Age, Growth, Reproduction, and Diet of the Finetooth Shark, Carcharhinus isodon, in the Northern Gulf of Mexico

Jeremy Michael Higgs
University of Southern Mississippi

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AGE, GROWTH, REPRODUCTION, AND DIET OF THE FINETOOTH SHARK,

*CARCHARHINUS ISODON*, IN THE NORTHERN GULF OF MEXICO

by

Jeremy Michael Higgs

A Thesis
 Submitted to the Graduate School
 and the Department of Coastal Sciences
 at The University of Southern Mississippi
 in Partial Fulfillment of the Requirements
 for the Degree of Master of Science

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ABSTRACT

AGE, GROWTH, REPRODUCTION AND DIET OF THE FINETOOTH SHARK, 
*CARCHARHINUS ISODON*, IN THE NORTHERN GULF OF MEXICO

by Jeremy Michael Higgs

May 2016

The current study examined life history parameters of the finetooth shark, 
*Carcharhinus isodon*, in the northern Gulf of Mexico (nGOM) to provide an accurate 
description of the species’ reproductive biology, age, growth, and diet composition. A 
total of 1,489 finetooth sharks (830 female; 659 male) were collected from coastal waters 
of the nGOM between Apalachicola Bay, Florida (29.873° N and 84.514° W) and East 
Bay, Louisiana (28.959° N and 89.279° W) from June 2006 through October 2013. Peak 
reproductive development occurred during May/June for both males and females, which 
was followed by mating and an 11-12 month gestation period. It was noted that mature 
females exhibited both annual and biennial reproductive periodicity, and it appears that 
the amount of energy reserves present could be driving this. The maximum observed age 
was 9.4 and 6.5 years, and the age at 50% maturity was 4.1 and 3.6 years for females and 
males, respectively. The von Bertalanffy growth model estimates for females and males 
were \( L_\infty = 1308\text{-mm FL and } k = 0.26/\text{yr} \) and \( L_\infty = 1164\text{-mm FL and } k = 0.32/\text{yr} \),
respectively. Diet analysis was conducted on 518 sharks and revealed that teleosts 
dominated the diet, with Gulf menhaden, *Brevoortia patronus*, being the most important 
prey species. The results of this comprehensive study better defines finetooth shark life 
history in the nGOM.
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LIST OF ABBREVIATIONS

wNAO Western North Atlantic Ocean
GOM Gulf of Mexico
nGOM Northern Gulf of Mexico
NMFS National Marine Fisheries Service
SEDAR Southeast Data Assessment and Review
TL Total length
STL Stretched total length
GSI Gonadosomatic index
HSI Hepatosomatic index
USM/GCRL University of Southern Mississippi, Gulf Coast Research Laboratory
DISL Dauphin Island Sea Laboratory
PCL Precaudal length
FL Fork length
MFL Median fork length
ANOVA Analysis of variance
VBGF3 Three parameter von Bertalanffy Growth Model
VBGF2 Two parameter von Bertalanffy Growth Model
APE Average percent error
Lt Predicted length at age “t”
L∞ Asymptotic length
L0 Size at birth
k Growth coefficient
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<td>$t_0$</td>
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<td>%W</td>
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<td>IRI</td>
<td>Index of relative importance</td>
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CHAPTER I

GENERAL INTRODUCTION

Elasmobranch fishes include more than 1,200 different species of sharks (n ≥ 503), skates (n ≥ 200), and rays (n ≥ 699), occupying a wide range of habitats, and are distributed throughout all the oceans of the world (Bone and Marshall 1982; Klimley 2013). In order to understand life strategies used by elasmobranchs, it is essential that the methods to determine life history parameters be fully developed and evaluated (Fisk et al. 2001). Elasmobranch life history patterns are commonly characterized by slow growth, long life, large adult size, late sexual maturity, long gestation periods, reduced fecundity, and precocial offspring. Furthermore, it has been recently suggested that three distinct life history-trait patterns are represented among elasmobranchs: 1) large litters, moderate to high longevity, large size, small offspring, slow growth, 2) small litters, high longevity, large size, large offspring, slow growth and 3) small litters, low longevity, small size, small offspring, fast growth (Cortés 2000).

Life history patterns can be influenced by several factors including food limitation, geographic separation, latitudinal variation, and light and temperature levels (Jones and Green 1977; Branstetter 1987; Parsons 1993; Lombardi-Carlson et al. 2003; Driggers et al. 2004). Recent research has established that life history traits and patterns have the potential to vary between members of one population of a species or between geographically separate populations of a species (Cortés 2000; Cope 2006). For example, blacknose sharks (Carcharhinus acronotus) exhibit biennial reproduction in the western North Atlantic Ocean (wNAO) and reproduce on an annual basis in the northern Gulf of Mexico (nGOM) (Driggers et al. 2004; Sulikowski et al. 2007). In addition, the Atlantic
sharpnose shark (*Rhizoprionodon terraenovae*) exhibits a smaller size-at-maturity and larger size-at-age in the wNAO as compared to the nGOM (Parsons 1983; Branstetter 1987; Loefer and Sedberry 2003). Furthermore, investigations into age and growth variability have shown possible regional and latitudinal differences in bonnethead sharks (*Sphyrna tiburo*) (Parsons 1993; Lombardi-Carlson et al. 2003). To fully understand the implications of life history variability, more species-specific research needs to be conducted at the population level.

Shark populations in the wNAO and nGOM, are managed as members of one of four complexes based upon known life history, habitat, size and fishery characteristics: pelagic, large coastal, small coastal, or protected (NMFS 1993; Carlson et al. 2003; NMFS 2006). Pelagic and large coastal sharks are typically characterized as long-lived species that exhibit slow growth and late age at maturity; whereas small coastal sharks are shorter-lived species with faster growth and earlier age at maturity (NMFS 1993; Carlson et al. 2003; Driggers et al. 2004; Dulvy et al. 2008). The small coastal complex is composed of four species: Atlantic sharpnose, blacknose, bonnethead and finetooth sharks (*Carcharhinus isodon*). In 2002 and 2007 the National Marine Fisheries Service (NMFS) reviewed the available life history data for this complex in the wNAO and nGOM. At the conclusion of the 2002 assessment, NMFS determined that small coastal sharks were not experiencing overfishing as a group; but on an individual level, finetooth sharks were experiencing overfishing (Cortés 2002). The 2007 assessment conducted by the Southeast Data Assessment and Review panel (SEDAR), determined that small coastal sharks as a whole were not found to be overfished and that overfishing was not occurring (NMFS 2007); but when assessed individually, it was shown that blacknose
sharks were overfished with overfishing occurring, while Atlantic sharpnose, bonnethead and finetooth sharks were not found to be overfished and no overfishing was occurring (NMFS 2007). In response the review panel noted that targeted research on the life history parameters for species in both the wNAO and nGOM was needed (NMFS 2007).

The finetooth shark has been documented as being caught in the wNAO and nGOM recreational and commercial shark fisheries; however, finetooth sharks only comprise about 1% of the catch for small coastal sharks (NMFS 2007). Due to their limited take in the fishery, finetooth sharks have not been extensively studied, and, as a result, their biology is poorly understood (Castro 1993). For example, much of the previous finetooth shark research was conducted on a small number of primarily immature specimens (Radcliffe 1916; Bigelow and Schroeder 1948; Baughman and Springer 1950; Clark and von Schmidt 1965). The few studies that have examined mature finetooth sharks were also limited to relatively small sample sizes (Springer 1950; Dahlberg and Heard 1969; Branstetter and Shipp 1980; Castro 1993; Carlson et al. 2003; Neer and Thompson 2004; Drymon et al. 2006; Driggers and Hoffmayer 2009).

Species Description

The finetooth shark was originally described in 1841 as *Carcharias* (*Aprion*) *isodon* and later updated to *Carcharhinus isodon*; *Carcharhinus* meaning sharp pointed or jagged and *isodon* meaning equal teeth, as demonstrated by the teeth being similar in the upper and lower jaws (Müller and Henle 1841; Compagno 1979; Garrick 1985; Castro 2011). Müller and Henle (1841) also state that the genus, *Carcharias*, can be broken into five subgenera, with the finetooth being a member of the subgenus *Aprion*, which is characterized as a subgenus with teeth of the upper and lower jaw being smooth,
and having a broad base and relatively narrow peak (Müller and Henle 1841). Compagno (1979) investigated the dentition and gill opening size of \textit{C.A. isodon} and found that while distinct from many within a separate genus, \textit{Carcharhinus}, the characters were relative similar. Juvenile spinner (\textit{Carcharhinus brevipinna}) and \textit{C. A. isodon} had similar dentition, while blacktip (\textit{Carcharhinus limbatus}), graceful (\textit{Carcharhinus amblyrhynchoides}) and spinner sharks had gill opening lengths similar to \textit{C. A. isodon}. Garrick (1985) continued the work Compagno had started and determined that \textit{C. A. isodon} was not distinctly different from members of the genus \textit{Carcharhinus}, despite the variability in tooth morphology. The finetooth was then formally updated to be a member of the \textit{Carcharhinus}.

The Order Carcharhiniformes, which contains finetooth shark family \textit{Carcharhinidae} is made up of 60 species, thirty of which are in the genus \textit{Carcharhinus} (Compagno 1988; Castro 2011). Carcharhinids are characterized by well-developed nictitating eyelids, the origin of first dorsal fin positioned anterior to the pelvic fin origin, a caudal fin that measures less than one third of the total length of the animal, an upper caudal lobe measuring close to twice the length of the lower lobe, and strong undulations on the dorsal caudal margin (Castro 1983; Compagno 1988). Within these overarching carcharhinid characteristics, the finetooth shark has several unique distinguishing features. Baughman and Springer (1950) noted the elongated length of the gill slits, in relation to body size, and Castro (2011) noted the light blue-grey coloration to be unique from conspecifics. Compagno and Vergara (1978) stated that finetooth sharks can reach a maximum size of 1890-mm and have the possibility of reaching 2000-mm in length; conversely Castro (1993) reports a maximum size of 1600-mm TL.
Finetooth sharks occur in the wNAO, primarily along the western boundary ranging from New York to Florida along the United States, and in the GOM from Florida to Texas (Baughman and Springer 1950; Castro 1983; Compagno 1984; Castro 1993; Carpenter 2002; Parsons 2006; Ebert and Stehmann 2013). They have also been reported in Mexican waters, South American waters off Brazil and Guyana (Compagno 1984; Castro 1993; Lessa et al. 1999; Carpenter 2002; Castro 2011; Ebert and Stehmann 2013), and in the Caribbean Sea specifically around Trinidad (Carpenter 2002; Castro 2011; Ebert and Stehmann 2013). Historical reports of finetooth sharks have been documented in Cuba and in the eastern Atlantic off Senegal and Guinea-Bissau (Baughman and Springer 1950; Compagno 1984; Carpenter 2002; Ebert and Stehmann 2013).

Finetooth sharks inhabit coastal waters, generally within the inner continental shelf (Castro 1983; Compagno 1984; Castro 1993; Carpenter 2002; Ebert and Stehmann 2013). They are known to exhibit latitudinal seasonal migrations in the northern hemisphere, migrating southward in the winter months and northward as water temperatures rise in the spring (Springer 1950; Dodrill 1977; Compagno 1984; Castro 1993).

It is not known if finetooth sharks in the wNAO interact with their conspecifics in the nGOM (Castro 1993), although, it has been suggested that life history differences occur in each distinct geographic location (Drymon et al. 2006), which could imply that interactions between the two populations are limited. Previous studies show it is unlikely that interactions between the populations exist in the nGOM and wNAO. Kohler et al. (1998) examined tagging data from 1962-1993 and did not find any information about movement between the nGOM and wNAO. Additionally, Bethea et al. (NMFS 2007)
examined tagging data from 1994-2006 and found that finetooth sharks tagged in the nGOM were recaptured in the nGOM. Conversely, Wiley and Simpfendorfer (2007) provided information on four finetooth sharks collected from Florida Bay (25°N: Florida Keys), a location further south than the previously recorded on both the Atlantic (27°N) and Gulf (27° N) sides of the state. The documented occurrence of these sharks in southern Florida could indicate an exchange of individuals between perceived nGOM and wNAO stocks (Wiley and Simpfendorfer 2007).

The diet of finetooth sharks has been described in both the wNAO and nGOM. In the wNAO, Castro (1993) found finetooth sharks feed predominately on Atlantic menhaden, *Brevoortia tyrannus*, with this species making up over 38% of their diet. In the nGOM, Hoffmayer and Parsons (2003) found that of the identifiable prey, *B. patronus*, Gulf menhaden, had the highest frequency of occurrence (20%). Additional work by Bethea et al. (2004) in the nGOM found that finetooth sharks predominately consumed *B. patronus* which when combined with *B. sp.*, composed over 50% of the diet.

Investigations of age and growth for finetooth sharks have been conducted in both in the nGOM and the wNAO. Aging was conducted using vertebral sectioning and annuli counting, an established method performed on several small coastal sharks species (Carlson et al. 2003). The previous studies on finetooth shark age and growth showed variability in parameter estimates between the geographic regions where samples were obtained. In the wNAO, the observed maximum age was 10.4 and 12.4 years old for males and females, respectively; whereas in the nGOM, the observed maximum age was 8.1 and 8.0 years for males and females, respectively (Carlson et al. 2003; Drymon et al.
2006). These studies also estimated the theoretical longevity to be 10.5 and 18.2 years in the wNAO, and 8.5 and 14.2 years in the nGOM, for males and females, respectively (Carlson et al. 2003; Drymon et al. 2006).

In the wNAO, finetooth sharks reach reproductive maturity at 1305 and 1350-mm stretched total length (STL) for females and males, respectively (Castro 1993). Mature females have oviducal glands measuring larger than 20-mm in width and developed uteri that are not embedded and can carry embryos. Mature males have claspers that are calcified, rotatable, and contain opening rhipidions, developed testis and are able to produce sperm (Clark and von Schmidt 1965; Castro 1993; Driggers and Hoffmayer 2009). Reproductive work has primarily been conducted in the wNAO by Castro (1993), and showed that finetooth sharks exhibit a placental, viviparous mode of reproduction (Castro 2011). Mating season occurs in May-June, and parturition occurs in late May to mid-June after approximately a 12-month gestation period (Castro 1993). Brood sizes range from two to six embryos, with the mean brood size being four (Castro 1993). These wNAO finetooth sharks exhibit a biennial reproductive cycle which consists of a consecutive ovarian and gestation cycle (Castro 1993; Driggers and Hoffmayer 2009). Due to this strategy, reproductively capable females in May should consist of equal numbers of gravid and non-gravid individuals within the population (Castro 1993).

Minimal research has been conducted on finetooth shark reproduction in the nGOM, which until recently, was assumed to follow the same strategy as their wNAO conspecifics. Driggers and Hoffmayer (2009) however, documented two gravid female finetooth sharks exhibiting annual reproductive tendencies in waters off Alabama and Mississippi. This was determined by the presence of large preovulatory follicles >20-mm
in diameter and near full term embryos in the same individuals. Biennially reproducing individuals were also caught during this sampling period, suggesting that both biennial and annual reproductive strategies are used in the nGOM. This is the first report of divergent reproductive strategies within a discrete geographic region for any shark species (Driggers and Hoffmayer 2009).

**Purpose and Hypothesis**

The goal of this study was to expand knowledge of the finetooth shark life history in the nGOM and make comparisons to previous studies from the wNAO. The specific objectives of this study were to describe: 1) reproductive biology; 2) age and growth parameters; and 3) feeding ecology of finetooth sharks. This was accomplished by testing the following general alternative hypotheses:

H$_a$: Finetooth sharks in the nGOM exhibit differences in reproductive biology from those in the wNAO, as highlighted by variability in reproductive periodicity.

