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Validated age, growth and maturity of the bonnethead *Sphyrna tiburo* in the western North Atlantic Ocean

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The age, growth and maturity of bonnetheads *Sphyrna tiburo* inhabiting the estuarine and coastal waters of the western North Atlantic Ocean (WNA) from Onslow Bay, North Carolina, south to West Palm Beach, Florida, were examined. Vertebrae were collected and aged from 329 females and 217 males ranging in size from 262 to 1043 mm and 245 to 825 mm fork length, L_F, respectively. Sex-specific von Bertalanffy growth curves were fitted to length-at-age data. Female von Bertalanffy parameters were $L_\infty = 1036$ mm L_F, $k = 0{\cdot}18$, $t_0 = -1{\cdot}64$ and $L_0 = 272$ mm L_F. Males reached a smaller theoretical asymptotic length and had a higher growth coefficient ($L_\infty = 782$ mm L_F, $k = 0{\cdot}29$, $t_0 = -1{\cdot}43$ and $L_0 = 266$ mm L_F). Maximum observed age was 17·9 years for females and 16·0 years for males. Annual deposition of growth increments was verified by marginal increment analysis and validated for age classes 2·5+ to 10·5+ years through recapture of 13 oxytetracycline-injected specimens at liberty in the wild for 1–4 years. Length (L_{F50}) and age (A_{50}) at 50% maturity were 819 mm and 6·7 years for females, and 618 mm and 3·9 years for males. Both female and male *S. tiburo* in the WNA had a significantly higher maximum observed age, L_{F50}, A_{50} and L_∞, and a significantly lower k and estimated L_0 than evident in the Gulf of Mexico (GOM). These significant differences in life-history parameters, as well as evidence from tagging and genetic studies, suggest that *S. tiburo* in the WNA and GOM should be considered separate stocks.

Key words: longevity; elasmobranch; life history; oxytetracycline.

INTRODUCTION

Over the past 400 million years, elasmobranchs have evolved life-history strategies that are unique among fishes. Elasmobranchs as a group are generally characterized as slow growing and late maturing, with relatively long gestational periods and low fecundity. These characteristics make this group of fishes especially vulnerable to fishing pressure when compared with teleosts (Holden, 1977), and once a stock is affected, it can be slow

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to recover (Hoenig & Gruber, 1990). Efforts to conserve and manage-depleted elasmobranch populations are further complicated by the lack of life-history information for commercially and recreationally important species such as the bonnethead *Sphyrna tiburo* (L. 1758).

Sphyrna tiburo is a relatively small shark, reaching a maximum size of 1500 mm total length (L_T) (Castro, 2011). This species inhabits the estuaries and shallow coastal waters of the western Atlantic Ocean from North Carolina to southern Brazil including the Gulf of Mexico (GOM) and the Caribbean Sea (Compagno, 1984). In the Atlantic Ocean waters off the east coast of the southern U.S.A. (western North Atlantic Ocean, WNA), *S. tiburo* are relatively common with juvenile and mature females inhabiting estuarine waters during late spring to early autumn, and juvenile and adult males primarily occurring in shallow coastal waters (Ulrich *et al.*, 2007).

Recent studies of small coastal shark species have shown significant differences in life-history parameters within species and among regions (Carlson *et al.*, 1999; Carlson & Baremore, 2003; Loefer & Sedberry, 2003; Driggers *et al.*, 2004; Carlson & Loefer, 2007). To account for these differences, the 2007 Southeast Data, Assessment and Review (SEDAR, 2007) small coastal shark stock assessment provided an all inclusive group assessment as well as species-specific assessments. Where data allowed, separate assessments were also conducted for the WNA and GOM regions to account for the spatial differences in life-history traits found in previous studies. When sufficient data exist and life-history differences are evident, stocks are assessed and managed by region (SEDAR, 2011*a*, *b*, *c*, *d*). A regional assessment allows the incorporation of localized life-history and mortality data giving managers population-specific assessment results that allow for more informed management of resources.

SEDAR (2007) listed *S. tiburo* as not overfished, with no overfishing occurring; however, separate regional assessments for *S. tiburo* were not conducted due to the paucity of life-history information for the WNA region. The GOM life-history parameter estimates were used for both regions, which could have led to incorrect conclusions regarding the status of the WNA population (SEDAR, 2007). No observations of individuals moving between the WNA and GOM have been reported (Kohler & Turner, 2007; Tyminski *et al.*, 2013), and preliminary genetic data (Diaz-Jaimes *et al.*, 2013) suggest the existence of two stocks. Therefore, area-specific life-history parameters for the WNA are probably necessary.

Studies completed by Parsons (1993*a*, *b*), Carlson & Parsons (1997) and Lombardi-Carlson *et al.* (2003) fully characterized the age, growth and reproduction of *S. tiburo* in the eastern GOM. Parsons (1993*a*) validated vertebral growth band periodicity with oxytetracycline (OTC) in age classes from 1 to 6 years old; however, the majority of these were animals kept in captivity. In order to attempt to validate all age classes, this project expands upon the OTC validation work completed by Parsons (1993*a*). The objectives of this study were to characterize the age, growth, and size and age at maturity of *S. tiburo* in the WNA, and validate the periodicity of vertebral band-pair formation. The life-history parameters generated from this study were compared to the parameters generated for *S. tiburo* in the eastern GOM (Lombardi-Carlson, 2007) to determine if regional differences were present.

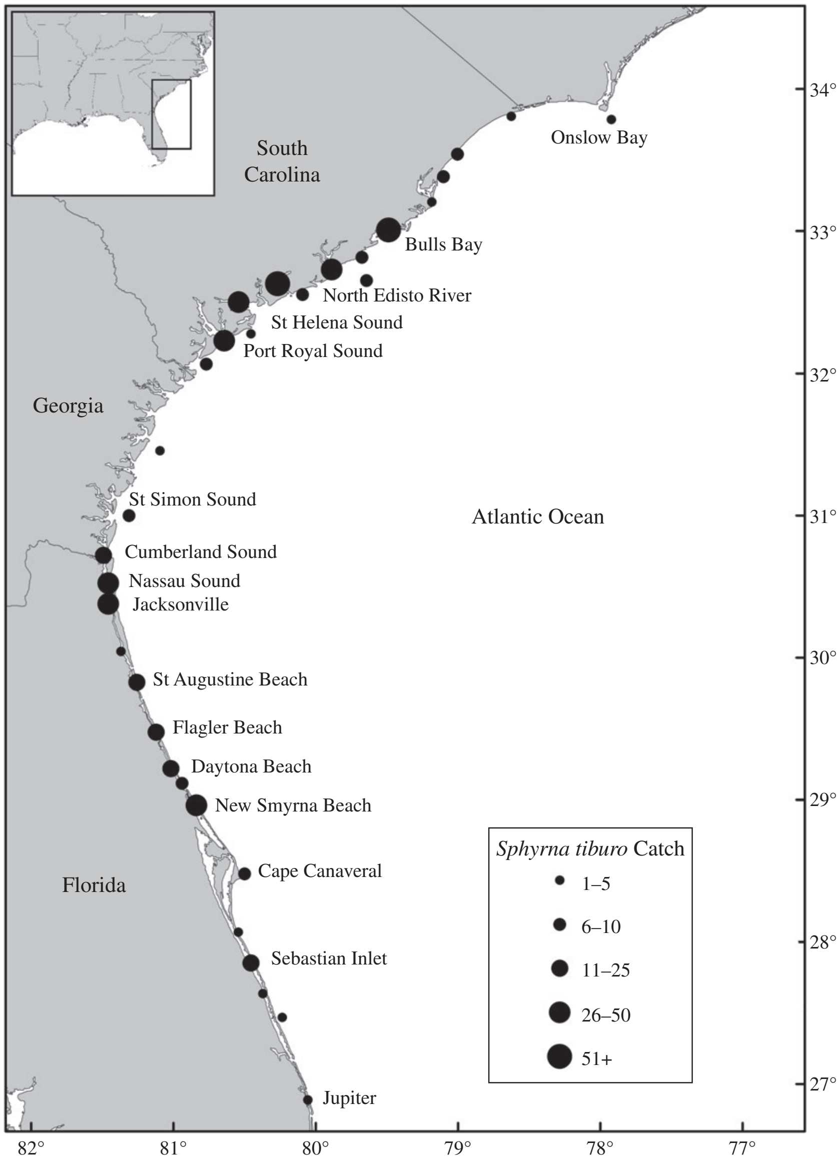

FIG. 1. Map of western North Atlantic Ocean with sampling locations and abundance.

MATERIALS AND METHODS

SAMPLE COLLECTION

Sphyrna tiburo were collected between April 2000 and September 2013 from the coastal and estuarine waters of North Carolina, South Carolina, Georgia and Florida (Fig. 1). Samples were provided by three surveys: the South Carolina Department of Natural Resources' (SCDNR) Cooperative Atlantic States Shark Pupping and Nursery Habitat Survey (COASTSPAN), the Southeast Area Monitoring and Assessment Program (SEAMAP) and the Florida Fish and

Wildlife Research Institute's (FWC-FWRI) Fisheries-Independent Monitoring Program. Gears used for collection included gillnets, seines, longlines, hook and line, and otter trawls. Specimens were also collected from fishery-dependent sources including recreational hook and line, and commercial longlines.

