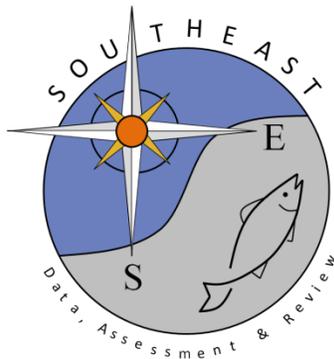


Age and growth of the smooth hammerhead, *Sphyrna zygaena*, in
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Age and growth of the smooth hammerhead, *Sphyrna zygaena*, in the Atlantic Ocean: comparison with other hammerhead species

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ABSTRACT

The smooth hammerhead *Sphyrna zygaena* (Sphyrnidae) is a pelagic shark occasionally caught as bycatch in pelagic longline fisheries, but is one of the least studied of all pelagic sharks. Age and growth of *S. zygaena* was studied along a wide Atlantic region covering both the northern and southern hemispheres. Data from 304 specimens, caught between October 2009 and September 2014, ranging in size from 126 to 253 cm fork length (FL), were analysed. Growth models were fitted using the three-parameter von Bertalanffy growth function (VBGF) re-parameterized to calculate L_0 (size at birth). Growth models were fitted to the sample data and data from several back-calculation models. The model fit to the quadratic modified Dahl-Lea back-calculated data seems to be the most appropriate to describe growth in this species, with resulting growth parameters of $L_{inf} = 285$ cm FL, $k = 0.09 \text{ year}^{-1}$ for males and $L_{inf} = 293$ cm FL, $k = 0.09 \text{ year}^{-1}$ for females. Compared with other species of the same genus, estimated growth coefficients for *S. zygaena* seem to fall in the low to middle range. Although further work is still needed, this study adds to knowledge of the vital life-history parameters of smooth hammerheads in the Atlantic Ocean, which can be used in the management and conservation of this species.

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Introduction

Even though elasmobranch fishes have never traditionally had a high value, they have become important fisheries resources in recent years (Barker & Schluessel 2005). In fact, these species are currently exploited both by directly targeted fisheries and as bycatch of fisheries targeting other species (Stevens et al. 2000). However, this increase in catches has not been mirrored by an increase in information on species biology (Stevens et al. 2000). In the Atlantic Ocean, pelagic sharks are a common bycatch of pelagic longline fisheries (e.g. Coelho et al. 2012a, 2012b). Oceanic sharks pose a particularly difficult problem when it comes to fisheries management and conservation due to their highly migratory nature that leads them to migrate between territorial waters of different countries and international waters (Barker & Schluessel 2005). Moreover, in general, elasmobranch species have K-strategy life cycles, characterized by slow growth rates and reduced reproductive potential (Cortés et al. 2010). These characteristics make these fishes extremely vulnerable to fishing pressure with

overexploitation occurring even at relatively low levels of fishing mortality. Due to these characteristics, once overfished, populations can take several decades to recover (Smith et al. 1998).

The smooth hammerhead *Sphyrna zygaena* (Linnaeus, 1758) is a cosmopolitan pelagic hammerhead shark occurring from close inshore to offshore oceanic waters (Compagno 1984). As with other pelagic shark species, *S. zygaena* is commonly caught as bycatch by pelagic longlines targeting swordfish, albeit in much lower numbers than the considerably more abundant blue *Prionace glauca* (Linnaeus, 1758) and shortfin mako sharks (*Isurus oxyrinchus* Rafinesque, 1810) (Mejuto et al. 2008). Despite being regularly caught as bycatch by these commercial fisheries, information on life history, movement patterns, essential habitats and population dynamics of *S. zygaena* over most of its range is still scarce.

Age and growth studies are fundamental in fisheries research as they provide some of the baselines for estimating important biological variables, including population growth rates, natural mortality and longevity of a

species; they are therefore crucial for successful fisheries management (Campana 2001; Hall et al. 2012). While other species of large pelagic hammerheads, such as the scalloped hammerhead *Sphyrna lewini* (Griffin & Smith, 1834), have been the focus of several growth studies (e.g. Branstetter 1987; Chen et al. 1990; Piercy et al. 2007; Harry et al. 2011; Kotas et al. 2011; Drew et al. 2015), only two studies are currently available on the life history parameters of *S. zygaena*, one in the Atlantic (Coelho et al. 2011) and the other in the Pacific Ocean (Liu & Tsai 2011).

In the Atlantic Ocean, the International Commission for the Conservation of Atlantic Tunas (ICCAT) is the inter-governmental fishery organization responsible for the management and conservation of migratory tunas and tuna-like species, including pelagic sharks such as *S. zygaena*. Since 2010 it has been prohibited to 'retain onboard, tranship, land, store, sell, or offer for sale any part or whole carcass of hammerhead sharks of the family Sphyrnidae, except for *Sphyrna tiburo* (Linnaeus, 1758), taken in the Convention area in association with ICCAT fisheries' (ICCAT 2010). More recently, the smooth hammerhead was included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which regulates the international trade of this species.

According to the International Union for the Conservation of Nature (IUCN) Red List Criteria, this species is globally classified as 'Vulnerable'; however, it is mentioned that more studies are still required to determine whether it may warrant a higher risk category in the future throughout its range (Casper et al. 2005). Cortés et al. (2010) conducted an ecological risk assessment for 11 species of pelagic elasmobranchs in the Atlantic Ocean and concluded that *S. zygaena* appeared to be one of the least vulnerable. However, Cortés et al. (2010) also mentioned that *S. zygaena* was one of the species for which there is the most urgent need for better biological data, due to many uncertainties regarding its life history. It is possible that the retention prohibition imposed by ICCAT and the international trade control regulated by CITES may not be enough to protect this species, as 71% of smooth hammerheads caught in the pelagic swordfish longline fishery have been estimated to be captured and released dead (Coelho et al. 2012a).

