Age, growth, and maturation of the Finetooth Shark, *Carcharhinus isodon*, in the Western North Atlantic Ocean

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Abstract Many elasmobranchs display K-selected life history characteristics, making species-specific life history parameters critical to development of the most accurate stock assessment models. Age, growth, and maturity were examined for Finetooth Sharks, *Carcharhinus isodon*, in coastal waters of the Western North Atlantic Ocean (WNA) from Winyah Bay, South Carolina to Cape Canaveral, Florida. Ages were estimated from the vertebrae of 200 males and 232 females. The maximum observed age for males and females was 21.9 years and 22.3 years, respectively. Sizes ranged from 376 mm to 1174 mm fork length (FL) for males and 380 mm to 1282 mm FL for females. Significant differences were detected between the sexes necessitating sex-specific von Bertalanffy growth models yielding the following parameters: male, $L_\infty = 1140$ mm FL, $k = 0.29$, $L_0 = 460$ mm FL; female, $L_\infty = 1253$ mm FL, $k = 0.20$, $L_0 = 464$ mm FL. Median length (L_{50}) at maturity was 1010 mm FL for males and 1043 mm FL for females corresponding to an age at median maturity (A_{50}) of 6.6 years and 6.8 years, respectively. Significant differences in growth and maturity were detected between the current study and previously published parameters for the WNA and Gulf of Mexico (GOM). Observed differences in the WNA were driven by ageing methods, with current methods yielding significant differences in age estimates between studies. Results from the current study, in conjunction with previously published reproductive, tag-recapture and genetic studies, provide support for separate stocks between the WNA and GOM.

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Introduction

Elasmobranchs display K-selected life history characteristics which include slow growth, delayed maturity, low fecundity, and long-life spans (Musick 1999). These qualities also make them less resilient and more susceptible to potential stock collapse through habitat degradation, overfishing by targeted commercial and recreational fisheries, and bycatch mortality in mixed species fisheries (Hoenig and Gruber 1990; Hoff and Musick 1990; Musick 1999; Musick et al. 2000). To properly assess and facilitate management of this important group of fishes in coastal waters off the United States, the National Marine Fisheries Service (NMFS) divides shark species into pelagic, large coastal shark, and small coastal shark (SCS) complexes. However, within these

complexes, age-at maturity, size-at-maturity, fecundity, growth rates, and theoretical maximum lengths still vary considerably; therefore, species-specific age and growth studies are critical to developing the most accurate stock assessment models.

Finetooth sharks, *Carcharhinus isodon* (Müller & Henle, 1839), are distributed in shallow coastal waters (< 20 m) from North Carolina to Florida (here-after referred to as the western North Atlantic, WNA) and throughout the Gulf of Mexico (GOM) (Compagno 1984; Castro 1993a). In South Carolina, *C. isodon* are frequently found in high salinity estuaries and nearshore waters from early spring to late autumn before migrating to overwintering grounds off the east coast of Florida (Castro 1993a; Ulrich et al. 2007). The estuaries and nearshore waters of South Carolina are considered primary and secondary nurseries, and coastal waters are used by all life stages with mating and parturition occurring concurrently (Castro 1993b).

Differences in life history parameters, reproductive periodicity, and genetic population structure have been observed in other small coastal sharks, suggesting separate stocks in the GOM and the WNA (Carlson and Parsons 1997; Carlson et al. 1999; Loefer and Sedberry 2003; Driggers III et al. 2004; Carlson and Loefer 2007; Sulikowski et al. 2007; Frazier et al. 2014; Portnoy et al. 2014; Escatel-Luna et al. 2015). Additionally, tag-recapture studies provide support for differences in longevity between the GOM and WNA (Frazier et al. 2015) and suggest limited movement between the two regions (Kohler et al. 1998; Kohler and Turner 2001; Tyminski et al. 2007). Contrary to other small coastal sharks, a study by Drymon et al. (2006) found no significant differences in von Bertalanffy growth model (VBGM) parameters for *C. isodon* in the WNA when compared to those in the GOM (Carlson et al. 2003). According to the most recent stock assessment (SEDAR 2007), *C. isodon* is considered a single stock in the GOM and WNA; however, recent studies suggest differences in reproduction (Driggers III and Hoffmayer 2009; Brown 2015) and genetic structure (Portnoy et al. 2016) between the two regions suggesting distinct regional populations.

The 2002 SCS Stock Assessment determined that *C. isodon* was not overfished but was experiencing overfishing, particularly related to bycatch in gillnet fisheries targeting non-highly migratory species (Cortes 2002). Additional indices were compiled and included in the 2007 SCS stock assessment (Carlson et al. 2003;

Neer and Thompson 2004; Drymon et al. 2006), which concluded that *C. isodon* is not overfished and is not experiencing overfishing; however, assessment scientists felt there were deficiencies in life history data and recommended updating age, growth, and reproductive data for *C. isodon* in the WNA (SEDAR 2007). This study will provide updated age, growth, and maturity parameters for *C. isodon* in the WNA and compare growth and maturation models to previously published results from the WNA (Drymon et al. 2006) and the GOM (Carlson et al. 2003) to assess regional differences. Results of this study will help inform fisheries managers by providing accurate and up to date information regarding growth and maturity for the *C. isodon* population along the southeastern United States.

Materials and methods

Collection

Carcharhinus isodon were collected from April 2002 through September 2016 from the South Carolina Department of Natural Resources (SCDNR) Cooperative Atlantic States Shark Pupping and Nursery Habitat (COASTSPAN) and the SCDNR Coastal Longline surveys using gillnets, hand-deployed longlines, and hydraulic longlines as described in Ulrich et al. (2007). Samples collected during 2002–2003 were from a previously published age and growth study which provided archived vertebrae as well as slides for each individual (Drymon et al. 2006). Spatial coverage ranged from Winyah Bay to Port Royal Sound, South Carolina with additional samples from Cape Canaveral, Florida provided by the University of North Florida and commercial fishermen during the winter migration (Fig. 1).

Once captured, specimens were brought aboard, sexed, measured for precaudal length (PCL, anterior tip of the rostrum to the precaudal pit), fork length (FL, anterior tip of the rostrum to the caudal fin fork), and stretch total length (STL, anterior tip of the rostrum to the posterior tip of the upper lobe of the caudal fin while extended along the body axis), and weighed to the nearest 0.25 kg using a hand-held spring scale. Individuals were sacrificed with the goal of providing two male and two female *C. isodon* per 10 mm FL size bins for lengths between previously reported length-at-birth (376 mm for males and 380 mm for females) and maximum observed FL (1174 mm for males and