For SCDNR and SEAMAP samples, the pre-caudal (L_{PC}), fork (L_F) and stretch-total (L_{ST}) lengths of all *S. tiburo* were measured in a straight line along the axis of the body to the nearest millimetre. The FWC-FWRI also measured L_{PC} and L_F, but measured L_T instead of L_{ST}. Mass was measured to the nearest 0·25 kg using a spring balance. Sharks collected were stored on ice and processed by the protocol described below. Initially, *S. tiburo* were randomly sacrificed for age estimates and maturity assessments. Once a sample of 100 individuals per sex was obtained, individuals were then sacrificed as encountered if they filled a gap in length of the existing dataset with the goal of obtaining at least two male and two female *S. tiburo* per 10 mm L_F increment from 250 to 1050 mm for females, and 240 to 850 mm for males, corresponding to observed L_F at birth and maximum observed L_F for each sex (Ulrich *et al.*, 2007).

REPRODUCTIVE CONDITION

Gross reproductive status was noted, and females were considered mature if they had developing pups, vitellogenic follicles (>10 mm) and developed uteri and oviducal glands (Parsons, 1983). Males were considered mature if they had fully calcified, rotating claspers, functional siphon sacs and functional rhipidions (Clarke & von Schmidt, 1965). When present, umbilical scars observed on neonates were characterized as: umbilical remains, fresh, partially healed, mostly healed and well healed according to Aubrey & Snelson (2007).

Morphometric conversions were generated using linear regression for L_F to L_{PC} and L_F to L_{ST}. Fork length to mass data were ln transformed and conversions were generated using two parameter power equations. All available SCDNR length data were used for L_F to L_{ST} regressions, only specimens sacrificed for this study were used for L_F to L_{PC} regressions. Analysis of covariance (ANCOVA) was used to test for significant differences between sexes. If no significant differences were encountered, combined conversions were generated. These and all subsequent statistical tests were considered significant at $\alpha < 0{\cdot}05$.

AGE ESTIMATION

Vertebral samples were removed from all sacrificed specimens and stored frozen. Each sample comprised a section of up to 12 vertebrae taken from the cervical region of the vertebral column. To prepare vertebrae for analysis, sections were thawed and excess tissue was removed from the vertebral column by scalpel. The column was separated into individual vertebra by severing connective tissues (*e.g.* intervertebral ligaments). Vertebrae were then soaked in 5% sodium hypochlorite for 3–15 min to remove remaining muscle tissue, rinsed under running tap water for 5 min and stored in 95% ethanol. Each vertebra was then mounted on a glass slide using Crystalbond 509 (www.2spi.com) and a 0·4 mm sagittal section containing the focus was removed using a Buehler isomet low-speed saw (www.buehler.com). The section was monitored while drying to ensure a preferred viewing state before being permanently mounted and preserved on a glass slide using Cytoseal-XYL (www.thermoscientific.com). If allowed to fully dry before mounting and preserving, band pairs may disappear, leading to underestimation of age (W. B. Driggers, pers. obs.). Each mounted vertebra was examined using a Nikon SMT-2T dissecting microscope (www.nikoninstruments.com) at ×20 magnification with a transmitted light source. A Scion Model CFW-1310C colour digital camera with Image-Pro Plus 6.0 digital imaging software (www.scioncorp.com) was used to record images, and to count and measure increments for marginal increment analysis.

Vertebral samples were selected at random and the number of translucent bands on the corpus calcareum was counted independently by two readers, each without knowledge of the other's reading or of the sex, size or date of capture of the shark from which the section was removed. Opaque bands representing summer growth and translucent bands representing winter growth (Fig. 2) were identified following the description and terminology of Cailliet & Goldman (2004). The birthmark, or change in angle of the corpus calcareum, was identified and counted as the first band. If there were discrepancies between readings, the section was re-read simultaneously

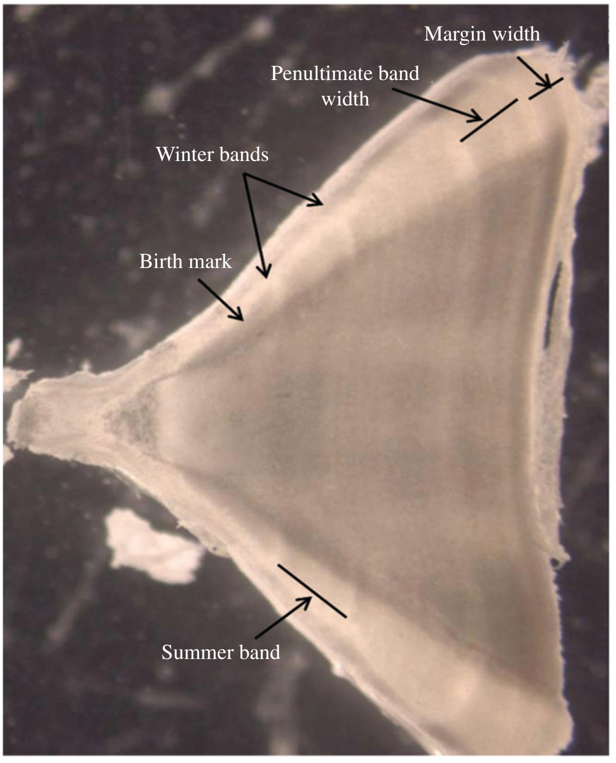

FIG. 2. Sagittal vertebra section from *Sphyrna tiburo* showing locations of birth mark, summer bands, winter bands, penultimate band width and margin width.

by both readers to resolve the difference. If no agreement was reached, the sample was discarded from all analyses.

A birth date of 30 September was assigned to all individuals based on the evidence that parturition in *S. tiburo* takes place over a period of several weeks during late September (SCDNR, unpubl. data). In the GOM, Parsons (1993*a*) found that the first translucent band, which represents winter growth, completes its formation in February at an age of 5 months. The first opaque band (summer growth) is completed 9 months later in November at an age of 14 months. Subsequent winter and summer band pairs were then laid down annually in the same months. Owing to variability in the presence of a translucent birthmark, the change in the angle of the corpus calcareum was counted as a birthmark or band for individuals without a discernible band (Goldman, 2004). The second band representing winter growth was assumed to form 5 months later. Therefore, for all band counts of two and above, the assigned age equals the band-pair count minus 1·5. In addition to assigned ages, fractional ages were calculated by setting the birth month as zero, and dividing the capture month by 12 (Loefer & Sedberry, 2003).

READER PRECISION AND BIAS

Multiple methods were used to examine reader bias and precision. Overall per cent agreement was the number agreed between readers divided by number read $\times 100$; the per cent agreement +1 year was calculated to evaluate the precision of data. Per cent agreement was also examined in 100 mm L_F groups as recommended by Goldman (2004). Age agreement tables were generated and tested for symmetry using Bowker's test of symmetry (Hoenig *et al.*, 1995). Age bias plots (Campana *et al.*, 1995) were used to evaluate reader bias. A sub-set of 100 randomly selected specimens was also re-read by reader 1 to examine within-reader bias. The index of average per cent error [I_{APE}; Beamish & Fournier (1981)] was calculated to assess between-reader error: $I_{APE} = n^{-1} \sum_{j=1}^{n} \left[R^{-1} \sum_{i=1}^{R} \left(x_{ij} - \bar{x}_j \right) x_j^{-1} \right]$, where n = number of sharks aged, R = number of times each fish is aged, x_{ij} = ith age estimation of jth fish at ith reading and $\bar{x}_j$ = mean age calculated for the jth fish. While I_{APE} assumes that S.D. of age estimates is proportional to the mean of the age estimates, Chang (1982) instead suggested that the coefficient of variation (C.V., Z) should be used to measure precision $Z = n^{-1} \sum_{j=1}^{n} 100 \left\{ \sqrt{\left[\sum_{i=1}^{R} \left(x_{ij} - \bar{x}_j \right)^2 (R-1)^{-1} \right]} x_j^{-1} \right\}$. Tests of precision and bias were generated using the FSA (Ogle, 2012) package in R (www.r-project.org).

AGE VERIFICATION

To verify the periodicity of band-pair formation, marginal increment analysis was used. The distance of the last opaque band to the edge of the corpus calcareum was divided by the width of the penultimate growth band pair. Verification of the annual period of band formation was performed using the relative marginal increment ratio (R_{MI}) (Conrath *et al.*, 2002) as recommended by Cailliet *et al.* (2006): $R_{MI} = W_M\ W_{PB}^{-1}$, where W_M is the margin width and W_{PB} is the penultimate band width. For specimens >1 year old, the margin width was divided by the penultimate band width (Fig. 2), whereas for specimens <1 year old, the margin width was divided by the distance to the birthmark. One-way analysis of variance (ANOVA) and Tukey's test for honestly significant differences (HSDs) were run in R to test for significant differences in R_{MI} between months. R_{MI} data were tested for normality using the Shapiro–Wilk test, and ln transformed if they did not meet the assumption of normality.