Due to the current lack of information on this species, the main objective of this study is to improve the knowledge and biological information for *S. zygaena*, by providing new data on the age and growth parameters of this species throughout a wide

Atlantic region comprising both the northern and southern hemispheres. A secondary objective is to compare growth between oceans and hammerheads of the same genus.

Materials and methods

Sampling and processing

All *Sphyrna zygaena* samples were obtained by Portuguese Institute for the Ocean and Atmosphere (IPMA) observers on board Portuguese commercial longline vessels targeting swordfish in the Atlantic Ocean. Vertebra collection started in October 2008, with a total of 304 *S. zygaena* sampled over a period lasting until September 2014. As per ICCAT Recommendation 13-10 (ICCAT 2013), samples were collected only from sharks that were dead at haulback when retrieving the longline and were taken in the framework of a research project notified to the Scientific Committee for Research and Statistics (ICCAT-SCRS) through the Shark Working Group (Coelho & Santos 2015; Santos & Coelho 2015). Samples were collected over a wide Atlantic region (latitudes 22°N to 29°S; longitudes 7° E to 43°W) (Figure 1). Some of these samples ($n = 139$) were used to estimate growth curves for the eastern equatorial Atlantic Ocean in a previous study (Coelho et al. 2011). Since the sample size and sample areas were limited, the aforementioned samples were also included in the present study in order to model the growth of this species for a wider Atlantic area.

All specimens were measured on board for fork length (FL, cm) in a straight line to the nearest cm, and the sex was determined. A section from 4 to 8 vertebrae was extracted from the region below the anterior part of the first dorsal fin. All samples were kept frozen while on the vessels and during transportation to the laboratory. In the laboratory, the covering connective tissue of the vertebrae was first removed manually with scalpels, and then by soaking the vertebrae in 4–6% sodium hypochlorite (commercial bleach) for 10–20 min, depending on size. Once cleaned, the vertebrae were stored in 70% ethanol, and then air-dried for 24 h before mounting on a microscope slide using thermoplastic cement or a synthetic polymer glue. Once mounted, the vertebrae were sectioned sagittally with a Buehler Isomet (Lake Bluff, IL) low-speed saw, using two blades spaced approximately 500 μm apart. The resulting section included the focus of the vertebra and the two halves (one on each side of the focus), in a form typically called 'bow-tie'. Finally, the sections were stained

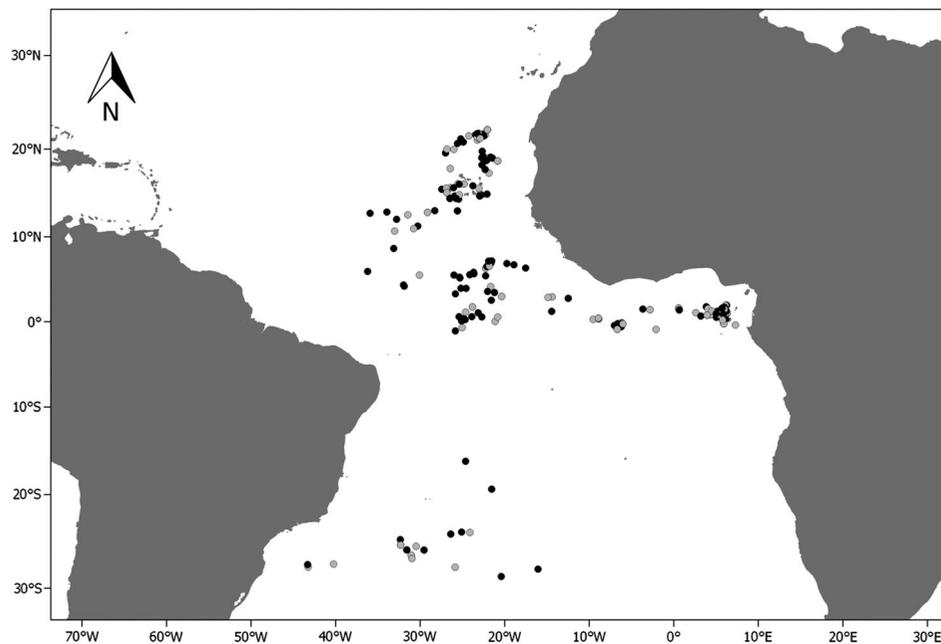


Figure 1. Map of the Atlantic areas with the location of the *Sphyrna zygaena* samples. Dark circles represent males and grey circles represent females.

with crystal violet (Sigma-Aldrich Co., St Louis, MO), found by Coelho et al. (2011) to be the best band enhancement technique for this species, for a better visualization of the growth band pairs (comprising one opaque and one translucent band). Once dried, the sections were mounted onto microscope slides with Cytoseal 60 (Thermo Fisher Scientific Inc., Waltham, MA). The visualization of the vertebral

sections was carried out under a dissecting microscope using transmitted white light (Figure 2).

Age estimation and comparison of age readings

For training and consistency between readings taken by different readers, a set of vertebrae ($n = 139$) was independently read by three readers, on three separate occasions, in order to guarantee quality control and precision. To prevent bias while counting the bands, the three readers had no knowledge of the length or sex of each shark. After this step, the remaining sample ($n = 165$) was then read three times by the primary reader and only those vertebrae whose band counts were the same for at least two of the three readings of the primary reader were accepted for the age and growth analysis. Each reading was finalized before starting the next one to prevent reader familiarity with any particular vertebra.