Fig. 1 Map of the Western North Atlantic Ocean with sample site locations. Relative abundance is indicated by increasing circle diameter (Winyah Bay, $n = 38$; Bull's Bay, $n = 294$; Charleston Harbor, $n = 30$; North Edisto, $n = 19$; Saint Helena Sound, $n = 24$; Port Royal Sound, $n = 18$; Cape Canaveral, Florida, $n = 12$)
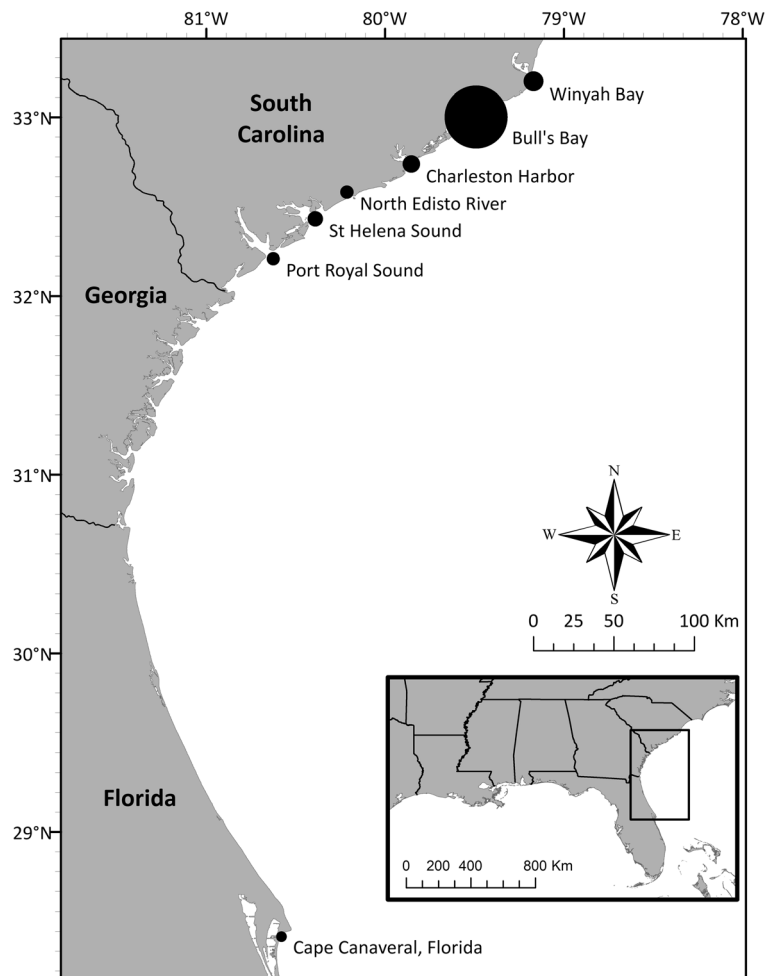
1262 mm for females) to accurately describe the population (Drymon et al. 2006). Parturition was estimated from umbilical scarring on neonates and characterized as umbilical remains, open, partially healed, mostly healed, or well healed (McCandless et al. 2007). Sexual maturity in males was determined based on fully calcified claspers, ability to rotate the clasper anteriorly, and presence of a freely opening rhipidion (Clark and von Schmidt 1965). Males who did not meet all three criteria were deemed immature. Females were considered mature if gravid or if the oviducal gland was larger than 20 mm in width and the uteri were uniformly enlarged (Castro 1993a; Walker 2007).

Morphometrics

Morphometric conversions for FL to STL and FL to PCL were generated using linear regressions.

Relationships between FL and mass were generated using non-linear least squares regressions. Analysis of covariance (ANCOVA) was used to test for significant differences ($\alpha < 0.05$) between the sexes, and if no differences were detected, sexes were combined.

Age estimation

A segment of 8–10 cervical vertebrae anterior to the origin of the first dorsal fin were removed in the field, placed in a bag on ice, and upon return to the laboratory, frozen at −20 °C. Vertebrae were allowed to thaw at room temperature for one hour prior to processing. Excess tissue was removed with a scalpel, individual vertebra were separated from the vertebral column by severing connective tissue, and vertebrae were soaked in 5% sodium hypochlorite for 5–15 min to remove remaining tissue. Residual sodium hypochlorite was

removed by rinsing the vertebrae under tap water for 5 min. Clean vertebrae were stored in tubes containing 95% ethanol until sectioned. Archived vertebrae from the previous WNA study (Drymon et al. 2006) had already been processed and were stored in 95% ethanol.

A 0.4–0.5 mm sagittal section was removed from each vertebra with a low-speed, paired diamond-bladed saw. While 0.4 mm sections work well for most vertebra, larger vertebra required slightly thicker sections to increase band pair visibility towards the margin. These sections were monitored while they dried to obtain the clearest band visibility before permanently fixing them to slides using Cytoseal-XYL (www.thermoscientific.com). If vertebrae are allowed to fully dry, band pairs may disappear which leads to under-estimation of ages (Frazier et al. 2014). Fixed slides were viewed with transmitted light on a binocular dissecting microscope at ×20 magnification. A digital camera and Image Pro-Plus 6.0 digital imaging software was used to record images. Two readers independently counted the number of translucent bands on the corpus calcareum for each vertebra without knowledge of size, sex, or date of capture. Following descriptions and terminology from Cailliet et al. (2006), translucent bands representing winter growth and opaque bands representing summer growth were identified. The birthmark (Fig. 2), represented as the change in angle of the corpus calcareum, was counted as the first band (Goldman 2005). If between-reader band counts did not match, the vertebrae were re-read simultaneously. If an agreement could not be reached, the sample was discarded from further analyses.

A birthdate of June 1 was assigned to all individuals based on umbilical scar evidence that parturition occurs from late-May to mid-June (Drymon et al. 2006). The birthmark was used as a reference point and counted as the first opaque band (Goldman 2005). The second opaque band representing summer growth was estimated to be laid down six months after birth, and the third opaque band laid down approximately one year later (Carlson et al. 2003; Drymon et al. 2006). Subsequent alternating translucent and opaque band pairs were counted as annual growth increments (Goldman 2005; Cailliet and Goldman 2012). Ages were assigned to band counts greater than two using the algorithm: estimated age = band pair count −1.5 (Carlson et al. 2003; Drymon et al. 2006). Fractional ages were calculated by setting the birth month to zero and adding the proportion of the year between the birth month and capture month
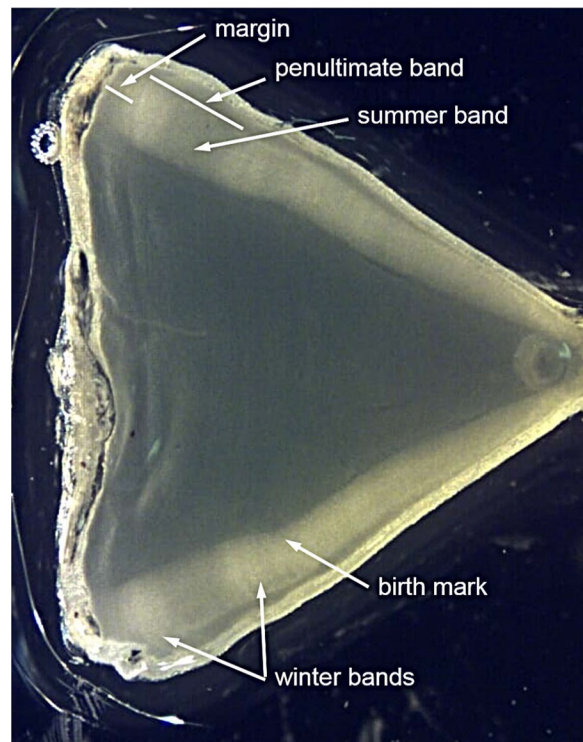

Fig. 2 Sagittal vertebra section identifying birthmark, bands and margin width for MIR analysis

using the algorithm: fractional age = band pair count − 1.5 + [(number of months between birth month and capture month)/12] (Carlson et al. 2003; Loefer and Sedberry 2003).

Precision and bias

To evaluate within reader precision and bias of age determination, a randomized subset of 100 vertebrae was read a second time by the primary reader. Original slides from the previous WNA study were also evaluated by the primary reader and compared to consensus reads from Drymon et al. (2006). To explore potential differences between vertebral drying time, newly prepared slides using archived vertebrae were aged by the primary reader and compared to consensus band counts from Drymon et al. (2006) for the same specimens to determine if age estimates varied between processing methods. Between reader precision and bias of age determinations utilized the duplicate reads of each vertebra as described above. Between reader and within reader overall percent agreement (number of vertebrae in agreement / number of vertebrae read × 100) and

percent agreement ±1 year was calculated. Reader precision was estimated using the index of average percent error (I_{APE}, Beamish and Fournier 1981):

$$I_{APE} = n^{-1} \sum_{j=1}^{n} \left[R^{-1} \sum_{i=1}^{R} \left(x_{ij} - \overline{x_j} \right) x_j^{-1} \right],$$

where n = number of sharks aged, R = number of readings for each fish, x_{ij} = age estimate of the jth fish at the ith reading, and $\overline{x_j}$ = mean age calculated for the jth fish.

In addition to I_{APE}, precision was evaluated using the coefficient of variation (C.V.) as recommended by Chang (1982):

$$CV_j = 100\% \times \left[\sqrt{\left(\sum_{i=1}^{R} \left(x_{ij} - x_j \right)^2 (R-1)^{-1} \right)} x_j^{-1} \right].$$

Following recommendations in Campana (2001), precision will be deemed acceptable with I_{APE} values less than 5.5% and C.V. values less than 7.6%. Bias was evaluated using age-bias plots (Campana et al. 1995) and tested for symmetry using Bowker's test of symmetry (Hoenig et al. 1995).

