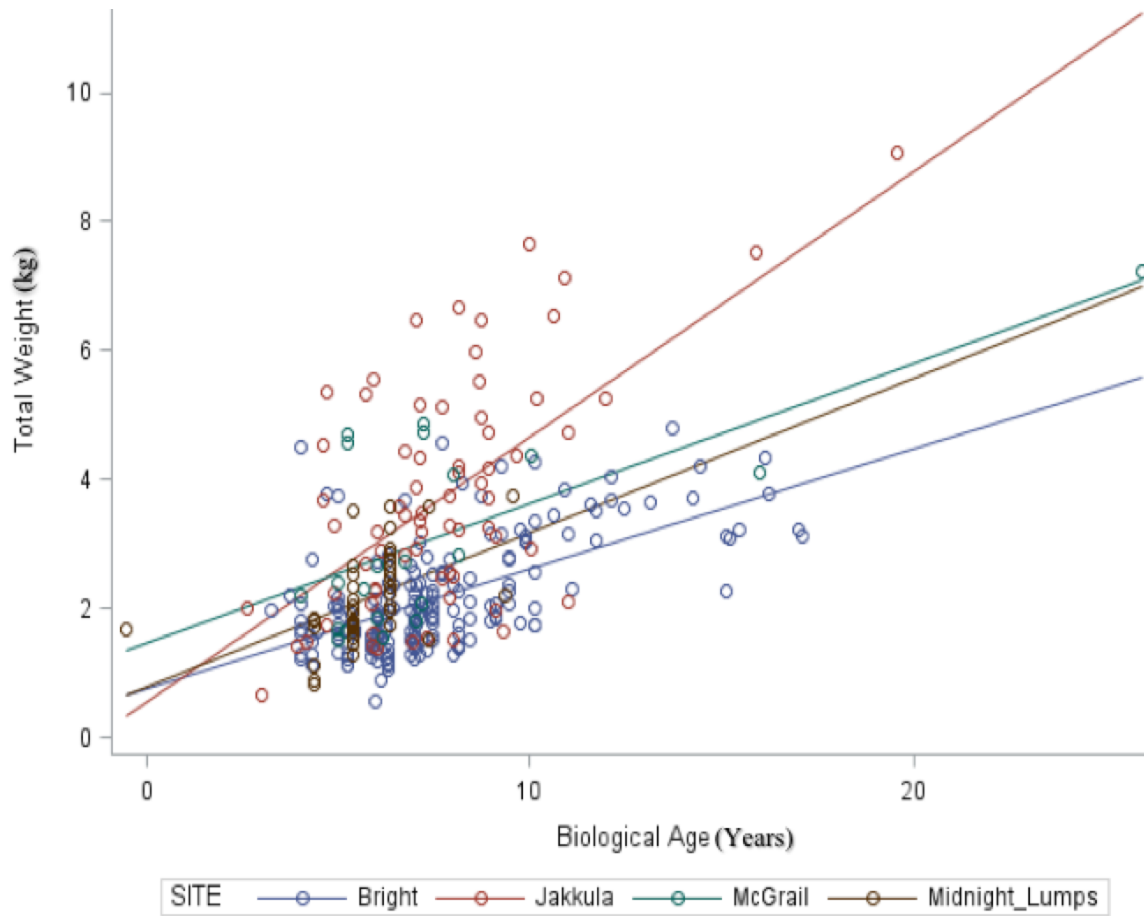


Figure 2.13. Linear ANCOVA models fit to total weight-at-age regression models for four shelf-edge reefs sampled off of Louisiana’s continental shelf for red snapper, *Lujantus campechanus*.

## 2.4 Discussion

### 2.4.1 Age Structure

My study was the first of its kind to examine age structure and growth at individual shelf-edge reefs, since the late 1970's, (Bradley and Bryan 1975, Davis 1975), for the economically important red snapper fishery in the northwestern GOM. Biological reference points, such as, age and growth studies, set benchmarks for comparisons to future fish stocks. However, biological reference points are not static and fluctuate with changes in the environment and rates of exploitation. Fishery induced evolution occurs when fishery managers in act 'precautionary' measures and when previous reference points are utilized in stock assessments. Updated red snapper biological reference points are needed to track changes in biological processes that 'drive' population dynamics (Heino et al. 2013).

This study found a truncated age structure at each shelf-edge reef sampled. Truncated age distributions usually result from natural and fishing mortality that selectively removes larger and older individuals from an exploited stock. This phenomenon is well documented, especially in long-lived species. Overfishing has lead to shifting age distributions of exploited populations and ecosystems (Hsieh et al. 2010). The 'spawn-at-least-once' principle states that current stock statuses are sustainable, if fish spawn at least once before they become vulnerable to commercial fishing gears (Myers and Barrowman 1996, Myers and Mertz 1998). The validity of the principle was examined with meta-analysis of 38 fish stocks of 13 fish species and reported that high fishing mortalities of immature fish has a significant negative effect on current stock statuses, *i.e.* age structure, as well as, patterns of exploitation (Vasilakopoulos et al. 2011).

A historical example is the California sardine fishery, which collapsed, in the late 1940's. Some researchers argued that fishing pressure was the primary cause, while others attributed it to cooling sea surface temperatures and shifting wind patterns. Hsieh et al. (2010) used ichthyoplankton assemblages from the 50-year California Cooperative Oceanic Fisheries Investigations as a proxy to separate the effects of fishing pressure from other biological variables. Their results demonstrated that fishing pressure increases the temporal variability in exploited fish populations and results in age truncation (Hsieh et al. 2010).

Red snapper in northern GOM produced relative strong red snapper year-classes between 2004, 2005, and 2006. My study found that red snapper at the four shelf-edge reefs were dominated by the strong year-classes 2004-2006, which represented approximately 82% of the cohort distribution. The addition of the red snapper 2007 cohort should be noted as established, as it was well represented (~15.37%) in the total cohort distribution. My research supports previous studies that have shown the presence of the strong red snapper year-classes sampled from pooled data at four eastern shelf-edge reefs in the northwestern GOM (Saari 2011). Furthermore, Saari et al. (2014) reported that red snapper from the 2004, 2005 and 2006 (~89%) year classes dominated the recreational landings of the species GOM-wide (Saari et al. 2014).

Historically, red snapper strong year-classes occurred in 1980, 1989, 1995, and 1996 (Cowan 2011), but individuals from these year-classes represented < 1% of the cohort distribution in this study. My findings are consistent with Saari (2011), who reported that <1% of the red snapper cohort distribution at four shelf-edge reefs belonged to the historically strong years classes. Allman and Fitzhugh (2007), in a 12-year (1991-

2002) red snapper survey of the GOM commercial and recreational red snapper landings, noted that the presence of cohorts 1989 and 1995 were abundant in both sectors.

The oldest red snapper sampled was 26 yrs old at McGrail, despite confirmed life spans >50 years (Render 1995, Wilson and Nieland 2001, Allman and Fitzhugh 2007). Overall, a larger red snapper mean age was observed (7.21 years) for all sites compared to a previous shelf-edge reef study (Saari 2011), but my research began in 2011 and is consistent with the age progression reported by Allman and Fitzhugh (2007) in their survey of commercial longlines (7.37 years) and in previous surveys. The absence of red snapper > 30 years in this study may be the result of GOM-wide overfishing that occurred in the late 1980s, which at that time may have depleted the fish that would represent the spawning population that would have been prevalent today (Cowan 2011, SEDAR 2013). In the absence of exploitation, periodic life history strategists, such as red snapper, produce strong-year classes every few years, while in intermediary years fewer eggs survive (Winemiller and Rose 1992).

I found that red snapper begin to recruit to the shelf-edge reefs at 4 years of age; this finding is consistent with Saari's (2011) comparison of red snapper age and growth between artificial and shelf-edge reefs. Furthermore, I found the majority of red snapper at the shelf-edge reefs were between 4 to 12 years of age; this may be attributable to an age-specific habitat preference. Red snapper exhibit an ontogenetic shift in habitat preference between the ages of 2 to 9 years of age, moving to deeper waters with higher vertical relief (Nelson and Manooch 1982, Wilson and Nieland 2001, Nieland and Wilson 2003, Wells et al. 2008). SEDAR (2009) reported a lack of red snapper >8 years in the commercial and recreational fisheries; our results suggest that red snapper >8 years are



present at the shelf-edge reefs, however red snapper >15 years were much less abundant at the shelf-edge reefs in this study. Red snapper site fidelity remains high during young ages, while older individuals are thought to have moderate site fidelity (Patterson et al. 2001b). The combination of older fish moving away from reefs and the depletion of the population biomass in the mid-to-late 1980's may offer plausible explanations for the lack of fish older than 15 years in this study (1987, n=1; 1995, n=2).