In order to compare intra-reader ageing precision between the three readers both the coefficient of variation (CV; Chang 1982) and the average percentage error (APE; Beamish & Fournier 1981) were calculated and compared. The percentage of agreement (PA) among the primary reader readings was also calculated. Bias plots were used to graphically assess the ageing accuracy between the three readings (Campana 2001). Precision analysis was carried out using the R language for statistical computing version 3.2.5 (R Core Team 2016), using the package 'FSA' (Ogle 2015).

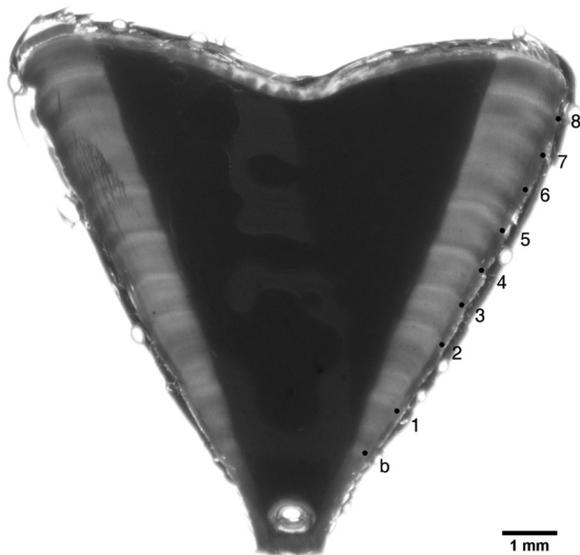


Figure 2. Microphotograph of a vertebral section of *Sphyrna zygaena* from a female specimen with 182 cm fork length, with the identification of the birth mark (b) and the estimated eight growth bands.

Growth modelling

Sphyrna zygaena is a viviparous species; parturition time is estimated to be around December–January in southern Brazilian waters (Vooren et al. 2005). As for other species, the first growth band is a birthmark, associated with an angle change along the *corpus calcareum* of sectioned vertebrae (Goldman 2004) (Figure 2). In order to verify the temporal periodicity of band formation in the vertebral centrum, an edge analysis and a marginal increment analysis were initially attempted. However, due to the lack of captures for each month and for every estimated age class, it was not possible to determine the periodicity of band formation. The deposition of a band pair (one translucent and one opaque band) per year was assumed (see Discussion for details). Vertebrae were aged accordingly in integer years.

Two models were used to describe the growth of this species. The first model was the three-parameter von Bertalanffy growth function (VBGF) re-parameterized to estimate L_0 (size at birth) instead of t_0 (theoretical age at which the expected length is zero), as suggested by Cailliet et al. (2006):

$$L_t = L_{\text{inf}} - (L_{\text{inf}} - L_0) \times \exp(-kt) \quad (1)$$

L_t = mean fork length at age t ; L_{inf} = asymptotic maximum fork length for the model of average fork length at age; k = growth coefficient; L_0 = fork length at birth.

A two-parameter VBGF was also used, where L_0 was fixed to the maximum size at birth described for this species. The maximum value of size at birth described for the species by Vooren et al. (2005) is 55 cm total length (TL). Because size data in our study refers to FL we used the conversion factor from Mas et al. (2014), to convert the size at birth from TL into FL:

$$FL = 0.78 \times TL \text{ (size range: 114 – 330 cm TL)} \quad (2)$$

A likelihood ratio test (LRT), as defined by Kimura (1980) and recommended by Cerrato (1990), was used to test the null hypothesis that there was no difference in growth parameters between males and females, using the ‘fishmethods’ package (Nelson 2014) in R (R Core Team 2016). The LRT was also used to test differences between the present study sample and the sample in Coelho et al. (2011).

Back-calculation

To account for the absence of smaller individuals in the sample, lengths at ages prior to the ages at capture were back-calculated from vertebral centrum

measurements. Back-calculation is a method for describing the growth history of each individual sampled by estimating lengths at ages prior to the ages at capture for each individual (Goldman 2004; see Francis 1990; Vigliola & Meekan 2009 for reviews). To obtain accurate parameter estimates from the growth models fitted to the resulting back-calculated lengths at ages it is necessary to choose the appropriate relationship between the vertebral radius (VR) and the specimen FL. Linear and quadratic models were used to describe the FL-VR relationship, respectively:

$$FL = a + bVR \quad (3)$$

$$FL = a + bVR + cVR^2 \quad (4)$$

For this analysis the vertebral sections of all specimens were micro-photographed, the distance from the focus to each annulus and the vertebral radius were measured digitally using Image J software (Abramoff et al. 2004) (Figure 2). Distances were measured to the nearest 0.01 mm or 0.007 mm, according to the dissecting microscope magnification used, as a straight line from the central focus to the outer margin of the *corpus calcareum*. When measuring the distance to each annulus it was assumed that a band pair constitutes one year of growth, and therefore the measurements were made from the outer edge of one translucent band to the outer edge of the next identifiable translucent band. These measurements were made only in vertebrae with an accepted count of growth rings, when two out of the three readings were the same. FL-VR models were fitted with a linear model in R (R Core Team 2016) and goodness-of-fit compared with the Akaike Information Criterion value (AIC) and the coefficient of determination (r^2), where the model with the lowest AIC and highest r^2 was considered the model that best fitted the data and described the FL-VR relationship.

Goldman (2004) recommends that several proportional back-calculation methods should be compared to examine the statistical and biological accuracy of back-calculated lengths relative to vertebral sample data. Four different proportion methods were used (Table I) and compared with our sample length at age data. The Dahl-Lea model assumes a direct proportion between fish length and vertebral radius (see Vigliola & Meekan 2009), while the linear and quadratic Dahl-Lea models use parameter estimates from the linear and quadratic fits that describe the FL-VR relationship, respectively (Francis 1990). The size at birth Fraser-Lee model includes a biologically derived intercept as the point of origin of back-calculations (Campana 1990).