Age verification

As recommended by Goldman (2005), in the absence of direct validation, indirect methods can be used to verify the periodicity of band formation as it relates to annual growth. For individuals >1 year, the margin distance from the last opaque band to the edge of the corpus calcareum was measured and divided by the width of the penultimate band pair (Fig. 2). As recommended by Cailliet et al. (2006), verification of annual band pair deposition was evaluated using the relative marginal increment ratio (MIR, Conrath et al. 2002):

$$MIR = MW \times PBW^{-1},$$

where MW = margin width and PBW = penultimate band width. For individuals <1 year lacking a penultimate band, the developing margin width was measured and divided by the width between the birthmark and first opaque band. These individuals were evaluated separately using the algorithm:

$$MIR = MW \times FBW^{-1},$$

where MW = margin width and FBW = distance from the birthmark to the first band. Age 0 individuals

lack opaque bands beyond the birthmark and were excluded from analysis (Cailliet et al. 2006). Ratios were plotted by age class and month in which the sample was collected, and ages were pooled when samples were present throughout the year. Differences between months were detected using post hoc Tukey's honestly significant differences tests.

Growth models

Observed lengths and estimated ages (assigned and fractional) were used to generate von Bertalanffy (von Bertalanffy 1938), Gompertz (Ricker 1975) and logistic (Karkach 2006) growth models as recommended by Cailliet et al. (2006). To facilitate comparisons between studies, observed FL and estimated ages were fitted to the von Bertalanffy growth model (VBGM) (von Bertalanffy 1938) as modified by Beverton and Holt (1957):

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)} \right),$$

where L_t = length at age t, L_∞ = asymptotic length, k = coefficient of growth, and t_0 = theoretical age at length zero. Observed FL and estimated ages were also fitted to the VBGM (von Bertalanffy 1938) modified by Fabens (1965):

$$L_{(t)} = L_\infty - (L_\infty - L_0)e^{-kt},$$

where L_0 = mean length at birth. Mean length-at-birth (L_0) is a more biologically relevant parameter than t_0 for elasmobranchs and prevents over or underestimation of other life history parameters (Cailliet et al. 2006; Cailliet and Goldman 2012). This value can be compared to observations of free-swimming neonates with umbilical remains, providing a means of corroborating the model's estimated parameter (Frazier et al. 2014).

To provide the most accurate description of growth, two additional models were generated for comparison: the Gompertz growth model as modified by Ricker (1975):

$$L_t = L_0 \left(e^{G(1-e(kt))} \right),$$

where $G = \ln(L_0/L_\infty)$, and the logistic model by Karkach (2006):

$$L_t = \frac{L_0 L_\infty}{L_0 + (L_\infty - L_0)e^{-kt}}.$$

Original age and length data from the previous WNA study (Drymon et al. 2006) and GOM study (Carlson et al. 2007) were fitted to VBGM to facilitate comparisons between studies and regions. Significant differences between sexes and studies were examined using maximum likelihood ratio tests (Kimura 1980). Confidence intervals were generated by bootstrapping (5000 replicates) and model fit was evaluated using Akaike information criterion (AIC), residual plots, and residual sums of squares.

All growth modeling was completed using the FSA (Ogle 2016) or Fishmethods (Nelson 2015) packages in R (R Core Team 2016).

Maturity models

To estimate maturity, a logistic model $Y = [1 + e^{-(a + bx)}]^{-1}$ was fitted to binomial maturity data where $0 =$ immature and $1 =$ mature. A generalized linear model with a logistic link function was used to determine fork length (L_{50}) and fractional age (A_{50}) at 50% maturity. Original age, length and maturity data from the previous WNA study (Drymon et al. 2006) was also modeled to facilitate comparisons between studies. Confidence intervals were calculated by bootstrapping (5000 replicates) using the FSA (Ogle 2016) package in R (R Core Team 2016).

Results

Sample collection

A total of 435 specimens was collected ranging in size from 380 to 1282 mm FL for females ($n = 235$) and from 376 to 1174 mm FL for males ($n = 200$). Samples were collected off the coast of South Carolina (SC) from April – October ($n = 423$) with a few samples collected during the winter migration off Cape Canaveral, Florida covering the months of December, January, March, April and early May ($n = 12$) (Fig. 1). While the majority of samples were collected from 2012 to 2016 (60%, $n = 262$), the remainder of samples (40%, $n = 173$) were from 2002 to 2003.

Morphometrics

No significant differences were detected between sexes for body length measurements (ANCOVA, FL → STL: $F(2, 429) = 63,510$, $P = 0.84$; FL → PCL: $F(2, 377) = 24,590$, $P = 0.20$); therefore, sexes were combined for conversions (Table 1). Differences were detected between sexes for length to mass conversions (ANCOVA, FL → mass: $F(2, 331) = 2077$, $P < 0.001$) and are reported separately (Table 1).

Precision and bias

Of the 435 individuals aged, three specimens were discarded because a consensus could not be reached between readers. Precision results for Beamish's I_{APE} and Chang's C.V. (Table 2) were within acceptable ranges. Bowker's test of symmetry did not indicate bias between readers or between subset reads by reader 1 (Table 2). When comparing first reads, overall percent agreement for age estimates between readers was 64.1% and percent agreement ±1 band was 89.4%. Percent agreement ±1 between reader 1 and reader 2 was also evaluated for first reads in 100 mm FL bins with agreement ranging from 57.9–100% (mean ± SD: 84.2 ± 15.1). The majority of 100 mm FL size bins had percent agreement ±1 year ≥80% which increased to >90% for percent agreement ±2 years. However, there were a few exceptions. For individuals between 800 and 899 mm FL ($n = 19$), percent agreement ±1 dropped to 57.9% and 73.7% ±2 years. For individuals in the 900–999 mm FL group ($n = 27$), percent agreement was 74.1% ±1 year which increased to 92.6% ±2 years (Table 3). Females who were reaching or had reached asymptotic lengths >1200 mm FL ($n = 30$) had age estimates ranging from 10.5–22.3 years of age, and precision for this group was high at 80% ±1 year and increased to 96.7% ±3 years. Age bias plots between readers (Fig. 3a) and a random sub-set of 100 samples read twice by reader 1 (Fig. 3b) did not show systemic differences, indicating that there was no bias between readings.

Age bias plots do not show systemic differences between reader 1 and published consensus band counts for slides produced by the previous study (Fig. 4a). Percent agreement was 66.3%; however, this increased to 87.3% ±1 band count due to the previous study assigning neonates and young-of-year individuals a band count = 1, while the current study differentiated

Table 1 Morphometric conversions for length and mass of Finetooth Sharks, *Carcharhinus isodon,* in the Western North Atlantic Ocean. FL, fork length (mm); STL, stretch total length (mm); PCL, precaudal length (mm); mass (kg)

Conversion	Sex	Equation	r^2	P	n
FL to STL	Combined	$STL = 1.24 * FL + 8.56$	0.997	<0.001	432
FL to PCL	Combined	$PCL = 0.92 * FL - 12.58$	0.992	<0.001	380
FL to Mass	Female	$Mass = 3.28 \times 10^{-5} * FL^{2.84}$	0.922	<0.001	194
FL to Mass	Male	$Mass = 2.36 \times 10^{-5} * FL^{2.88}$	0.943	<0.001	140

between these groups based on umbilical scarring and complete formation of the birthmark band. Conversely, systemic bias is evident in age bias plots comparing consensus band counts for newly prepared slides to consensus band counts for the same specimens from the previous study (Fig. 4b), and percent agreement was 57.8% and 78.9% ± 1 band count.

Age verification

Annual band formation was verified by MIR for ages 0–3 years (Fig. 5). Due to decreased margin width visibility and insufficient sample sizes by month for older juveniles and adults (> 4 years of age), it was not possible to elucidate seasonal growth patterns in these age categories. For age 0–1-year individuals, mean MIR was lowest in May and greatest in October, consistent with a unimodal pattern of deposition. Differences were detected between the months ($n = 177$, ANOVA, F (5, 225.5, $P < 0.001$; Fig. 5a) with significant differences detected between every month except May and June (Tukey's HSD test). A similar unimodal pattern of deposition was observed for juveniles age 1–3 years ($n = 61$, ANOVA, F (6,23.1), $P < 0.001$; Fig. 5b); significant differences were detected between multiple months (Tukey's HSD test) with the lowest mean MIR occurring in April and the greatest in October (Fig. 5b).