H$_a$: Finetooth sharks reach sexual maturity at a smaller size and younger age in the nGOM than this species in the wNAO.

H$_a$: Finetooth sharks exhibit a specialized diet of teleost prey, rather than exhibiting opportunistic feeding on all available prey.
CHAPTER II
REPRODUCTIVE BIOLOGY OF THE FINETOOTH SHARK, CARCHARHINUS ISODON, IN THE NORTHERN GULF OF MEXICO

Abstract

The reproductive biology of finetooth sharks (Carcharhinus isodon) was investigated in the northern Gulf of Mexico (nGOM), a region where information on this species is lacking. A total of 1,489 finetooth sharks (830 female; 659 male) were collected from the coastal waters of the nGOM between Apalachicola Bay, Florida (29.873° N and 84.514° W) and East Bay, Louisiana (28.959° N and 89.279° W) from June 2006 through October 2013. The size at which 50% of the population reaches maturity was determined to be 1037-mm and 961-mm fork length for females and males, respectively. In males, the peak gonadosomatic index (GSI) in March and presence of semen in the seminal vesicles in April suggest spermatogenesis occurs from March to May. In females, ovulation occurred from May to June with a peak GSI occurring in May and maximum vitellogenic follicle diameter occurring in May and June. Gestation was found to be 11-12 months with parturition occurring in May and June, and a mean brood size of 3.8 ± 0.1 embryos. Fifty females were examined during the ovulatory period to determine reproductive periodicity, resulting in a split of 32 sharks exhibiting annual reproduction and 18 sharks exhibiting biennial reproduction. The current study provides detailed reproductive information that will ultimately benefit future management plans for finetooth sharks in the nGOM.
Introduction

Elasmobranch life history has been studied extensively for many species, and as a whole, they are commonly characterized as having a slow rate of growth, late onset of maturity and low fecundity (Musick 1999). These traits, in conjunction with increased fishing pressure, have made elasmobranchs susceptible to stock depletion, but the degree of risk is yet unknown for many species (Steven et al. 2000; Shepard and Myers 2005). To fully understand the potential for stock depletion, it is critical that continued detailed investigations of life history parameters occur. Specifically, a detailed assessment of reproductive biology will better assist with species management as more accurate stock assessments can be generated. This is especially true for species that are encountered in the commercial and recreational fisheries.

The finetooth shark (*Carcharhinus isodon*) is a small coastal species that inhabits the inner continental shelf of the western Atlantic Ocean, primarily ranging from New York to Florida, and throughout the Gulf of Mexico (Castro 1983; Compagno 1984). The finetooth shark is a commercially targeted species, but makes up a very small percentage of the overall catch for the small coastal shark complex (NMFS 2007). Due to the limited take in the commercial and scientific fishery, the finetooth shark has not been extensively studied and, existing studies have been from geographically isolated areas within the western North Atlantic Ocean (wNAO) and the northern Gulf of Mexico (nGOM).

Despite limited opportunities for collection, life history parameters for finetooth sharks were documented in several previous studies (e.g. Castro 1993; Carlson et al. 2003; Drymon et al. 2006; Driggers and Hoffmayer 2009). However, there have only been a few studies describing their reproductive biology, with the most comprehensive
work performed by Castro (1993) in the wNAO. Castro (1993) found that finetooth sharks in the wNAO demonstrated mating in May-June, parturition during May-mid June, and a two-year consecutive ovarian and gestation cycle, resulting in biennial reproduction. In contrast, little information about finetooth shark reproductive biology is available from the nGOM (Carlson et al. 2003; Driggers and Hoffmayer 2009).

Based on a small sample size of only seven sharks, Driggers and Hoffmayer (2009) highlighted the potential for variable reproductive periodicity for this species within the nGOM; a first for any elasmobranch species within a discrete region. The variable reproductive periodicity was documented based on two individuals demonstrating concurrent ovarian and gestation cycles (annual reproduction) and five specimens with consecutive ovarian and gestation cycles (biennial reproduction) (Driggers and Hoffmayer 2009). Carlson et al. (2003) noted size at maturity for finetooth sharks, however their study was mainly focused on defining age and growth in the nGOM. Other than these two studies, little information exists on finetooth shark reproductive biology in the nGOM. Further research is warranted to understand the reproductive biology in this region and to determine the degree of variability in the reproductive periodicity exhibited by the population. The objectives of the current study were to investigate the reproductive biology of finetooth sharks in the nGOM, describe the variability of reproductive periodicity found in the nGOM, and compare these findings to prior studies in the wNAO, in order to provide a more complete assessment of life history for this species.
Materials and Methods

Sample collection and location

Finetooth sharks were collected in nGOM waters between Apalachicola Bay, Florida (29.873° N and 84.514° W) and East Bay, Louisiana (28.959° N and 89.279° W) (Figure 1). Samples were obtained from June 2006 through October 2013 from fisheries independent surveys conducted by The University of Southern Mississippi’s Gulf Coast Research Laboratory (USM/GCRL), National Marine Fisheries Service (NMFS) Panama City Laboratory, and Dauphin Island Sea Laboratory (DISL), and through a contracted commercial fisher. Finetooth sharks obtained from fishery independent surveys were collected by means of a 183-m anchored gillnet, a 152-m hand-deployed bottom longline supporting 50 gangions with 12/0 hooks baited with Gulf menhaden, *Brevoorta patronus*, or a 1,609-m bottom longline supporting 100 gangions with 15/0 circle hooks baited with Atlantic mackerel, *Scomber scombrus*. Finetooth sharks obtained from the commercial fishers were collected using a 915-m anchored gillnet.
Figure 1. Collection locations for finetooth sharks (*Carcharhinus isodon*) in the northern Gulf of Mexico from 2006 to 2013. Map inserts are magnified collection locations in Mississippi and Alabama (left) and Florida (right).

The length (mm), weight (kg), sex, liver weight (g), and maturity state of each shark were determined and recorded. Length measurements included: pre-caudal (PCL), from the tip of the snout to the precaudal pit; fork (FL), from the tip of the snout to the caudal fork; and stretched total (STL), and from the tip of the snout to the stretched length of the upper lobe of the caudal fin. Length measurements were used to develop morphometric relationships in order to compare measurements from other studies; linear regressions were generated for FL to STL and for PCL to FL. Finetooth sharks collected from commercial fishers were examined at the dock, all organs were removed, and the
carcass was left with the fisher for commercial processing. Once removed, the organs were stored on ice for in-depth examination upon return to the laboratory. Finetooth sharks collected from fishery independent surveys were placed on ice and dissected upon return from the field.

Maturity assessment and size at maturity

Male finetooth were considered mature when (1) the clasper rhipidion was fully formed and could be spread open; (2) the clasper was rigid due to calcification of the supporting cartilage; and (3) the base of the clasper easily rotated 180° (Clark and von Schmidt 1965). Female finetooth sharks were considered mature when they had an oviducal gland larger than 20-mm in width, developed uteri that were not embedded in the body wall, and had oocytes larger than 26-mm, or if they were gravid, (Castro 1993).

Size-at-maturity was calculated at the point in which 50% of the assessed finetooth sharks were mature. This was determined by use of a logistic model, which has been fitted to binomial maturity data using least squares nonlinear regression, where immature = 0 and mature = 1 (Mollet et al. 2000), as described by the equation:

\[ y = \frac{1}{1 + e^{-(a+bx)}} \]

where \( y \) is the binomial maturity data,
\( x \) is the FL (mm),
\( a \) is the \( y \)-intercept and
\( b \) is the slope

Median FL at maturity was expressed by the equation: \( MFL = -a/b \). The model was fit using a Gauss-Newton algorithm for nonlinear regression in R (R Development Core Team 2011).
Male reproductive measurements

In male finetooth sharks, inner clasper length, taken on the lateral clasper margin (medial to the shark) from the anterior cloacal opening to the clasper tip, and outer clasper length, taken on the lateral clasper margin (lateral to the shark) from the pelvic fin insertion to the clasper tip, were measured to the nearest tenth of a millimeter (Castro 1993). Internal measurements consisted of right testis length (cm), width (mm) and mass (g), and right epididymis head width (g). The testis and epididymis were removed from the peritoneal cavity and measured on a flat surface to ensure accuracy of the measurement. Male finetooth sharks were also assessed for presence of sperm within the seminal vesicles.

Female reproductive measurements

Internal reproductive condition was assessed in the laboratory for each female collected. Internal measurements consisted of oviducal gland width (mm), ovary weight (g), and examination of the ovary for development of follicular structure. Follicle stage of development was determined by the following criteria: 1) non-vitellogenic follicles (follicles white in color and small in size), 2) vitellogenic follicles (follicles yellow in color, uniformly round, and larger in size when compared to non-vitellogenic follicles), and 3) atretic follicles (follicles showing a decrease in yellow coloration and lacking a defined round shape). Each follicle type was enumerated, and the largest 3-6 follicles of each stage were measured to the nearest tenth of a millimeter.

In non-gravid and postpartum finetooth female sharks, the uterus width (mm) was measured at the widest point prior to removal and dissection. Postpartum females were defined as having an expanded uterus containing no embryos or exhibiting placental
scarring inside the uterus, indicating they had recently given birth. The presence of sperm in the uterus and/or placental scaring was noted. If the female was gravid, the embryos in each uterus were enumerated and their mass (g), length (STL, mm) and sex recorded.

Embryonic development and gestation period

Date of parturition and length of gestation were determined by plotting the stage of reproduction (gravid, non-gravid, and postpartum) by month and by plotting embryo length (STL, mm) by month. Size at birth was ascertained by plotting embryo length (STL, mm) by month and comparing these results to collected free swimming neonates. Linear regression analysis was used to determine the relationship between maternal FL (mm) and brood size (Driggers et al. 2004; Sulikowski et al. 2007). The number of embryos and the associated sex ratio in each uterus were analyzed with a chi square test to determine if the ratio deviated from a 1:1 ratio (Hoffmayer et al. 2013).

Seasonality

A gonadosomatic index (GSI) was calculated for male and female finetooth sharks to analyze reproductive seasonality using the equation by Nikolsky (1963):

\[
GSI = \left( \frac{gonad \ weight}{mass - gonad \ weight} \right) \times 100
\]

For gravid female sharks, the Nikolsky (1963) equation was modified to also remove embryo weight from the denominator of the equation. Gonadosomatic indices were compared among months using an analysis of variance (ANOVA) to determine peak reproductive activity for males and females, which was followed by a post hoc Tukey’s test to identify significant variability between months (Zar 1999; Hoffmayer et al. 2013). Hepatosomatic indices (HSI) were calculated for each sex to analyze available energy in
relation to seasonality using a modification of the GSI equation, wherein liver mass is substituted for gonad mass. In the case of gravid female sharks, the HSI equation was modified to remove embryo weight from the denominator. Hepatosomatic indices were compared among months using an ANOVA to determine the peak period of stored energy in the liver for males and females; and a post hoc Tukey’s test to identify significant variability among months (Zar 1999; Hoffmayer and Parsons 2006).

In addition to GSI and HSI, monthly plots of the oviducal gland width and maximum follicle diameter determined reproductive seasonality for females. Similarly, monthly plots of epididymis head width, testis width and length were done for males. An ANOVA determined significant variation in female follicle size and oviducal width, as well as in male epididymis and testis widths and lengths by month (Zar 1999; Driggers et al. 2004).

**Periodicity**

Reproductive periodicity for mature female finetooth sharks was determined by examining the reproductive state of the female in relation to the ovarian cycle. To determine periodicity, mature female sharks were only examined from April to June, a time just prior to ovulation when embryos would be near full term if present (Castro 1993; Driggers and Hoffmayer 2009). Females utilizing annual reproduction exhibit vitellogenesis and gestation concurrently (Castro 1989; Castro and Wourms 1993; Castro 2009). Annual classification was assigned if the female was: 1) gravid with vitellogenic follicles (Figure 2); or 2) postpartum, as defined by being non-gravid with placental scaring (indicating recent birth), and possessing vitellogenic follicles. Females utilizing biennial reproduction exhibit vitellogenesis and gestation consecutively (Castro 1999).
Biennial classification was assigned if the female was: 1) gravid with non-vitellogenic follicles (Figure 3); or 2) postpartum and possessed non-vitellogenic follicles.

*Figure 2.* Example of annual reproduction in a female finetooth shark (*Carcharhinus isodon*). Annual reproduction was determined by the presence of vitellogenic follicles (1) in conjunction with near full term embryos (2), as represented by this female collected in April of 2012. Maximum follicle size was 21.3-mm and the five embryos ranged in size from 485-mm to 519-mm stretched total length.
Figure 3. Example of biennial reproduction in a female finetooth shark (Carcharhinus isodon). Biennial reproduction was determined by the lack of vitellogenic follicles (1) in conjunction with near full term embryos (2), as represented by this female collected in April of 2015. Maximum follicle size was 9.5-mm and the five embryos ranged in size from 448-mm to 472-mm stretched total length.

The assessment of periodicity was limited to gravid females that were within the ovulatory period to ensure an accurate and clear characterization of reproductive periodicity for finetooth sharks in the nGOM. This conservative approach was taken due to the difficulty in differentiating reproductive values for earlier months. For instance, not all collecting parties noted the presence of intrauterine scarring or uterus width, which is necessary for determining if a female had given birth recently, thus not allowing classification as a postpartum female (Hazin et al. 2001; Natanson and Gervelis 2013). Additionally, oocyte classification was difficult to discern in earlier months as follicles were either skipping vitellogenesis or were in early stages of vitellogenesis. Additionally,
non-gravid females exhibiting vitellogenic follicles were not considered for analysis due to the complications with first time reproducers; if a female was mating for the first time, a definitive decision on periodicity could not be made.

Annual and biennial reproducers were additionally examined in terms of FL, HSI, age, and catch location in order to determine if any of these factors played a role in determining periodicity. An analysis of variance was used to test for variability due to FL, HSI, or age. Additionally, FL, HSI, age and longitude were tested with a generalized linear model with logit transformation to determine if multiple factors contributed to variability in periodicity (Zar 1999). Ages of female finetooth sharks were obtained from a concurrent investigation of age and growth (J. Higgs unpubl data). Catch location of finetooth sharks were plotted by periodicity in ArcMap 10 (Environmental Systems Research Institute, Inc (ESRI), Redlands, California) with date and time of catch data.

Results

A total of 1,489 finetooth sharks (female n = 830, male n = 659) were collected over the duration of this study. Specimens ranged in size from 387 to 1384-mm FL and from 380-mm to 1131-mm FL, for females and males, respectively (Figure 4). Morphometric regressions between FL and STL (n = 816) and PCL and FL (n = 1128) were developed in order to compare current findings with previous studies, the resulting regression formulas were: $\text{STL} = 1.225\text{FL} + 23.224$ (Linear regression, $r^2 = 0.99, F_{1,814} = 9.1 \times 10^4, P < 0.001$) and $\text{FL} = 1.0975\text{PCL} + 5.5602$ (Linear regression, $r^2 = 0.99, F_{1,1126} = 6.5 \times 10^5, P < 0.001$).
Figure 4. Length frequency of male and female finetooth sharks (*Carcharhinus isodon*) arranged in 100-mm size bins. Males (n = 659) ranged in size from 387-mm to 1384-mm FL; females (n = 830) ranged in size from 380-mm to 1131-mm fork length.