Table 1. Summary of the four back-calculation models examined in this study: Dahl-Lea (see Vigliola & Meekan 2009), linear modified Dahl-Lea (Francis 1990), quadratic modified Dahl-Lea (Francis 1990), and size at birth modified Fraser-Lee (Campana 1990).

Back calculation models	
Dahl-Lea	$L_i = (VR_i/VR_0)L_c$
Linear modified Dahl-Lea	$L_i = [(a + bVR_i)/(a + bVR_c)]L_c$ a and b are estimated from $FL = a + bVR$
Quadratic modified Dahl-Lea	$L_i = L_c \{[(a + bVR_i + cVR_i^2)/(a + bVR_c + cVR_c^2)]\}$ a, b and c are estimated from $FL = a + bVR + cVR^2$
Size at birth modified Fraser-Lee	$L_i = L_c + (VR_i - VR_0)[(L_c - L_0)/(VR_c - VR_0)]$

Note: FL fish fork length; VR vertebral radius; L_0 fish length at birth; L_i length at age i ; L_c length at capture; VR_0 vertebral radius at birth; VR_i radius at age i ; VR_c radius at capture.

Size at birth in the modified Fraser-Lee size at birth was set to the maximum observed size at birth.

Vertebral radii-at-birth (R_0) were averaged from all sectioned vertebrae to obtain a mean value. An R_0 of $1.61 \text{ mm} \pm 0.31$ standard deviation (SD) was estimated.

Biological accuracy was determined by plotting the sample mean length at age data against the difference between mean back-calculated length at age and the sample mean length at age to determine which method provides the best results (Goldman 2002). This plot shows which back-calculation method most accurately reflects sample mean lengths at age (Goldman 2004). The three-parameter VBGF was then fitted to the back-calculated length data.

The FSA package (Ogle 2015) in R (R Core Team 2016) was used for the back-calculations. The VBGF model was then fit using non-linear mixed effects models ('nlme', Pinheiro et al. 2016) in R (R Core Team 2016), as suggested by Vigliola & Meekan (2009) due to the longitudinal nature of the back-calculated data. A block variance-covariance structure was used to allow L_{inf} and k to be correlated (Pinheiro & Bates 2000) and the convergence tolerance was set to 1^{-4} . For each model, the parameters were estimated, as were the corresponding standard errors (SE) and the limits of the 95% confidence intervals (CI). Plots were created using 'ggplot2' (Wickham 2009).

Results

Sample characteristics

A total of 304 sampled sharks (175 males, 128 females, one specimen with undetermined sex) were collected for this study (Figure 3). From these individuals, 291 vertebra had at least two identical readings and were considered to have valid age readings; they were thus used for the age and growth analysis. As the growth modelling was performed for the separate sexes, the specimen with undetermined sex was not included in this part of the analysis. Females ranged in size between 126 and 252 cm FL (mean \pm SD: 193.5 ± 25.2 cm), while males ranged in size between 131 and 253 cm FL (mean \pm SD: 190.5 ± 22.5 cm).

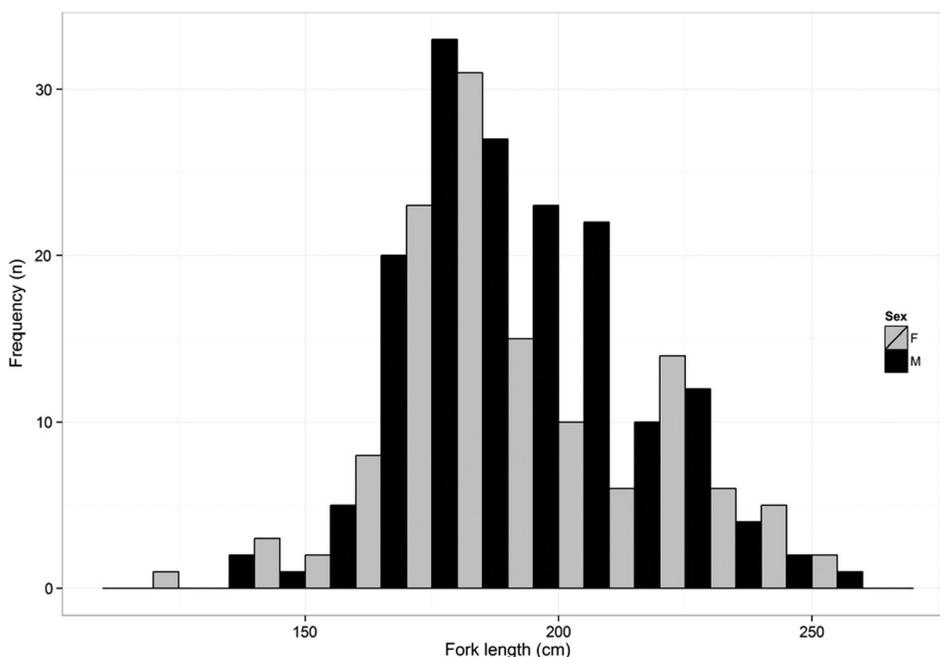


Figure 3. Size (fork length, in cm) frequency distribution of male ($n = 175$) and female ($n = 128$) *Sphyrna zygaena* caught in the Atlantic Ocean and used for this study.

Age estimation and comparison of age readings

Inter-specific percentage agreement between the first and second, first and third, and second and third readings was 46%, 38% and 50%, respectively, demonstrating that vertebrae can be read consistently. A total of 95.7% of the vertebrae had at least two identical readings (97.8% within one growth band) and thus were accepted for the growth modelling. The CV between the three readings was 7.00% and the APE was 5.36%. A high agreement with no systematic bias was

observed between the readings when comparing graphically the three readings of the primary reader using the age-bias plots (Figure 4).