Growth models

No significant temporal differences were detected based on sample collection years (2002–2003 vs. 2012–2016) (likelihood ratio test (LRT), $\chi^2 = 4.20$, d.f. = 3, $P = 0.24$) therefore all samples were combined. Significant differences were detected between sexes, necessitating sex-specific von Bertalanffy growth models (LRT, $\chi^2 = 55.58$, d.f. = 3, $P < 0.001$) (Fig. 6). Model fit was improved using fractional ages for all growth models (VBGM, Gompertz, and Logistic) based on residual

sums of squares and Akaike Information Criterion (AIC). Therefore, all age information in the results are presented using fractional ages. The VBGM provided the best fit of the models tested (Table 4) and will be presented for the remaining figures.

All free-swimming neonates with umbilical remains were captured between May 8 and June 20. No significant difference was detected in size-at-birth between the sexes (Welch t-test: t = 0.31, d.f. = 32.68, $P = 0.76$) with observed mean (± standard deviation) lengths-at-birth of 442 ± 21 mm FL (range = 331–482, $n = 68$).

Previous studies

Significant differences in von Bertalanffy growth curves (Fig. 7) were detected between the current and previous WNA studies for all model parameters for females (LRT, $\chi^2 = 8.33$, d.f. = 3, $P = 0.04$) and males (LRT, $\chi^2 = 14.98$, d.f. = 3, $P = 0.002$). No significant differences were detected between female and male *C. isodon* in the GOM (LRT, $\chi^2 = 6.60$, d.f. = 3, $P = 0.09$), but due to significant differences in the WNA, all comparisons were separated by sex. Growth models were significantly different between the regions for females (LRT, $\chi^2 = 26.23$, d.f. = 3, $P < 0.001$), and for males (LRT, $\chi^2 = 8.74$, d.f. = 3, $P = 0.03$) with significant differences detected between all parameters for both sexes (Fig. 7; Table 5).

Maturity

Maturity data was available for all individuals with age estimates. The youngest mature and oldest immature female specimens were 5.92 and 7.92 years respectively, and the smallest mature and largest immature females were 1046 and 1070 mm FL. respectively (Table 6). The L_{50} for females was 1043 ± 11.9 mm which is larger than previously reported in the WNA (Table 7, Fig. 8a). In addition, the A_{50} for females was 6.8 ±

Table 2 Precision and bias test results for Finetooth Sharks, *Carcharhinus isodon,* age estimates. Included are percent agreement, percent agreement ±1 year, Bowker's test, degrees of freedom for Bowker's test, Beamish's average percent error (I_{APE}) and Chang's coefficient of variation (C.V)

Comparison	Percent Agreement	Percent Agreement ±1	Bowker's test χ^2	Bowker's test d.f.	Bowker's test P value	Beamish's I_{APE}	Chang's C.V.
Reader 1 vs. Reader 1	71.0	88.0	23.0	22	0.40	2.6	3.6
Reader 1 vs. Reader 2	64.1	89.4	63.8	50	0.09	3.6	5.1
Reader 1 vs. Consensus	70.6	88.9	53.5	48	0.27	3.0	4.2
Reader 2 vs. Consensus	85.0	97.2	31.0	27	0.27	1.2	1.7

0.5 years which is older than previously reported (Table 7, Fig. 8b). The youngest mature and oldest immature male specimens were 5.08 and 9.25 years respectively, and the smallest mature and largest immature males were 916 and 1022 mm FL respectively (Table 6). Similar to the pattern observed in females, the L_{50} for males was 1010 ± 24.9 mm which is larger than previously reported in the WNA (Table 7, Fig. 8c). Male A_{50} in the current study was 6.6 ± 0.6 years which is older than previously reported (Table 7, Fig. 8d).

Discussion

This study found significant differences in age, growth and maturity compared to previously published studies, with observed differences in the WNA likely driven by ageing methods. Delayed age and larger lengths at maturity were found for both sexes in the WNA relative to the GOM with significantly older individuals observed in this study than previously reported in either region. These results are consistent with more recent observations of increased longevity for other species in the WNA compared to the GOM (Driggers III et al. 2004; Frazier et al. 2014; Frazier et al. 2015). The observed differences in growth between regions coupled with differences in genetic structure (Portnoy et al. 2016), tagging (Kohler et al. 1998; Kohler and Turner 2001; Tyminski et al. 2007), and reproduction (Brown 2015) provide evidence for separate populations which may benefit from regional management.

Significantly increased longevity estimates were found in the current study which is consistent with recent findings for other elasmobranchs based on genetics (Brooks et al. 2016), radiocarbon dating (Andrews et al. 2011; Natanson et al. 2014; Passerotti et al. 2014; Andrews and Kerr 2015), tag recaptures (Frazier et al. 2015), and near infrared spectroscopy (NIR) (Rigby et al. 2016). There is increasing evidence that age underestimation is frequent in elasmobranch studies and even newer methods may underestimate true age (Harry 2018). Several studies have suggested that as somatic growth slows, some species continue to lay down visible band pairs (Skomal and Natanson 2003) while other species have no discernable banding

Table 3 First-read precision of age estimates for Finetooth Sharks, *Carcharhinus isodon,* between readers as represented by percent agreement ± year. Agreement is broken down by 100 mm fork length (FL) size bins with sexes combined

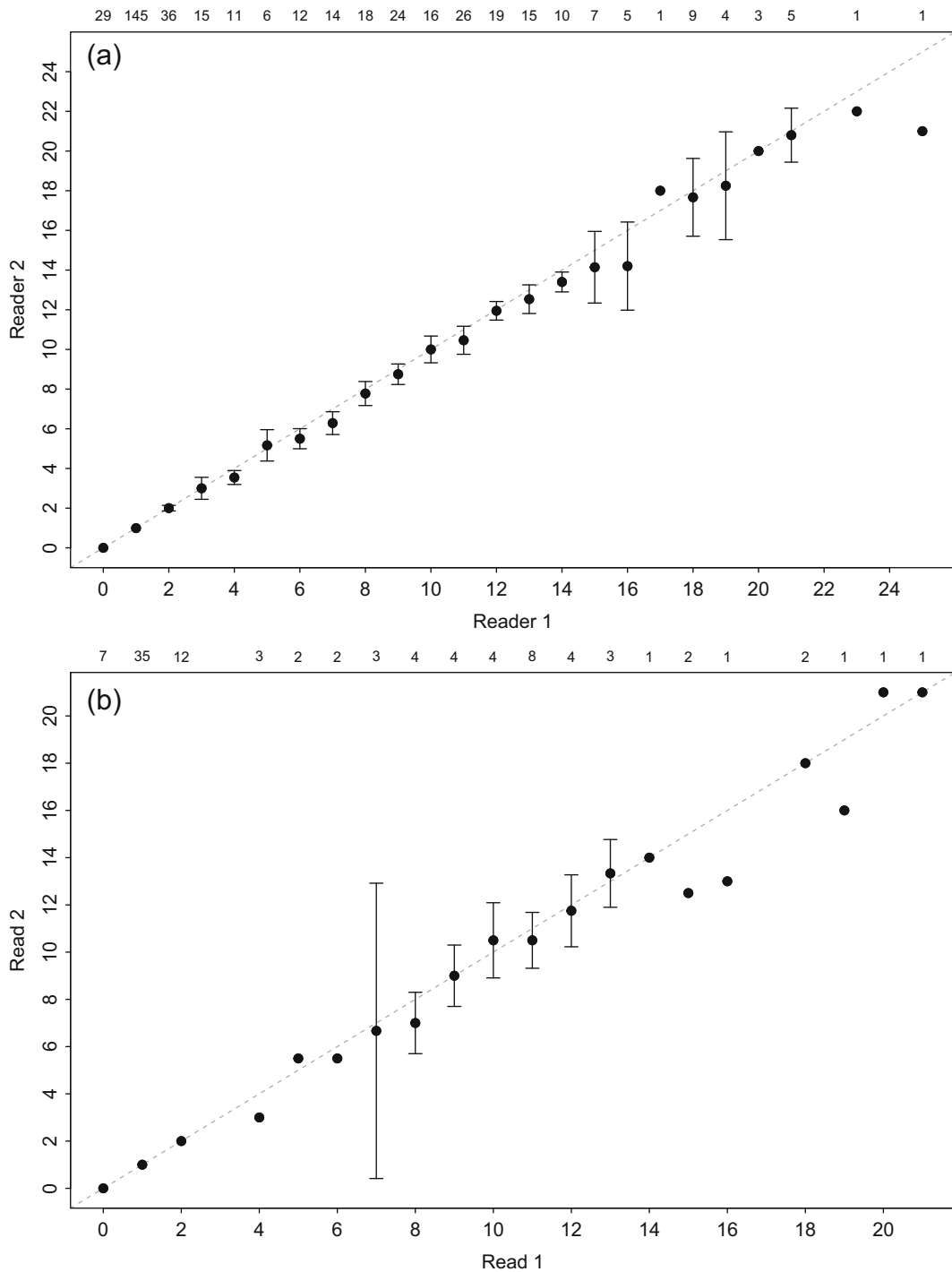| FL (mm)	n	% ± 1 year	% ± 2 years	% ± 3 years	% ± 4 years	% ± 5 years
< 600	175	100				
600–699	36	100				
700–799	15	100				
800–899	19	57.9	73.7	78.9	100	
900–999	27	74.1	92.6	100		
1000–1099	46	80.4	93.5	95.7	100	
1100–1199	84	81.0	92.9	96.4	98.8	100
> 1200	30	80.0	86.7	96.7	100	