AGE VALIDATION

The periodicity of vertebral band-pair formation was validated using recaptured specimens that had previously been injected with OTC. During routine and targeted gillnet sampling by the SCDNR COASTSPAN survey in the North Edisto River, South Carolina (Fig. 1), healthy *S. tiburo* were transported by holding tank to Bears Bluff National Fish Hatchery (located on Wadmalaw Island, South Carolina <1·6 km from sampling location) where biologists measured, weighed, tagged and intra-muscularly injected OTC at a dosage of 25 mg kg^{-1} body mass (Gelsleichter *et al.*, 1998). The *S. tiburo* were then released into holding tanks in groups of no more than six fish. They were fed a mix of Atlantic mackerel *Scomber scombrus* L. 1758, blue crab *Callinectes sapidus* and Atlantic white shrimp *Litopenaeus setiferus* to satiation daily. Owing to the potential for angler's catching and consuming OTC-injected *S. tiburo*, they were held for 30 days to allow the dispersal of OTC from edible tissues before being released back into the North Edisto River.

Post-release, an index station in the North Edisto River was sampled twice a month as part of routine COASTSPAN sampling. Recaptured individuals were sacrificed if they had been at liberty for >9 months and processed as previously described. Vertebrae with assumed OTC reference marks were stored in 95% ethanol in the dark to prevent degradation of photosensitive OTC reference marks. The vertebral sections were examined under ultraviolet (UV) light to determine the presence of an OTC mark. The position of a detected OTC mark was then compared with the observed band pairs to validate the hypothesis of deposition of one band pair per year. Age at initial tagging was backcalculated for OTC- and non-OTC-sacrificed recaptures by subtracting time-at-liberty from estimated age. The L_F at initial tagging, backcalculated ages, estimated ages and L_F at recapture were plotted against the preferred growth model curves to allow visual comparison of observed growth *v.* predicted growth.

GROWTH MODELS

Observed L_F and age estimates (actual and fractional) were used to generate von Bertalanffy (von Bertalanffy, 1938), Gompertz (Ricker, 1975) and logistic (Ricker, 1979) growth models. The von Bertalanffy growth model as adapted by Beverton (1954) and Beverton & Holt (1957) is:

$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right)$, where L_t is length-at-age t and L_∞ (asymptotic length), k (coefficient of growth) and t_0 (theoretical age at which length equals zero) are fitted parameters. The original von Bertalanffy growth model was also fitted to data as recommended by Cailliet *et al.* (2006) $L_t = L_\infty - (L_\infty - L_0)e^{-kt}$, where L_0 (mean length at birth) is a fitted parameter. For comparisons, mean size-at-birth was determined for males and females through measurements of free swimming neonates with an umbilical stage of open, partly healed or mostly healed. The modified form of the Gompertz growth model was generated (Ricker, 1975), and is expressed following Mollet *et al.* (2002) as $L_t = L_0 \left(e^{G\left(1-e^{(-kt)}\right)}\right)$, where $G = \ln(L_0 L_\infty{}^{-1})$ is a fitted parameter. A logistic model was generated for both length and mass (Ricker, 1979) $L_t = L_\infty\{1 + e^{[-k(t-a)]}\}^{-1}$ and $W_t = W_\infty\{1 + e^{[-k(t-a)]}\}^{-1}$, where W_t is mass at age t and W_∞ (theoretical maximum mass), k (instantaneous rate of growth when W approaches 0) and a [time at which the absolute rate of increase in mass begins to decrease or the inflection point of the curve, equivalent to t_0 in Ricker (1979)] are fitted parameters. Confidence intervals for all model parameters were generated by bootstrapping (1000 replicates). Models and confidence intervals were generated using the FSA (Ogle, 2012) package in R. Model fit and selection were assessed by examination of residuals, Akaike information criterion [AIC, Akaike (1973)] and residual sums of squares. Examination of residuals and residual sums of squares was used to assess relative strength of models fit to assigned or fractional age data sets.

To examine potential differences in growth parameters between males and females, sex-specific growth curves were estimated. Maximum likelihood ratio tests (Kimura, 1980) generated using the fishmethods (Nelson, 2013) package in R were used to detect if there were significant differences between male and female parameters in the WNA, as well as sex-specific latitudinal differences (South Carolina *v.* Florida). Original L_F at age raw data from Lombardi-Carlson (2007) were used to generate GOM von Bertalanffy parameters for comparison. New curves needed to be generated as L_T at band count was originally used to generate parameters for the GOM *v.* L_F at age for the WNA. If L_F was missing from an aged GOM individual, a GOM-specific L_T to L_F regression from Lombardi-Carlson (2007) was used to convert measurements. Likelihood ratios were used to test for regional differences in sex-specific parameters between the GOM and WNA. Theoretical maximum age was estimated to be the age at which 95% of the theoretical maximum length is reached, using the formula $[5 (\ln 2)]\, k^{-1}$ (Fabens, 1965).

MATURITY MODELS

To determine median fork length (L_{F50}) and age (A_{50}) at which 50% of the population was considered mature, a logistic model $Y = [1 + e^{-(a+bx)}]^{-1}$ was fitted to binomial maturity data using non-linear least squares regression, where 0 = immature and 1 = mature. Median L_{F50} and A_{50} at maturity was determined by $-a\, b^{-1}$ (Mollet *et al.*, 2002). Models and confidence intervals were generated using the FSA (Ogle, 2012) package in R. Confidence intervals were generated by bootstrapping (1000 replicates). The parameters generated by this study were compared with GOM L_{F50} and A_{50} generated by Frazier *et al.* (2013) using original raw L_F and age data from Parsons (1993*a*) and Lombardi-Carlson (2007).

RESULTS

SAMPLE COLLECTION

A total of 555 specimens were collected with a size range of 245–825 mm L_F for males ($n = 219$) and 262–1043 mm L_F for females ($n = 336$). The majority of specimens were collected from April to October ($n = 544$), with limited samples ($n = 11$) collected in March, November and December. Owing to seasonal growth that occurred when *S. tiburo* had migrated away from waters sampled by participating surveys, not

TABLE I. Morphometric conversions for length and mass of *Sphyrna tiburo* in the western North Atlantic Ocean

Conversion	Sex	Equation	r^2	P	n
$L_F \rightarrow L_{ST}$	Combined	$L_{ST} = 1 \cdot 198(L_F) + 39 \cdot 1$	0·994	<0·001	2747
$L_F \rightarrow L_{PC}$	Combined	$L_{PC} = 0 \cdot 925(L_F) - 9 \cdot 03$	0·999	<0·001	507
$L_F \rightarrow M_T$	Female	$M_T = 3 \cdot 462 \times 10^{-6} \times L_F^{3 \cdot 208}$	0·984	<0·001	200
$L_F \rightarrow M_T$	Male	$M_T = 4 \cdot 482 \times 10^{-6} \times L_F^{3 \cdot 126}$	0·968	<0·001	155

L_{ST}, stretch total length (mm); L_F, fork length (mm); L_{PC}, precaudal length (mm); M_T, mass (kg).

all size bins were filled. Samples were collected in coastal waters throughout the WNA (Fig. 1) with most samples from South Carolina (59·3%) and Florida (37·8%).

MORPHOMETRICS

There were no significant differences for body length measurements; therefore, sexes were combined for morphometric conversions (ANCOVA, $L_F \rightarrow L_{ST}$: $F_{1,534} = 0{\cdot}52$, $P > 0{\cdot}05$; $L_F \rightarrow L_{PC}$: $F_{1,504} = 0{\cdot}37$, $P > 0{\cdot}05$; Table I). Mass data were only available for SCDNR and SEAMAP specimens. Significant differences were found for L_F and mass data for males and females (ANCOVA, $F_{1,352} = 80{\cdot}65$, $P < 0{\cdot}001$); therefore, equations for these conversions are reported separately (Table I).

READER PRECISION AND BIAS

Of the 555 specimens aged, nine were discarded because a consensus age could not be reached. Age estimates between readers agreed for 59·5% of samples examined and per cent agreement ± 1 band was 90·8%. Per cent agreement ± 1 band was also examined in 100 mm increments with sexes separate and combined. Female increment agreement ranged from 78·6 to 100% (mean ± S.D. = 91·0 ± 7·7), male increment agreement ranged from 86·2 to 100% (mean ± S.D. = 96·4 ± 5·9) and combined increment agreement ranged from 84·1 to 100% (mean ± S.D. = 92·9 ± 5·8). Bowker's test of symmetry did not indicate bias between reader 1 and reader 2, and no bias was observed in a sub-set of 100 samples read twice by reader 1 (Table II). Results from Beamish's I_{APE} and Chang's C.V. (Table II) suggest that assigned ages are acceptably precise based on resulting C.V.s all being <5%, (Campana, 2001). Age bias plots for reader 1 *v*. reader 2 revealed no systematic differences between readers among age classes [Fig. 3(a)] and a sub-set of 100 samples read twice by reader 1 showed no bias between readings [Fig. 3(b)].