Despite low sampling effort at Midnight Lumps, the reef had the largest number of 4 years old recruits (17%) and is consistent with Saari (2011) who reported red snapper at 4 yrs represented approximately 35% of the distribution at four eastern shelf-edge reefs in the northwestern GOM. I suggest that Midnight Lumps proximity to the established West Delta Artificial reef block (~36 km) may explain the abnormally higher percentage of 4-year-old recruits than at the more westerly shelf-edge reefs. Additionally, the data suggest that red snapper may disappear from Midnight Lumps at 7 years of age due either to age-specific habitat preferences or to recreational fishing mortality. Older red snappers in the northwestern GOM become less reef-associated once they reach a size threshold that allows them to escape predation and emigrate away from artificial reefs to lower habitat quality (Render 1995, Workman et al. 2002, Nieland and Wilson 2003, Szedlmayer and Lee 2004, Geary et al. 2007, Wells et al. 2008).

Species that produce relatively infrequent strong year-classes present difficulties for fishery managers. As strong-years classes recruit to the fishery, an increase in catch-per-unit-effort occurs in the recreational and commercial fisheries, which in turn adds pressure to increase catches, as well as the fishing effort needed to catch fish, which has been the case with red snapper for the last 25 years (Cowan et al. 2011). As a strong

year-class moves through the fishery, to a size when they become less desirable or less vulnerable, it is much more difficult to reduce catches and effort to a level that is sustainable (Cowan 2011). This is a well-known phenomenon referred to as the ratchet effect by Ludwig et al. (1993). It is possible that the natural shelf-edge reefs provide some refuge from fishing pressure because of their distance from shore (>150 km), enabling more fish to reach reproductive maturity and maximum spawning potential. In this study, the lack of red snapper >20 yrs is consistent with previous reports that a deep-water cryptic red snapper biomass does not exist at the shelf-edge reefs in the northwestern GOM (SEDAR 2009, Cowan et al. 2011), but the sheer number and complexity of the habitats may indeed make them the historical center of abundance in the northern GOM (Goodyear 1995)

#### 2.4.2 Growth

Size selectivity from fishing gear and fisher preference for larger individuals removes genetic diversity from the red snapper population leading to fishery-induced juvenescence (Jackson et al. 2007). I found that the von Bertalanffy parameter  $k$  did not differ across the longitudinal gradient that the reefs provided, suggesting that as red snapper recruit to the shelf-edge reefs, growth becomes uniform, however this may not be biologically significant. Overall, I found greater estimates of red snapper growth parameter  $k$  compared to those across the GOM and in all fisheries with the exception of red snapper off the coast of Texas (Nelson and Manooch 1982, Szedlmayer and Shipp 1994, Render 1995, Patterson et al. 2001a, Wilson and Nieland 2001, Fischer et al. 2004). This study found a larger estimate of the von Bertalanffy parameter  $k$  and was not consistent with Saari's (2011) fishery-independent study that reported smaller estimates

of the growth parameter  $k$  at the shelf-edge reefs, toppled and standing platforms in the northwestern GOM.

In this study, red snapper growth estimates from von Bertalanffy growth models estimated smaller  $L_{\infty}$  than in all previous studies in the northern GOM (Nelson and Manooch 1982, Szedlmayer and Shipp 1994, Render 1995, Wilson and Nieland 2001, Fischer et al. 2004, Saari 2011, SEDAR 2013, Saari et al. 2014). Fischer (2004) reported that the smallest estimate of  $L_{\infty}$  (778 mm) and the largest growth parameter ( $k=0.38$ ) of red snapper occurred off the coast of Texas and this is consistent with the shelf-edge reefs in this study. Red snapper von Bertalanffy growth parameters at all reefs are smaller for both  $L_{\infty}$  and  $k$  in the northwestern GOM compared to the eastern and western GOM and among fishing sectors (SEDAR 2013).

The latest red snapper stock assessment recommended further growth studies (SEDAR 2013), especially those based on fishery-independent sampling to further determine if regional and sub-regional differences in the demographics of red snapper indeed occur. Many red snapper growth estimates in the GOM have been based upon fishery-dependent data collected from portside sampling where sub-regional differences are impossible to address. Fishery-dependent studies have the great advantage of larger sample sizes, including larger and older fish, effectively pulling  $L_{\infty}$  downward allowing for better estimates of  $k$ . When investigating von Bertalanffy growth parameters, researchers must assume that the sample population reflects the natural red snapper population that the model reflects. The parameter estimates  $L_{\infty}$  and  $k$  are strongly correlated (Kirkwood and Somers 1984, Wang and Thomas 1995), however they are estimated parameters and variation occurs with only small changes in sampling

demographics (Wang and Milton 2000). Furthermore, differences in year class strength and between year differences in growth rates may result in differing growth estimates. Therefore, comparisons of von Bertalanffy growth models between studies is problematic; parameter estimates reflect growth in a particular region over a certain time period, and ignores the recruitment of younger red snapper over time and the difficulty of capturing older individuals (Fischer 2007).

Red snapper reproductive studies at Bright, Jakkula, and McGrail and artificial reefs in the northern GOM have reported that red snapper spawning potential, batch fecundity, and reproductive maturity are more favorable at the shelf-edge reefs (Kulaw 2012, Glenn 2014). Red snapper at natural shelf-edge reef habitats are maturing at younger ages and smaller sizes than artificial sites. During peak spawning season red snapper at Bright, McGrail, and Jakkula showed 98% maturity compared to 52% maturity on artificial habitats. A recent study found that red snapper at natural shelf-edge reef habitats are maturing at younger ages and smaller sizes than artificial sites. Glenn (2014) found that female red snapper with hydrated oocytes collected from natural shelf-edge reef habitats had significantly higher batch fecundities, then their artificial counterparts, contributing more significantly to the spawning stock biomass in northwestern GOM (Glenn 2014).

Differences in red snapper age and growth estimates at each shelf-edge reef may be due to habitat specific characteristics. A recent red snapper diet study at the three natural shelf-edge reefs (Bright, McGrail, and Jakkula) reported a wider diversity of prey items, largely consisting of demersal reef-fish and concluded that the natural shelf-edge reefs are bioenergetically more favorable to red snappers than artificial reefs. Red

snapper diets did not differ through size-classes at the shelf-edge reefs, however size-class was correlated with dietary intake at the East Cameron Planning Area (Schwartzkopf 2014). However other studies have found prey composition to be similar between artificial and natural reefs, and suggest that the lack of ocean currents in the upper water column at artificial reefs may be more bioenergetically favorable (Simonsen et al. 2014).

The main goal of my research was to examine the age and growth of the economically important red snapper populations on four natural shelf-edge reefs in the northwestern GOM. The fishery began in the central Gulf coast in modern day Pensacola, Florida. The fishery grew due to the availability of ice and the availability of trains to cities in the northern U.S. Through the early 1900's the fishery grew to exceed 10 million pounds but the fishery declined and moved eastward into Tampa Bay and westward in Texas. Landings peaked in the mid 1960's through the 1980's with the advent of modern fishing vessels and fishing methods (Hood et al. 2007).

To accelerate the rebuilding of the red snapper stock, stock assessments, and sustainable management decisions require accurate estimations of age distributions and growth rates. Egregious ageing errors result in over-exploitation of fish stocks world-wide, as was the case with the orange roughy (*Hoplostethus atlanticus*) off the coast of New Zealand. Precise and unbiased age and growth estimates provide fishery managers with the tools necessary to improve stock assessments, population models, and size-at-maturity data. My study will help define biological reference points at the four natural shelf-edge reefs and to track the progression of strong year-classes at individual shelf-edge reefs.