**Maturity**

A total of 659 male finetooth sharks were collected; of those, 154 were mature and 505 immature. Immature, male finetooth sharks were collected every month except November, December, January, and February; whereas mature sharks were collected every month except January and February. The calculated length at which 50% of the male population reached maturity was 961-mm FL (a = 196.253, b = 0.204) (Figure 5). Inner clasper length (n = 223) exhibited sigmoidal growth when plotted against FL; with gradual growth in male sharks below 850-mm FL, rapid growth between 850-mm and 950-mm FL, and resumed slowed growth above 950-mm FL (Figure 6). The largest immature male was 1000-mm FL while the smallest mature male was 910-mm FL.
Figure 5. Length at 50% maturity for male finetooth sharks (Carcharhinus isodon) was calculated as 961-mm fork length.

Figure 6. Relationship between inner clasper length and fork length for immature (open circles) and mature (closed circles) male finetooth sharks (Carcharhinus isodon).
Collections of female finetooth sharks comprised of 573 immature specimens and 257 mature specimens. Immature females were collected every month except November, December, January, and February; and mature females were collected every month except January. The calculated length at which 50% of the female population reached maturity was 1037-mm FL (a = 40.663, b = 0.039) (Figure 7). Oviducal gland width (n = 452) exhibited slow growth in female sharks below 1000-mm FL, followed by rapid sigmoidal growth with the onset of maturity (Figure 8). Additionally, uterus width (n = 127) exhibited little to no growth below 1000-mm FL, followed by rapid growth with the onset of maturity (Figure 9). The largest immature female was 1108-mm FL, and the smallest mature female was 992-mm FL.

Figure 7. Length at 50% maturity for female finetooth sharks (Carcharhinus isodon) was calculated as 1037-mm fork length.
Figure 8. Relationship between oviducal width and fork length for immature (open circles) and mature (closed circles) female finetooth sharks (*Carcharhinus isodon*).

Figure 9. Relationship between uterus width and fork length for immature (open circles) and mature (closed circles) female finetooth sharks (*Carcharhinus isodon*).
Male finetooth sharks exhibited a peak in GSI during March, followed by a drastic decline until May at which point GSI remained low through the remainder of the calendar year (ANOVA, $F(9,96) = 40.0, P < 0.001$) (Figure 10). The GSI in March and April is significantly different from each other and they were both significantly different from the rest of the year (Figure 10). Epididymis width, testis width and testis length reflected the trend shown by GSI, with the highest values occurring in the spring (March – May) followed by a decline in values in late spring and early summer, and subsequently lower relative values during the remainder of the year. Epididymis head width showed a statistically significant change throughout the year (ANOVA, $F(9,118) = 16.9, P < 0.001$), peaking in March/April (Figure 11). Testis width also exhibited a statistically significant change throughout the year (ANOVA, $F(9,128) = 25.7, P < 0.001$), peaking in March and April (Figure 12). Testis length similarly change throughout the year (ANOVA, $F(9,128) = 11.18, P < 0.001$), with March and April values being significantly higher than the rest of the months (Figure 13). Initial presence of semen in the seminal vesicles was noted in April, which is consistent with a peak spermatogenesis period of March through May, as suggested by the GSI, epididymis width, testis width, and testis length data. Male HSI also changed significantly throughout the year (ANOVA, $F(8, 82) = 18.33, P < 0.001$), peaking in November and December (13.7 and 13.5, respectively) (Figure 11).
Figure 10. Mean gonadosomatic index by month for mature male finetooth sharks (*Carcharhinus isodon*). Points with different letters are significantly different at $\alpha = 0.05$ (error bars represent 1 standard error).

Figure 11. Mean epididymis width by month for mature male finetooth sharks (*Carcharhinus isodon*). Points with different letters are significantly different at $\alpha = 0.05$ (error bars represent 1 standard error).
Figure 12. Mean testis length (black circles) and width (open circles) for mature male finetooth sharks (*Carcharhinus isodon*). Points with different letters are significantly different at $\alpha = 0.05$ (error bars represent 1 standard error).

Figure 13. Mean hepatosomatic index by month for mature male finetooth sharks (*Carcharhinus isodon*). Points with different letters are significantly different at $\alpha = 0.05$ (error bars represent 1 standard error).
Female reproductive cycle

Examination of female GSI revealed statistically significant change throughout the year (ANOVA, $F(10, 200) = 10.28, P < 0.001$) with a peak GSI value in May that was not statistically different from February, March, April, and June. May was statistically different from the remainder of the year; whereas all months other than May were not statistically different from one another (Figure 14). When GSI was compared between non-gravid and gravid (gravid for this comparison included postpartum) female sharks, this study found non-gravid individuals to have higher GSI values in the spring but very similar values in the fall to sharks which were gravid. Both non-gravid and gravid sharks peaked in May (Figure 15). No significant difference between gravid and non-gravid sharks was exhibited during the ovulatory period of May and June, when investigated by GSI (ANOVA, $F(1,44) = 0.204, P = 0.653$).
Figure 14. Mean gonadosomatic index (GSI) by month for mature female finetooth sharks (*Carcharhinus isodon*). Points with different letters are significantly different at $\alpha = 0.05$ (error bars represent 1 standard error).

Figure 15. Mean gonadosomatic index (GSI) by month for gravid and non-gravid female finetooth sharks (*Carcharhinus isodon*) (error bars represent 1 standard error).
Maximum follicle diameter of vitellogenic oocytes changed significantly throughout the year (ANOVA, $F(9, 108) = 29.2$, $P < 0.001$), peaking during May and June (26.9-mm and 29.6-mm, respectively). Peak months were significantly different from August (6.8-mm), when the minimum mean maximum follicle diameter occurred (Figure 16). Maximum follicle diameter for non-gravid and gravid (including postpartum) sharks showed non-gravid sharks had larger follicle diameters throughout the duration of the year; maximum follicle diameter for non-gravid sharks peaked in May; whereas, the maximum was in June for gravid sharks (Figure 17). The ovulatory period of gravid and non-gravid sharks did not differ (May and June), as indicated by maximum follicle diameter (ANOVA, $F(1,16) = 0.078$, $P = 0.784$). Together, GSI and maximum follicle diameter values indicate an ovulation period during May and June.

![Graph of maximum follicle diameter by month](image)

*Figure 16. Mean maximum follicle diameter (mm) by month for female finetooth sharks (*Carcharhinus isodon*). Points with different letters are significantly different at $\alpha = 0.05$ (error bars represent 1 standard error).*
Figure 17. Mean maximum follicle diameters by month for gravid and non-gravid finetooth sharks (*Carcharhinus isodon*) (error bars represent 1 standard error).

Inspection of female HSI revealed significant change throughout the year (ANOVA, \(F(10,210) = 35.01, P < 0.001\)), with peak HSI values in November and December (14.7 and 14.5, respectively) which were not statistically different from February but were statistically different from all other months (Figure 18). When HSI was compared between non-gravid and gravid (gravid for this comparison included postpartum) female sharks, it was found that non-gravid individuals have higher HSI values during winter and spring but similar values to gravid sharks during the summer; both non-gravid and gravid sharks showed a peak HSI in November (Figure 19). No significant difference in HSI was evident between gravid and non-gravid sharks was exhibited during the ovulatory period of May and June (ANOVA, \(F(1,48) = 0.022, P = 0.882\)).
Figure 18. Hepatosomatic index by month for mature female finetooth sharks (*Carcharhinus isodon*). Points with different letters are significantly different at $\alpha = 0.05$ (error bars represent 1 standard error).

Figure 19. Hepatosomatic index by month for mature gravid and non-gravid finetooth sharks (*Carcharhinus isodon*) (error bars represent 1 standard error).
**Reproductive periodicity**

Fifty adult female finetooth sharks collected during April, May, and June were examined to determine reproductive periodicity. A split between females with vitellogenic follicles and those possessing only non-vitellogenic follicles was evident; resulting in the classification of 32 females (64%) exhibiting an annual reproductive strategy and 18 females (36%) exhibiting a biennial reproductive strategy. Several factors were considered as possible correlates of the reproductive periodicity. Females exhibiting annual reproduction had FLs ranging from 1110 – 1215-mm, with a mean of $1163 \pm SE = 4.85$-mm; whereas those exhibiting biennial reproduction ranged from 1120 – 1208-mm, with a mean of $1158 \pm SE = 6.19$-mm. Results from maternal FL comparisons between periodicities showed no significant difference (ANOVA, $F(1,48) = 0.4$, $P = 0.53$).

Females exhibiting annual reproduction ranged in age between 3.8 – 7.8 years with a mean of $5.5 \pm SE = 0.19$ years; whereas those exhibiting biennial reproduction ranged between 4.8 – 6.9 years with a mean of $5.7 \pm SE = 0.19$ years. Ages were not statistically different between reproductive periodicity strategy groups (ANOVA, $F(1,43) = 0.402$, $P = 0.529$). It should be noted that not all finetooth examined for periodicity were assigned an agreed age by researchers. Twenty eight annual and 17 biennial females investigated for age exhibited variability but no reproductive variability was noted. Hepatosomatic index values for females exhibiting annual reproduction ranged between 4.0 – 12.5%, and averaged $7.3 \pm SE = 0.31$%; whereas, as those exhibiting biennial reproduction ranged between 3.9 – 9.6%, and averaged $6.0 \pm SE = 0.34$%. A significant difference was found between annual and biennial finetooth sharks for HSI during the study period (ANOVA, $F(1,48) = 6.897$, $P = 0.0115$). The generalized linear regression model with logit
transformation identified HSI as the only significant factor associated with the expression of reproductive strategy; and failed to identify any interaction between factors (HSI, $SE = 0.25$, $Z$ value $= 2.294$, $P = 0.0218$). Catch location also showed no difference between periodicity; as both annual and biennial sharks were collected from the same locations during the same times (Figure 20).

![Map of Gulf of Mexico with collection locations marked](image)

*Figure 20.* Collection locations for female finetooth sharks (*Carcharhinus isodon*) classified as showing annual (+) and biennial (○) reproductive periodicity.

**Embryonic Development**

A total of 524 embryos were collected from 140 broods in this study. Mean brood size was $3.8 \pm 0.1$ individuals; with a minimum brood size of one and maximum of nine. Brood size was not strongly correlated with maternal FL but was statistically significant (ANOVA, $F(1,276) = 84252.1$, $P < 0.001$; $r^2 = 0.04$; $y = 0.0053x - 2.278$) (Figure 21). The ratio of in utero embryos between uterine branches was 1:1.008, which was not significantly different from 1:1 (Chi-square test, $X^2 = 0.0082$, $P = 0.928$). The ratio of
male to female embryos within the broods (i.e., 1:1.012) was also not significantly different from 1:1 (Chi-square test, \(X^2 = 0.0186, P = 0.891\)). Gestation time was found to be between 11 and 12 months. The first developing embryos were observed in June, and the largest embryos occurred in May and June, further indicating that the time of parturition is likely May and early June (Figure 22). Embryos ranged in size from 38.6-mm to 549-mm STL, and 43.6-g to 1021.8-g. Mean embryo size at parturition was 508-mm STL, and ranged from 470-mm to 546-mm STL. The smallest free swimming finetooth shark neonates collected in this study were 435 and 478-mm STL. Mean embryo sizes for annual (497-mm STL) and biennial (487-mm STL) reproductive groups were not statistically different (ANOVA, \(F(1,46) = 1.87, P = 0.178\)).

![Figure 21. Relationship between brood size and maternal fork length (mm) for finetooth sharks (Carcharhinus isodon).](image-url)
Discussion

This study represents the most comprehensive reproductive study of finetooth sharks in the nGOM. The results of this study have expanded upon the knowledge of finetooth shark life history and reproduction previously reported for the wNAO (Castro 1993) and nGOM (Driggers and Hoffmayer 2009). Reproductive parameters reported in this study were similar to those reported in the aforementioned studies.

Estimated size at maturity for male finetooth sharks in this study was slightly larger than the existing estimate for the GOM (Carlson et al. 2003). Both estimates were smaller than those reported for the wNAO (1001-mm FL, Castro 1993; 1015-mm FL, Drymon et al. 2006). Females showed a trend similar to males and were found to be mature at a slightly larger size in this study as compared to Carlson et al. (2003); however, both sexes were larger at maturity than reported by Drymon et al. (2006) and...
smaller than reported by Castro (1993). The inconsistency with female size of maturity could be attributed to the difference in sample size between studies; the current study examined 831 females compared to the studies in the wNAO: 97 (Drymon et al. 2006) and 107 (Castro 1993), and in the GOM: 117 (Carlson et al., 2003). Additionally, it could be due to the variability reported in maximum immature length and minimum mature length of females collected, since the maturity curve is directly comparing the ratio of immature/mature sharks and the associated overlap between respective sizes. The model with a larger range of overlap would potentially allow for a more accurate estimation of size at maturity. The current study showed an overlap between maximum immature length and minimum mature length of 116-mm; while Carlson et al. (2003) reported 43-mm, Drymon et al. (2006) exhibited no overlap, and Castro (1993) did not specify values.

Seasonality of male reproductive parameters was apparent from the epididymis head width, testis length and width, and GSI, which all peaked in spring followed by a rapid decline during the summer months. This suggests that spermatogenesis occurs in late spring and early summer prior to the regression of testicular tissue. Similar trends have been observed in other coastal carcharhinids, such as the blacknose (Carcharhinus acronotus), blacktip (Carcharhinus limbatus), and bonnethead sharks (Sphyrna tiburo), where testis weight increases along with spermatogenesis and subsequently decreases as the mating season progresses (Parsons and Grier 1992; Castro 1996; Maruska et al. 1996; Engel and Callard 2005, Sulikowski et al. 2007). Seminal vesicles in males were found to contain semen between April and August, with 82% of engorged vesicles occurring from April through June.
Castro (1993) noted that emaciated livers were common in near-term gravid females which could reflect the energy requirement of a placental brood, or the provision of proteins necessary for vitellogenesis by the liver (Lutton et al. 2005). If it is due to the latter, it might also explain variability in maximum follicle diameter. This is likely not the case in the current study, as there were no differences in maximum follicle diameter, liver mass or HSI between gravid and non-gravid finetooth sharks during the ovulatory period in May and June. This peak ovulatory period also coincided with reproductive trends in males from the current study. Castro (1993) reported similar patterns showing May and June to be the peak time for spermatogenesis, ovulation and subsequently mating in the wNAO.

Recent studies of two sharpnose shark species (*Rhizoprionodon lalandi* and *R. terraenovae*) that reproduce annually reported that nulliparous females mate earlier than females that have undergone reproduction previously (Motta et al. 2007; Hoffmayer et al. 2013). In those two studies the variance in mating time (based on maximum follicle diameter values) ranged from a few weeks to several months. The mating time for finetooth in the current study was also expanded over two months and may indicate that non-gravid females (either nulliparous females or those exhibiting biennial reproduction) are capable of mating prior to annually reproducing gravid females. This is exhibited by the non-gravid females having larger follicle diameters earlier in the mating period. Further research needs to be conducted to help clarify this variability.

The estimated gestation period of 11-12 months is supported by the presence of newly fertilized embryos in June, and the presence of full-term embryos in May and early June; whereas, no near-term embryos were found after June. The observed gestation
period in this study is consistent with the reported 12-month period in the wNAO (Castro 1993). Additionally, the observed gestation period for finetooth sharks is comparable to other species of the family Carcharhinidae in the GOM, which exhibit similar gestation periods ranging from 9-10 months for blacknose sharks, 10-11 months for Atlantic sharpnose sharks, and 12 months for blacktip and sandbar sharks (*Carcharhinus plumbeus*) (Sulikowski et al. 2007; Baremore and Hale 2012; Baremore and Passerotti 2013; Hoffmayer et al. 2013).