Fig. 3 (a) Age bias plot for reader 1 vs. reader 2 and (b) age bias plot for a sub-set of 100 samples which was read twice by reader 1. Axis numbers are band counts for Finetooth Sharks, *Carcharhinus* *isodon,* lines represent a one to one relationship, circles represent the mean, and bars represent ±95% CI. Numbers at the top of each graph represent number of samples read

after a certain age (Francis et al. 2007; Harry 2018). Others suggest that banding may be more representative of somatic growth and vertebral function than

annual growth increments (Natanson et al. 2018). However, vertebra remain the most widely used method of ageing sharks and are crucial for
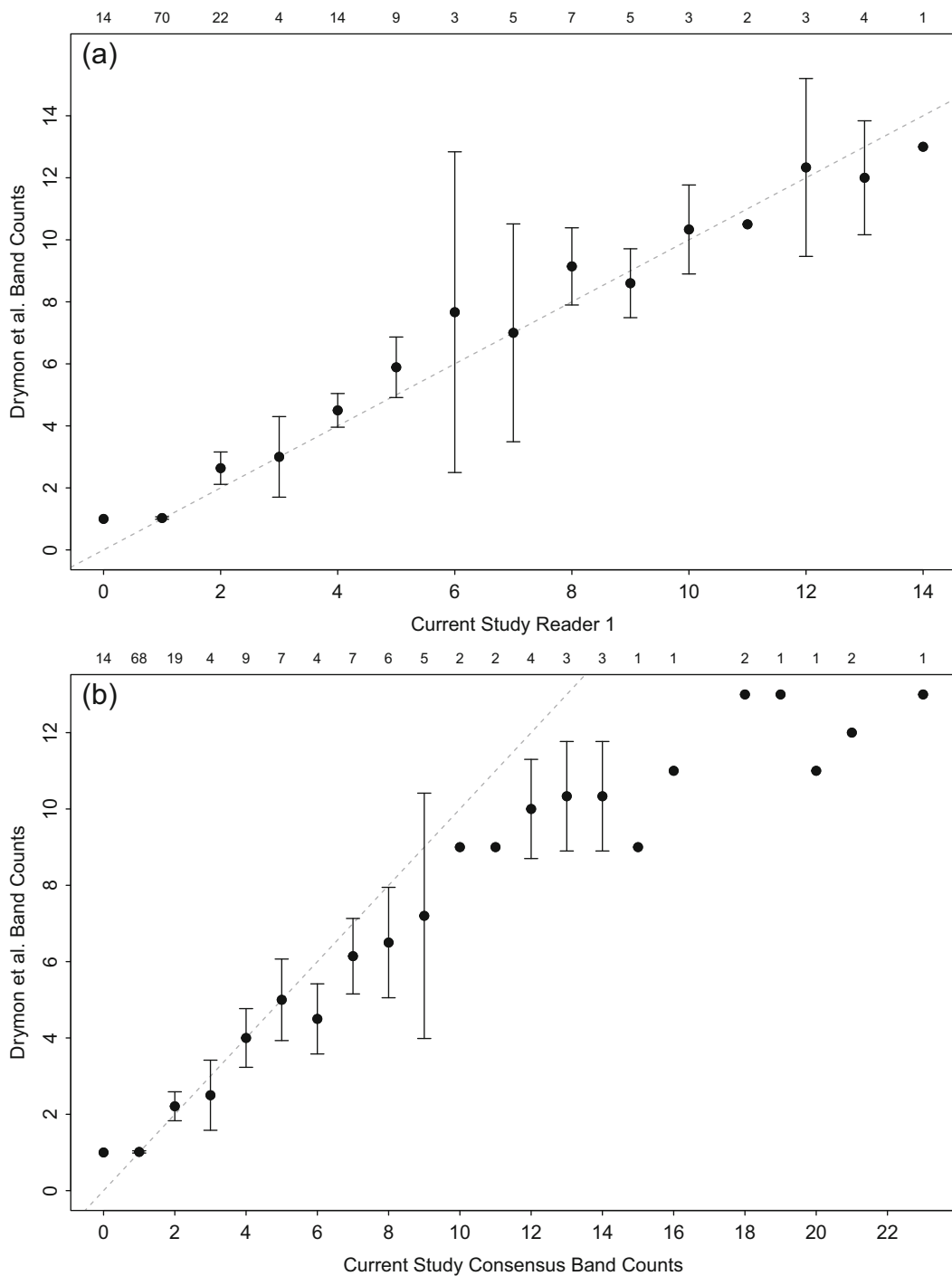
Fig. 4 Age bias plots comparing slides from a previous WNA study to slides produced during the current study for the subset of vertebral samples collected during 2002–2003. **(a)** Age bias plot for original slides comparing reader 1 vs. consensus reads from the previous study (Drymon et al. 2006) and **(b)** age bias plot comparing consensus reads for re-sectioned and "wet"-mounted vertebral slides to consensus reads of the same specimens from the previous study (Drymon et al. 2006). Axis numbers are band counts for Finetooth Sharks, *Carcharhinus isodon*, lines represent a one to one relationship, circles represent the mean, and bars represent ±95% CI. Numbers at the top of each graph represent number of samples read
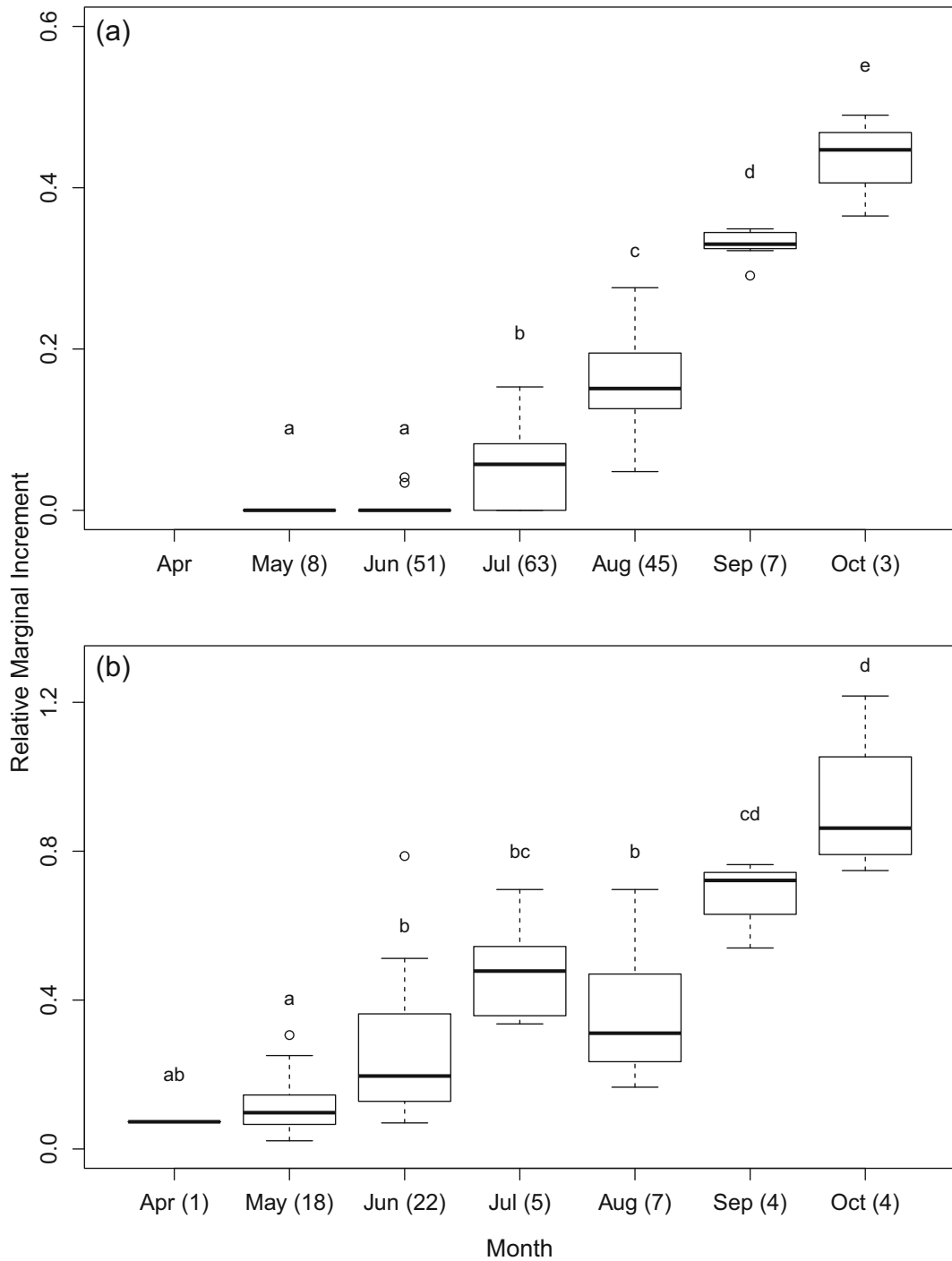
Fig. 5 Box plots of marginal increment ratios (MIR) for **(a)** age 0–1 ($n = 177$) and **(b)** age 1–3 ($n = 61$) year old Finetooth Sharks, *Carcharhinus isodon*,. Sexes are combined. Lines (——) represent mean ratio by month with boxes encompassing the 25–75% quartiles. Whiskers reflect the remaining 25% with outlying individuals represented by open circles. Sample size per month is indicated within parentheses. Significant differences between months (Tukey's HSD test, $P < 0.05$) are indicated by lower case letters