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## CHAPTER 3: AGE AND GROWTH COMPARISONS OF FRESHWATER DRUM, *APLODINOTUS GRUNNIENS*, BETWEEN ANCIENT AND MODERN POPULATIONS IN SOUTHEASTERN LOUISIANA

### 3.1 Introduction

Humans have been exploiting aquatic ecosystems for millennia and the presence of extant virgin fish stocks around the world is questionable. Records of exploitation in antiquity to the 19<sup>th</sup> century exist but removal rates are difficult to quantify (Pinnegar and Engelhard 2008). For example, early explores in the Gulf of California during the 16<sup>th</sup>-19<sup>th</sup> centuries wrote about ‘innumerable’ whales, sea-turtles, and the great abundance of fish (Saenz-Arroyo et al. 2006). George Wilhelm Stellar published notes of his expedition aboard the vessel *St. Peter*, which provided detailed anatomical information about the now extinct Stellar sea cow *Hydrodamalis gigas*. The International Whaling Commission has used 18<sup>th</sup> and 19<sup>th</sup> century whaler’s log books to reconstruct population dynamics pre-and-post exploitation (Baker and Clapham 2004). Financial records have been used to reconstruct 300-year time series for Mediterranean tuna (Ravier and Fromentin 2001) and Norwegian cod abundance (Oiestad 1994). These studies offer insight into historical fish stocks but frequently lack quantifiable data.

The use of paleological fish remains, such as otoliths or vertebrae, offer quantifiable data to access fish stocks in antiquity. Numerous studies have focused on comparisons between fishery exploitation in antiquity and modern times. For example, in Parita Bay, Panama, marine fish bones were used to compare fish faunas from the Cerro Mangote (6000 B.P.) and Sitio Sierra site (1800 B.P.) (Cooke 1992). That author suggested that regional fishing practices had developed from a shore-based fishery to a more complex gear type, namely fine meshed gill nets.

In southern Louisiana at the end of the Pleistocene period deglaciation increased stream entrenchment broadening the alluvial Mississippi Valley and eroded Pleistocene landforms. Raising sea levels approached modern levels by the Middle Archaic period (8,000-4,000 BCE), which produced lower gradients and meandering river courses, such as, abandoned channels, natural levees, back swamps and over-back deposits seen in the modern Lower Mississippi Valley (Saucier 1994). A warming interval known as the Hypsithermal period caused channel movement and distributary formation that reshaped the alluvial valley and deltaic plain during the Early and mid-Holocene that supported the development of Cypress-gum wetlands, mixed hardwood forests, and modern vegetation (Hays and Weinstein 2011).

The Tchefuncte is a well-know culture of the Early Woodland Period, a time period identified as the Tchula period in the Lower Mississippi Valley. The extensive occurrence of shell middens at Tchefuncte sites offers rich assemblages of pottery, bone and otolith artifacts, and cultural remains. The Tchefuncte were primarily hunter-gatherers who lived in small communities in the lowlands and coastal areas of the Gulf of Mexico. They fed primarily on a variety of seafood, especially clams and fish; they hunted deer, raccoons, alligators and migratory birds (Ford et al. 1945). Another important quality of the Tchefuncte culture is the distinct departure from its Late Archaic predecessor, the Poverty Point culture. As found in the Poverty Point culture, the Tchefuncte lack long-distance exchange systems, large mound complexes, and exotic stone industries (Hays and Weinstein 2011). The decline in cultural complexity is viewed as the most vital aspect of research on the Tchefuncte. The chronology of the Tchefuncte culture is complicated, but most archaeologists would agree that it begins at

least by about 1000 BCE and ends around 200 BCE with the beginning of the Marksville culture (Gibson 2000, Fullen 2005, Kidder 2006, Hays and Weinstein 2011).

A freshwater drum (FWD) growth study published in 1960 used ancient FWD otoliths recovered from Native American middens at Modoc Rock Shelter, Illinois to estimate body lengths and body weights of ancient FWD from sagittal otoliths. First, the authors established a relationship between sagittal otolith weight and body length with data from contemporary freshwater drum. Those authors used this relationship to back-calculate ancient FWD body lengths and weights from sagittal otoliths found within the Native American middens (Witt 1960).

In this new study, I used modern FWD otoliths to estimate the month of capture for ancient FWD by developing a classification key based on marginal increment analysis from modern FWD otoliths. The modern FWD classification key serves to estimate biological age at time of capture. However, the strength of my work is that age structure and growth were empirically derived from ancient FWD otoliths.

Empirically deriving growth information from ancient FWD otoliths is both advantageous and problematic. Back calculating growth estimates cannot account for environmental factors that control growth, such as temperature, density-dependence, prey availability, environmental degradation, sea level rise, and perhaps, the selectivity of the fishing methods used to capture the fish. A disadvantage of this methodology is that the burial within a submerged Native American midden diminishes otolith quality by exposure to biological, chemical, and geological processes. My goal is to estimate age and growth information from ancient FWD sagittal otoliths and then by comparison

elucidate similar and contrasting age distributions and growth rates with a modern FWD population.

### 3.1.1 Life History

Freshwater Drum, *Aplodinotus grunniens*, also known commonly as gaspergou and sheepshead, is a freshwater species known for their '*grunniens*' or grunting, a behavior observed in males as a mechanism to attract females. Freshwater drum are listed in the United States Endangered Species Act as being of 'little concern', indicating the species is not threatened (Minnesota Department of Natural Resources 2014).

Freshwater drum are the most latitudinally wide-ranging fish in North America, from Hudson Bay, Canada to Guatemala in Central America. Longitudinally, FDW can be found from the Appalachian Mountains to the eastern slopes of the Rocky Mountains. Although FWD are considered a trash fish in some regions, in other areas anglers prize them and their otoliths are considered lucky. Freshwater drum are cannibalistic and prey upon smaller freshwater drum. They are prey for many other species including, walleye *Sander vitreus*, muskellunge *Esox masquinongy*, and migratory birds. However, humans are the primary predator with estimated commercial landings of 435,000 kg per year (Minnesota Department of Natural Resources 2014).

Freshwater drum spawn in June and July when water temperatures increase following the winter (Swedberg and Walburg 1970) (Etnier and Starnes 1993). They spawn in open water and after fertilization the eggs become buoyant and are carried away by riverine currents. Eggs hatch within 48 to 96 hours post fertilization. Males reach maturity at age 4, while females reach maturity around age 5. A female FWD can produce from 40 to 60 thousand eggs, which are immediately exposed to high levels of



predation. Freshwater drum larvae remain trapped in the surface film until they develop enough muscle strength to swim into deeper waters (Swedberg and Walburg 1970).

Younger FWD feed selectively on zooplankton and larvae, which comprise the majority of their diet (Bur 1982). Older freshwater drum are generalists but feed primarily on fish, crayfish, and immature insects. Pharyngeal teeth assist in the digestion of various species of mollusks. They prefer turbid backwater habitats in areas of sluggish current and feed at night by rooting prey out of muddy substrates. Environmental alterations, such as dams and levees negatively impact FWD drum ecosystems by decreasing the diversity and abundance of macroinvertebrate communities that limits prey taxa (Rypel 2007).

#### 3.1.2 Age & Growth

Accurate age estimation is crucial to calculating age structure, growth rates and production estimates (Campana 2001). Freshwater drum age estimates have been used to determine maturation rates (Palmer et al. 1995), to compare growth rates between habitats (Rypel et al. 2006) and to detect sexual dimorphisms in growth (Rypel 2007). Previous studies of FWD growth before 1994 were based on the examination of fish scales (Butler and Smith 1950, Daiber 1952, Edsall 1967), which has been invalidated (Campana 2001). The most recent studies have used otoliths to estimate age (Pereira and Bingham 1994, Rypel et al. 2006). Annual otolith deposition in FWD has been validated with accelerator mass spectrometry bomb radiocarbon dating (Davis-Foust et al. 2009).

Freshwater drum can reach lengths up to 910 mm and weights greater than 36 kg (Page and Burr 1991). Rypel et al. 2006 analyzed differences in growth estimates between lotic and lentic habitats in Alabama. The authors concluded that lotic habitats support more robust and faster growing freshwater drum. Rypel (2007) estimated von

Bertalanffy growth parameters for each sex. Female FWD grow faster and reach larger sizes at age than males.

Little is known about the age structure and growth rates of ancient fish populations of important recreational and commercial fishes worldwide. Age and growth estimates are the basis for determining age structure, production estimates, and insuring sustainable harvests. Collecting this information is difficult because of the remoteness of antiquity and the scarcity of preserved otoliths from which we can derive estimates. However, if the information can be obtained, fishery managers get a snapshot of fish populations that have not been exposed to industrial fishing pressure, raising sea-levels, man-made freshwater diversions, and point-source pollution. The goal of this study is to compare age and growth estimates between ancient and modern FWD to provide a temporal ‘snapshot’ between populations and contribute to our understanding of shifting baselines with respect to age and size distributions, and the increasing need for more emphasis on sustainability in coming decades.