The time of parturition noted in this study was consistent with the time period noted by Castro (1993) in the wNAO of May and June. Overall, late spring and early summer is the general pupping period for sharks within the family Carcharhinidae in the nGOM (e.g. Sulikowski et al. 2007; Baremore and Hale 2012; Baremore and Passerotti 2013). During the parturition period, the smallest free swimming finetooth shark collected during this study was 435-mm FL, which is similar to the smallest free swimmer found in the wNAO with a size of 430-mm FL (Castro 1993). However, the mean and maximum size of the embryos from this study was larger than those found in the wNAO (Castro 1993). Variability in embryo size during similar periods of gestation between geographically distinct collection sites has been noted previously, and it has been suggested that water temperature could account for the difference in growth rates (Yamaguchi et al. 2000). Temperature plays a critical role in embryo development, as demonstrated by increased embryonic growth with warmer temperatures in the small-spotted catshark (*Scyliorhinus canicula*) and by female Atlantic stingrays (*Dasyatis sabina*), as exhibited by gravid females that inhabit warmer water temperature regions compared to non-gravid individuals (Harris 1952; Wallman and Bennett 2006). Despite
the variability in maximum and mean sizes of near full-term embryos, both the current study and the wNAO study found similar mean brood sizes of $3.8 \pm 0.1$ and 4.0, respectively (Castro 1993).

The current study found two female finetooth sharks with brood sizes larger than the previously recorded maximum of six embryos (Castro 1993). A female collected during October 2011 had a brood size of seven embryos with a mean length and mass of 292-mm STL and 126-g, respectively. Length and mass measurements were consistent with other embryos examined during October. The second female was collected during November 2011 and had a brood size of nine embryos with a mean length and mass of 394-mm STL and 282-g, respectively. Similar to the brood in October, length and mass measurements from the November brood were consistent with other embryos collected throughout the month. As morphometric means from both broods were comparable for the month, these embryos were deemed to be in a healthy state and showed no signs of malnourishment, compared to “normal” broods; thus, the potential existed for gestation to continue to the time of parturition. These two females were 1142-mm and 1172-mm FL, respectively, which is not representative of the largest size class of gravid individuals sampled (1260-mm FL). Therefore, even though previous studies have confirmed that larger maternal size and age are directly related to brood size (e.g. Driggers et al. 2004; Baremore and Hale 2012; Baremore and Passerotti 2013), it is unlikely that this is the reason for these large broods. Castro (1993) collected gravid individuals up to 1283-mm FL in the wNAO so female size was similar in both sampling regions negating the possibility that this study encompassed females from larger size classes.
This study found that 32 out of 50 finetooth sharks collected in May and April exhibited annual periodicity, while the other 18 exhibited biennial periodicity. These results confirmed the initial hypothesis that finetooth sharks in the nGOM have the ability to reproduce on an annual basis (unlike the wNAO population) and that annually and biennially reproducing finetooth sharks are occurring within a discrete region of the nGOM (Driggers and Hoffmayer 2009). This variability in reproductive periodicity could have large implications for population management in the GOM. According to Carlson et al. (2003), female finetooth sharks in the GOM reach maturity at approximately age four and have a theoretical longevity of approximately 14 years, meaning there are 10 potential years of reproductive activity. Multiple reproductive periodicities allow for drastic variability in the total reproductive output of a population, especially in light of limitations on the number of reproductively active years and the mean brood size (i.e., four embryos) (Driggers and Hoffmayer 2009). A biennially reproducing female would produce half the number of offspring compared to an annually reproducing female. Using the results from the current study as an example, if 64% of the gravid population reproduces annually rather than biennially, over a 10 year reproductive lifetime the number of offspring produced would be underestimated by 39%; a gross underassessment of a population. Further research is needed on geographic separation in relation to reproductive strategy. Such research would help better define whether the entire population is being represented in the collection area or if a portion of the female population is exhibiting geographic segregation. Segregation based upon reproductive phase has been suggested for the sandtiger shark (Carcharias taurus) in Australian waters and for blacknose sharks in Brazilian waters, where mature female sharks exhibit
different migratory patterns depending on if they are pregnant or in a period of resting (Hazin et al. 2002; Bansemer and Bennett 2009).

In order to determine why variability in reproductive periodicity exists, several \textit{a posteriori} hypotheses have been proposed to explain life-history patterns. Thus, variability in reproductive periodicity may be related to maternal 1) size, 2) energy stores, 3) age, or 4) geographic location. Female size was examined because others have shown that new breeders and/or larger females may have reduced fecundity (Van Wyk 1991). In the current study, this was not found to be the case as there was no significant difference in maternal size between reproductive periodicities. Work by Van Wyk (1991) showed that size was not the driving factor in the giant girdled lizard (\textit{Cordylyus giganteus}); but Jouventin and Dobson (2002) found size to be at least partially responsible for reproductive periodicities of various species of albatross. Even though size was not a factor in the current study, this factor should always be considered when investigating the phenomenon of multiple reproductive periodicities.

In addition to maternal length, maternal age was investigated as a potential correlate of reproductive periodicity, as age has been shown to be a better indicator of offspring success in teleosts (Berkeley et al. 2004). The black rockfish (\textit{Sebastes melanops}) could be a good teleost model for comparison with elasmobranchs, as it demonstrates similar life history traits: long life, slow growth and live bearing reproduction (Love et al. 2002). Older female black rockfish were found to be able to provide supplemental nutritional support to offspring by means of increased lipids, thereby promoting better growth and survival (Berkeley et al. 2004). Conversely, the current study did not show similar results as there were no differences in periodicities and
maternal age. However, this is an interesting line of research that should be investigated further for elasmobranchs and potentially expanded to investigate other aspects of reproduction.

The current study also considered the possibility of stored energy as an underlying explanation for the variability in reproductive periodicity. Variability in available energy has been shown to be responsible for skip spawning events in other fish (Rideout and Tomkiewicz, 2011). In such scenarios, a period of poor feeding experienced by a portion of the spawning population leads to the lack of sufficient stored energy for a spawning event. Indeed, a significant difference in HSI between annual and biennial females was observed in this study, with annual reproducers showing a larger mean liver mass. To what extent energetics is responsible for reproductive variability is yet unknown, but further research should be conducted to determine if and how this factor is related.

Lastly, this study considered differences in reproductive periodicity due to variability in geographic catch locations in the nGOM. It has been shown in other carcharhinid species that reproductive periodicity could differ due to geographic separation. For example, the blacknose shark reproduces on an annual cycle in the GOM and on a biennial cycle in the wNAO (Driggers et al. 2004; Sulikowski et al. 2007). In the current study we did not find any geographic pattern in the expression of annual and biennial reproduction. However, it should be noted that the samples considered for variability in reproductive periodicity came from the north central GOM due to sampling constraints, and to fully investigate geographic variability in the nGOM samples should be tested from throughout the entire area.
Variability in reproductive parameters is not widespread in elasmobranchs; however, studies have concluded that variability does occur, but generally in geographically distinct locations. These studies included several families and species of sharks, including the blacknose shark (Driggers et al., 2004; Sulikowski et al., 2007), sand tiger shark (Lucifora et al. 2002; Bansemer and Bennett 2009), gummy shark (*Mustelus antarcticus*) (Walker 2007) and the star spotted smoothhound shark (*Mustelus manazo*) (Yamaguchi et al. 2000). Conversely, investigations of intraspecific variability within discrete geographic locations for elasmobranchs have been studied even less, as opportunities are not as prevalent. Investigating and comparing reproductive cycles inter- and intra-specifically in discrete regions are essential for careful study and subsequent management on a species level (Wourms 1977). Accordingly, this study represents an improved state of knowledge about the reproductive biology of finetooth sharks in the nGOM which can assist with future assessment and management of this geographically distinct population.

In conclusion, this study is the most comprehensive reproductive investigation of finetooth sharks in the nGOM. Results from male finetooth sharks indicate that their reproductive cycle peaked between March and May, and 50% of males reached maturity at 961-mm FL. Female reproductive cycle peaked between May and June, and 50% of females reached maturity at 1037-mm FL. Investigation of gravid females revealed that gestation was 11-12 months, and parturition occurred in May and June. The mean brood size was $3.8 \pm 0.1$ embryos. Finally, female finetooth sharks in the GOM display both annual and biennial reproductive periodicities; further analysis indicates that the differing periodicities could be due to energetics.
CHAPTER III

AGE AND GROWTH OF THE FINETooth SHARK, **CARCHARHINUS ISODON**, IN
THE NORTHERN GULF OF MEXICO

Abstract

Age, growth, and size of maturity estimates were defined for the finetooth shark (*Carcharhinus isodon*) to compare and expand on previous work in the northern Gulf of Mexico (nGOM) and western Atlantic Ocean (wNAO). A total of 711 finetooth sharks (424 female; 287 male) were examined from the coastal waters of the nGOM between Apalachicola Bay, Florida (29.873° N and 84.514° W) and East Bay, Louisiana (28.959° N and 89.279° W) from April 2007 through September 2013. The observed maximum age was 9.4 years (1384-mm fork length [FL]) and 6.5 years (1130-mm FL) for females and males, respectively. Two and three parameter von Bertalanffy, Gompertz, and logistic growth models were fitted to the size-at-age data and were found to be statistically significant *p* < 0.05, with the most parsimonious models being the logistic and three parameter von Bertalanffy (VBGF3) for females and males, respectively. The results of this study were compared with three prior studies conducted in the GOM and wNAO, with a focus on results from the VBGF3 model. The VBGF3 model estimates for females and males were: \( L_\infty = 1308\text{-mm FL} \) and \( k = 0.26/\text{yr} \) and \( L_\infty = 1164\text{-mm FL} \) and \( k = 0.32/\text{yr} \), respectively. Age at which 50% of the finetooth population was estimated to be mature was 4.1 and 3.6 years for females and males, respectively.

Introduction

Investigation of life history parameters is essential for stock assessments and proper management of elasmobranch populations (Cortés 2002; Natanson et al. 2014).
However, the common approach of mixed species fisheries management is widely applied to elasmobranchs, and studies have shown that this may not be the most appropriate management strategy. Musick (1999) noted that species with higher production rates are often driving the fishery by overshadowing less productive species. Thus, some sharks in a mixed species fishery are likely being put in a position of peril because they are not being managed individually (Musick et al. 2000). One solution would be to investigate life history parameters on a species-specific basis to create more appropriate management plans and ensure a sustainable future fishery.

To confound the matter even further, recent studies demonstrate intraspecific variability in life history characteristics for various elasmobranch species (Frisk et al. 2001; Cope 2006). For example, blacknose sharks (*Carcharhinus acronotus*) have exhibited regional variability in age and growth estimates and reproductive biology between populations in the western North Atlantic Ocean (wNAO) versus the northern Gulf of Mexico (nGOM) (Driggers et al. 2004; Sulikowski et al. 2007), and bonnetheads (*Sphyrna tiburo*) have shown latitudinal variability for age and growth estimates within the GOM and regional variability between the wNAO and nGOM (Carlson and Parsons 1997; Lombardi-Carlson et al. 2003; Fraizer et al. 2014); whereas, finetooth sharks (*Carcharhinus isodon*) have exhibited rather unique inconsistency of life history parameters, in terms of reproductive periodicity, as well as age and growth estimates in regions where they occur. Variability in reproductive periodicity, as well as in age and growth estimates, has been noted for this species in the wNAO and nGOM; while variability in age and growth estimates has been noted within different geographic regions of the nGOM, and variability in reproductive periodicity has been identified
within a discrete region of the nGOM (Castro 1993; Carlson et al. 2003; Neer and Thompson 2004; Drymon et al. 2006; Driggers and Hoffmayer 2009).

The finetooth shark is a small coastal species that inhabits the inner continental shelf of the western Atlantic Ocean, primarily ranging from New York to Florida and throughout the GOM in US waters (Castro 1983; Compagno 1984). It is a commercially targeted species but makes up a very small percentage of the overall catch for the small coastal shark complex (NMFS 2007). Due to the limited take in the commercial and scientific fishery, the finetooth shark has not been extensively studied. Existing studies were conducted in geographically isolated areas within the wNAO and the neGOM.

Variability of age and growth estimates and reproductive biology in finetooth sharks was identified as an area of needed research in order to allow for accurate reassessment and future management of the species on a regional level (Carlson et al. 2003; Drymon et al. 2006; Driggers and Hoffmayer 2009). Accordingly, the objective of this study was to reassess the age, growth, and age at maturity for finetooth sharks in the nGOM, and compare findings with estimates provided by prior studies in the wNAO (Drymon et al. 2006) and nGOM (Carlson et al. 2003; Neer and Thompson 2004) to discern any regional similarity or variability between the populations.

Materials and Methods

Sample collection and location

Finetooth sharks were collected in nGOM waters between Apalachicola Bay, Florida (29.873° N and 84.514° W) and East Bay, Louisiana (28.959° N and 89.279° W). Samples were obtained throughout the year from April 2007 to September 2013 from fisheries independent surveys conducted by the University of Southern Mississippi’s Gulf
Coast Research Laboratory (USM/GCRL), National Marine Fisheries Service (NMFS) Panama City Laboratory, and Dauphin Island Sea Laboratory (DISL), and through a contracted commercial fisher. Finetooth sharks obtained from fishery independent surveys were collected by means of a 183-m anchored gillnet, a 152-m hand-deployed bottom longline supporting 50 gangions with 12/0 hooks baited with Gulf menhaden, *Brevoortia patronus*, or a 1,609-m bottom longline supporting 100 gangions with 15/0 circle hooks baited with Atlantic mackerel, *Scomber scombrus*. Finetooth sharks obtained from the commercial fishers were collected using a 915-m anchored gillnet.

The length (mm), weight (kg), sex, liver weight (g) and maturity state of each shark was determined and recorded. Length measurements included: pre-caudal (PCL), from the tip of the snout to the precaudal pit; fork (FL), from the tip of the snout to the caudal fork; and stretched total (STL), from the tip of the snout to the stretched length of the upper lobe of the caudal fin. Length measurements were used to develop morphometric relationships in order to compare measurements from other studies; linear regressions were generated for FL to STL and for PCL to FL. Finetooth sharks collected from commercial fishers were examined at the dock, vertebrae were removed, and the carcass was left with the fisher for commercial processing. Once removed, the vertebrae were stored on ice for in-depth examination upon return to the laboratory. Finetooth sharks collected from fishery independent surveys were placed on ice and dissected upon return from the field.

Length (mm), weight (kg), sex and maturity state of each shark were determined and recorded for each specimen. Length measurements included: pre-caudal (PCL), as measured from the tip of the snout to the precaudal pit; fork (FL), as measured from the
tip of the snout to the caudal fork; and stretched total (STL), as measured from the tip of
the snout to the stretched length of the upper lobe of the caudal fin. Length measurements
were used to develop morphometric relationships for comparison with other studies;
linear regressions formulas were generated for FL to STL and for PCL to FL.

Male finetooth sharks were considered mature when (1) the clasper rhipidion was
fully formed and could be spread open, (2) the clasper was rigid due to calcification of
the supporting cartilage, and (3) the base of the clasper rotated easily 180° (Clark and von
Schmidt 1965). Female finetooth sharks were considered mature when they had an
oviducal gland larger than 20 mm in width, developed uteri that were not embedded in
the body wall, or were gravid (Castro 1993).