Fig. 6 von Bertalanffy growth models for Finetooth Sharks, *Carcharhinus isodon,* in the Western North Atlantic Ocean. The model was fitted to observed fork length (mm) and estimated fractional ages (years). Female (open triangles, $n = 232$) growth parameters are $L_\infty = 1253$ mm, $k = 0.20$, $L_0 = 464$ mm, and male (solid triangle, $n = 200$) parameters are $L_\infty = 1140$ mm, $k = 0.29$, $L_0 = 460$ mm
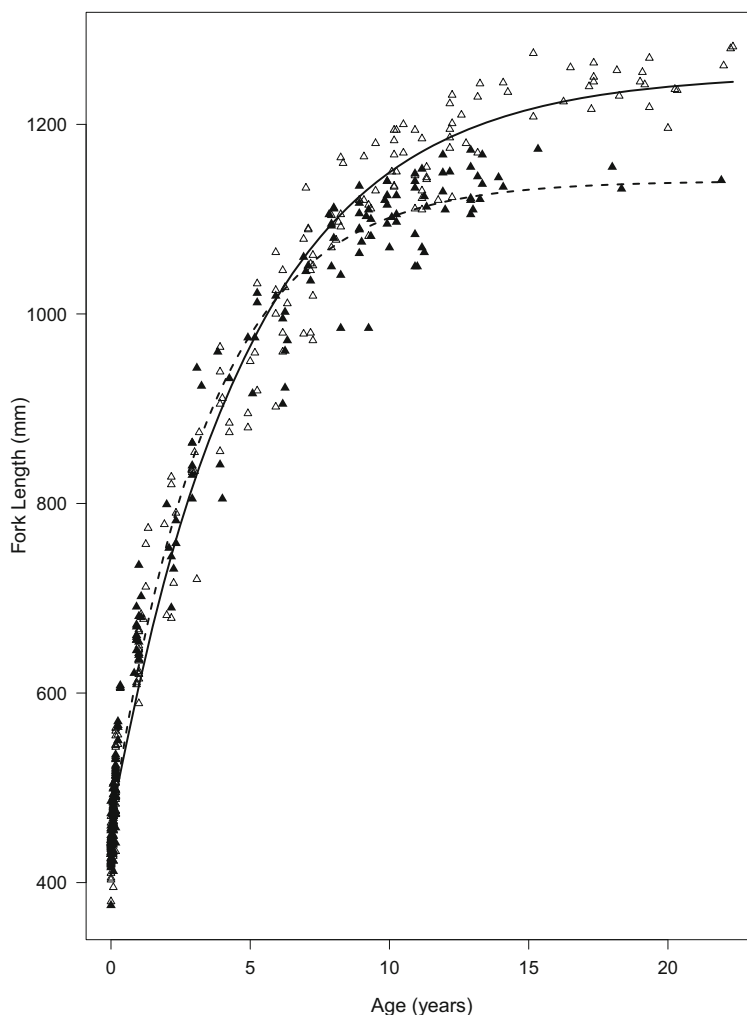
generating calibration models both for NIR and radiocarbon dating as well as providing life history parameters necessary for management decisions. Radiocarbon dating and NIR have provided validation for vertebral band pairs in multiple species up to 10–12 years but may still underestimate true age in older individuals (Andrews et al. 2011; Natanson et al. 2014; Passerotti et al. 2014; Rigby et al. 2016). In the absence of direct validation across all age ranges, it may be beneficial to use multiple methods to verify longevity whenever possible.

Unfortunately, validation in *C. isodon* has not yet been achieved. Radiocarbon dating requires either long-lived specimens of known age or historical samples collected during the pre- and post- influx of ^{14}C in the region in order to generate calibration curves (Kalish 1993). Other validation methods such

as release of aged/marked fish and the use of OTC labeling is impractical for *C. isodon* due to low recapture rates. Since 1992, SCDNR has tagged 2773 *C. isodon* in coastal waters and has recaptured or had reports of recapture from recreational and/or commercial fishermen of only 52 individuals (1.88%; SCDNR, unpubl. data). While it was not possible to validate age estimates of *C. isodon* in the current study, MIR verified the annual periodicity of band deposition for individuals aged 0–3 years. A pattern of increasing band width relative to the penultimate band width was observed from April through October, similar to results from previous studies of small coastal shark growth in the WNA (Driggers III et al. 2004; Drymon et al. 2006; Frazier et al. 2014). Based on this information, despite missing data from November thru March,

Table 4 Results from growth models fitted to observed fork lengths (mm) and estimated fractional ages (years) for Finetooth Sharks, *Carcharhinus isodon,* in the Western North Atlantic Ocean. Values in parentheses represent 95% confidence intervals (bootstrapped 5000 times). Akaike Information Criterion (AIC), residual sums of squares (RSS), and goodness of fit (r^2) are also reported. L_∞ is the mean asymptotic length, k is the growth coefficient, and L_0 is the theoretical length-at-birth

Model	Sex	L_∞	k	L_0	AIC	RSS	r^2
VBGM	Female	1253	0.20	464	2373	362,953	0.984
	95% CI	(1237–1271)	(0.19–0.22)	(455–472)			
	Male	1140	0.29	460	2023	278,335	0.983
	95% CI	(1125–1155)	(0.26–0.31)	(451–468)			
Gompertz	Female	1231	0.27	472	2417	439,347	0.981
	95% CI	(1215–1246)	(0.26–0.29)	(464–481)			
	Male	1124	0.38	466	2055	326,238	0.980
	95% CI	(1111–1138)	(0.35–0.41)	(457–475)			
Logistic	Female	1215	0.35	479	2459	527,205	0.980
	95% CI	(1201–1231)	(0.33–0.37)	(470–488)			
	Male	1114	0.48	472	2085	378,233	0.977
	95% CI	(1102–1127)	(0.45–0.52)	(463–481)			

winter band deposition likely occurs approximately six months after parturition, between December– January.