AGE VERIFICATION

Marginal increment analysis verified annual band formation for ages 0–4 years. *Sphyrna tiburo* specimens aged 0–1 R_{MI} ($n = 55$) reflected a shorter time period of optimum growth for the previous band (birthmark to first winter band) than R_{MI} in older specimens ($n = 85$). Observed age 0–1 R_{MI} approached and was even larger than an R_{MI} of 1 [Fig. 4(a)]. Significant differences between months were detected (ANOVA, $F_{6,57} = 8{\cdot}44$, $P < 0{\cdot}001$). Significant differences in age 0–1 R_{MI} were

TABLE II. Results for tests of precision and bias of *Sphyrna tiburo* age estimates including: per cent agreement, per cent agreement ± 1 year, Bowker's test (χ^2, d.f. and *P*-value), Beamish's average per cent error (I_{APE}) and Chang's coefficient of variation (C.V.)

Reader comparison	Per cent agreement	Per cent 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 *v.* reader 2	59·5	90·8	35·57	40	0·669	3·30	4·66
Reader 1 *v.* final	80·0	98·0	27·49	25	0·332	1·33	1·88
Reader 2 *v.* final	73·9	93·6	28·11	35	0·789	2·19	3·09
Reader 1 *v.* reader 1	63·0	99·0	8·87	15	0·884	2·71	3·83

detected between April and June to August, and May and August (Tukey's HSD test). The largest observed differences between mean R_{MI} were between April and August.

Increments beyond 4 years of age were excluded as margin widths became too small to elucidate seasonal differences. Ratios for age-1–4 year fish followed a similar pattern to R_{MI} from age-0–1 year specimens [Fig. 4(b)], and significant differences between months were detected (ANOVA, $F_{8,76} = 5·2$, $P < 0·001$). Significant differences were detected between April and September to November, May and October to November, and June and September to October (Tukey's HSD test). The largest observed differences in R_{MI} were observed between May and October.

AGE VALIDATION

A total of 60 *S. tiburo* were captured and injected with OTC, held at Bear's Bluff National Fish and Wildlife Hatchery and subsequently released. Of those, 13 were recaptured, with time-at-liberty ranging from 10·5 months to 4·1 years (Table III). All recaptured specimens had a visible OTC reference mark in the vertebral section when viewed under UV light. Ages of specimens ranged from 2·8 to 7·0 years at initial tagging, and 3·7 to 10·5 years when sacrificed. On the basis of length, six were noted as immature at initial tagging, two mature and five were unknown. Five were immature and eight were mature when sacrificed after being recaptured. Twelve of the 13 specimens validated annual band deposition (Fig. 5). The specimen that did not show annual band deposition (531833) was at liberty for 707 days, yet only grew 16 mm L_F (860–876 mm L_F). The fluorescent reference mark was visible in close proximity to the edge of the corpus calcareum and no bands were observed distal to the reference mark (Fig. 6).

Yearly growth of OTC recaptures was highly variable, ranging from 8 to 105 mm year^{-1} (mean ± S.D. = 50 ± 30 mm year^{-1}). Two OTC-injected individuals were recaptured twice. Specimen 531829 was first recaptured after 121 days (growth = 35 mm) and again after a total of 372 days at liberty (growth = 18 mm); this individual was sacrificed after the second recapture. Specimen 531845 was originally tagged in 2007, and had been at liberty for 305 days before it was recaptured and injected with OTC giving it a total liberty of 1817 days (1512 days liberty after injection with OTC; Table III).

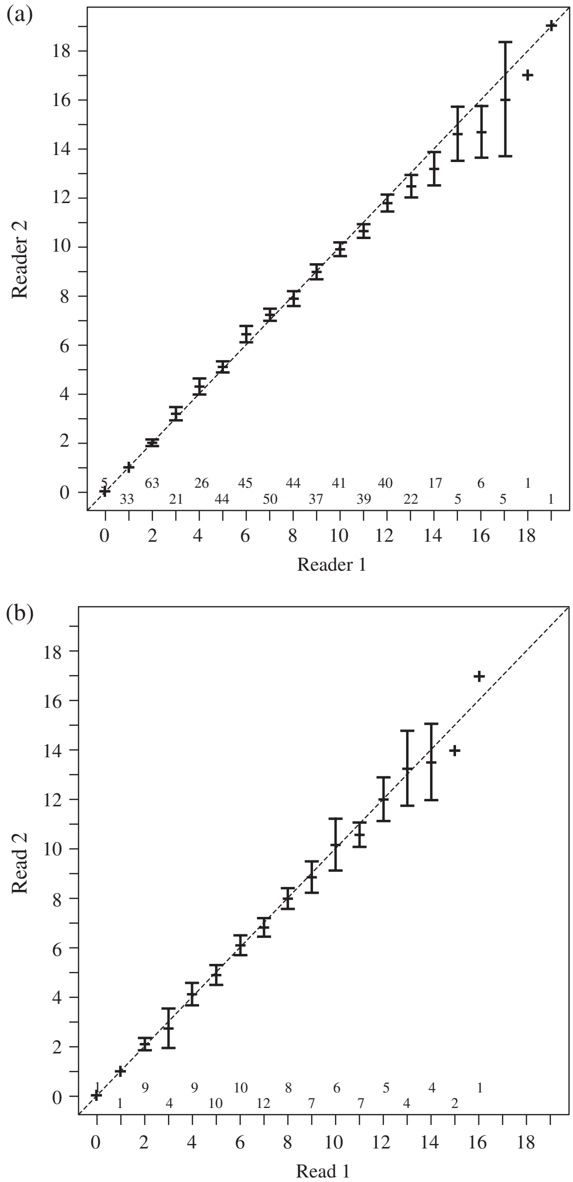

FIG. 3. (a) Inter-reader age bias plot for reader 1 *v.* reader 2 and (b) intra-reader age bias plot for a sub-set of 100 samples read twice by reader 1. Numbers represent *Sphyrna tiburo* aged by band count. Values are means ± 95% C.I. -----, a one to one relationship.

GROWTH MODELS

Significant differences were not detected between von Bertalanffy curves for South Carolina ($n = 334$) and Florida ($n = 211$) captured *S. tiburo* (likelihood ratio test, $\chi^2 = 4{\cdot}8$, d.f. $= 3$, $P > 0{\cdot}05$), so all data were combined. Significant differences in von Bertalanffy curves were detected for males ($n = 219$) and females ($n = 336$) (likelihood

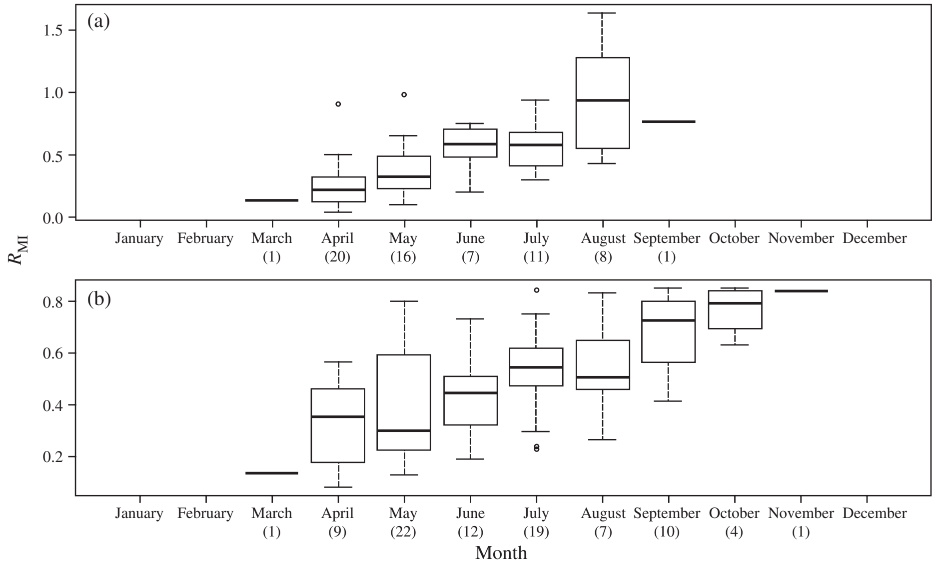

FIG. 4. Box plots of monthly average marginal increment ratio (R_{MI}) for (a) age 0–1 and (b) age 1–4 year-old *Sphyrna tiburo*. Sexes are combined. ——, median monthly R_{MI}, the top and bottom of the box equates to 75 and 25% quartiles. Whiskers encapsulate the remaining upper and lower 25% R_{MI} values. Individual points are considered outliers. Sample size per month is indicated in parentheses.

ratio test, χ^2=159·0, d.f. = 3, P <0·001) indicating that sex-specific growth curves were necessary. Residual sums of squares indicated that fractional age data produced better fits of the Gompertz and von Bertalanffy curves than assigned ages. Additionally, in the original von Bertalanffy model, the fractional age L_0 (Table IV) was more realistic than assigned age L_0 (male = 281 mm, 95% C.I. = 269–295, female = 291 mm, 95% C.I. = 271–310), when compared with observed mean size-at-birth. Observed mean ± S.D. size-at-birth was 274 ± 14 mm L_F (range = 245–300 mm, n = 22) for males, and 278 ± 12 mm L_F (range = 265–302 mm, n = 15) for females. Based on the more realistic L_0 and residual sums of squares, as well as its prevalence in literature and widespread use in stock assessments, sex-specific fractional age von Bertalanffy models were chosen as the most appropriate models for this study (Fig. 7); therefore, only fractional age model results are presented (Table IV). The Gompertz growth curve produced the best fit for female length-at-age data whereas the Gompertz and von Bertalanffy for male length-at-age data had identical AIC values and were therefore indistinguishable (Table IV). The logistic length model produced the poorest fit for both sexes (Table IV). The original von Bertalanffy model and Beverton & Holt (1957) model produced nearly identical L_∞ and k parameters with parameter differences occurring in non-significant digits. Examination of growth model residuals suggested that the logistic model for mass was inferior to the length-based models due to increased variability with mass at age. Theoretical maximum age was estimated to be 19·3 years for females, and 12·0 years for males and the oldest aged female and male were 17·9 and 16·0 years, respectively.