### 3.2 Methods

#### 3.2.1 Otolith Collection Sites

Ancient otoliths were collected from two archaeological strata (II, III) within a submerged prehistoric midden at the Bayou Jasmine site (16SJB2), in St. John the Baptist Parish, Louisiana, USA. Ancient otoliths are associated with the Tchefuncte tribe of the Early Woodland period (1000 BCE-1000 CE). Ancient otoliths were radiocarbon dated to approximately 650 BCE (Rebecca Saunders<sup>1</sup>).

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<sup>1</sup> Rebecca Saunders. Louisiana State Museum of Natural History. Louisiana State University.

Modern freshwater drum otoliths were collected from Henderson swamp, Atchafalaya River Basin, and Prophet Island in the Mississippi River between 1987-1989. Modern FWD came from a commercial fishery and were caught on trotlines and then collected by the Simmesport Fish Company in Simmesport, Louisiana. Otoliths were processed at the Age and Growth laboratory at Louisiana State University.

### 3.2.2 Otolith Processing

Ancient FWD sagittal otolith weight (g), length (mm), and width (mm) were measured. The otoliths were sectioned transversely anterior to the core as described in Cowan et al. (1995). Otolith sections were cut with a Hillquist 800 thin-sectioning machine equipped with a diamond embedded wafering blade and precision grinder (Cowan et al. 1995). Otolith sections were then polished, mounted on a petrographic slides, and recut to produce a 200  $\mu\text{m}$  section of the otolith's core showing the opaque annuli along the ventral margin of the sulcus groove. The number of opaque annuli and the edge condition were determined under a dissecting microscope under transmitted light with a polarized light filter at 20x to 64x magnifications. Edge conditions were recorded after the methods of Beckman et al. (1998) (Table 1.1).

Modern FWD sagittal otolith weights (g) were recorded and processed by the Department of Oceanography and Coastal Sciences at Louisiana State University. Otoliths were embedded in resin and sectioned transversely to the core with a diamond-embedded, low-speed Isomet saw. Otolith sections were then polished, and recut to produce a section of the otolith's core showing opaque annuli along the ventral margin of the sulcus groove (personal communication, Daniel Beckman<sup>2</sup>). The number of opaque

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<sup>2</sup> Daniel Beckman. Department of Biological Sciences. Missouri State University.

annuli and the edge condition were determined under a dissecting microscope at 20x and 60x magnification. Edge conditions were recorded after the methods of Beckman et al (1988)

Table 1.1. Summary of sagittal otolith edge conditions used in marginal increment analysis to estimate month of capture in ancient freshwater drum from a modern freshwater drum classification key.

Summary of Edge Conditions	
Edge Condition 1	Opaque zone on edge from point of initial formation to roughly 1/3 complete
Edge Condition 2	Opaque zone 1/3 to 2/3 complete
Edge Condition 3	Opaque zone 2/3 to entirely complete
Edge Condition 4	Outer opaque zone complete, translucent zone from point of initial formation to 1/3 complete
Edge Condition 5	Translucent zone on edge 1/3 to 2/3 complete
Edge Condition 6	Translucent zone 2/3 to entirely complete

### 3.2.3 Age Estimations

Ancient FWD opaque annulus counts and edge conditions were determined by the author and a second reader without referencing morphometric data. Precision of ancient and modern annulus counts was evaluated with the Coefficient of Variation (CV) and Average Percent Error (APE) (Beamish and McFarlane 1983). Cohen's Kappa coefficient was used to measure the inter-rater agreement for qualitative data and reader agreement by chance (Viera and Garrett 2005).

To assign all fish to a uniform hatching date of July 1<sup>st</sup> age estimates were made using the following algorithm (Equation 1). The age in days algorithm is as follows:

$$Age = -182 + (annulus\ count * 365) + ((m - 1) * 30) + d \quad \{1\}$$

Where  $m$  is the ordinal number of the month of capture, and  $d$  is the day within month captured. In order to correct for a uniform hatching date of July 1<sup>st</sup>, 182 days was

subtracted from each estimate. To calculate the age in years, the ordinal number of days was divided by 365.

A classification key was developed using the otolith edge-condition from modern FWD to estimate the month of capture for ancient freshwater drum. Probabilities were assigned using a discrete uniform probability distribution to determine temporal ranges of otolith edge-conditions by month as established with modern otolith data. Probabilities from this key were then applied to the edge conditions observed in the ancient otoliths.

#### 3.2.4 Age, Size, and Growth Estimations

ANOVA models were used to compare age distributions of FWD between time periods using Tukey-Kramer pairwise comparisons. Kolmogorov-Smirnov tests compared age frequency distributions between ancient and modern freshwater drum.

Freshwater drum sagittal otolith weight and age were regressed to establish a relationship between otolith weight and FWD age. Sagittae mean weights-at-age were compared between populations for all ages sampled. An ANCOVA (the most common ages in this study 1-9 years) was used to compare sagittal weight-at-age for ancient and modern freshwater drum populations.

### 3.3 Results

Ancient FWD sagittae were removed from two archaeological strata within a submerged Native American midden in St. John the Baptist Parish, Louisiana. Due to the low sample size in stratum III and its general similarity to stratum II, both strata were combined for all analyses. A total of 364 modern FWD and 71 ancient FWD sagittal otoliths were used for all analysis (Table 3.1).

Table 3.1. Numbers of freshwater drum, *Aplodinotus grunniens*, sample size and damaged sagittal otoliths sampled from an ancient Native American midden and Henderson swamp and Prophet Island, Louisiana.

Time Period	Strata	<i>n</i>	Damaged
Ancient	II	42	3
	III	37	5
Modern		365	1

Age accuracy of modern FWD otoliths was determined from a subset of 142 sagittae otoliths (Table 3.2). The first and only enumeration of modern FWD otoliths the readers agreed on 87.51% of otolith opaque increments, an APE of 2.14%, CV of 0.19 and a Kappa Statistic of 0.745.

Ancient FWD ages were determined from counts of opaque increments in 71 transverse otolith (sagittal) sections. After the initial reading, the two readers agreed on 43.73% of otoliths, an APE of 10.58%, CV of 0.239, and a Kappa statistic of 0.36 (Table 3.2).

Table 3.2. Differences between two readers for modern freshwater drum, *Aplodinotus grunniens*, otoliths in average percent error (APE), coefficient of variation (CV), Kappa statistic, percentages of agreement (O) for opaque annulus counts, and percentages of differences in age estimates ( $\pm 1, 2$ ) after first reading.

	1st
APE	2.14
CV	0.19
Kappa	0.745
O	87.51%
$\pm 1$	14.98%
$\pm 2$	6.76%

Second reading produced better values for all tests. A third reading significantly improved the estimates between readers. The two readers agreed on 79.54% of annulus counts, with an APE of 1.198%, CV of 0.106 and a Kappa statistic of 0.689.

Table 3.3. Differences between two readers for ancient freshwater drum, *Aplodinotus grunniens*, otoliths in average percent error (APE), coefficient of variation (CV), Kappa statistic, percentages of agreement (O) for opaque annuli counts, and percentages of differences in age estimates ( $\pm 1, 2$ ) after first, second, and third reading.

	1st	2nd	3rd
APE	10.583	3.443	1.198
CV	0.239	0.134	0.106
Kappa	0.284	0.569	0.689
O	43.73%	65.24%	79.54%
$\pm 1$	40.98%	25.66%	17.44%
$\pm 2$	10.58%	6.15%	3.52%

### 3.3.1 Ancient Freshwater Time of Capture Estimation.

Marginal edge conditions in otoliths of modern FWD occurred over a discrete range of months (Fig. 3.1), however the modern FWD data did not fit a normal distribution. Sample sizes from the middens were too small to determine frequencies directly from modern otolith edge conditions. Therefore, modern FWD edge conditions were fit to a uniform probability distribution and a key was created based on the 0.1 and 0.9 quantiles (Table 3.4). The first edge condition (initial formation of opaque portion of annulus) begins in early October and sequential edge conditions are added throughout the year. While each FWD edge condition occurs over a discrete time range throughout the calendar year, temporal overlap occurs between neighboring edge conditions. However, modern FWD median edge conditions are distinctly staggered approximately two months apart (Table 3.4).