In this study a high degree of band count agreement was found, even with older specimens, which suggests that consistency in sample location along the vertebral column, processing, and reader experience may be crucial for accurate vertebral age estimations. The "wet" method of reading used in this study may also prevent loss of band visibility and has produced older age estimates in several species (Driggers III et al. 2004; Francis et al. 2007; Frazier et al. 2014) and increased longevity in the WNA has been corroborated for several species by tag recapture studies (Frazier et al. 2014; Frazier et al. 2015). This processing methodology also likely explains differences between the current and previous WNA studies (Drymon et al. 2006). The systemic bias detected between the original slides and vertebral samples re-sectioned and mounted following the "wet" methodology (Fig. 4b), as well as the high degree of precision between a wide range of ages for mature individuals nearing asymptotic lengths, suggests that changes in band clarity due to drying may be a factor in vertebral age under-estimation. However, as noted by the decrease in precision for certain size classes (Table 3), future studies may benefit from collecting additional samples in the 800– 999 mm FL size range to explore individual variability in growth prior to reaching maturity.

In the current study, length-at-birth (L_0) calculated using the original von Bertalanffy equation was compared to observations of free-swimming neonates with umbilical remains. Size estimates and 95% confidence intervals for the model fell within observed size ranges indicating the model is well anchored and provides a measure of confidence in the other parameter estimates. The previous study in the WNA reported comparable sizes at birth and dates of parturition but did not calculate mean length-at-birth (L_0). To be able to compare between the studies, L_0 values were calculated using raw data from Drymon et al. (2006) and were found to be within observed size ranges. In the GOM however, Carlson et al. (2003) reported known size-at-birth ranges of 374–414 mm FL (480–530 mm total length) which are smaller than observed size-at-birth in the WNA (389–482 mm FL). To determine if L_0 values calculated by the VBGM were consistent with observations in the GOM, raw data from Carlson et al. (2007) was used. The model generated larger and more variable L_0 size estimates (Table 5) which could mean that the original VBGM is underestimating k and overestimating L_∞ in this region.

Significant differences in *C. isodon* growth curves were detected between the sexes, which is in-agreement with the previous WNA study (Drymon et al. 2006). The current study found smaller L_∞ for both sexes compared to Drymon et al. (2006) which is likely due to a larger sample size of mature individuals (female, $n = 84$; male, $n = 67$) vs. the previous WNA study

Fig. 7 von Bertalanffy growth models fitted to estimated fractional ages (years) and observed fork lengths (mm) comparing Finetooth Sharks, *Carcharhinus isodon,* from the current study in the Western North Atlantic (WNA) to previously published studies from the WNA and eastern Gulf of Mexico (GOM) (**a**) females [WNA, current study (——); WNA, Drymon et al. 2006 (–––); GOM, Carlson et al. 2007 (⋯)] and (**b**) males [WNA, current study (——); WNA, Drymon et al. 2006 (–––); GOM, Carlson et al. 2007 (⋯)]. Parameters are listed in Table 5
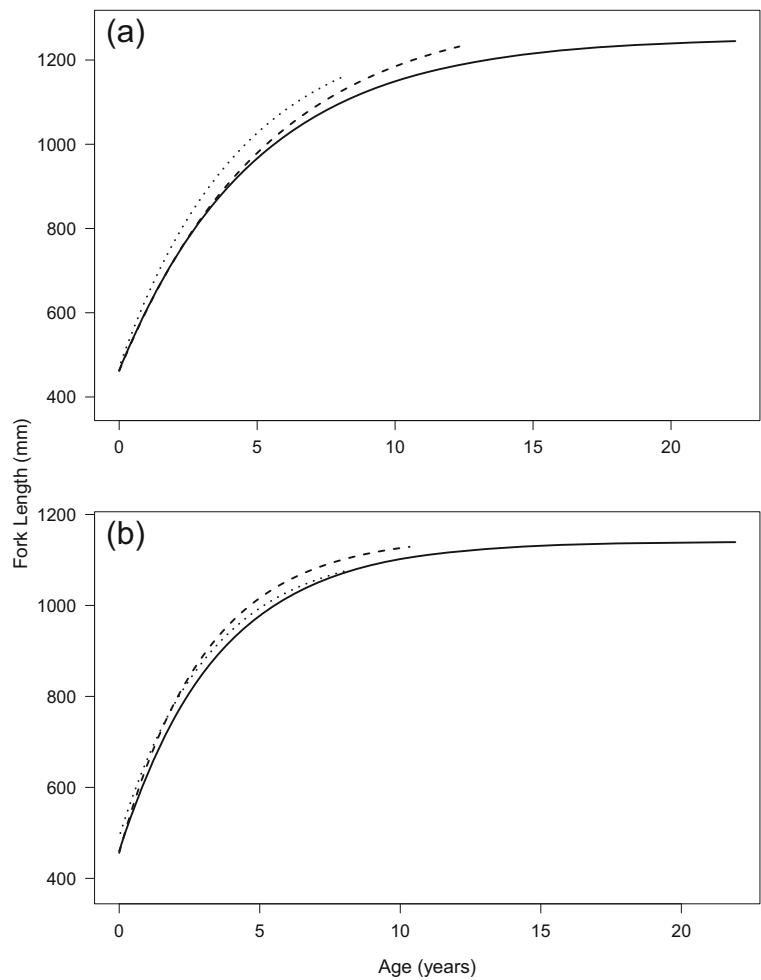
Table 5 Life history parameters reported by Carlson et al. (2007), Drymon et al. (2006) and the current Finetooth Shark, *Carcharhinus isodon,* study. Results were generated from von Bertalanffy models using observed fork length (FL (mm)) at fractional age (years) for *C. isodon* in the Gulf of Mexico and the Western North Atlantic ±95% confidence intervals. L_∞ is the mean asymptotic length, K is the growth coefficient, t_0 is the theoretical age at length = 0, and L_0 is the theoretical length-at-birth

Parameter	Sex	Sample size	L_∞ (mm FL)	K	t_o	L_o (mm FL)	Observed maximum size (mm FL)	Observed maximum age (years)
Gulf of Mexico Carlson et al. 2007[a]	Female	$n = 147$	1291 ± 120	0.23 ± 0.06	−2.00 ± 0.47	471 ± 32	1208	8.1
	Male	n = 147	1127 ± 66	0.31 ± 0.07	−1.83 ± 0.46	491 ± 34	1103	8.2
Western North Atlantic Drymon et al. 2006[a]	Female	$n = 97$	1320 ± 90	0.18 ± 0.04	−2.32 ± 0.38	461 ± 18	1262	12.3
	Male	$n = 71$	1153 ± 46	0.33 ± 0.06	−1.54 ± 0.25	456 ± 16	1174	10.3
Western North Atlantic Current Study	Female	n = 232	1253 ± 17	0.20 ± 0.02	−2.28 ± 0.14	464 ± 8.5	1282	22.3
	Male	n = 200	1140 ± 15	0.29 ± 0.03	−1.80 ± 0.14	460 ± 8.5	1174	21.9

[a] Life history parameters were calculated using original length-at-age data from Carlson et al. (2007) and Drymon et al. (2006)

Table 6 Oldest and largest immature Finetooth Sharks, *Carcharhinus isodon,* as well as the youngest and smallest mature individuals sampled during the current study in the WNA. Measurements in parenthesis are corresponding age or fork length (FL mm) of the individual

	n	Immature		Mature	
		Oldest (years)	Largest (mm FL)	Youngest (Years)	Smallest (mm FL)
Female	232	7.92 (1070)	1070 (7.92)	5.92 (1065)	1046 (6.17)
Male	200	9.25 (985)	1022 (5.25)	5.08 (916)	916 (5.08)

(female, $n = 18$; male, $n = 16$). This representative increase of mature individuals allowed the models to better estimate asymptotic lengths. Comparisons between age and length-at-maturity found increased A_{50} and L_{50} for males and females relative to previously reported values (Drymon et al. 2006).