Assigned age von Bertalanffy models were used for comparisons of WNA and GOM data due to a poorer fit of GOM data with a fractional age von Bertalanffy model. Both

TABLE III. Recaptures of oxytetracycline (OTC)-injected and non-OTC-tagged *Sphyrna tiburo* from South Carolina's Cooperative Atlantic States Shark Pupping and Nursery Habitat Survey: tag number, sex (F, female; M, male), initial fork length (L_F) at tagging, length at recapture (sacrifice), growth, liberty, maturity status (Imm, immature; Mat, mature), backcalculated age at tagging, age at recapture and bands after OTC reference mark for OTC-injected samples

Tag number	Sex	Initial L_F (mm)	Recapture L_F (mm)	Growth (mm)	Liberty (days)	Initial maturity	Maturity at recapture	Age at tagging (years)	Age at recapture (years)	Bands after OTC mark
OTC-sacrificed recaptures										
532720	F	650	713	63	322	Imm	Imm	2·8	3·7	1
531774	F	739	765	26	332	Imm	Imm	4·8	5·8	1
531801	F	814	850	36	360	Imm	Imm	5·7	6·8	1
531809	F	715	788	73	372	Imm	Imm	6·7	7·8	1
531829*	F	808	843/861	35/53	121/372	Imm	Mat	5·7	6·8	1
531839	F	834	861	27	372		Mat	4·7	5·8	1
532714	F	802	835	33	706		Mat	5·5	7·7	2
531833	F	860	876	16	707		Mat	6·7	6·7	0†
532709	F	680	890	210	776	Imm	Imm	4·7	6·8	2
531783	F	670	930	260	1329	Mat	Mat	7·0	10·5	4
531793	F	779	930	151	1329	Mat	Mat	7·0	10·5	4
531799	F	756	916	160	1415		Mat	7·0	10·8	4
531845†	F	830	924	94	1512		Mat	4·7	8·8	4
Non-OTC-sacrificed recaptures										
B13223	F	565	685	80	351	Imm	Imm	3·8	4·8	
B2603	F	941	940	−1	356	Mat	Mat	8·8	9·8	
B2620	F	960	974	14	417	Mat	Mat	8·7	9·9	
B11584	F	551	800	249	680	Imm		4·7	6·7	
B11584	F	551	866	315	1062	Imm	Mat	4·7	7·7	
B13929	F	954	975	21	1526	Mat	Mat	7·7	11·9	
531845‡	F	799	924	125	1817		Mat	3·9	8·8	
B11084	F	865	905	40	1853		Mat	5·7	10·8	
B1933	F	804	940	136	2138		Mat	6·9	12·8	
B13104	M	738	765	27	2613	Mat	Mat	6·7	13·8	
B13326	M	763	805	42	2659	Mat	Mat	9·75	16·0	
B2916	F	980	1008	28	3263	Mat	Mat	6·7	15·7	

*Multiple recaptures.
†Derivation from expected band count after OTC reference mark.
‡Recaptured prior to OTC injection.

females [likelihood ratio test, $\chi^2 = 34{\cdot}8$, d.f. = 3, $P < 0{\cdot}001$; Fig. 8(a)] and males [likelihood ratio test, $\chi^2 = 45{\cdot}1$, d.f. = 3, $P < 0{\cdot}001$; Fig. 8(b)] had significantly different von Bertalanffy growth model parameter estimates among regions (Table V). For both sexes, regional differences were driven by significant differences between L_∞ (likelihood ratio test, females $\chi^2 = 12{\cdot}9$, d.f. = 1, $P < 0{\cdot}001$, males $\chi^2 = 8{\cdot}7$, d.f. = 1, $P < 0{\cdot}01$) and k (females $\chi^2 = 9{\cdot}3$, d.f. = 1, $P < 0{\cdot}01$, males $\chi^2 = 7{\cdot}7$, d.f. = 1, $P < 0{\cdot}01$) (Table V). Significant differences were not detected for t_0 (likelihood ratio test, females $\chi^2 = 0{\cdot}2$, d.f. = 1, $P > 0{\cdot}05$, males $\chi^2 = 0{\cdot}2$, d.f. = 1, $P > 0{\cdot}05$).

In addition to the OTC recaptures, 11 previously tagged non-OTC-injected *S. tiburo* were recaptured and sacrificed during the course of the study. Length of non-OTC recaptures ranged from 561 to 980 mm L_F at initial tagging to 685–1008 mm L_F at recapture (Table III). Time at liberty ranged from 351 to 3263 days. Average growth was highly variable and ranged from −1 to 134 mm year^{-1} (mean ± S.D. = 34 ± 46 mm year^{-1}). Recapture B2916 had the greatest time-at-liberty

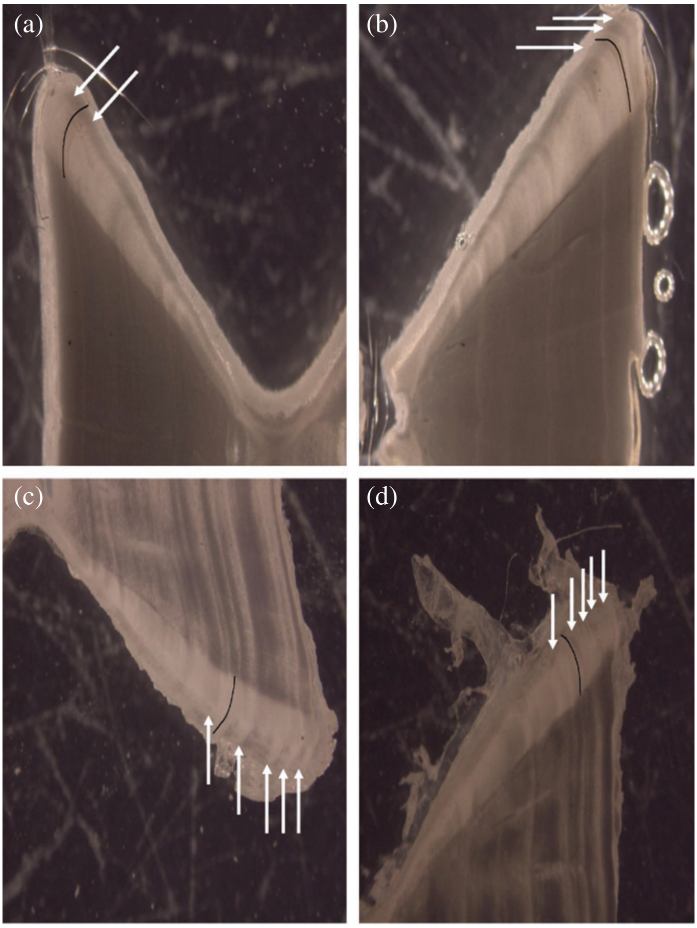

FIG. 5. Sectioned vertebrae showing oxytetracycline (OTC) reference marks (___) and winter bands around reference mark (➡). (a) Recapture 532720, at liberty 322 days, fork length (L_F) at injection was 650 mm, L_F at sacrifice was 713 mm, one band after reference mark. (b) Recapture 532714, at liberty 706 days, L_F at injection was 802 mm, L_F at sacrifice was 835 mm, two bands after reference mark. (c) Recapture 531799, at liberty 1415 days, L_F at injection was 756 mm, L_F at sacrifice was 916 mm, four bands after reference mark. (d) Recapture 531845, at liberty 1512 days, L_F at injection was 830 mm, L_F at sacrifice was 924 mm, four bands after reference mark.

and was already at asymptotic length when tagged 9 years prior to recapture, average growth was 3 mm year^{-1} and age was estimated at 15·7 years. Recapture B11584 was recaptured twice; this specimen grew an average of 123 mm year^{-1} before the first recapture (680 days), and 66 mm year^{-1} between the first recapture and the second (382 days). Recapture 531829 showed within-year variation of growth, growing 35 mm over the first 121 days of liberty (summer) before slowing down to 18 mm over the next 251 days (autumn to spring). Sacrificed non-OTC and OTC recaptures were plotted against the generated von Bertalanffy curves for comparison of observed *v*. modelled growth (Fig. 9). The slopes of plotted recaptures fit the trajectory of the generated growth curves well, lending additional verification to the results.