Growth modelling

Estimated ages of the analysed specimens ranged from 3 to 24 years for females and from 4 to 25 years for males. The LRT showed significant differences between the samples used in Coelho et al. (2011) and

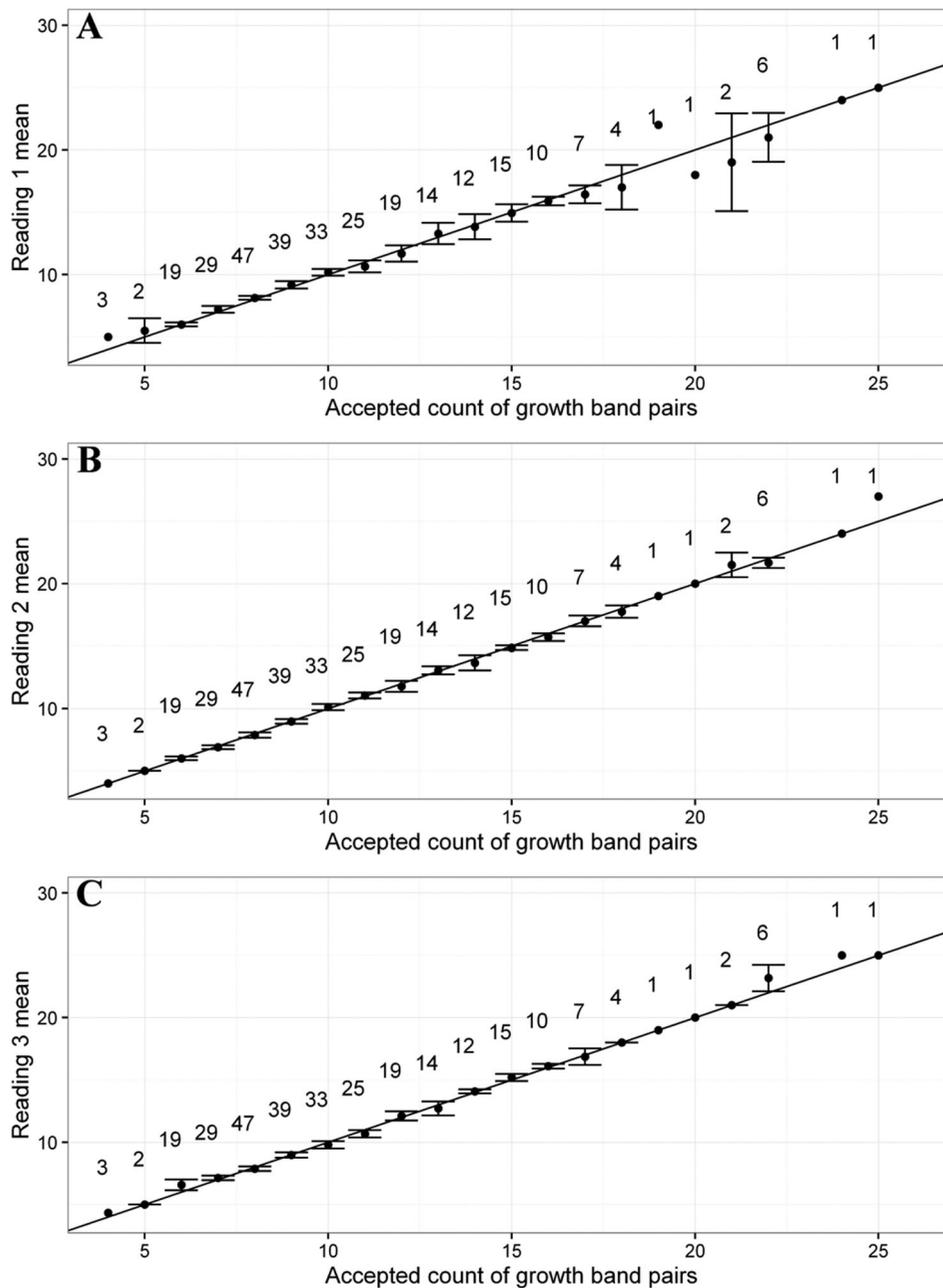


Figure 4 . Age-bias plots of pairwise age comparisons between (A) reading 1, (B) reading 2 and (C) reading 3 and the final accepted count of growth band pairs (when two out of the three readings agreed) carried out by the primary reader based on examination of *Sphyrna zygaena* vertebrae. Numbers represent number of samples and dots with error bars represent the mean counts of reading (\pm 95% confidence intervals) relative to the accepted age. The diagonal line indicates a one-to-one relationship.

Table II. Growth parameters for *Sphyrna zygaena* (sexes separate) from the Atlantic Ocean, fitted with individual observed data. The presented models are the re-parameterized von Bertalanffy growth function (VBGF) and the VBGF with fixed L_0 at 43 cm fork length (FL). For each model, parameters are presented with the respective standard errors (SE) and 95% confidence intervals (CI). L_{inf} = asymptotic maximum length (cm FL), k = growth coefficient (year^{-1}), L_0 = size at birth (cm FL).

Sex	Model	AIC	Parameter	Estimate	SE	95% CI	
						Lower	Upper
Males	VBGF	1136	L_{inf}	259.3	8.5	245.5	280.9
			k	0.09	0.01	0.07	0.11
	VBGF $L_0 = 43$	1152	L_0	89.6	8.5	71.2	105.00
			L_{inf}	237.57	2.72	232.26	243.28
Females	VBGF	927	k	0.14	0.005	0.14	0.15
			L_{inf}	303.6	24.2	270.6	385.1
	VBGF $L_0 = 43$	949	k	0.06	0.01	0.03	0.09
			L_0	99.1	9.00	80.2	115.2
	L_{inf}	251.81	4.45	243.23	261.46		
	k	0.13	0.006	0.12	0.14		

the remaining samples used in the present study (LRT: $\chi^2 = 10.11$, $df = 3$, $P = 0.02$). The LRT revealed significant differences between males and females (LRT: $\chi^2 = 14.52$, $df = 3$, $P = 0.002$); therefore, growth models were calculated for each sex.