Vertebral preparation and interpretation

Vertebrae used for age determination were collected below the first dorsal fin as
these vertebrae are larger in diameter and it allowed for consistency between aging
studies (Goldman 2005). Extracted vertebrae were placed on ice at the time of collection
and were then frozen upon arrival at the laboratory. Prior to processing, vertebrae were
thawed and all excess tissue was removed. Two complete centra were separated from the
sample and used for age determination. A sagittal cross section was cut from each centra
with a Jem Saw 45 (Raytech Industries, Middletown, Connecticut, USA), housing two
lapidary blades separated by a 0.3-mm spacer (Sulikowski pers comm), resulting in a
cross-section 0.3-mm thick. The sections cut from the two centra were then mounted on a
clear glass slide with Cytoseal 60 (Fisher Scientific, Pittsburgh Pennsylvania, USA). The
growth bands were clearly visible and needed no further staining.
Sagittal cross-sections were analyzed and photographed using an image capturing, dissecting microscope (Leica Microsystems, Wetzlar, Germany). Under 10x magnification, growth bands were imaged, digitally marked, and counted. A single growth band was defined as a pair of opaque and translucent bands that traverse the intermedialia and clearly extend into the corpus calcareum (Sulikowski et al. 2003, 2005; Cailliet and Goldman 2004). The birth mark (age zero) was defined as the first distinct band distal to the focus coinciding with the change in angle of the corpus calcareum (e.g. Wintner and Cliff 1996; Carlson et al. 2003; Cailliet and Goldman 2004). Estimated age of each shark collected was based upon the following assumptions: (1) the birthmark was formed prior to parturition, (2) parturition occurred in June (J. Higgs unpubl data), (3) the second band formed approximately six months later during the first winter, and (4) the third band formed one year later during the second winter. Consequently, ages were calculated by using the algorithm: age = [total increment count – 1.5, + the proportion of the year from the winter mark until the date of capture] (Carlson et al. 2003, Driggers et al. 2004; Drymon et al. 2006).

Two independent readers conducted non-consecutive band counts of all vertebrae sections without prior knowledge of the shark’s length, or the other reader’s count. Count reproducibility was estimated by using the index of average percent error (APE) as described by Beamish and Fournier (1981):

\[
APE = \left( \frac{1}{N} \sum_{j=1}^{N} \left( \frac{1}{R} \sum_{i=1}^{R} \left| \frac{X_{ij} - X_j}{X_j} \right| \right) \right) \times 100
\]

where \(N = \) the number of sharks aged,

\(R = \) the number of readings,
$X_{ij} =$ the $i$th age determination of the $j$th fish, and 

$X_j =$ the average calculated for the $j$th fish.

If a confirmed age was not agreed upon by the first and second reader after reevaluation of an age discrepancy, the specimen was discarded from analysis.

**Modeling growth**

Following previous elasmobranch aging studies, multiple growth models were fit to the observed length-at-age data for male and female finetooth sharks to estimate age and growth parameters (Carlson and Baremore 2005; Neer and Thompson 2005; Chen et al. 2007). The three parameter von Bertalanffy growth model (VBGF3) (von Bertalanffy 1938) is described by the equation:

$$L_t = L_\infty (1 - e^{-kt_0})$$

where $L_t$ is the predicted length at age ‘$t$’,

$L_\infty$ is the asymptotic or maximum length,

$t_0$ is the age or time when length theoretically equals zero and

$k$ is the growth coefficient.

The two parameter von Bertalanffy growth model (VBGF2) was also considered, which includes a size at birth intercept “$L_0$” instead of the theoretical “$t_0$” parameter (Goosen and Smale 1997; Carlson et al. 2003; Romine et al. 2006). Size at birth was estimated from observed at-term embryos and free swimming neonates collected during this study. The VBGF2 (Fabens 1965) model is described by the equation:

$$L_t = L_\infty (1 - be^{-kt}) = L_\infty - (L_\infty - L_o)e^{-kt}$$

where $L_t$ is the predicted length at age ‘$t$’,

$L_\infty$ is the asymptotic or maximum length,
$L_0$ is the size at birth,

$k$ is the growth coefficient and

\[ b = (L_{\infty} - L_0)/L_\infty. \]

Following Neer and Thompson (2005) and Chen et al. (2007) the Gompertz growth model (Gompertz, 1825) was also fit to the data, as described by the equation:

\[ L_t = L_\infty (e^{-k(t-t_0)}) \]

where $L_t$ is the predicted length at age ‘$t$’,

$L_\infty$ is the asymptotic or maximum length,

$k$ is the growth coefficient and

$t_0$ is the age or time when length theoretically equals zero.

The logistic growth model (Ricker 1975) was also considered, as described by the equation:

\[ L_t = L_\infty / (1 + e^{-k(t-t_0)}) \]

where $L_t$ is the predicted length at age ‘$t$’,

$L_\infty$ is the asymptotic or maximum length,

$k$ is the growth coefficient and

$t_0$ is the age or time when length theoretically equals zero.

Growth models were evaluated to determine the model of best fit through the Akaike information criterion (AIC) (Akaike 1974) as described by the equation:

\[ AIC = 2LL + 2p \]

where $LL$ is the negative log-likelihood and

$p$ is the number of parameters in the model.
The model with the lowest AIC value is considered to be the model of best fit of those tested based upon the best tradeoff between fit and number of parameters (Haddon 2011). The AIC values were compared between models to determine the magnitude of difference (ΔAIC) between each model. The model with the lowest AIC was found to be the best fit. Models with ΔAIC < 2 show evidence of good fit whereas models with ΔAIC > 10 are unlikely candidates for accurate models (Burnham and Anderson 2002).

Akaike information criterion was also used to determine whether there was a difference between sexes for growth models (Natanson et al. 2014). Theoretical longevity was estimated at the age in which 95% of the maximum size is reached using the term, \([5/(\ln2)/k}\) (Fabens 1965; Carlson et al. 2003, Drymon et al. 2006). The software system, \(R\) (R Development Core Team 2011), was used to calculate AIC values as well as to estimate growth model parameters. Growth model parameters were estimated with a Gauss-Newton algorithm for nonlinear regression, and AIC values were calculated using the \(R\) package \(qpcR\) (R Development Core Team 2011; Spiess 2012).

**Marginal increment analysis**

Verification of the annual periodicity of band formation was attempted using marginal increment analysis (MIA). Marginal increment analysis was calculated by measuring the distance from the last ring to the centrum edge and dividing by the width of the previous fully formed annulus (Branstetter and Musick 1994). Mean incremental percent by month of capture was plotted to identify trends in band formation using a single factor analysis of variance (ANOVA) (Simpfendorfer 1993, 2000; Carlson et al. 2003). Age zero animals were not used for MIA as they do not have fully formed growth increments (Goldman 2005).
**Estimation of age at maturity**

Age and size-at-maturity was calculated at the point in which 50% of the finetooth population was mature. This was determined by fitting the logistic model, which has been fitted to binomial maturity data using least squares nonlinear regression, where immature = 0 and mature = 1 (Mollet et al. 2000) as described by the equation:

\[
Y = \frac{1}{1 + e^{-(a+bx)}}
\]

where \( y \) is binomial maturity data,

\( x \) is the FL (mm),

\( a \) is the \( y \)-intercept and

\( b \) is the slope

Median FL at maturity was expressed by the equation: \( MFL = -a/b \). The model was fit using a Gauss-Newton algorithm for nonlinear regression in R (R Development Core Team 2011).

**Results**

A total of 745 finetooth sharks were collected during the duration of this study. The specimens ranged in size from 420 – 1384-mm FL and 397 – 1130-mm FL for females and males, respectively. Morphometric relationships between FL and STL and PCL and FL were developed in order to compare current findings with previous studies. The resulting regression formulas were: \( STL = 1.225FL + 23.224 \) (Linear regression, \( r^2 = 0.99, F1,1814 = 9.14 \times 10^{-4}, P < 2.2 \times 10^{-16} \)) and \( FL = 1.0975PCL + 5.5602 \) (Linear regression, \( r^2 = 0.99, F1,1126 = 6.512 \times 10^{-5}, P < 2.2 \times 10^{-16} \)). A total of 711 sharks (424 female; 287 male) were used to model growth after excluding disqualified specimens (Table 1). Precision of band counts for all aged finetooth sharks was high
among readers (J. Higgs and D. Bethea) with an APE of 4.46%. Vertebrae were disqualified when an agreement in aging was not reached (n = 6) or if information was missing for modeling growth (n = 28).

Table 1

*Number, by month and sex, of northern Gulf of Mexico finetooth sharks used in age deriving estimations.*

<table>
<thead>
<tr>
<th>Month</th>
<th>Female</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>February</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>March</td>
<td>39</td>
<td>10</td>
</tr>
<tr>
<td>April</td>
<td>79</td>
<td>37</td>
</tr>
<tr>
<td>May</td>
<td>68</td>
<td>50</td>
</tr>
<tr>
<td>June</td>
<td>51</td>
<td>38</td>
</tr>
<tr>
<td>July</td>
<td>53</td>
<td>38</td>
</tr>
<tr>
<td>August</td>
<td>42</td>
<td>46</td>
</tr>
<tr>
<td>September</td>
<td>33</td>
<td>29</td>
</tr>
<tr>
<td>October</td>
<td>23</td>
<td>20</td>
</tr>
<tr>
<td>November</td>
<td>18</td>
<td>5</td>
</tr>
<tr>
<td>December</td>
<td>16</td>
<td>14</td>
</tr>
</tbody>
</table>

Mean MIA was calculated for select, immature finetooth sharks greater than age 0 (n = 112). Mean MIA plotted by month exhibited increased growth from March through November, followed by a drastic decline in December (Figure 23). Despite monthly variability, MIA was not significantly different across months (ANOVA, $F(1,8) = 2.676$, $P = 0.141$). The continuous incremental growth from March through November indicates that band formation likely occurs annually between December and February.
Figure 23. Mean marginal increment ratio plotted month for immature finetooth sharks (*Carcharhinus isodon*), combined sexes (n = 112) (error bars represent 1 standard error).

Growth models incorporating separate parameter estimates for the sexes showed improved fit in comparison to models using common parameters for the sexes (Table 2). For females, the logistic model was best supported; whereas for males, the VBGF3 and the Gompertz models were best supported (ΔAIC < 2). Combined gender models showed minimal to no support based upon AIC model selection criteria (ΔAIC > 10; Table 2). Accordingly, female and male parameter estimates were calculated separately in order to find the model of best fit for the observed data for each sex (Table 3).
Table 2

Relative goodness of fit for each candidate growth model for finetooth sharks, ranked in order of best fit to observed data.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>∆AIC</th>
<th>Akaike weight</th>
<th>LL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Logistic w/sex</td>
<td>4842.59</td>
<td>0</td>
<td>7.62E-01</td>
<td>-2417.30</td>
</tr>
<tr>
<td>Gompertz w/sex</td>
<td>4845.04</td>
<td>2.44</td>
<td>2.25E-01</td>
<td>-2418.52</td>
</tr>
<tr>
<td>VBGF3 w/sex</td>
<td>4850.67</td>
<td>8.08</td>
<td>1.34E-02</td>
<td>-2421.33</td>
</tr>
<tr>
<td>VBGF2 w/sex</td>
<td>4914.42</td>
<td>71.82</td>
<td>1.93E-16</td>
<td>-2454.21</td>
</tr>
<tr>
<td>VBGF3</td>
<td>8114.73</td>
<td>3272.14</td>
<td>0</td>
<td>-4053.37</td>
</tr>
<tr>
<td>Gompertz</td>
<td>8115.07</td>
<td>3272.48</td>
<td>0</td>
<td>-4053.53</td>
</tr>
<tr>
<td>Logistic</td>
<td>8119.33</td>
<td>3276.74</td>
<td>0</td>
<td>-4055.67</td>
</tr>
<tr>
<td>VBGF2</td>
<td>8227.65</td>
<td>3385.06</td>
<td>0</td>
<td>-4110.83</td>
</tr>
</tbody>
</table>

Note. Models that indicate “w/sex” represent models with parameters that vary by sex. The other four models include general parameter estimates for both sexes. AIC = Akaike information criterion. ∆AIC = Akaike difference. LL = log-likelihood.

Table 3

Estimates of growth model parameters for finetooth sharks.

<table>
<thead>
<tr>
<th>Model</th>
<th>Asymptotic size (mm FL)</th>
<th>Growth coefficient (/yr)</th>
<th>t0 (yr)</th>
<th>AIC</th>
<th>∆AIC</th>
<th>Relative likelihood</th>
<th>Akaike weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Logistic</td>
<td><strong>1214</strong></td>
<td><strong>0.50</strong></td>
<td>-0.50</td>
<td><strong>4842.59</strong></td>
<td>0.00</td>
<td><strong>1.00</strong></td>
<td>0.76</td>
</tr>
<tr>
<td>Gompertz</td>
<td>1248</td>
<td>0.38</td>
<td>-0.41</td>
<td>4845.04</td>
<td>2.44</td>
<td>0.29</td>
<td>0.22</td>
</tr>
<tr>
<td>VBGF3</td>
<td>1308</td>
<td>0.26</td>
<td>-1.97</td>
<td>4850.67</td>
<td>8.08</td>
<td>0.02</td>
<td>0.01</td>
</tr>
<tr>
<td>VBGF2</td>
<td>1224</td>
<td>0.37</td>
<td></td>
<td>4930.91</td>
<td>88.31</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Male</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VBGF3</td>
<td><strong>1164</strong></td>
<td><strong>0.32</strong></td>
<td>-1.75</td>
<td><strong>3214.44</strong></td>
<td>0.00</td>
<td><strong>1.00</strong></td>
<td>0.59</td>
</tr>
<tr>
<td>Gompertz</td>
<td>1116</td>
<td>0.46</td>
<td>-0.54</td>
<td>3215.70</td>
<td>1.26</td>
<td>0.53</td>
<td>0.32</td>
</tr>
<tr>
<td>Logistic</td>
<td>1089</td>
<td>0.60</td>
<td>-0.16</td>
<td>3218.19</td>
<td>3.76</td>
<td>0.15</td>
<td>0.09</td>
</tr>
<tr>
<td>VBGF2</td>
<td>1087</td>
<td>0.48</td>
<td></td>
<td>3265.44</td>
<td>51.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Note. The best fit model for each sex is indicated in bold. t0 = the length that age theoretically equals 0. AIC = Akaike information criterion. ∆AIC = Akaike difference.
Aforementioned ΔAIC values dictated separation of models by sex more accurately describe asymptotic length and growth coefficient (Table 3, Figures 24 and 25). Female asymptotic length was estimated to be the greatest from the VBGF3 model (1308-mm FL), followed by the Gompertz (1248-mm FL) and VBGF2 models (1224-mm FL), and by the lowest estimate from the logistic model (1214-mm FL). Male asymptotic length was estimated to be the greatest from the VBGF3 model (1164-mm FL), followed by estimates from the Gompertz (1116-mm FL) and the logistic models (1089-mm FL), and by the lowest estimate from the VBGF2 model (1087-mm FL).

*Figure 24.* The von Bertalanffy (VBGF3), von Bertalanffy with size-at-birth intercept (VBGF2), Gompertz and logistic growth models fitted to observed length at age data for female finetooth sharks (*Carcharhinus isodon*) (n = 424).
Figure 25. The von Bertalanffy (VBGF3), von Bertalanffy with size-at-birth intercept (VBGF2), Gompertz and logistic growth models fitted to observed length at age data for male finetooth sharks (*Carcharhinus isodon*) (n = 287).

The greatest female growth coefficient was estimated from the logistic model (0.5/year), followed by similar estimates from both the Gompertz and VBGF2 models (0.38 and 0.37/year, respectively), and finally by the lowest estimate from the VBGF3 model (0.26/year). The greatest male growth coefficient was estimated from the logistic model (0.6/year), followed by similar estimates from both the Gompertz and VBGF2 models (0.46 and 0.48/year, respectively), and finally by the lowest estimate from the VBGF3 model (0.32/year). The logistic model yielded the lowest AIC value for female
growth, indicating it was the model of best fit; conversely, the VBGF3 model yielded the lowest AIC value for male finetooth sharks (Table 3).