Most ancient FWD otolith edge conditions consisted of 4, 5, and 6 (deposition of translucent material) edge conditions, while 1, 2, and 3 edge conditions (deposition of opaque material) were less prevalent. Using the classification key (Table 3.4), most ancient FWD were probably caught between May and January (Table 3.5)(Figure 3.2).

Table 3.4. Temporal distributions of edge conditions from modern freshwater drum, *Aplodinotus grunniens*. Shown are sample size (*n*), 10% and 90% quantiles, and median.

Edge Condition	<i>n</i>	Quantiles		
		0.1	Median	0.9
1	63	October	January	March
2	29	January	March	April
3	51	March	April	May
4	107	May	June	July
5	52	July	August	October
6	60	August	October	January

Seasonal classifications were based on the beginning a period of the slower growth; winter is classified as December through February, spring as March through May, summer as June through August, and autumn as September through November. Historical seasonal data was interpreted as the percent catch by season (Table 3.5). Freshwater drum from both archaeological strata exhibited the same temporal distribution. Overall, estimated mean time of capture in summer was 35%, fall (40%), leaving 25% caught in the winter and spring (Table 3.5).

Table 3.5 Seasonal relative frequencies of freshwater drum, *Aplodinotus grunniens*, sampled from an ancient Native American midden. Absolute errors are given in red.

Strata	<i>n</i>	Winter	Spring	Summer	Fall
III	43	0.13	0.15	0.36	0.36
		0.01	0.02	0.04	0.04
IV	21	0.10	0.10	0.35	0.44
		0.01	0.01	0.04	0.04
Combined	64	0.11	0.13	0.35	0.40
		0.01	0.01	0.04	0.04

### 3.3.2 Age Structure

Modern freshwater drum exhibited a truncated age distribution. Freshwater drum ages ranged from 1 to 14 years of age with the majority (~80%) of individuals between



the ages of 4-6 years (Table 3.6). Mean biological age for modern FWD was  $4.76 \pm 0.1$  years and individuals younger than 4 years accounted for < 2% of the age distribution.

Freshwater drum older than 6 years of age accounted for < 14% of the age distribution.

Table 3.6. Freshwater drum, *Aplodinotus grunniens*, minimum, maximum, range and mean  $\pm$  standard error of ages, sampled from an ancient Native American midden and Henderson swamp and Prophet Island, Louisiana between 1987 and 1989.

Site	Minimum	Maximum	Range	Mean $\pm$ Standard Error
Ancient	0.42	9.42	9.02	$3.02 \pm 0.266$
Modern	0.98	13.92	13.83	$4.76 \pm 0.082$

Ancient FWD ages were less truncated and dominated by 1-5 years of olds (70.6%). Mean biological age for ancient FWD was  $3.02 \pm 0.08$  years, while ancient FWD older > 7 years of age accounted for 7.7% of the age distribution. Ancient FWD otoliths were dated to *circa* 650 BCE by radiocarbon dating.

A Tukey-Kramer grouping of mean age was significantly different between sites (Table 3.7). A Kolmogorov-Smirnov test for equal age frequency distributions were significantly different between ancient and modern freshwater drum (Table 3.8).

### 3.3.3 Growth

Ancient FWD sagittal otolith weights ranged from 0.12 g to 2.32 g with a mean otolith weight of  $0.51 \pm 0.05$  g (Table 3.9). Modern otolith weights ranged from 0.09 to 2.73 g with a mean otolith weight of  $1.04 \pm 0.02$  g (Table 3.9). Ancient FWD otolith weight increased rapidly from 0 to 8 years of age, plateaued from 8 to 10 years of age and due to low sample sizes after 10 years mean sagittal weight-at-age could not be evaluated. Similarly, modern FWD sagittal otoliths followed a linear trend growing from

0 to 8 years of age, plateauing from 8 to 10 years and increasing in weight from 10 to 12 years of age.

Table 3.7. Freshwater drum, *Aplodinotus grunniens*, pairwise comparison of mean age with a Tukey-Kramer *post hoc* adjustment, sampled from an ancient Native American midden and Henderson swamp and Poverty Point Island, Louisiana in the 1980's. Model significance:  $F_{1,447}=60.68$ ,  $p<0.0001$ .

Site	Estimate	Tukey-Kramer Grouping by Site
Ancient	3.02	A
Modern	4.76	B

Table 3.8. Kolmogorov-Smirnov test for age frequency distributions sagittal otolith weight and biological age of Freshwater Drum for sagittal otolith weight and biological age, sampled from an ancient Native American midden and Henderson swamp and Poverty Point Island, Louisiana in the 1980's.

Kolmogorov-Smirnov Two Way Test		
	Ksa	Pr > Ksa
Sagittal Wt (g)	5.03	$p<0.0001$
Biological Age	4.13	$p<0.0001$

Sagittal otoliths from older individuals (modern) displayed large variability after 10 years of age, which may be attributable to low sample sizes in age classes older than 10 years (<1% of the total). Mean sagittal otolith weight-at-age was limited to the most common ages in this study (1-9 yrs). Results from an ANCOVA indicate that sagittae mean weight-at-age differed, as modern FWD apparently grew more rapidly (steeper slope) than ancient FWD (Table 3.10)(Figure 3.4).

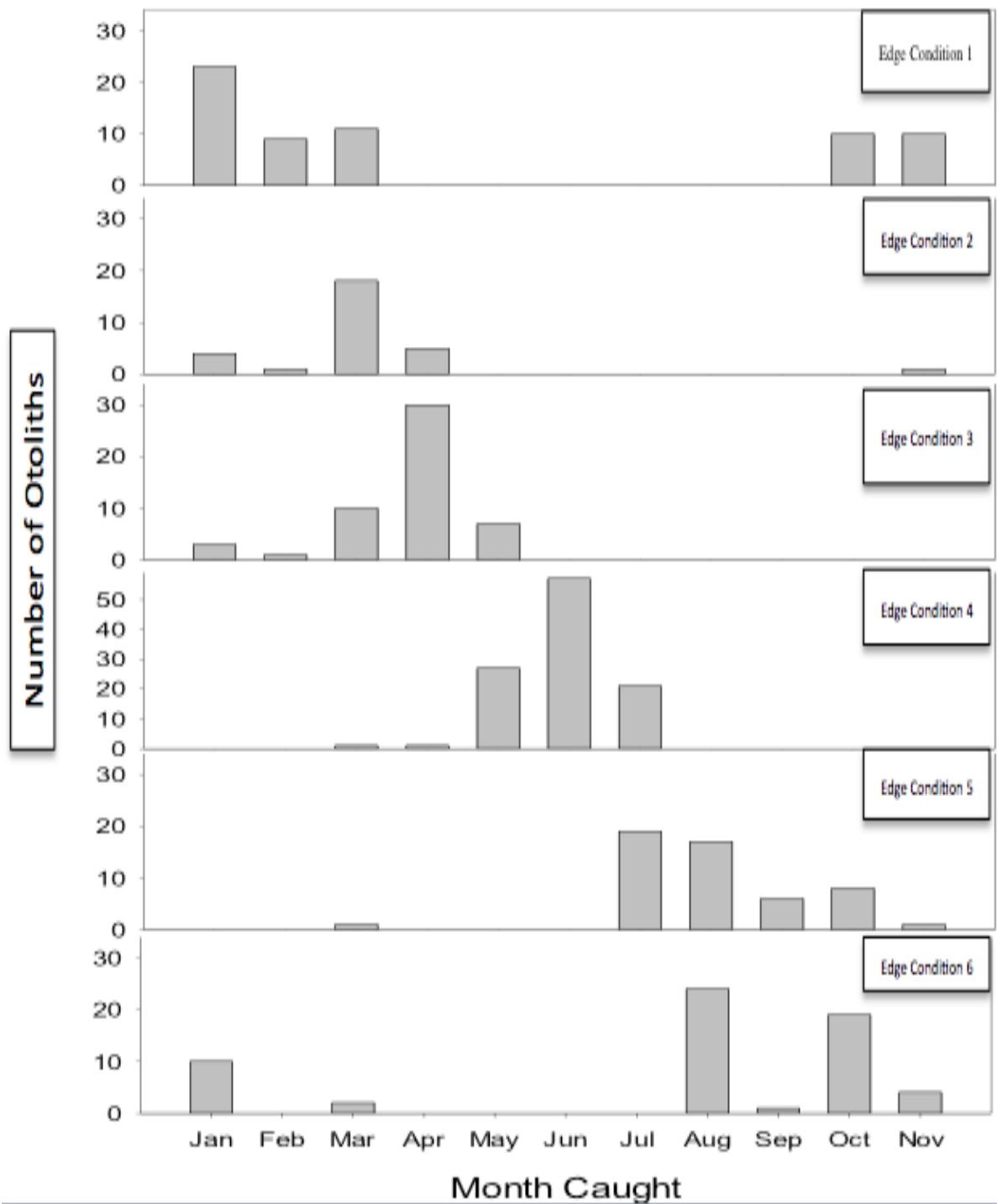


Figure 3.1. Modern freshwater drum, *Aplodinotus grunniens*, sagittal otolith counts by edge condition plotted against month of capture, sampled from Henderson swamp and Poverty Point Island, Louisiana.