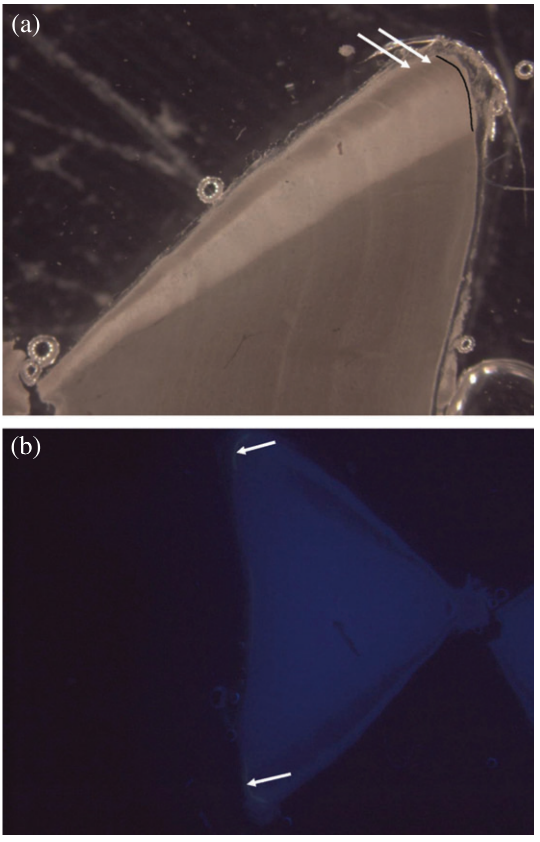

Fig. 6. Sectioned vertebral images from recapture 531833 showing oxytetracycline (OTC) reference marks and no visible bands after reference mark. (a) Image showing OTC reference mark (——) and counted winter bands prior to reference mark (➡). (b) Image illuminated by ultraviolet light showing actual OTC reference marks (➡). Liberty was 707 days, fork length (L_F) at injection was 860 mm, L_F at sacrifice was 876 mm.

MATURITY MODELS

Fork length and age at maturity data were available for all aged specimens. The largest immature male was 655 mm L_F (5·6 years old) and the smallest mature male was 582 mm L_F (4·7 years old). The oldest immature male was 6·8 years old (640 mm L_F) and the youngest mature male was 3·6 years old (657 mm L_F). The L_{F50} for males [Fig. 10(a)] in the WNA was 618 mm (95% c.i. = 605–629), which was larger than the GOM (572 mm L_{F50}, 95% c.i. = 562–583; Table V). The A_{50} for males [Fig. 10(b)] in the WNA was 3·9 years (95% c.i. = 3·6–4·3), which was over double the A_{50} reported for the GOM (1·7 years old, 95% c.i. = 1·5–1·9).

The largest immature female was 890 mm L_F (6·8 years old) and the smallest mature female was 743 mm L_F (4·8 years old). The oldest immature female was 9·8 years old (870 mm L_F) and the youngest mature female was 4·8 years old (743 mm L_F). The L_{F50} for females in the WNA [Fig. 10(c)] was 819 mm (95% c.i. = 799–831), which was larger than reported for the GOM (663 mm L_{F50}, 95% c.i. = 652–673). The A_{50} for

TABLE IV. Results from growth models generated to fork length (L_F) in mm and mass (kg) at fractional age (years) for *Sphyrna tiburo* inhabiting the western North Atlantic Ocean. Sex (F, female; M, male) and growth parameters (±95% C.I.) are reported. Akaike information criterion (AIC) and residual sums of squares (RSS) for models are reported. t_0 is reported for von Bertalanffy models and a is reported for the logistic regression models

Model	Sex	L_∞ (mm)	k	t_0/a	L_0 (mm)	G	W_∞ (kg)	AIC	RSS
von Bertalanffy*	M	782	0·29	−1·43	266			2240·1	$3·73 \times 10^5$
(95% C.I.)		(761–805)	(0·26–0·33)	−(1·63–1·23)	(251–280)				
	F	1036	0·18	−1·64	272			3565·3	$9·56 \times 10^5$
(95% C.I.)		(1011–1065)	(0·17–0·20)	−(1·89–1·42)	(252–291)				
Gompertz	M	761	0·40		278	1·01		2240·1	$3·73 \times 10^5$
(95% C.I.)		(740–783)	(0·36–0·44)		(265–290)	(0·96–1·05)			
	F	1036	0·27		292	1·22		3560·5	$9·42 \times 10^5$
(95% C.I.)		(1008–1063)	(0·26–0·30)		(276–308)	(1·17–1·27)			
Logistic Length	M	751	0·51	0·94				2255·3	$3·82 \times 10^5$
(95% C.I.)		(738–767)	(0·47–0·56)	(0·82–1·07)					
	F	969	0·38	2·02				3566·7	$9·60 \times 10^5$
(95% C.I.)		(955–984)	(0·35–0·40)	(1·88–2·16)					
Logistic mass	M		0·69	3·43			3·08	227·4	34·7
(95% C.I.)			(0·62–0·80)	(2·98–3·52)			(2·91–3·21)		
	F		0·45	6·05			8·30	967·3	356
(95% C.I.)			(0·40–0·51)	(5·51–6·18)			(7·90–8·66)		

*von Bertalanffy parameters L_∞ and k for the Beverton & Holt (1957) and original model only differ in non-significant digits and are presented together.

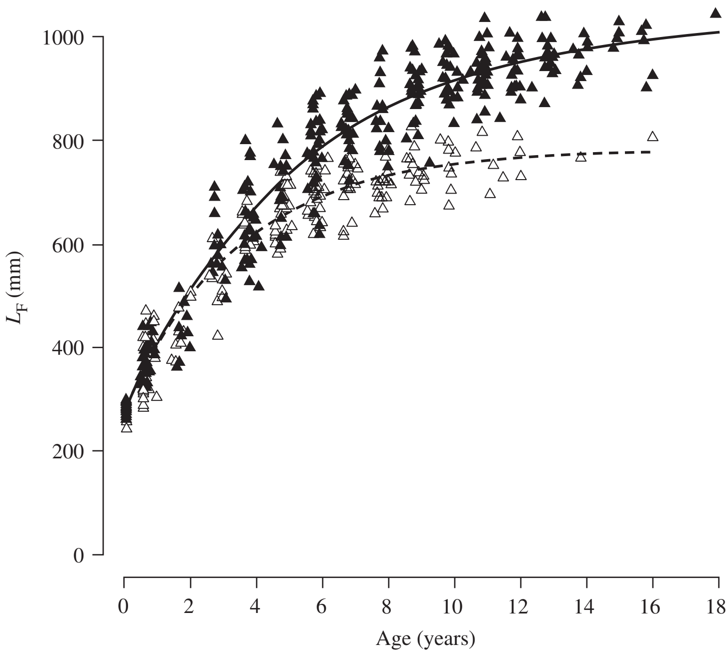

FIG. 7. von Bertalanffy growth models for *Sphyrna tiburo* inhabiting the western North Atlantic Ocean fitted to fork length (L_F) at fractional age data. Female (▲, ——) model parameters are $L_\infty = 1036$ mm (L_F), $k = 0{\cdot}18$, $L_0 = 272$ mm (L_F), $t_0 = -1{\cdot}64$, $n = 329$, and male (△, - - -) parameters are $L_\infty = 782$ mm (L_F), $k = 0{\cdot}29$, $L_0 = 266$ mm (L_F), $t_0 = -1{\cdot}43$, $n = 218$.

females in the WNA [Fig. 10(d)] was 6·7 years (95% C.I. = 6·3–7·0), which was over double the A_{50} reported by Lombardi-Carlson (2007) for the GOM (2·9 years old, 95% C.I. = 2·7–3·1).

DISCUSSION

This study has generated valuable life-history data that inform the conservation and management of *S. tiburo* by providing validated age and growth parameters and maturity data. This study suggests that *S. tiburo* have slower growth, take longer time to reach maturity and have greater longevity than populations of *S. tiburo* in the eastern GOM. The use of OTC and long-term recapture data validates these results; however, age underestimation was documented, which could mean that *S. tiburo* could have even greater longevity than that the age estimates indicate. The life-history parameters estimated by this study suggest that *S. tiburo* in the WNA may be more sensitive to fishing mortality than populations in the eastern GOM. The data generated will allow fisheries managers to assess and, if necessary, manage populations at appropriate regional levels.