Theoretical longevity estimates were calculated separately for female and male finetooth sharks. Female longevity estimates were 13.4, 9.3, 9.2, and 7.0 years for VBGF3, VBGF2, Gompertz and logistic models, respectively. Male longevity estimates were 10.7, 7.2, 7.5, and 5.8 years for VBGF3, VBGF2, Gompertz and logistic models, respectively. Observed maximum age for the oldest aged sharks was 9.4 and 6.5 years for females and males, respectively.

Length and age of maturity differed between males and females. Fifty percent of the female population reached maturity at 1032-mm FL, which corresponds to an approximate age of 4.1 years. Fifty percent of the male population reached maturity at 962-mm FL, corresponding to an approximate age of 3.6 years. The smallest mature female collected was 910-mm FL and the largest immature female collected was 1108-mm FL. The smallest mature male collected was 910-mm FL and the largest immature male collected was 1000-mm FL.
Discussion

The use of multiple growth models to fit observed data is becoming more prevalent in elasmobranch age and growth studies (e.g. Carlson and Baremore 2005; Chen et al. 2007; Frazier et al. 2014; Natanson et al. 2014). The current study elected to examine multiple models, VBGF3, VBGF2, Gompertz and logistic, as this has previously not been attempted for finetooth sharks. Separate analysis of sexes for each suite of models resulted in the logistic and VBGF3 models being those of best fit to the observed data for females and males, respectively. In contrast, prior studies on finetooth sharks focused only on the VBGF3 and the VBGF2 models, which are the more common models associated with estimating age and growth parameters in elasmobranchs.

While the VBGF2 model has consistently been used as a standard for estimating age and growth parameters, it has recently been proposed that this model is potentially ill
suited for the job in regard to elasmobranchs and teleost fishes (Pardo et al. 2013). Pardo et al. (2013) showed that the VBGF2 model often yields biased growth parameter estimates, and despite this bias, it is often selected by AIC to be the model of best fit. This is partially due to the decrease of one degree of freedom, which is heavily considered when selecting models by the means of AIC (Akaike 1974). Conversely, the VBGF2 has been found to be useful when studies have a small sample size, but the provided length-at-birth values must be carefully chosen, otherwise parameter estimates could be reported inaccurately (Thorson and Simpfendorfer 2009). Despite potential problems with the VBGF2 model, it was considered in this study and found that while statistically significant (p < 0.05), it was the least parsimonious of all models for both female and male finetooth sharks.

The Gompertz and logistic models were also considered, even though these models are traditionally used to model population growth rather than individual growth (Grosjean 2001). Notwithstanding, these models are being used considerably more often to investigate individual growth in many marine species and are commonly included when multiple growth models are being considered for elasmobranchs (e.g. Grosjean 2001; Wintner et al. 2002; Carlson et al. 2005; Chen et al. 2007). This study revealed the logistic model to be the most parsimonious for female sharks, but ranked low by AIC for males. For both sexes, the logistic model estimated the highest rate of growth and the lowest asymptotic size compared to other models, and thus a younger theoretical maximum age as well. Gompertz model estimates were found to provide the second best fit to the observed data for both females and males along with parameter values similar to previous studies for finetooth sharks. However, since the three prior studies describing
finetooth shark age and growth in the western Atlantic all used the VBGF3 model, the remainder of the Discussion will focus on the comparison of the VBGF3 model results.

The theoretical maximum sizes of finetooth sharks reported in the current study were comparable to other studies conducted in the wNAO and nGOM. Carlson et al. (2003) reported lower estimated $L_\infty$ values for finetooth sharks from the northeastern GOM compared to the current study (Table 4). On the other hand, Neer and Thompson (2004) reported higher estimated $L_\infty$ values in the nGOM than in the current study (Table 4). Conversely, $L_\infty$ estimates from the wNAO (Drymon et al. 2006) were nearly identical to those in the current study (Table 4). The variability observed in $L_\infty$ across these four studies could be attributed to the size of the individuals collected and/or the number of sharks collected by the studies. Neer and Thompson (2004) reported the largest finetooth sharks collected as 1177-mm, but did not differentiate sizes by sex. The maximum reported size falls between the maximum size that Carlson et al. (2003) reported of 1183-mm and 1089-mm FL for females and males, respectively. Despite similar maximum sizes, the parameter estimates generated by Neer and Thompson (2004) for $L_\infty$ are larger than those generated by Carlson et al. (2003). This disparity might be attributed to the number of samples collected between these two studies. Neer and Thompson (2004) collected 30 female and 24 male sharks; whereas, Carlson et al. (2003) collected more robust sample sizes of 117 female and 123 male sharks. Neither study necessarily fully represented the entire size range of the population, as the number of samples collected was still fairly low. The current study reported $L_\infty$ estimates in-between the other two studies, but collected the largest sized individuals, 1384-mm and 1130-mm for females and males, respectively, and sampled a larger portion of the population, 424 female and
287 male finetooth sharks. Due to the collection of larger individuals and a larger portion of the population, the model parameter estimates of the current study are likely a more accurate representation for the nGOM.

Table 4

Comparison of von Bertalanffy growth function estimates for the current study.

<table>
<thead>
<tr>
<th>von Bertalanffy growth estimates</th>
<th>Gulf of Mexico current study</th>
<th>Atlantic Ocean Drymon et al., 2006</th>
<th>Gulf of Mexico Neer and Thompson, 2004</th>
<th>Gulf of Mexico Carlson et al., 2003</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Females  Males</td>
<td>Females  Males</td>
<td>Females  Males</td>
<td>Females  Males</td>
</tr>
<tr>
<td>L∞ (mm FL)</td>
<td>1308  1164</td>
<td>1311  1151</td>
<td>1386  1196</td>
<td>1254  1073</td>
</tr>
<tr>
<td>k</td>
<td>0.26  0.32</td>
<td>0.19  0.33</td>
<td>0.25  0.3</td>
<td>0.24  0.41</td>
</tr>
<tr>
<td>t0 (yr)</td>
<td>-1.97 -1.75</td>
<td>-2.2 -1.4</td>
<td>-1.367 -1.806</td>
<td>-2 -1.39</td>
</tr>
<tr>
<td>Thr. long. (yr)</td>
<td>13.4  10.7</td>
<td>18.2  10.5</td>
<td>13.8  11.6</td>
<td>14.2  8.5</td>
</tr>
<tr>
<td>n</td>
<td>424  287</td>
<td>97  71</td>
<td>30  24</td>
<td>117  123</td>
</tr>
</tbody>
</table>

Note. Data from Carlson et al., (2003) and Neer and Thompson (2004) was converted to FL. Additionally, theoretical longevity was calculated from provided growth values for Neer and Thompson (2004). Thr. long. = Theoretical longevity.

Age estimates derived from growth band counts were based upon the assumption of annual growth band deposition which is commonly found for several species within the small coastal shark complex (e.g. Parsons 1993; Carlson et al. 2003; Driggers et al. 2004; Barreto et al. 2010). The present study attempted to verify annual deposition through MIA. Results indicated that annual formation is likely during the winter months, as shown by the highest MIA value in November and the lowest MIA value in March.

The finding of winter deposition of annual growth bands has been previously supported for finetooth sharks (Carlson et al. 2003; Drymon et al. 2006), as well as other carcharhinid species in the nGOM (e.g. Branstetter and Stiles 1987; Carlson et al. 1999; Carlson and Baremore 2005). Despite the current findings, additional sampling should be conducted to verify the time period of band deposition, with increased sampling.
occurring during November through February. Furthermore, verification of band formation should be investigated through other independent means, such as tag recapture in conjunction with oxytetracycline markers (e.g. Carlson et al. 2003; Driggers et al. 2004).

Age at which 50% of the finetooth shark population reached maturity (4.1 and 3.6 years for females and males) in this study was slightly younger than the previous study conducted in the nGOM (4.3 and 3.9 years for females and males; Carlson et al. 2003). In comparison, the work by Drymon et al. (2006) in the wNAO reported ages older than both studies conducted in the nGOM (6.3 and 5.0 years for females and males). Older age of maturity in the wNAO is not uncommon for sharks as was reported for several shark species, including tiger (*Galeocerdo cuvier*), blacktip (*Carcharhinus limbatus*), and blacknose and may be due to a varying physiological response to environmental conditions such as sea surface temperature (Driggers et al. 2004; Begg 2005; Carlson et al. 2006).

The results of all three studies imply a smaller age and size at maturity in the nGOM than in the wNAO, which suggests a potential difference in overall reproductive productivity between these two regions (Drymon et al. 2006). Data from the present study suggests that mature finetooth sharks in the nGOM would potentially have nine reproductive years, whereas sharks in the wNAO would potentially have twelve years. Since finetooth sharks were shown to exhibit a biennial reproductive cycle with an average of four embryos per brood (Castro 1993) this would result in four reproductive events producing on average 16 embryos in the nGOM versus six reproductive events producing on average 24 embryos in the wNAO. However, Driggers and Hoffmayer
(2009) recently suggested the potential for annual reproduction in the nGOM; if these initial findings are found to be accurate then the number of potential reproductive opportunities for finetooth sharks in the nGOM would more than double during their lifespan. Such a doubling of reproductive output could have major implications for the management of this species, and needs to be investigated further.

The current study provides further evidence of finetooth sharks exhibiting life history parameters that are intermediate to members of the small and large coastal shark complexes (Carlson et al. 2003; and Driggers and Hoffmayer 2009). For example, the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) growth coefficient ranges between 0.46-0.52 (Loefer and Sedberry 2003) and the bonnethead shark coefficient ranges from 0.18-0.44 (Lombardi-Carlson et al. 2003), which indicate that both species have a high rate of growth, as expected for small coastal sharks. Whereas another member of the small coastal shark complex, the blacknose shark, exhibits a growth coefficient ranging between 0.18-0.21, a value which is similar to rates exhibited by members of the large coastal shark complex, such as the blacktip, (0.19-0.27), bull (*Carcharhinus leucas*), (0.12 – 0.17), spinner (*Carcharhinus brevipinna*), (0.14-0.21), silky (*Carcharhinus falciformis*), (0.15), and tiger sharks, (0.18) (Branstetter 1987; Branstetter and Stiles 1987; Killam and Parsons 1989; Driggers et al. 2004; Carlson and Baremore 2005; Cruz-Martínez et al. 2005). The growth coefficient for finetooth sharks in the current study was between 0.26-0.32, which is most similar to that of blacknose sharks, supporting the notion that the growth coefficients of these two species are intermediate between those representing the small and large coastal shark complexes.
In conclusion, a multi-model approach of investigating growth in finetooth sharks has shown that the logistic and the three parameter von Bertalanffy models provide the best fit to the observed age/growth data for female and male finetooth sharks, respectively. Age at maturity estimates from this study are in agreement with previous studies and indicate maturity is reached at a younger age and smaller size in the GOM compared to the wNAO, which when taken into consideration along with reproductive capabilities, leads to different life history outputs. The current study investigated a larger number of finetooth sharks across a larger spatial area of the nGOM than covered in previous studies and thus provides a more accurate regional depiction of age and growth estimates. Additionally, the present study is the first to have investigated models other than von Bertalanffy for finetooth sharks. The findings documented by this study have increased the knowledge of the biology of finetooth sharks in the nGOM and provided valuable estimates of life-history parameters for this species, particularly within the context of single-species management.
CHAPTER IV

FOOD HABITS OF THE FINETOOTH SHARK, CARCHARHINUS ISODON, IN THE NORTHERN GULF OF MEXICO

Abstract

The diet composition of finetooth sharks (Carcharhinus isodon) was quantitatively analyzed from sharks collected in the northern Gulf of Mexico (nGOM) between Gulf Shores, Alabama (30.178° N and 87.937° W) and East Bay, Louisiana (28.959° N and 89.279° W) from May 2010 through October 2013. Of the 518 sharks collected, 79% (n = 411) contained empty stomachs. The 107 finetooth sharks with stomach contents contained primarily teleost prey that represented six families and eight genera and comprised 99% of the total diet. Overall, the diet was dominated by Gulf menhaden (Brevoortia patronus), an important ecological and commercial fishery resource in the nGOM. Cumulative prey curve analysis indicated that a sufficient number of finetooth sharks were examined to describe diet. The current study helped refine predator-prey linkages between these two commercially important species in the region.

Introduction

Elasmobranchs play an important role in the trophic ecology of coastal waters (Cortés 1999; Hoffmayer and Parsons 2003; Bizzarro et al. 2007). The trophic ecology of sharks is often viewed from a top-down perspective, in which the apex predator can potentially regulate and maintain lower trophic levels within the food web (Cortés 1999; Estrada et al. 2003). As top predators, sharks directly influence lower trophic levels and thus fill an important ecological niche within the marine ecosystem (Stevens et al. 2000;
Heithaus et al. 2008; Bornatowski et al. 2014). However, to better understand their role in the north central GOM ecosystem, it is necessary to investigate the feeding ecology of sharks in order to determine what ecological interactions are occurring.

Despite the importance of understanding the feeding ecology of top predators, there has historically been limited literature available defining the ecological role of shark species (Cortés 1999; Hoffmayer and Parsons 2003; Heithaus 2004; Wetherbee and Cortés 2004). However, studies are becoming more common on diet and trophic relationships; several of these studies focused on larger sharks, including scalloped hammerhead (*Sphyrna lewini*), dusky (*Carcharhinus obscurus*), blacktip (*Carcharhinus limbatus*) and sandbar (*Carcharhinus taurus*) sharks, and better defined the ecological importance of the large shark complex (Gelsleichter et al. 1999; Bush 2003; Ellis and Musick 2007; Barry et al. 2008). Conversely, there have been few studies on small coastal shark species, despite the fact that they likely fill equally important ecological roles as those of larger sharks. These few studies focused on small coastal shark species (blacknose, *Carcharhinus acronotus*; bonnethead, *Sphyrna tiburo*; finetooth, *Carcharhinus isodon*) have been limited in scope, with the exception of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, which has been studied extensively (e.g. Cortés et al. 1996; Hoffmayer and Parsons 2003; Bethea et al. 2004; Bethea et al. 2006; Bethea et al. 2007; Barry et al. 2008; DeLorenzo et al. 2014).

The investigation of finetooth shark diet has been limited to a single study in the wNAO and two studies in the nGOM. All studies were based on relatively small sample sizes and varied in their degree of detail. The study in the wNAO (Castro, 1993) focused on a basic description of diet, as did one study in the nGOM (Hoffmayer and Parsons,
whereas, the other nGOM study investigated diet in relation to early life stages (Bethea et al. 2004). These investigations of basic diet analyses are a crucial step in providing the framework for more exhaustive future research, including but not limited to the investigation of: predator prey interactions, diet breadth, trophic level, resource competition, and diet overlap with other predators (Bornatowski et al. 2014). With continued research, clarification of the trophic interactions of sharks and other large predators, will allow for better interpretation of the role these apex predators have in the trophic ecology within marine ecosystems (Lucifora et al. 2009; Heithaus et al. 2013; Bornatowski et al. 2014). Accordingly, the goal of the current study was to further describe and quantify the diet and food habits of finetooth sharks in the nGOM.