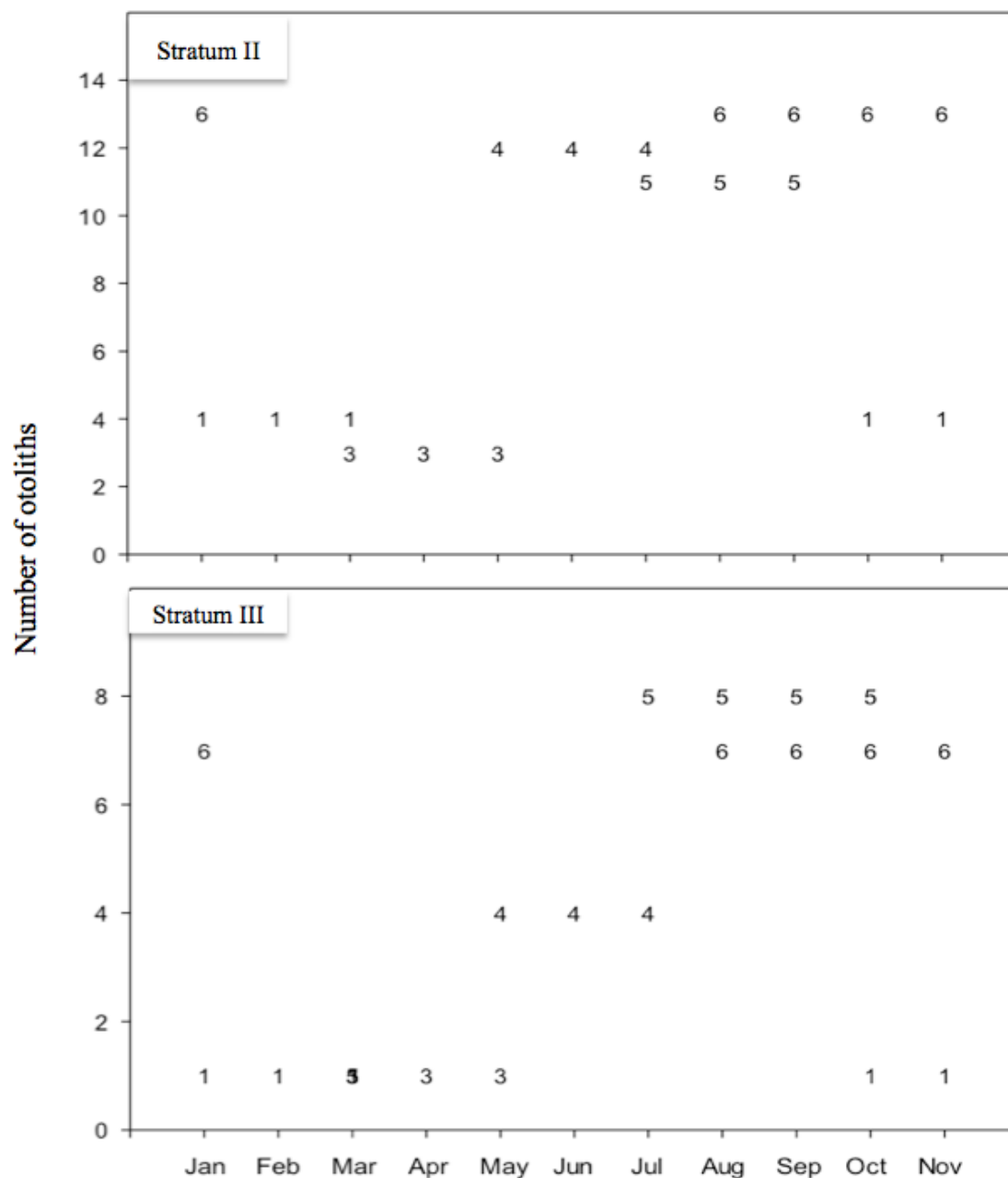


Figure 3.2. Ancient Freshwater drum, *Aplodinotus grunniens*, otolith counts (y-axis) by month (x-axis). Numbers represent edge condition observed at each month, sampled from an ancient Native American midden. Median month of capture for each edge condition (EC): EC 1 (January), EC 2 (March), EC 3 (April), EC 4 (June), EC 5 (August), EC (October).

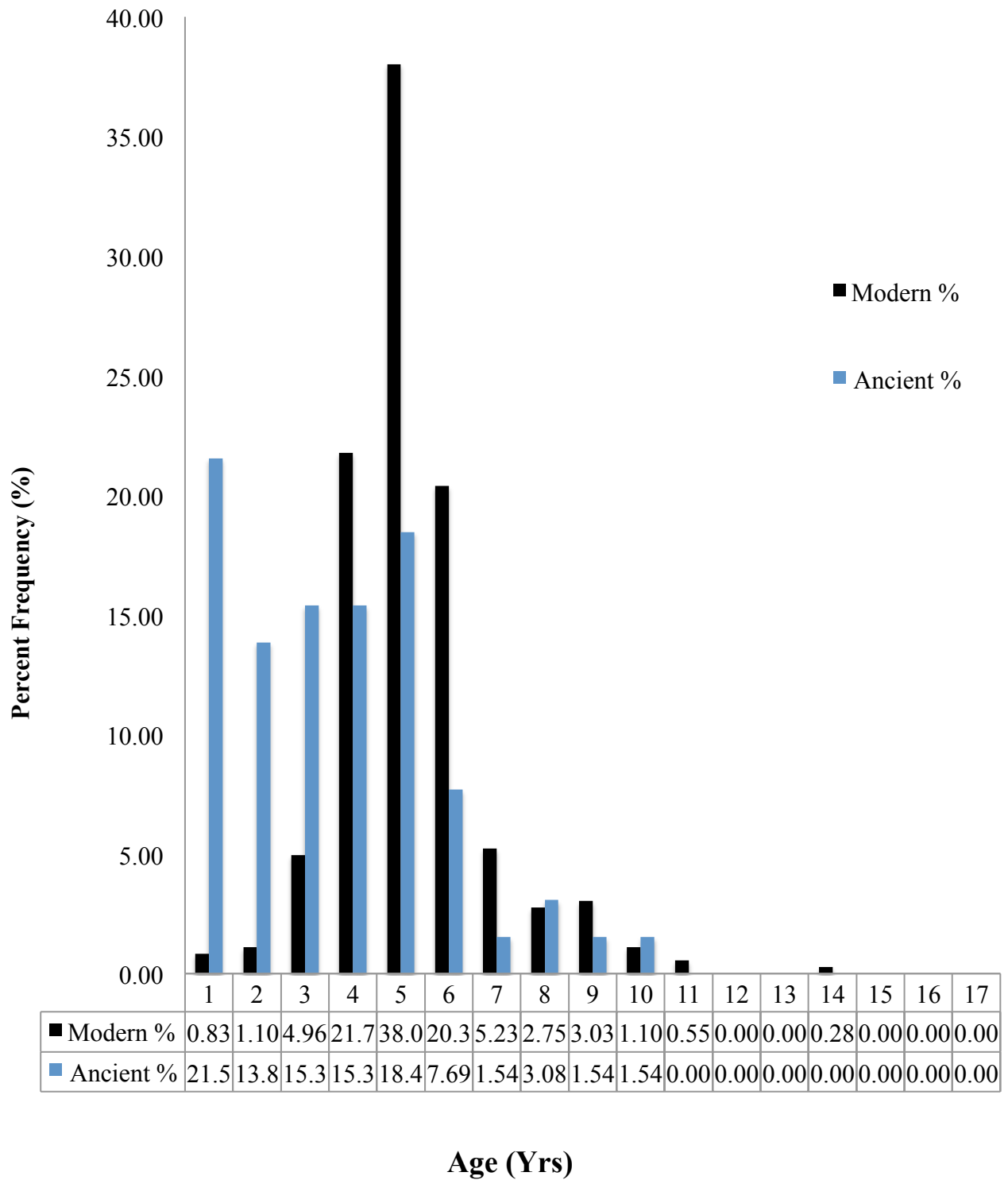


Figure 3.3. Distributions of ages in years for freshwater drum, *Aplodinotus grunniens*, sampled from an ancient Native American Midden and Henderson swamp and Poverty Point Island, Louisiana.