Estimates of precision and bias, marginal increment analysis, as well as OTC injection results support the use of vertebrae for estimating age of *S. tiburo*. Precision was relatively high, with a minimum of >84·1% agreement ± 1 year for all 100 mm size classes and an overall agreement ± 1 year of 90·8%. The analyses of OTC-injected

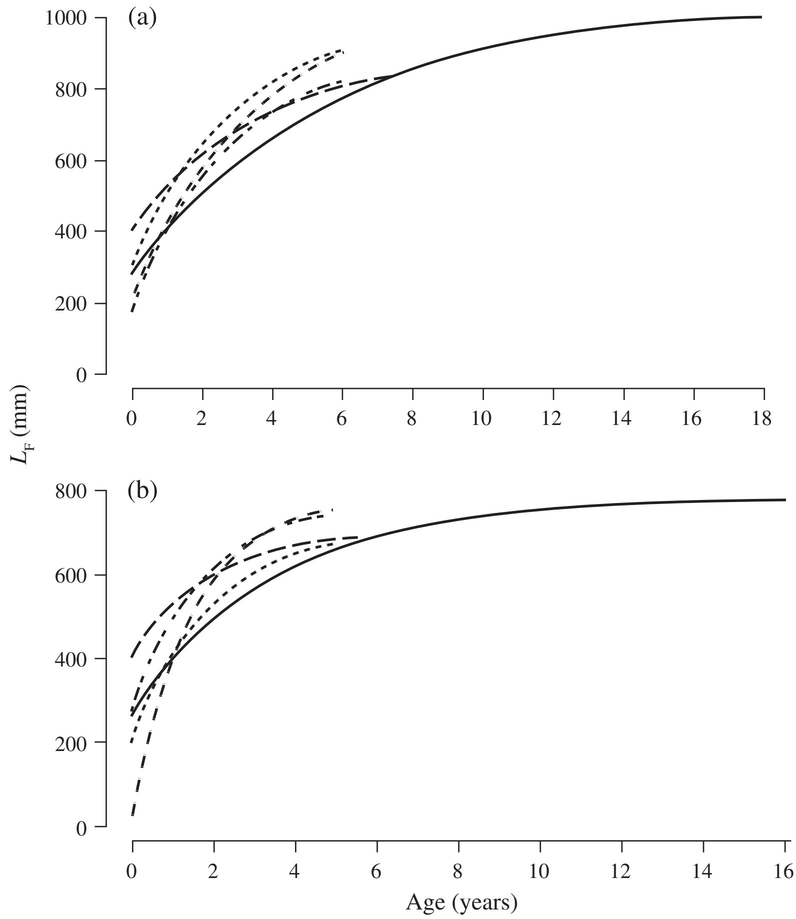

FIG. 8. A comparison of von Bertalanffy growth curves fitted to fork length (L_F) at assigned age data for (a) female and (b) male *Sphyrna tiburo* from this study (——) to previous studies from the eastern Gulf of Mexico [– – –, Lombardi-Carlson *et al.* (2003); - - - -, Carlson & Parsons (1997); ...., Parsons (1993*a*) (Tampa Bay); –·–·–, Parsons (1993*a*) (Florida bay)]. Parameter values are presented in Table V.

and OTC-recaptured specimens complement the results presented by Parsons (1993*a*). While predominantly captive reared sharks were injected with OTC for validation of the periodicity of growth band formation by Parsons (1993*a*), this study used all wild-captured and wild-recaptured specimens. In addition to the validation of age-1·5+ to age-4·5+ year sharks completed by Parsons (1993*a*), this study further validated annual band deposition for age-2·7–10·5 years females. Band deposition was validated across as many as 4 years. Validation, however, was not achieved for any male *S. tiburo*, as recaptures were rare.

Growth band formation was found to be aberrant in recapture 531833 (Table III). Two bands would be expected to be evident after the OTC reference mark; however, no bands were present after the mark. This specimen was probably reaching the asymptotic length as growth had reduced to 8 mm year^{-1}. Parsons (1993*a*) reported anomalies in two of his captive-held OTC-injected sharks. One specimen failed to

TABLE V. Life-history parameters from Parsons (1993*a*), Carlson & Parsons (1997), Lombardi-Carlson (2007) and this study. Results from von Bertalanffy models generated to fork length (L_F) in mm at assigned age (years) and logistic models for age (A_{50}) and length (L_{F50}) at 50% maturity for *Sphyrna tiburo* in the western North Atlantic Ocean (this study) and Gulf of Mexico are reported. Sex (F, female; M, male) and life-history parameters ± symmetrical 95% C.I. are reported

Parameter	Parsons (1993*a*) Tampa Bay	Parsons (1993*a*) Florida Bay	Carlson & Parsons (1997)	Lombardi-Carlson (2007) combined	This study
Sample size	48 (M)	44 (M)	50 (M)	245 (M)	218 (M)
	96 (F)	45 (F)	65 (F)	254 (F)	329 (F)
L_∞ (mm)	772 ± 83 (M)	710 ± 81 (M)	780 ± 51 (M)	703 ± 51 (M)	780 ± 21 (M)
	994 ± 67 (F)	895 ± 83 (F)	1058 ± 153 (F)	894 ± 95 (F)	1032 ± 26 (F)
k	0·58 ± 0·27 (M)	0·53 ± 0·25 (M)	0·69 ± 0·20 (M)	0·54 ± 0·20 (M)	0·30 ± 0·04 (M)
	0·34 ± 0·09 (F)	0·37 ± 0·12 (F)	0·28 ± 0·10 (F)	0·28 ± 0·10 (F)	0·19 ± 0·02 (F)
t_0 (years)	−0·77 ± 0·54 (M)	−0·64 ± 0·54 (M)	−0·04 ± 0·27 (M)	−1·60 ± 0·31 (M)	−1·51 ± 0·21 (M)
	−1·10 ± 0·43 (F)	−0·60 ± 0·40 (F)	−0·79 ± 0·43 (F)	−2·13 ± 0·63 (F)	−1·75 ± 0·24 (F)
L_0 (mm)				406 ± 25 (M)	281 ± 13 (M)
				404 ± 24 (F)	291 ± 19 (F)
A_{50} (years)	2·0 (M)	2·0 (M)	2·0 (M)	1·7 ± 0·2 (M)*	3·9 ± 0·3 (M)
	2·4 (F)	2·4 (F)	2·4 (F)	2·9 ± 0·2 (F)*	6·7 ± 0·3 (F)
L_{F50} (mm)				572 ± 11 (M)*	618 ± 12 (M)
				663 ± 10 (F)*	819 ± 14 (F)
Observed maximum size (L_F, mm)	774 (M)	774 (M)	834 (M)	808 (M)	825 (M)
	1002 (F)	1002 (F)	1071 (F)	952 (F)	1043 (F)
Observed maximum age (years)	5+ (M)	5+ (M)	5+ (M)	5·5+ (M)	16·0 (M)
	6+ (F)	6+ (F)	6+ (F)	7·5+ (F)	17·9 (F)

*Parameters for L_{F50} and A_{50} were calculated using original raw L_F at age data from Parsons (1993*a*) and Lombardi-Carlson (2007) by Frazier *et al.* (2013).

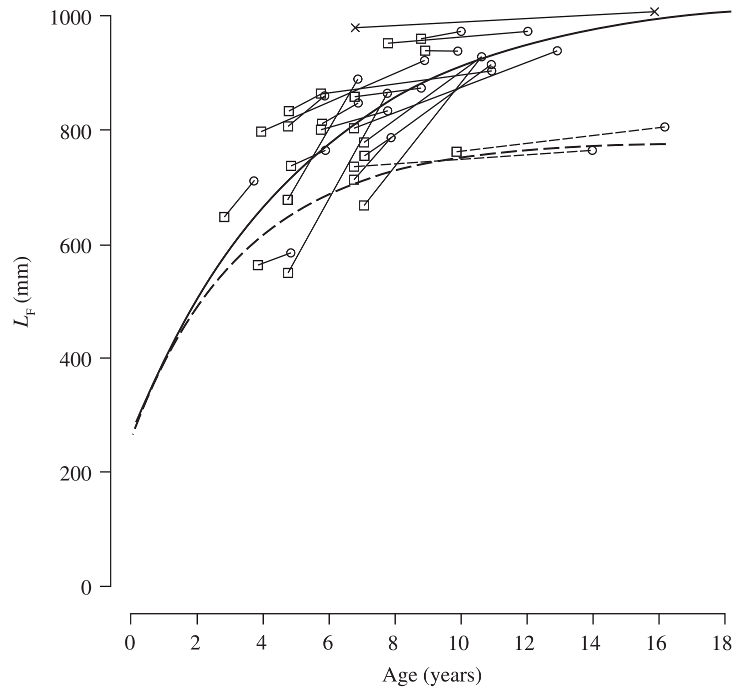

FIG. 9. von Bertalanffy growth curves for female (——), and male (– – –) *Sphyrna tiburo* inhabiting the western North Atlantic Ocean with all aged recaptures (Table III) plotted. Initial fork length (L_F, mm) and back-calculated age (years) at capture (□) and recaptured L_F and estimated age (○) are also plotted. Recapture B2916 (×) highlights potential age underestimation.

form a band after 0·3 years and the other specimen formed two bands 1·5 years after injection. There was no evidence of the formation of multiple bands per year in this study, and the anomalies observed between the OTC recapture in this study and Parsons (1993*a*) were probably unrelated.

Age underestimation due to asymptotic length also probably occurred in long-term recapture B2916 (Table III). This individual was near maximum-recorded length when it was initially tagged (980 mm L_F). Over 9 years of liberty, its average growth was 3 mm year^{-1}. Age estimates produced a band count of 17 (15·7 years old at recapture and 6·7 years old at initial tagging). If the length at initial tagging was applied to the von Bertalanffy equation with the parameters generated in this study, this specimen could have been as old as 14·5+ years at initial tagging (23·5+ years at sacrifice). Analysis of lengths of all age-6·5+ year *S. tiburo* reveals a range of 723–890 mm L_F (mean ± S.D. = 823 ± 44 mm), adding further evidence that age was probably underestimated in B2916.