For the VBGF fit to the sample data, females exhibited lower growth coefficients (k values) and higher asymptotic size (L_{inf}) than males. L_{inf} parameter estimates are 259.3 cm for males and 303.6 cm for females; k is 0.09 year^{-1} for males and 0.06 year^{-1} for females. L_0 estimates are 89.6 cm for males and 99.1 cm for females (Table II, Figure 5). L_{inf} estimates from the model with fixed L_0 were lower than the estimates from the standard model, with estimates of 237.6 cm and 251.8 cm for males and females, respectively. Inversely, k estimates were higher, being 0.14

year^{-1} and 0.13 year^{-1} for males and females, respectively. The model with fixed L_0 presented higher AIC than the model with three-parameters (Table II), indicating that the models with estimated L_0 better represented the data.

Back-calculation

Of the 291 individuals with valid age readings, only 287 individuals were included in the back-calculation analysis, 125 males and 162 females, because it was not possible to measure the distances from the focus to each annulus for some individuals.

There was a slight curvilinear relationship between VR and FL (Figure 6). A linear regression gave a significant fit to the data ($FL = 64.04 + 11.77 \times VR$; $r^2 = 0.86$;

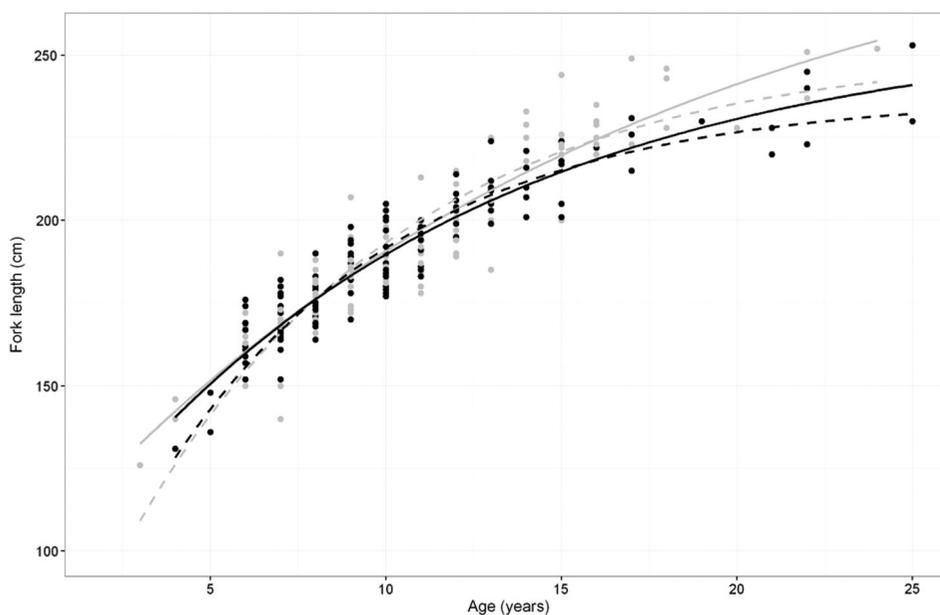


Figure 5. The von Bertalanffy growth function (VBGF) for *Sphyrna zygaena* based on age estimations by vertebrae growth marks. Circles represent observed data and line represents VBGF, dashed line represents VBGF with fixed L_0 (43 cm fork length). Black represents males and grey represents females.

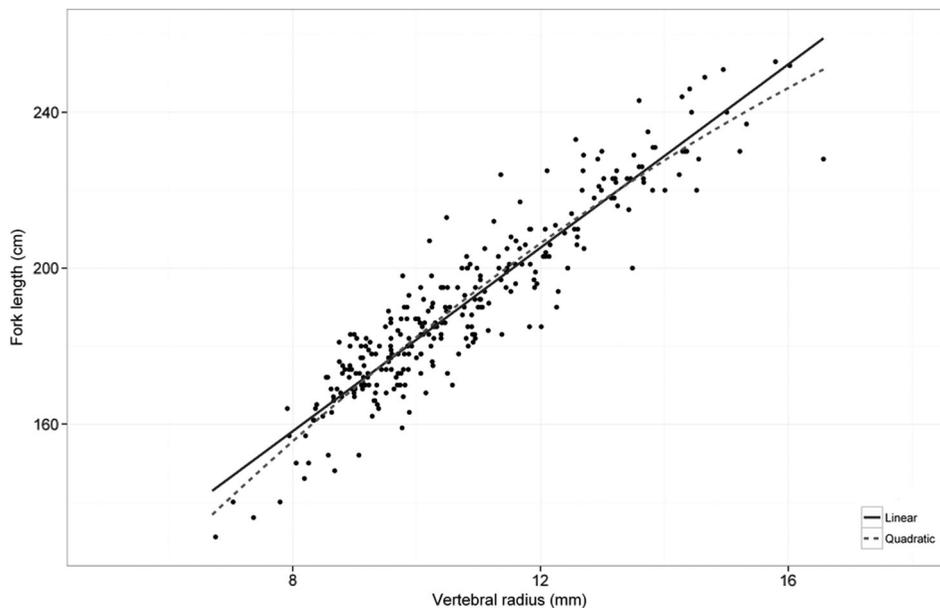


Figure 6. Relationship between fork length (cm) and vertebrae centrum radius (mm) for *Sphyrna zygaena*. Dots represent individual observations. Solid line represents linear regression where: $FL = 64.04 + 11.77 \times VR$. Dashed line represents quadratic regression where: $FL = 21.45 + 19.49 \times VR - 0.34 \times VR^2$. FL = fork length; VR = vertebral radius.