Table 3.9. Descriptive statistics for freshwater drum, *Aplodinotus grunniens*, sagittal otolith weights, sampled from an ancient Native American midden and Henderson swamp and Poverty Point Island, Louisiana (modern samples collected in the 1980's).

Site	Minimum	Maximum	Mean $\pm$ Standard Error
Ancient	0.12	2.32	0.536 $\pm$ 0.051
Modern	0.09	2.73	1.044 $\pm$ 0.024

Table 3.10. Analyses of covariance (ANCOVA) for freshwater drum, *Aplodinotus grunniens*, model significance, tests for equality of intercepts and slopes, and regression models fitted to observed sagittal weight at biological age (Bioage).

Model (Sagittal TW)	$F_{3,396}=167.37, p<0.0001, r^2=0.56$
Equality of Intercepts	$F_{1,396}=149.29, p=0.68$
Equality of Slopes	$F_{1,419}=4.11 \quad p<0.0001$

Site	Regression Model
Modern	Sagittal TW=0.1549(BioAge)+0.1871
Ancient	Sagittal TW=0.1429(BioAge)+0.1479

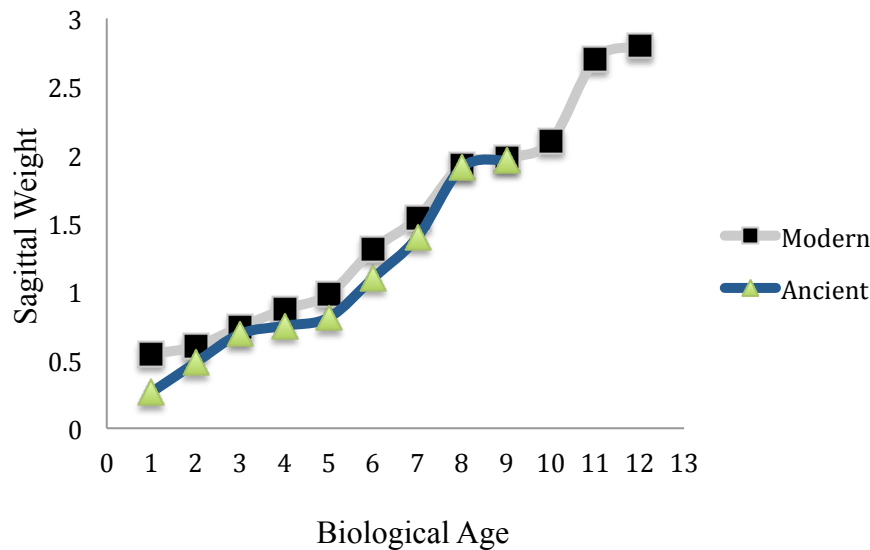


Figure 3.4. Freshwater drum, *Aplodinotus grunniens*, mean total sagittal weight-at-age sampled from an ancient Native American midden and Henderson swamp and Poverty Point Island, Louisiana.

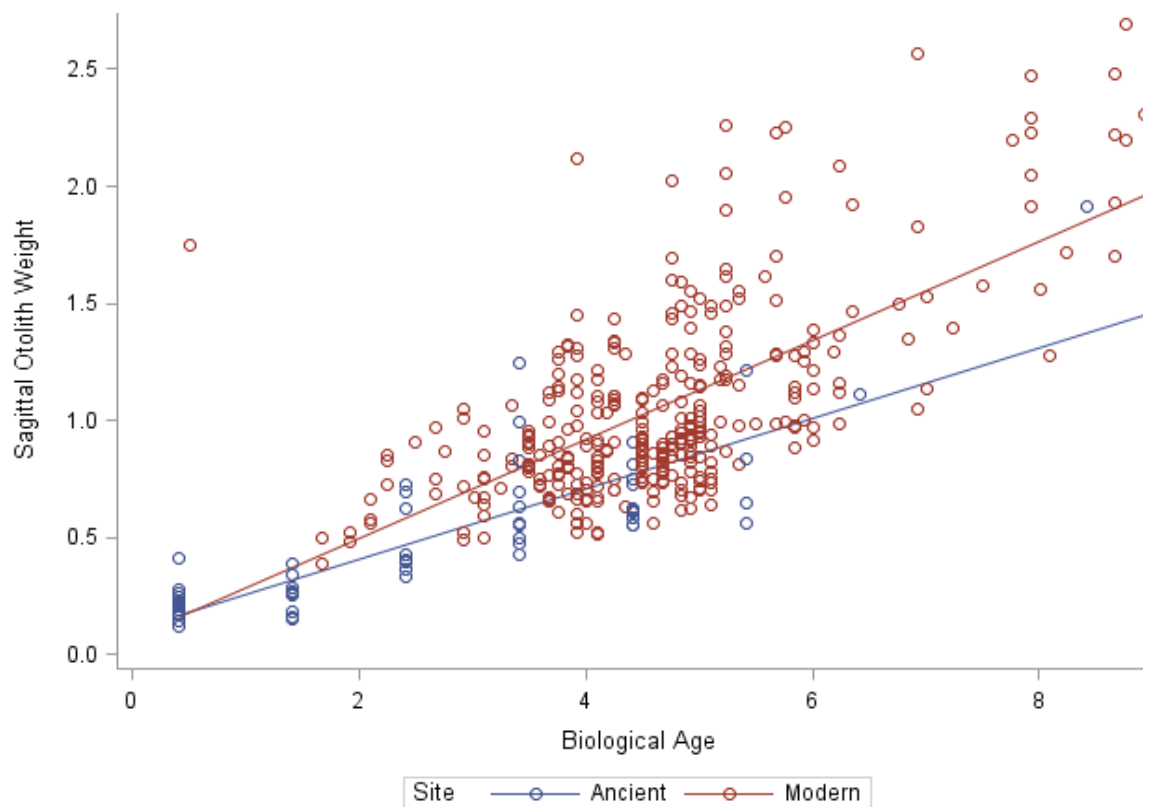


Figure 3.5. Regressions of weight-at-age of sagittal otoliths collected from an ancient Native American midden, and Henderson swamp and Poverty Point Island, Louisiana in the 1980s.

### 3.4 Discussion

#### 3.4.1 Age Structure

This study found that the modern FWD age structure was strongly truncated for individuals caught in 1987-1989. Selective removal of large mature individuals, natural mortality, fishing pressure and size specific emigration can result in a truncated age distribution (Anderson et al. 2008, Hsieh et al. 2010). Modern FWD drum < 4 years of age represented 8.67% of the age distribution, which suggest to me that younger individuals may not emigrate from juvenile habitats and recruit to the fishery at ages < 4 yr. Freshwater drum > 6 years of age accounted for < 12.98% of the age distribution;

factors that can effect nominal age distribution include age-specific habitat preference individuals, gear selectivity, or fisher preference.

The ancient FWD age distribution differed significantly from the modern FWD population ( $K_{sa} < 0.0001$ ); younger FWD ( $< 4$  yrs) composed 50.62% of the distribution. The Tchefuncte may have used woven nets with chiseled stone weights to capture younger fish (Ford et al. 1945), increasing the probability of capture at young ages (Page and Burr 1991). Evidence of older FWD in the middens dramatically decreased after 6 years of age. Older FWD may have been more difficult to catch with bone hooks and spear fishing (Ford et al. 1945) or not present at the seasonal fishing grounds of Tchefuncte.

#### 3.4.2 Growth

Ancient FWD sagittal otoliths displayed a smaller mean weight-at-age than did their modern counterparts. However, ancient FWD otoliths followed the same general trend in accumulation of inorganic material when compared to age estimates in both populations. Due to the biological, chemical, and geological decay processes that weathered and mineralized the ancient FWD sagittal otoliths, it could be inferred that mean sagittal otolith weight-at-age may be equal or greater than modern FWD sagittal otoliths.

In a two-dimensional plane sagittal otoliths may not increase in width as evident in smaller annual increments as individuals reach older ages, however in a three-dimensional plane deposition should remain consistent over a fish's lifetime, as fish continue to assimilate inorganic material into the calcium carbonate matrix.