These two anomalies cast doubt over the ability to properly age individuals that have reached asymptotic length. As the growth of an individual slows down, so too does vertebral growth, making it difficult to count bands that could be present on the edge of the corpus calcareum. Therefore, while annual band deposition was validated for female age classes 1·0–10·5 years, age underestimation may still occur for individuals that have reached asymptotic length. Several other recaptured specimens had slow to no growth, including one individual with a recorded growth of −1 mm year^{-1} (probably

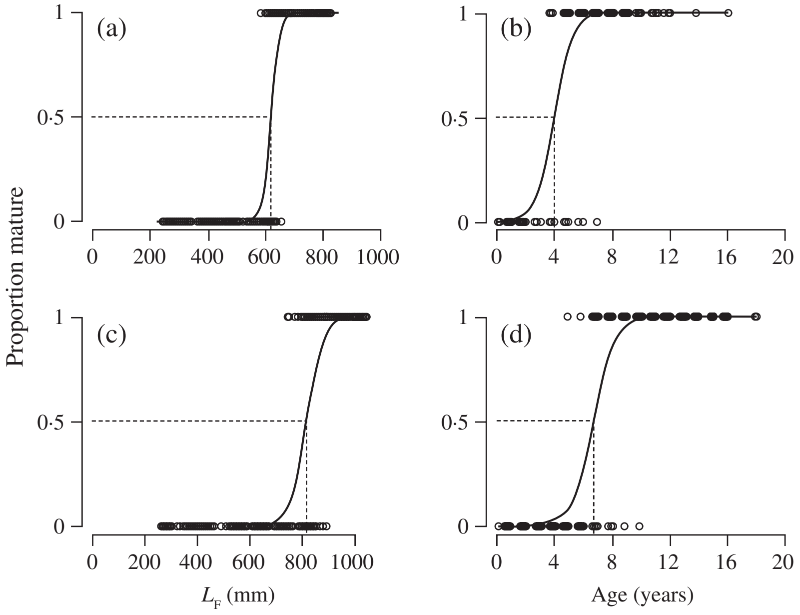

FIG. 10. (a, c) Fork length (L_F) and (b, d) age at maturity ogives for (a, b) male and (c, d) female *Sphyrna tiburo* in the western North Atlantic Ocean. ——, the expected proportion mature at a given L_F or age. ○, observed data points.

due to measuring error). Maximum observed age estimates for this study, however, were similar or equal to the theoretical maximum ages, indicating that the observed age underestimation is probably uncommon.

Although there was no indication that age underestimation was a biasing factor in this study, it is important to note that there is evidence that it occurred. Age underestimation of up to 50% has been documented in porbeagle *Lamna nasus* (Bonnaterre 1788) (Francis *et al.*, 2007) and school sharks *Galeorhinus galeus* (L. 1758) (Kalish & Johnston, 2001) using bomb radiocarbon validation analysis. These species have greater longevity than *S. tiburo* and if age underestimation occurred in this study, it probably only affects older age classes and occurs at a much lower level than observed in previous studies.

Marginal increment ratios were only available from March to November, as no specimens from age 0 to 4 years old were collected during the winter months. Age 0–1 R_{MI} approached and was even >1·0 for the month of August. While normal R_{MI} should be <1·0, this result can be explained by parturition date, formation of the first winter band, as well as by environmental effects on early growth. *Sphyrna tiburo* are born in late September and the birthmark forms shortly after in October. The first winter band is assumed to form 5 months later in February. This early autumn parturition date is unique among viviparous sharks found in the coastal waters of the WNA. Evidence suggests that parturition may occur prior to, or during, autumn adult migration. For example, numerous post-partum females have been documented in South Carolina waters, and free swimming neonates with open umbilical scars were captured in both South Carolina and Georgia waters (SCDNR, unpubl. data). The combination of slow initial growth after parturition, migration to nursery grounds shortly after birth, as well as slower growth with colder water temperatures (Cailliet *et al.*, 1986; Branstetter, 1987), probably results in slower initial growth over the first 5–6 months of life for neonate *S. tiburo*. Marginal increment growth after the first winter band takes place in warmer spring and summer months where conditions could be better for rapid growth. Therefore, measured growth between the birthmark and first winter band may be smaller than the margin width, and R_{MI} over 1·0 would not be unexpected. The R_{MI} analysis verifies that annual bands are formed in age-0–4 year classes. Unfortunately, the month of winter band completion could not be confirmed, but the present data do not refute Parsons' (1993*a*) hypothesis of winter band completion occurring in February.

The von Bertalanffy parameters generated in this study were not statistically compared with Parsons (1993*a*) and Carlson & Parsons (1997) due to differences in age estimate methodology. These previous studies aged whole vertebrae, rather than using sagittal vertebral sections, which has become the preferred and more common methodology in recent studies (Goldman, 2004). Growth models were generated using original L_F at age data to allow for visual comparisons of growth curves for females [Fig. 8(a)] and males [Fig. 8(b)], and general comparisons show that estimates of L_∞ were similar with the exception of Florida Bay (Parsons, 1993*a*), *k* values were higher for all GOM studies and t_0 values were lower (Table V).

Observed growth was directly measured from recaptured *S. tiburo* and compared with modelled growth. Growth in recaptured specimens was observed to be highly variable. While growth slowed as some individuals approached maturity, other individuals experienced rapid growth as they progressed from immature to mature. Several *S. tiburo* were recaptured multiple times before being sacrificed. The measured growth of multiple-recapture B11584 showed that average yearly growth slowed as the specimen approached asymptotic length. The measured growth of multiple recapture 531829 showed within-season variation in *S. tiburo* growth, with more rapid growth in summer months, and slower growth from later autumn to spring. Plots of OTC- and non-OTC-recaptured individuals over the von Bertalanffy curves (Fig. 9) show slight variation in observed growth, but the recaptures lend additional verification to the generated curve. The plotted growth of recapture B2916 appears to confirm the assertion that age was underestimated.

Mean length at birth (L_0) was not originally calculated by Lombardi-Carlson *et al.* (2003), but for comparative purposes, GOM L_0 was calculated using the original von Bertalanffy equation with length-at-age data from Lombardi-Carlson (2007) (Table V). Estimated mean length-at-birth (L_0) was larger for the GOM than WNA. Observed mean length at birth for the WNA was within the confidence intervals for L_0 parameter estimates. Umbilical stages were not available for the GOM data and reported time of parturition varies by several months among regions, so it was not possible to get an estimate of length at birth in order to compare with estimated mean length at birth for the WNA. Lengths of near-term embryos from the GOM were reported to range from 215 to 297 mm L_T (Lombardi-Carlson *et al.*, 2003) and near-term (<2 weeks from parturition) embryos from the WNA ranged from 245 to 356 mm L_T (mean ± s.d. = 313 ± 29 mm, n = 92). Therefore, observed length at birth for the regions is probably similar, if not smaller for the GOM. This suggests that the original von Bertalanffy models for the GOM could overestimate mean length at birth (L_0), and consequently underestimate *k*.

The findings of this study are consistent with previous studies on small coastal sharks by Loefer & Sedberry (2003), Driggers *et al.* (2004) and Drymon *et al.* (2006).

Generally, these studies found that small coastal sharks in the WNA have a larger L_∞, a lower k, a larger maximum estimated age and older A_{50} compared with the GOM, although Drymon *et al.* (2006) found no significant differences in finetooth sharks *Carcharhinus isodon* (Müller & Henle 1839). Loefer & Sedberry (2003) initially found the opposite when compared with Parsons (1985) and Branstetter (1987), however, when compared with the most recent study on Atlantic sharpnose *Rhizoprionodon terraenovae* (Richardson 1836) life history in the GOM by Carlson & Baremore (2003), the results matched the trends observed in the other small coastal species. The only exception was female blacknose sharks *Carcharhinus acronotus* (Poey 1860), which were reported to have a larger theoretical maximum size in the GOM by Carlson *et al.* (1999); however, the larger L_∞ may have been driven by a lack of larger adults in the GOM model (Driggers *et al.*, 2004).

Observed life-history differences between *S. tiburo* in the GOM and WNA could be due to differences in age estimation procedures (*e.g.* allowing sectioned vertebra to fully dry) or they may be manifested by migration patterns or differential mortality of *S. tiburo*. Anecdotal evidence suggests that a large portion of the young-of-year and younger juvenile *S. tiburo* do not recruit to South Carolina's coastal waters until they are several years old, instead remain in Florida waters (Hueter & Tyminski, 2002; Ulrich *et al.*, 2007). Similar population structure may exist in the GOM and it is possible that sampling locations for previous GOM studies are located in areas that do not contain individuals of all sizes and ages represented in the GOM population. If samples were drawn from these areas and assumed to be representative of the entire GOM population, it could result in inaccurate growth parameters, especially if large animals were poorly represented (Goldman, 2004). Differential mortality of larger adult *S. tiburo* in the GOM could also lead to observed life-history differences between the GOM and WNA.

Significant regional differences in age and growth have been documented by this study. *Sphyrna tiburo* in the WNA were found to grow more slowly to a larger size, take longer time to mature and reach an older age than populations from the GOM. The annual periodicity of growth band deposition was validated for a large portion of female age classes, and several long-term recaptures further verified age estimates and generated growth curves. Age underestimation was documented, however, and *S. tiburo* may have greater longevity than reported. Significant differences in important life-history characteristics between regions, together with the lack of stock mixing as shown by tagging and genetic studies, suggest that, if possible, these stocks be managed and assessed separately.

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