AIC = 2054; $P < 0.001$); however, the quadratic equation produced a slightly better goodness-of-fit ($FL = 21.45 + 19.49 \times VR - 0.34 \times VR^2$; $r^2 = 0.86$; AIC = 2048; $P < 0.001$). Nonetheless, it was still necessary to compare the back-calculated data with the mean sample length at age to check if the slightly better statistical fit of the quadratic equation translated into better biological accuracy for modelling growth.

Lee's phenomenon, the tendency for older aged fish lengths at previous ages to underestimate sample mean length of fish of that age class (see Ricker 1969) was observed in individual back-calculated lengths. This is apparent in the mean back-calculated lengths of smaller length classes particularly for the Dahl-Lea and size at birth modified Fraser-Lee models. For the linear modified Dahl-Lea model the mean back-calculated lengths were, overall, very similar to the mean sample length at age data, with males and females within 14 and 13 cm for males and females, respectively. Likewise the quadratic Dahl-Lea provided similar back-calculated lengths to the mean length at age, especially for males and females larger than 165 cm FL (Figure 7).

For all back-calculated methods the female VBGF estimates had higher L_{inf} than males and similar k estimates. Between VBGF models, fit to the different back-calculation methods, L_0 estimates varied from 29 to 83 cm for males and 29 to 84 cm for females (Table III). L_{inf} estimates varied from 436.33 cm to 284.58 cm for males, and 461.31 cm to 293.94 cm for females. Although similar, estimates of k varied

inversely from L_{inf} , where the quadratic Dahl-Lea had the highest k estimate for both sexes (Figure 8).

Discussion

The fact that age precision is highly influenced by species and the nature of the structure being read makes it difficult to establish target levels of precision indexes such as the CV and APE. Campana (2001) suggested 7.6% as a reference level for CV and 5.5% for APE, but mentioned that most studies reporting shark ages based on vertebrae did so with CV values exceeding 10%. In this study, values for intra-reader precision of 7.00% CV and 5.36% APE were determined, which taken together with the age bias plots indicates that our age estimates were consistent and seem adequate for this species.

Although no age validation was carried out in the present study, previous studies on other hammerhead shark species have discussed this issue, with different criteria and results. For the scalloped hammerhead, Chen et al. (1990) assumed that two pairs of bands per year were being deposited in the NW Pacific (Taiwan), while Piercy et al. (2007) assumed a pattern of one pair of bands per year in the NW Atlantic. For the great hammerhead shark, *Sphyrna mokarran* (Rüppell, 1837), Passerotti et al. (2010) validated the annual deposition pattern of the growth bands with the bomb radiocarbon technique, demonstrating that indeed one band pair was being deposited annually. For the bonnethead (*Sphyrna tiburo*) in the Gulf of

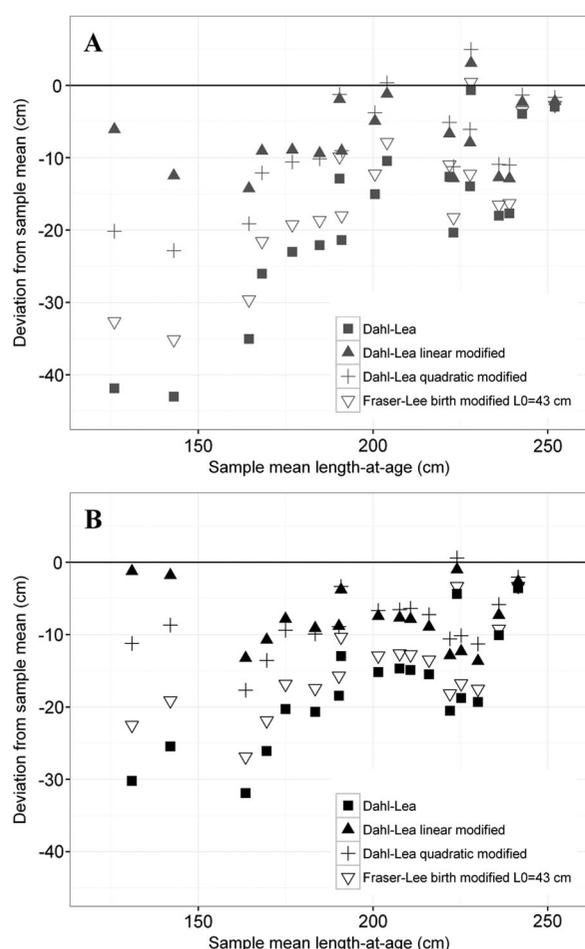


Figure 7. Mean deviation from mean sampled fork length of four proportional back-calculation methods for (A) female and (B) male *Sphyrna zygaena*. Data points represent mean back-calculated lengths at age for each model. A point on the x-axis (black horizontal line) would represent zero deviation from the sample mean length at age.

Mexico and western North Atlantic, Parsons (1993) and Frazier et al. (2014) also validated the periodicity of growth band deposition as one pair of bands per year by analysing vertebrae of specimens marked with oxytetracycline. As such, our assumption of the deposition of one band per year in *Sphyrna zygaena* seems to be valid, but a confirmation of this annual pattern is still lacking for this species and future work should address this issue.

The observed growth curves of both sexes were similar until age 10, after which males exhibited a considerable reduction in the growth rate, while females showed a straighter growth curve, with a less acute reduction in the growth rate than males and at a later age. This difference in growth between sexes has also been described for other shark species (e.g. Kotas et al. 2011; Parsons 1993; Piercy et al. 2007; Frazier et al. 2014; Drew et al. 2015).