Materials and Methods

Finetooth sharks were collected in nGOM waters between Gulf Shores, Alabama (30.178° N and 87.937° W) and East Bay, Louisiana (28.959° N and 89.279° W) (Figure 27). Samples were obtained from May 2010 through October 2013 from fisheries independent surveys conducted by the University of Southern Mississippi’s Gulf Coast Research Laboratory (USM/GCRL), and through a contracted commercial fisher. Finetooth sharks obtained from fishery independent surveys were collected by means of a 183-m anchored gillnet, a 152-m hand-deployed bottom longline supporting 50 gangions with 12/0 hooks baited with Gulf menhaden, *Brevoortia patronus*, or a 1,609-m bottom longline supporting 100 gangions with 15/0 circle hooks baited with Atlantic mackerel, *Scomber scombrus*. Finetooth sharks obtained from the commercial fishers were collected using a 915-m anchored gillnet.
Figure 27. Collection locations for finetooth sharks (*Carcharhinus isodon*) in the northern Gulf of Mexico from 2010 to 2013.

The length (mm), weight (kg), sex, liver weight (g), and maturity state of each shark were determined and recorded. Length measurements included: pre-caudal (PCL), from the tip of the snout to the pre-caudal pit; fork (FL), from the tip of the snout to the caudal fork; and stretched total (STL), from the tip of the snout to the stretched length of the upper lobe of the caudal fin. Length measurements were used to develop morphometric relationships in order to compare measurements from other studies; linear regressions were generated for FL to STL and for PCL to FL. Finetooth sharks collected from commercial fishers were examined at the dock, all organs were removed, and the carcass was left with the fisher for commercial processing. Once removed, the organs
were stored on ice for in-depth examination upon return to the laboratory. Finetooth sharks collected from fishery independent surveys were placed on ice and dissected upon return from the field. Identification of prey items was conducted to the lowest taxonomic level and weighed to the nearest gram.

Finetooth shark diet composition was analyzed using three indices: percent by weight (%W), percent frequency of occurrence (%O), and percent mean proportion by weight (%MW). The %W was determined by taking the total weight of individual prey items and dividing by the total weight of all prey items in stomachs containing contents. Similarly, %O was calculated by taking the number of stomachs containing a prey type divided by the total number of stomachs containing prey (Hyslop 1980; Chipps and Garvey 2007). The %MW was calculated using the equation:

\[ MW = \frac{1}{P} \sum \frac{W_{ij}}{\sum W_{ij}} \]

where P is the number of stomachs containing prey, and Wij is the weight of prey in a single stomach and the \( \sum W_{ij} \) is the total weight of all prey items in the single stomach; to calculate %MW for a prey item, all MW of single prey items were summed and then divided by the total number of stomachs with prey (Chipps and Garvey 2007).

Sample processing techniques varied during the collection process. As such, some samples only had associated occurrence and weight data available and not prey count. To fully utilize all the diet data, a subset of specimens where all prey were counted was analyzed using two additional indices: percent by number (%N) and index of relative importance (IRI). The %N was determined by taking the total count of individual prey items and dividing by the total count of all prey items in stomachs containing contents.
The overall prey importance was assessed by calculating IRI through the equation (Pinkas et al. 1971):

\[ IRI = (\%N + \%W) \times \%O \]

IRI was expressed as a percentage in order to facilitate comparisons among prey types (Cortés 1997; Bizzarro 2007).

Diet specialization was investigated on a family level for all finetooth sharks containing identifiable prey remains. The method of Amundsen et al. (1996) was followed to generate values for prey specific abundance \( (P_i) \) through the equation:

\[ P_i = \frac{\sum S_i}{\sum S_{ti}} \]

where \( S_i \) is the stomach content (weight) comprised of prey \( i \), and \( S_{ti} \) is the total stomach content for only those predators with prey \( i \) in their stomachs. The \( P_i \) is then plotted against \%O in order to visualize prey importance and feeding strategy; specialization or generalization of the diet is determined by the position of prey points in regard to the vertical axis and prey importance is determined by the position on the diagonal axis starting in the lower left and ending in the upper right of the plot (Amundsen et al. 1996). A prey group located in the upper right portion of the plot identifies it as the dominant prey taxon and exhibits diet specialization by the predator population (Amundsen et al. 1996).

Identifiable prey items were categorized to genera in order to perform cumulative prey curve analysis, which was conducted for the entire sample, by sex and by maturity state. Cumulative prey curves were constructed in order to determine if the number of
finetooth shark stomachs with contents was sufficient to accurately describe the diet (Ferry and Cailliet 1996). Matlab (version 7.8.0.347, The MathWorks, Inc., Natick, MA) was used to generate cumulative prey curves via 500 randomizations of stomach samples to determine mean and standard error for each sample (Bizzarro et al. 2007). Sample size was considered adequate if an asymptotic stabilization of the curve occurred, demonstrating that the minimum number of stomachs were analyzed to accurately define the diet (Bizzarro et al. 2007). Linear regression was used to determine if the cumulative prey curve reached an asymptote, endpoint slope, as generated by the final four stomachs in the curve, was compared to a line with zero slope (Bizzarro et al. 2007). Statistical analysis of slopes was conducted by using a Student’s t-test; if slopes were found not to differ from zero (P > 0.05), the asymptote of the cumulative prey curve was considered to be reached (Zar 1999; Bizarro et al. 2007). Additionally, cumulative prey curve analysis was used to further investigate difference between sexes and maturity states. If an asymptote was reached then a chi square test was preformed to determine if significant differences were evident between the groups.

Empty stomach data were examined to determine if any seasonal trends were present. Seasons were defined as Spring (March – May), Summer (June – August), Fall (September – November) and Winter (December – February). A one-tailed analysis of variance (ANOVA) was used to test for differences in the proportions of empty stomachs among seasons (Sokal and Rohlf 1994; Zar 1999), followed by a post hoc Tukey’s test to determine which seasons differed (Zar 1999). The proportion data were arcsine square root transformed prior to analysis (Sokal and Rohlf 1994).
Results

A total of 518 finetooth sharks, ranging in size from 380-mm FL to 1384-mm FL, were collected during study. Stomachs containing contents were observed in 107 sharks of which 10.3% (n = 11) showed evidence of multiple prey types. Empty stomachs were observed in 79% (n = 411) of sharks collected (78% female; 81% male). Furthermore, there were no significant differences in the percent of empty stomachs among seasons (ANOVA, \( F(3,8) = 1.889, P = 0.21 \)).

Cumulative prey curve analysis revealed that the number of prey items reached an asymptote, indicating that sample size was large enough to accurately describe the diet of finetooth sharks in this study (\( r^2 = 0.755, F_{1,2} = 6.157, P = 0.131 \)) (Figure 27). Prey curve analysis revealed that a sample size consisting of 61 finetooth sharks appeared sufficient to accurately describe the diet from this region (\( r^2 = 0.879, F_{1,2} = 14.564, P = 0.062 \)). Cumulative prey curve analysis by sex indicated insufficient sample sizes to accurately describe diet in this study; male (n = 31) (\( r^2 = 0.983, F_{1,2} = 114.286, P = 0.009 \)) and female (n = 71) (\( r^2 = 0.964, F_{1,2} = 54.180, P = 0.018 \)). Conversely, cumulative prey curve analysis indicated that sample sizes were sufficient to describe diet of immature and mature finetooth sharks from this study; immature (n = 35) (\( r^2 = 0.726, F_{1,2} = 5.289, P = 0.148 \)) and mature (n = 66) (\( r^2 = 0.822, F_{1,2} = 9.229, P = 0.093 \)). Even though sample sizes were large enough to accurately describe the diets of mature and immature sharks, no ontogenetic shift was evident in the diet (Chi-square test, \( \chi^2 = 13.374, p = 0.270 \)).
Pelagic teleosts made up the largest portion of the diet composition for finetooth sharks, occurring in 99 stomachs (92.5 %O) (Table 5). Six families and eight genera of teleosts were identified within stomach contents. The Gulf menhaden was found to be the most abundant species representing 67.3 % of the diet, followed by mullet, *Mugil* sp., which was the second most abundant prey item in 16.8% of stomachs. Only eight stomachs contained unidentifiable teleost remains (7.5%). Crustacean remains (Penaeidae) were found in three stomachs; each occurrence was represented by only a single prey item. Further analysis of the subset of stomachs with prey count data (n = 76) showed a similar pattern as the entire dataset, with pelagic teleost (89.6%O) being the majority of the diet composition and Gulf menhaden (70.2%O) being the most abundant prey species (Table 2). Additionally, %IRI showed pelagic teleosts to be the most
important prey group (97.2%) while Gulf menhaden was the most important prey item (95.1%) (Table 6).

Table 5

*Diet composition of finetooth sharks (n = 107) from the northern Gulf of Mexico (nGOM).*

<table>
<thead>
<tr>
<th>Prey Item</th>
<th>W (g)</th>
<th>%W</th>
<th>O</th>
<th>%O</th>
<th>MW</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pelagic teleosts</strong></td>
<td>6984.36</td>
<td>86.39</td>
<td>99.00</td>
<td>92.52</td>
<td>84.63</td>
<td>2642.27</td>
</tr>
<tr>
<td><em>Chloroscombrus chrysurus</em></td>
<td>88.90</td>
<td>1.10</td>
<td>1.00</td>
<td>0.93</td>
<td>0.93</td>
<td>9.67</td>
</tr>
<tr>
<td><em>Brevoortia patronus</em></td>
<td>5644.50</td>
<td>69.81</td>
<td>72.00</td>
<td>67.29</td>
<td>63.18</td>
<td>47.16</td>
</tr>
<tr>
<td><em>Anchoa hepsetus</em></td>
<td>36.80</td>
<td>0.46</td>
<td>1.00</td>
<td>0.93</td>
<td>0.93</td>
<td>9.67</td>
</tr>
<tr>
<td><em>Anchoa sp.</em></td>
<td>91.70</td>
<td>1.13</td>
<td>6.00</td>
<td>5.61</td>
<td>3.24</td>
<td>16.00</td>
</tr>
<tr>
<td><em>Mugil sp.</em></td>
<td>1037.26</td>
<td>12.83</td>
<td>18.00</td>
<td>16.82</td>
<td>15.40</td>
<td>35.64</td>
</tr>
<tr>
<td><em>Pomatomus saltatrix</em></td>
<td>85.20</td>
<td>1.05</td>
<td>1.00</td>
<td>0.93</td>
<td>0.13</td>
<td>1.36</td>
</tr>
<tr>
<td><strong>Epibenthic teleosts</strong></td>
<td>896.68</td>
<td>11.09</td>
<td>8.00</td>
<td>7.48</td>
<td>6.26</td>
<td>213.42</td>
</tr>
<tr>
<td><em>Leiostomus xanthurus</em></td>
<td>530.40</td>
<td>6.56</td>
<td>1.00</td>
<td>0.93</td>
<td>0.79</td>
<td>8.13</td>
</tr>
<tr>
<td><em>Menticirrhus americanus</em></td>
<td>78.20</td>
<td>0.97</td>
<td>1.00</td>
<td>0.93</td>
<td>0.93</td>
<td>9.67</td>
</tr>
<tr>
<td><em>Micropogonias undulatus</em></td>
<td>288.08</td>
<td>3.56</td>
<td>6.00</td>
<td>5.61</td>
<td>4.39</td>
<td>19.96</td>
</tr>
<tr>
<td><strong>Unknown teleost remains</strong></td>
<td>145.50</td>
<td>1.80</td>
<td>8.00</td>
<td>7.48</td>
<td>7.26</td>
<td></td>
</tr>
<tr>
<td><em>Unknown teleost remains</em></td>
<td>145.50</td>
<td>1.80</td>
<td>8.00</td>
<td>7.48</td>
<td>7.26</td>
<td>25.71</td>
</tr>
<tr>
<td><strong>Crustaceans</strong></td>
<td>58.40</td>
<td>0.72</td>
<td>3.00</td>
<td>3.00</td>
<td>1.85</td>
<td></td>
</tr>
<tr>
<td><em>Farfantenpeaeus azteicus</em></td>
<td>43.40</td>
<td>0.54</td>
<td>1.00</td>
<td>0.93</td>
<td>0.93</td>
<td>9.67</td>
</tr>
<tr>
<td><em>Litopenaeus setiferus</em></td>
<td>12.00</td>
<td>0.15</td>
<td>1.00</td>
<td>0.93</td>
<td>0.93</td>
<td>9.67</td>
</tr>
<tr>
<td><em>Penaeus sp.</em></td>
<td>3.00</td>
<td>0.04</td>
<td>1.00</td>
<td>0.93</td>
<td>0.93</td>
<td>9.67</td>
</tr>
</tbody>
</table>

Note. Composition represented by weight (W) percent weight (%W), occurrence (O), percent occurrence (%O), and mean proportion by weight (MW) with standard deviation. Bold indicates prey groups.
Table 6

*Diet composition of finetooth shark subset (n = 76) from the northern Gulf of Mexico (nGOM).*

<table>
<thead>
<tr>
<th>Prey Item</th>
<th>N</th>
<th>%N</th>
<th>W</th>
<th>%W</th>
<th>O</th>
<th>%O</th>
<th>IRI</th>
<th>%IRI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pelagic teleosts</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Chloroscombrus chrysurus</em></td>
<td>79.00</td>
<td>29.48</td>
<td>88.90</td>
<td>1.40</td>
<td>1.00</td>
<td>1.49</td>
<td>46.08</td>
<td>0.57</td>
</tr>
<tr>
<td><em>Brevvoorta patronus</em></td>
<td>111.00</td>
<td>41.42</td>
<td>4358.14</td>
<td>68.57</td>
<td>47.00</td>
<td>70.15</td>
<td>7715.81</td>
<td>95.05</td>
</tr>
<tr>
<td><em>Anchoa hepsetus</em></td>
<td>1.00</td>
<td>0.37</td>
<td>36.80</td>
<td>0.58</td>
<td>1.00</td>
<td>1.49</td>
<td>1.42</td>
<td>0.02</td>
</tr>
<tr>
<td><em>Anchoa sp.</em></td>
<td>13.00</td>
<td>4.85</td>
<td>77.90</td>
<td>1.23</td>
<td>5.00</td>
<td>7.46</td>
<td>45.35</td>
<td>0.56</td>
</tr>
<tr>
<td><em>Mugil sp.</em></td>
<td>8.00</td>
<td>2.99</td>
<td>637.50</td>
<td>10.03</td>
<td>5.00</td>
<td>7.46</td>
<td>97.13</td>
<td>1.20</td>
</tr>
<tr>
<td><em>Pomatomus saltatrix</em></td>
<td>1.00</td>
<td>0.37</td>
<td>85.20</td>
<td>1.34</td>
<td>1.00</td>
<td>1.49</td>
<td>2.56</td>
<td>0.03</td>
</tr>
<tr>
<td><strong>Epibenthic teleosts</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Leiostomus xanthurus</em></td>
<td>13.00</td>
<td>4.85</td>
<td>530.40</td>
<td>8.35</td>
<td>1.00</td>
<td>1.49</td>
<td>19.70</td>
<td>0.24</td>
</tr>
<tr>
<td><em>Menticirrhus americanus</em></td>
<td>1.00</td>
<td>0.37</td>
<td>78.20</td>
<td>1.23</td>
<td>1.00</td>
<td>1.49</td>
<td>2.39</td>
<td>0.03</td>
</tr>
<tr>
<td><em>Micropogonias undulatus</em></td>
<td>27.00</td>
<td>10.07</td>
<td>288.10</td>
<td>4.53</td>
<td>6.00</td>
<td>8.96</td>
<td>130.82</td>
<td>1.61</td>
</tr>
<tr>
<td><strong>Unknown teleost remains</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Unknown teleost remains</em></td>
<td>11.00</td>
<td>4.10</td>
<td>115.90</td>
<td>1.82</td>
<td>6.00</td>
<td>8.96</td>
<td>53.09</td>
<td>0.35</td>
</tr>
<tr>
<td><strong>Crustaceans</strong></td>
<td>3.00</td>
<td>1.12</td>
<td>58.40</td>
<td>0.92</td>
<td>3.00</td>
<td>4.48</td>
<td>9.13</td>
<td>0.06</td>
</tr>
<tr>
<td><em>Farfantepenaeus aztecus</em></td>
<td>1.00</td>
<td>0.37</td>
<td>43.40</td>
<td>0.68</td>
<td>1.00</td>
<td>1.49</td>
<td>1.58</td>
<td>0.02</td>
</tr>
<tr>
<td><em>Litopenaeus setiferus</em></td>
<td>1.00</td>
<td>0.37</td>
<td>12.00</td>
<td>0.19</td>
<td>1.00</td>
<td>1.49</td>
<td>0.84</td>
<td>0.01</td>
</tr>
<tr>
<td><em>Penaeus sp.</em></td>
<td>1.00</td>
<td>0.37</td>
<td>3.00</td>
<td>0.05</td>
<td>1.00</td>
<td>1.49</td>
<td>0.63</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Note. Metrics include number (N) percent number (%N), weight (W) percent weight (%W), occurrence (O), percent occurrence (%O), index of relative abundance (IRI) and percent IRI (%). Bold indicates prey groups.
Finetooth sharks collected in this study exhibited diet specialization (Figure 28).