The ANCOVA model reported significant differences in the equality slopes between ancient and modern populations. However, the model exhibited a poor fit to the



FWD sagittal weight-at-age data ( $r^2=0.495$ ), which is not unexpected when modeling biological parameters. The poor fit to the FWD populations may result from the subjective nature of age determination from sagittal otoliths. The interpretation of the first annual opaque deposition resulting from the protracted FWD spawning season, which determines the amount of translucent material between the otolith core and the first opaque annulus. Secondly, a parameter was not added to account for the decay of the ancient FWD sagittal otoliths, which may explain the large variations between ancient and modern FWD slopes. Therefore, mean sagittal weight-at-age may be a more appropriate method of comparing growth between ancient and modern FWD populations. Further research in the growth of otoliths should target a long-lived fish >100 years with a large sample size of fish in older age classes to appropriately model otolith growth. The Sebastidae family, which includes the genus *Sebastes* (pacific rockfish) and the Trachichthyidae family (orange roughy) have reached ages greater than 200 years and would be an appropriate specimen to model otolith growth.

Overall, this study was more successful in the comparison of age structure than of growth rates. Freshwater drum age structure was more easily assessed due to the preservation of annual opaque annuli within the transverse otolith plane and less successful in growth estimates due the decay of the three-dimensional otolith. However, if decay rates of otoliths can be incorporated into growth models, accurate comparisons between ancient and modern populations may be more correctly equated. Modern advances in both terrestrial and marine archaeology are continually discovering areas of human habitation in close proximity to rivers and coastal waters. Is it likely that future opportunities will present themselves for the collection of ancient otoliths allowing

researchers to reconstruct fishery-dependent estimates of age and growth of important fisheries world-wide.

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## CHAPTER 4: SUMMARY AND IMPLICATIONS

### 4.1 Red Snapper Age and Growth Estimates

The goal of my red snapper research was to examine the age and growth of individual natural shelf edge reefs in the northwestern GOM. The majority of red snapper studies have investigated the biological parameters of red snapper at and among artificial and natural shelf-edge reefs. A wide range of analyses have been utilized, including comparisons of age and growth, diet analysis, stable isotopes, hydroacoustics, and reproduction studies (Saari 2011, Kulaw 2012, SEDAR 2013, Glenn 2014, Schwartzkopf 2014, Simonsen et al. 2014a). I found that red snapper age demographics differed between all sites. With over a 100 natural shelf-edge reefs in the northwestern GOM, results suggests that each individual shelf-edge reef may differ in age structure with significant differences in size-at-age compositions. Geographic location on the shelf-edge, biotic zones, and biological assemblages may be important factors in growth rates and age structure at reef site.

Different geographical locations along the continental shelf edge are either advantageous or retarding. Hydrodynamic flow at shelf-edge reefs west of 91 degrees longitude is more favorable to the transport of reef-building larva, spores, and juvenile fish from the Gulf of Campeche, the Yucatan shelf and the Caribbean Sea that sustains the development of tropical reef communities (Rezak et al. 1985). East of 91 degrees longitude the shelf-edge reefs are dominated by the cold, sediment rich outflow of the Mississippi River delta that decreases the thermocline and results in increased vertical relief of the turbidity layer. The density of particulate matter within the turbidity layer creates differences in biological complexity in light suffused communities (Rezak et al. 1985).

Proximity of the shelf-edge reefs to one another may play an important factor in age and growth estimates. Reefs supporting different biological assemblages, biotic zones, and geological features may differ seasonally in prey availability, predation, and density-dependence coupled with interspecies competition. Bright reef for example is located in close proximity to the East and West Flower Gardens National Marine Sanctuary (EFGNMS), 28 Fathom and Rankin reefs. Bright reef had the largest sample size, which may be attributable to a higher relative abundance but the lowest estimated  $L_{\infty}$ . Conversely, Jakkula and McGrail reefs had the lowest sample sizes (lower relative abundance), and larger estimates  $L_{\infty}$  suggesting that prey-availability and density-dependent growth may be an important factor regulating age structure and growth at each shelf-edge reef site.

The natural shelf-edge reefs have long been considered primary habitat and the historical centers of abundance of the red snapper in the northwestern GOM (Camber 1955). More than 100 shelf-edge reefs have been identified along the continental shelf in the northwestern GOM (Rezak et al. 1985); it has been suggested that the natural reefs act as ‘habitat highways’ that create large scale ecological communities (Schmahl et al. 2008).

A new fishery management plan may be critical to maintain the ecological integrity of the reefs (Office of National Marine Sanctuaries 2012). The National Marine Sanctuaries division of the National Oceanic and Atmosphere Administration has developed a Sanctuary Expansion Action Plan (SEAP) to further extend the protection of marine resources along the TX-LA continental shelf. The SEAP has set forth criteria for the inclusion of shelf-edge reefs, which include biological, geological, structural,

biological connectivity, and sensitivity to anthropomorphic degradation. Our study supports SEAP inclusion of Bright and McGrail, and our study further suggests the inclusion of Jakkula because of the large presence of the strong red snapper year-classes at the shelf-edge reef. Inclusion within the EFGNMS would allow the historically overfished red snapper population to rebuild by allowing red snapper to reach reproductive maturity and thus increasing the spawning stock biomass. I suggest that red snapper travel between individual shelf-edge reefs in response to seasonal changes in biotic and abiotic environmental factors providing variations in prey availability between trophic levels. Further research should focus on the movement of red snapper in and among the numerous (>100) natural shelf-edge reefs. For example, sub-regional tagging studies should address the interconnectivity of shelf-edge reefs with respect to site-fidelity and elucidate seasonal trends in habitat preference in the northwest GOM.

#### 4.2 Ancient and Modern Freshwater Drum Age and Growth Estimates

I compared age structure and growth estimates between ancient and modern freshwater drum. The two FWD populations are separated by nearly 2600 years. However, the collection sites are less than 200 km apart. Novel elements of this study, including the calculation of biological ages and growth estimates directly from ancient sagittal annuli counts and growth rates were estimated without back-calculating allometric relationships from modern FWD morphometrics.

The differences in age distributions between the two FWD populations may be due to habitat limitation and fishing gear selectivity. Freshwater drum populations in antiquity may not have been habitat limited due to sediment flow from Mississippi River that continued to sustain and create new habitats. Conversely, the Lower Mississippi River is now constrained by levees and spillways to control flooding. These man-made

diversions serve to manipulate the flow of water, reducing habitat availability and the reduction of the ecological community that supports FWD populations.

Gear selectivity also plays an important role in age distributions between the ancient and modern FWD populations. Currently, freshwater drum commercial landings in the U.S.A are estimated to exceed 435,000 kg per year (Minnesota Department of Natural Resources 2014). The majority of individuals caught in the modern FWD population were 4, 5, and 6 year olds, suggesting that modern fishers target habitats associated with adult freshwater drum. Conversely, artisanal fishing methods, such as woven nets employed by the Tchefuncte culture (Ford et al. 1945) in lotic waters had increased success rates in young age-classes.

Mean sagittal weight-at-age was the most successful analysis to model growth between the two FWD populations due to the lower samples sizes in older individuals. Mean sagittal otolith weight-at-age was limited to the most common ages in this study (1-9 yrs), however the results suggest that mean otolith weight-at-age between the FWD populations increased in concert with one another. Ancient otoliths are assumed to have lost density, altering the allometric relationship by the gradual decay within the submerged midden. In the absence of environmental degradation, ancient otoliths may have weighed as much as, or more than, their modern counterparts. Therefore, it plausible to assume that FWD in antiquity were less susceptible to fishing pressure and size selectivity that reduces genetic diversity, with respect to slower and faster growing individuals.

Terrestrial and marine archaeological studies continue to find evidence of human habitation in close proximity to rivers and coastal waters. The use of ancient fish otoliths



is not limited to temporal comparisons of age and growth estimates in fishery science. Modern techniques in paleobiology and solution-based assays, such as Inductively Coupled Plasma Mass Spectrometry (ICPMS) and Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES), gives researchers insight into the elemental composition within the otolith's calcium carbonate matrix. Therefore, the elemental composition within the otolith, such as the ratios of Sr: Ca and  $^{18}\text{O}/^{16}\text{O}$  isotopes, act as paleo-indicators to reconstruct environmental and oceanographic conditions in antiquity.

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## VITA

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