Contrary to previously published data, significant differences in life history parameters were detected between the WNA and GOM. The current study found increased length-at-maturity and nearly double the age-at-maturity for both sexes relative to published data for the GOM (Carlson et al. 2007). Both sexes had lower growth coefficients, with males displaying larger L_∞. Contrary to expectations, the current study found females reached smaller asymptotic lengths (L_∞) than those in the GOM; however, maximum observed sizes in the WNA are greater than those reported in the GOM (Carlson et al. 2003). These regional trends of increased length and age-at-maturity, slower growth, and larger asymptotic lengths in the WNA compared to the GOM have been observed in several other small coastal sharks (Carlson and Baremore 2003; Driggers III et al. 2004; Frazier et al. 2014). Discrepancies between regions may be due to interpretation of ageing structures, genetic differences, environmental conditions, sampling that doesn't represent the population due to migration or habitat usage, gear selectivity restricting sizes captured, or even differential mortality between areas.

Maximum observed ages in the current study were almost double those previously reported likely due to differences in procedures (e.g. allowing sectioned vertebrae to fully dry before mounting). Since longevity estimates are typically based on parameters generated by growth models, values based on theoretical average maximums may not necessarily be representative of true longevity and observations of older individuals should be expected (Harry 2018). In addition, observations of significantly older individuals highlight the importance of sampling larger and older individuals in ageing studies, and it's plausible that *C. isodon* live even longer than suggested in the current study. Since age underestimation has been documented in multiple species, additional methods of validation, such as tag recaptures, would be beneficial since significantly greater longevity can influence mortality and fecundity estimates used in stock assessments.

This study provides valuable life history data for *C. isodon* in the WNA, which can help guide fishery management and conservation. Results indicate that *C. isodon* in the WNA have slower growth and greater

Table 7 Comparison of mean size (mm FL) ± 95% CI and mean age (years) ± 95% CI at maturity for Finetooth Sharks, *Carcharhinus isodon*, as reported for the GOM (Carlson et al. 2007), the WNA (Drymon et al. 2006), and the current study

Parameter	Sex	Sample size	Mean Size-at-Maturity FL mm (L_{50})	Mean Age-at-Maturity (A_{50})
Gulf of Mexico Carlson et al. 2007	Female	n = 147	990	4.2
	Male	n = 147	935	3.5
Western North Atlantic Drymon et al. 2006[a]	Female	n = 97	1022 ± 21	6.2 ± 1.2
	Male	n = 71	988 ± 60	4.9 ± 1.5
Western North Atlantic Current Study	Female	n = 232	1043 ± 12	6.8 ± 0.5
	Male	n = 200	1010 ± 25	6.6 ± 0.6

[a] Parameters were calculated using original maturity and length-at-age data from Drymon et al. (2006)
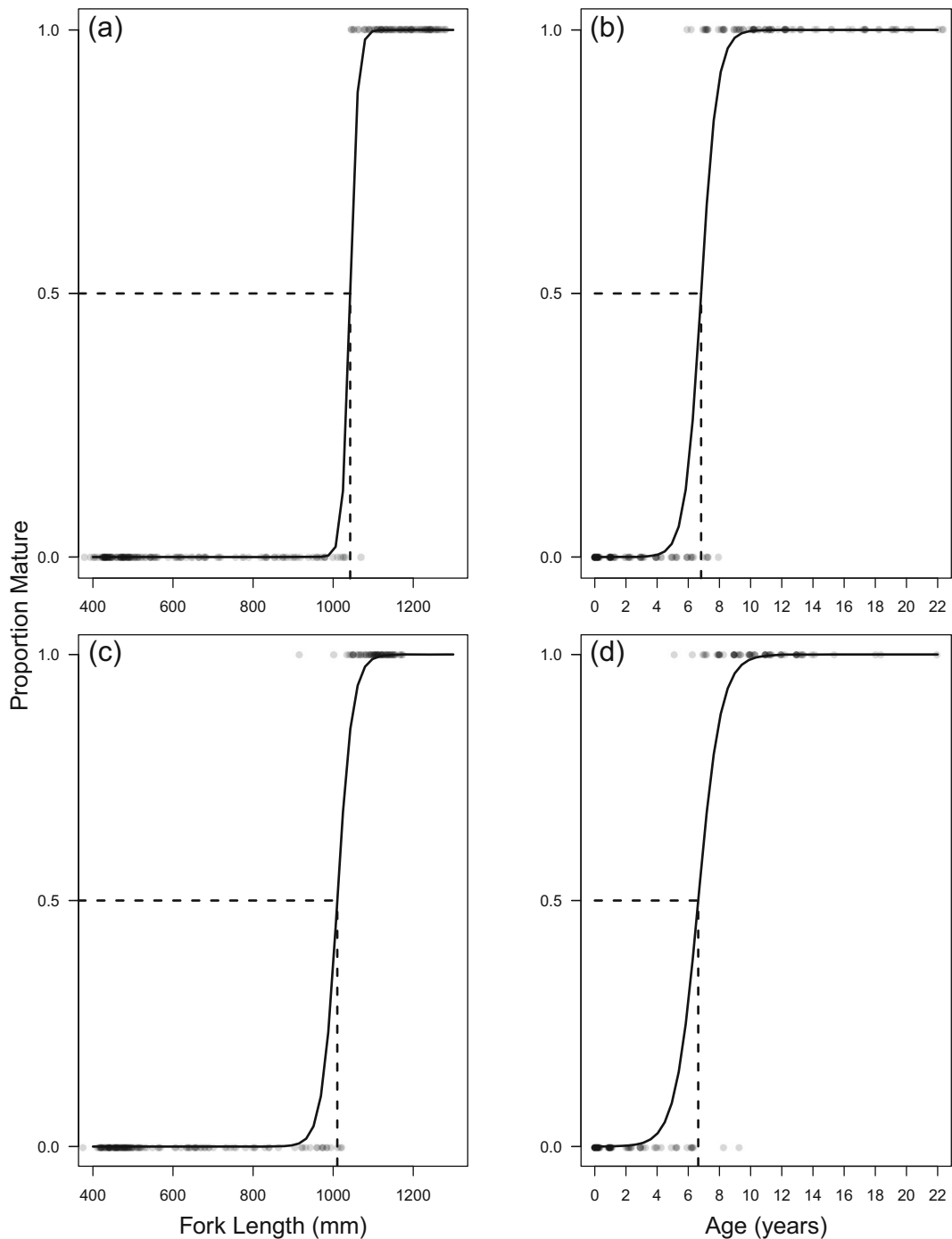
Fig. 8 Estimated fork length (mm) and age (years) at maturity for Finetooth Sharks, *Carcharhinus isodon*, in the Western North Atlantic Ocean. Lines indicate the expected proportion mature at a given fork length or age. Dashed lines indicate L_{50} and A_{50}. Diamonds indicate observed data points. Female fork length (**a**) and age (**b**); male fork length (**c**) and age (**d**)

longevity relative to conspecifics in the GOM. Additionally, delayed maturity, greater length-at-maturity, and significantly increased longevity was noted for both

sexes of *C. isodon* relative to previous studies from the WNA and GOM. These results provide additional data for use by fishery managers to assess the status of the

C. isodon stock and provide additional support for separate stocks.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical statement Specimens were collected following protocols outlined in Institutional Animal Care and Use Committee permit IACUC-2014-015 or under SCDNR scientific collection permit.

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