The most important prey group was Clupeidae as exhibited by diet specialization on a population level. Engraulids and mugilids were minor contributors to the finetooth shark diet.

*Figure 29.* Prey specific abundance index for finetooth shark (*Carcharhinus isodon*) diet from the northern Gulf of Mexico. Specialization of diet based upon prey groups is represented by the location on the y-axis; importance of prey groups to diet is represented by the location on the x-axis. (e.g. the position of Clupeidae in the upper right portion of the graph indicates population specialization) ▲ = Clupeidae, ★ = Mugilidae, ■ = Engraulidae, • = Sciaenidae, + = Penaeidae, ○ = Carangidae, ✶ = Pomatomidae.
Discussion

The current study found that finetooth sharks feed almost exclusively on teleost prey (99%) and predominately on Gulf menhaden. The previous studies conducted in the wNAO and within discrete regions of the GOM showed similar findings with the majority of the diet composed of teleost (Castro 1993; Bethea et al. 2004; Hoffmayer and Parsons 2003), and a heavy emphasis on *Brevoortia*. Castro (1993) found that Atlantic menhaden (*B. tyrannus*) was the most abundant prey item (38% O) in the diet of finetooth sharks. Similarly, the two studies in the GOM found Gulf menhaden, a close relative of the Atlantic menhaden (Bowen and Avise 1990; Anderson 2007), to be the primary prey item consumed by finetooth sharks (36 and 20% O) (Bethea et al. 2004; Hoffmayer and Parsons 2003). It is not surprising that *Brevoortia* dominates the diet of finetooth sharks in the GOM because these sharks are a known bycatch species in the GOM menhaden fishery (de Silva et al. 2001). Furthermore, in the wNAO, commercial shark fishers are known to target menhaden schools when deploying their gear for sharks (Trent et al. 1997).

Investigation of teleost prey location in the water column in this study indicates finetooth sharks are primarily feeding in the pelagic zone and minimally using the epibenthos. Though not directly investigated by Hoffmayer and Parsons (2003) these results are similar in terms of identifiable prey items. Additionally, Bethea et al. (2004) found that finetooth sharks primarily feed in the pelagic zone and epibenthic prey were of little importance. Due to the heavy reliance on pelagic teleosts, the potential exists for dietary overlap with other predators. For instance, Atlantic sharpnose sharks are known to prey upon menhaden in varying amounts, depending on ontogenetic stage; immature (1.6
– 8.3%) and more frequently in mature sharks (27.9%) (Hoffmayer and Parsons 2003; Bethea et al. 2004; Bethea et al. 2006). Additionally, prior studies of the blacktip shark diet showed similar ontogenetic trends as Atlantic sharpnose sharks, with menhaden occurring less frequently in immature individuals (24.6%) than in mature sharks (46.1%) (Hoffmayer and Parsons 2003; Bethea et al. 2004). The aforementioned studies suggest dietary overlap is occurring among these three species in the nGOM, which in fact, has been shown to exist between blacktip and finetooth sharks (Bethea et al. 2004). However, further research should better define the degree of overlap and potential competition among these three species and ideally should include other abundant coastal sharks in the nGOM.

A large number of empty stomachs (79%) was found in the current study. This was also observed by Hoffmayer and Parsons (2003) in the Mississippi Sound, where 70% stomachs were empty. However, both the current study and that by Hoffmayer and Parsons (2003) found substantially more empty stomachs than reported by Bethea et al. (2004) for the eastern GOM and Castro (1993) for the wNAO as 49% and 39%, respectively. Similar values for empty stomachs have been seen for the blacktip shark, which showed the percent empty ranging between 32% and 60% (Hoffmayer and Parsons 2003; Bethea et al. 2004; Barry et al. 2008). As previously mentioned, both finetooth and blacktip sharks feed primarily on Gulf menhaden, and as such, competition may be a factor related to the high percentage of empty stomachs. Further research is necessary to determine the dietary overlap between finetooth sharks and other coastal shark species.

The current study found no seasonal trends in the frequency of empty stomachs. This is interesting because prior studies in fish have shown that warmer water
temperatures can increase the rate of digestion (Brett and Higgs 1970). Accordingly, a higher frequency of empty stomachs might be expected during the warmer months when digestion is occurring more rapidly. This does not appear to be the case in this study and may indicate other factors are of more importance concerning the presence of prey items in diet. One confounding issue could be stomach eversion. Sharks are known to regurgitate their stomach contents when stressed, and this may have occurred with the commercial gillnet specimens. This is proposed because during routine collection, several sharks exhibited stomachs protruding from the oral cavity (pers. obs.), which could account for some of the empty stomachs. Determination of causation of empty stomachs would provide a better understanding of finetooth feeding ecology. Further investigation should be conducted to determine if finetooth sharks have a reduced feeding rate during certain periods of the year or have high evacuation rates/regurgitation tendencies. One potential way to elucidate this would be to investigate gastric acid secretion in the stomachs of captured sharks and make comparisons to those held in captivity. Papastomatiou and Lowe (2005) demonstrated variability in gastric acid presence by a fluctuation of pH levels in nurse sharks as they were either fasting (higher pH levels) or in a period of feeding (lower pH levels). Continued research will help determine potential reasons for the large number of empty stomachs.

Diet variability based on distinct geographic regions has been noted in several shark species and could be attributed to different life stages being associated with specific distinct regions (Cortés and Gruber 1990; Bethea et al. 2006; Ellis and Musick 2006). Finetooth sharks do not appear to exhibit such regional trends as there is not much variability in dominant prey items across the nGOM or wNAO. However, due to the
limitations of the previous studies, regional diet variability cannot be completely ruled out. Hoffmayer and Parsons (2003) did not fully describe the diet or specify the maturity of the animals examined. However, the current study encompassed the same study area of Hoffmayer and Parsons (2003) potentially negating the proposed variability. Another study in the eastern GOM (Bethea et al. 2004) focused on immature individuals and as such may not reflect the feeding habits of mature finetooth sharks, the predominant specimens sampled in the present study. To definitively document the lack of geographic variability in the diet of this shark, further research should focus on mature sharks in the eastern and western GOM.

The results of the \( P_i \) investigation substantiated that Clupeidae are the most important prey group, and diet specialization is occurring within the finetooth shark population. Although seldom applied to sharks (e.g. Vögler et al. 2003; Lucifora et al. 2006; Braccini 2008), prey specific abundance has been applied in many other elasmobranch diet studies, especially in regard to batoids and specifically to skates (e.g. Scenna et al. 2003; Ajemian and Powers 2012; Molina and Cazorla 2015). The limited use of \( P_i \) in sharks may reflect the notion that sharks are typically considered opportunistic predators (Lucifora et al. 2006). However, in order to confirm this notion, the \( P_i \) index should be applied to other shark feeding studies; particularly those focusing on closely related species within the small coastal shark complex.

The current study aimed to expand the knowledge of finetooth shark diet by investigating a larger number of samples across the geographic breadth. Finetooth sharks appear to have a specialized diet focused almost exclusively on teleosts, primarily Gulf
menhaden. The results of this study have contributed to a greater understanding of diet and trophic role of finetooth sharks within coastal waters of the nGOM.
CHAPTER V

GENERAL CONCLUSION

Investigations of life history parameters are paramount for a thorough biological understanding of a species and are essential for stock assessments and implementation of effective management of populations (Cortés 2002; Natanson et al. 2014). However, species are commonly assessed as a group of closely related taxa in a mixed species model, which has been widely applied to elasmobranchs. A mixed species model might conceal the decline of individual species stocks, as other species with higher production rates may continue to drive the fishery (Musick 1999). This can lead to a potential stock collapse of species in peril because they are not being managed individually (Musick et al. 2000). One viable solution to this problem would be to investigate life history parameters on a species-specific basis, thus facilitating more appropriate management plans to be implemented and ensuring a sustainable fishery. To assist in accomplishing such species-specific management, the current study focused on obtaining detailed life history parameter aspects for finetooth sharks in the nGOM.

The current study investigated the age and growth parameters of finetooth sharks (Carcharhinus isodon) in the nGOM to update the known parameters from a larger geographic breadth. The observed maximum age calculated for finetooth sharks was 9.4 years (1384-mm fork length [FL]) and 6.5 years (1130-mm FL) for females and males, respectively. Following the work of Carlson and Baremore (2005), four growth models were fit to the data in order to determine the model of best fit. All four models (two and three parameter von Bertalanffy, Gompertz, and logistic growth) were found to be statistically significant p < 0.05. For comparability with other studies, the three parameter
von Bertalanffy model was used for evaluation; \( k \) and \( L_\infty \) estimates were 1308-mm FL and 0.26/yr for females and 1164-mm FL and 0.32/yr for males. The age at which 50% of the finetooth population was mature was 4.1 and 3.6 years for females and males, respectively.

The current study revealed similar age and growth estimates for finetooth sharks compared to previously conducted studies in the nGOM and wNAO (Carlson et al. 2003; Neer and Thompson 2004; Drymon et al. 2006). All studies reported similar theoretical maximum size values for male and female sharks; the theoretical maximum size in the current study falls within the ranges reported by the two previous studies in the nGOM. The reported \( k \) values from the current study were also similar to those values given in both the wNAO and the GOM. Results suggest an earlier onset of maturity for finetooth sharks in the GOM, which could have management implications due to the potential for higher reproductive productivity. The present study also indicates that GOM finetooth sharks exhibit age and growth parameters that are intermediate between the species of the small coastal and large coastal shark complexes.

The present study also investigated the reproductive biology of finetooth sharks in the nGOM, a region where such critical information is lacking. The length at which 50% of the population reaches maturity was 1037-mm and 961-mm fork length for females and males, respectively. For males, a combination of peak gonadosomatic index (GSI) in March and first noted presence of semen in the seminal vesicles in April suggest spermatogenesis occurs from March to May. In females, ovulation occurred from May to June, which corresponded with a peak GSI in May with maximum vitellogenic follicle diameter occurring from May to June. Gestation period was 11-12 months with
parturition occurring from May to June, as represented by a mean brood size of 3.8 ± 0.1 embryos. After examining fifty gravid females during the ovulatory period to determine reproductive periodicity, 32 sharks exhibited annual periodicity and 18 sharks exhibited biennial periodicity.

The present study is comparable to previous work on finetooth sharks in the wNAO, including the seasonality for male spermatogenesis, the female ovulatory period, and for initiation of the mating season. (Castro, 1993). Additionally, this study and that by Castro (1993) in the wNAO observed an approximate 12-month gestation period, a parturition period occurring in May and June, and a mean brood size of approximately four embryos. Despite the many similarities, two striking reproductive differences exist between the regional populations. Finetooth sharks in the wNAO exhibited a larger maximum size and older age at maturity (Castro, 1993) compared to the present study in the GOM. In addition, finetooth sharks in the nGOM exhibited intraspecific variability in reproductive periodicity and more variability in reproductive parameters than finetooth sharks in the wNAO (Castro 1993; Driggers and Hoffmayer 2009). This variability in reproductive periodicity could have major implications for fishery management models in terms of stock recruitment. When considered together with variable reproductive periodicity, the smaller size of maturity would potentially allow for a higher number of offspring produced per lifetime in the GOM compared to the wNAO (nGOM: annual = 40 embryos, biennial = 20 embryos; wNAO: biennial = 24 embryos). The reproductive findings in this study represent improved knowledge of finetooth shark life history in the nGOM and will be of considerable interest for the future assessment and management of this geographically distinct population.
The diet composition of GOM finetooth sharks was also quantified for a detailed comparison of this species across regions. A total of 518 sharks were collected, of which 411 (79%) contained empty stomachs. The remaining 107 finetooth sharks revealed that teleosts were the primary prey, composing 99% of the diet and as represented by six families and eight genera. Cumulative prey curve analysis indicated that a sufficient number of finetooth sharks were sampled to accurately describe the diet within this region. The Gulf menhaden (*Brevoortia patronus*) was consumed by 67% of finetooth sharks examined and was the most abundant prey species consumed. The second highest frequency prey type, *Mugil* sp., was consumed by 15% of examined sharks with content.

The findings from the present study agree with previous diet work conducted on finetooth sharks in both the nGOM and wNAO. In the wNAO, Castro (1993) found that finetooth sharks primarily feed on Atlantic menhaden, whereas Bethea et al. (2004) and Hoffmayer and Parsons (2003) found they primarily feed on Gulf menhaden in the nGOM. While dietary studies conducted in the nGOM and wNAO revealed that finetooth sharks feed on different species, they were of the same genus (Bowen and Avise 1990; Anderson 2007) and indicated that members of family Clupeidae were the dominant prey in both regions. The findings of the current study demonstrate that finetooth sharks tend to exhibit a fairly specialized and homogeneous diet focused almost exclusively on Gulf menhaden. The results of this study provide a better understanding of diet and the trophic role that finetooth sharks play in the coastal waters of the nGOM. Additionally, this thesis provides valuable insights into the life history of finetooth sharks by defining reproductive habits, age and growth estimates, and diet metrics, which are critical for the future management and conservation of this species.
Appendix A

Institutional Review Board Notice of Committee Action

Institutional Animal Care and Use Committee Notice of Committee Action

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

Protocol Number: 09031203
Project Title: Investigation into the Reproductive Parameters of the Sharpnose, Blacktip, and Finetooth Shark
Proposed Project Dates: 03/01/09 to 10/31/10
Project Type: New Project
Principal Investigator(S): Eric Hofmayer, Ph.D.
College/Division: Department of Coastal Sciences
Department: Center for Fisheries Research & Development
Funding Agency/Sponsor: Departmental
IACUC Committee Action: Full Committee Review Approval
Protocol Expiration Date: 09/30/11

Robert C. Bateman, Jr., Ph.D.
IACUC Chair

Date
APPENDIX B

INSTITUTIONAL REVIEW BOARD NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER: 11092202
PROJECT TITLE: Investigation into the Reproductive Parameters of the Sharptail, Blacknose, and Finetooth Shark
PROPOSED PROJECT DATES: 10/01/2011 to 09/30/2014
PROJECT TYPE: Renewal/Continuation of a Previously Approved Project
PRINCIPAL INVESTIGATOR(S): Jill Hendon
COLLEGE/DIVISION: Research & Development
DEPARTMENT: Center for Fisheries
FUNDING AGENCY/SPONSOR: NOAA & Departmental
IACUC COMMITTEE ACTION: Full Committee Review Approval
PROTOCOL EXPIRATION DATE: 09/30/2014

Jodie M. Jawor, Ph. D.
IACUC Chair

DATE

9/28/2011
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