Newborn *S. zygaena* must have a very high growth rate in the early years (our youngest individual was assigned an age of 3 years and measured 126 cm FL, a rate of 28 cm FL year⁻¹ if it was born at 43 cm). As this size/age range is not represented in our dataset, it might be the reason the growth model is not able to estimate L_0 as low as the observed size at birth. The estimated L_0 values from the growth curves fitted to the sample data (90–100 cm) are much higher than the values reported by Vooren et al. (2005), i.e. between 38 and 43 cm FL. By overestimating L_0 the model estimates of k and L_{inf} will also be biased. Also, when setting L_0 to 43 cm FL, k estimates are forced to be higher, in order to explain the rapid increase in size in the first few years. As k and L_{inf} are inversely correlated, this makes L_{inf} estimates lower than expected. Back-calculation was used to complete the gap by calculating length at ages prior to the ages at capture based on the relationship between fork length and vertebral radii.

Lee's phenomenon was observed in individual data and resulted in an underestimation of mean back-calculated length at age regarding the observed mean length at age in some age classes. This phenomenon describes the apparent change in back-calculated growth rates with increasing age, which can occur as a result of length-dependent mortality, non-representative sampling, use of the wrong back-calculation equation, or ageing errors (see Ricker 1969; Duncan 1980). Both modified Dahl-Lea equations were more accurate in representing the mean length at age than the standard Dahl-Lea or the size at birth Fraser-Lee. Besides not representing the mean back-calculated lengths at age, the Dahl-Lea and the size at birth modified Fraser-Lee L_{inf} estimates are very high compared with the largest observed individuals in our dataset for each sex.

The linear modified Dahl-Lea equation was the best predictor of length at ages prior to capture; however, L_0 estimates fit to this data were much higher than the values previously reported for this species by Vooren et al. (2005), as well as having a large L_{inf} estimate. The models with highest L_{inf} were fitted to data from back-calculation models that are based on a linear relationship, even if implicit. The lack of smaller individuals in the sample may be affecting the form of the FL-VR relationship, which might lead to the overestimation of L_0 in the linear modified Dahl-Lea and to the overestimation of L_{inf} in the Dahl-Lea, linear modified Dahl-Lea and size at birth modified Fraser-Lee.

The VBGF fit to the back-calculated lengths obtained using the quadratic modified Dahl-Lea represented mean lengths at age accurately and L_{inf} estimates are

Table III. Growth parameters for *Sphyrna zygaena* (separate sexes) from the Atlantic, fitted with back-calculated length at age data. The presented model is the re-parameterized von Bertalanffy growth function (VBGF). For each back-calculation model parameters are presented with the respective standard errors (SE) and 95% confidence intervals (CI). L_{inf} = asymptotic maximum length (cm fork length), k = growth coefficient (year^{-1}), L_0 = size at birth (cm fork length).

Sex	Back calculation model	Parameter	Estimate	SE	95% CI	
					Lower	Upper
Males	Dahl-Lea	L_{inf}	436.33	11.85	413.10	459.56
		k	0.054	0.002	0.050	0.057
		L_0	29.04	0.53	27.99	30.09
	Dahl-Lea linear modified	L_{inf}	355.95	7.00	342.23	369.68
		k	0.051	0.002	0.048	0.055
		L_0	82.85	0.39	82.08	83.62
	Dahl-Lea quadratic modified	L_{inf}	284.58	4.21	276.71	293.19
		k	0.091	0.003	0.087	0.097
		L_0	52.15	0.50	51.18	53.12
	Fraser-Lee birth modified $L_0=43$	L_{inf}	413.53	10.53	392.89	434.17
		k	0.054	0.002	0.050	0.057
		L_0	43.24	0.49	42.29	44.19
Females	Dahl-Lea	L_{inf}	461.32	13.53	434.81	487.84
		k	0.050	0.002	0.046	0.054
		L_0	29.16	0.59	28.01	30.31
	Dahl-Lea linear modified	L_{inf}	384.97	9.18	366.98	402.96
		k	0.047	0.002	0.043	0.050
		L_0	83.85	0.49	82.89	84.91
	Dahl-Lea quadratic modified	L_{inf}	293.94	4.66	284.80	303.07
		k	0.087	0.003	0.082	0.093
		L_0	52.73	0.57	51.61	53.85
	Fraser-Lee birth modified $L_0=43$	L_{inf}	441.16	12.42	423.23	442.66
		k	0.049	0.002	0.045	0.053
		L_0	43.25	0.52	42.23	44.26
Combined	Dahl-Lea	L_{inf}	444.65	8.84	427.33	461.96
		k	0.052	0.001	0.049	0.055
		L_0	29.06	0.40	28.29	29.84
	Dahl-Lea linear modified	L_{inf}	367.43	5.66	356.35	378.52
		k	0.049	0.001	0.047	0.052
		L_0	83.27	0.31	82.67	83.87
	Dahl-Lea quadratic modified	L_{inf}	288.20	3.16	282.00	294.40
		k	0.090	0.002	0.087	0.094
		L_0	52.38	0.37	51.65	53.11
	Fraser-Lee birth modified $L_0=43$	L_{inf}	425.01	8.20	408.93	441.09
		k	0.052	0.001	0.049	0.055
		L_0	43.22	0.35	42.53	43.92

consistent with the largest individuals in our dataset, as well as L_0 being similar to that reported for this species by Vooren et al. (2005). There is also a statistical reason to prefer the quadratic modified Dahl-Lea, as the FL-VR relationship is slightly curvilinear.

Growth curves have been produced by Coelho et al. (2011) for the Eastern equatorial Atlantic Ocean but because the sample size and coverage areas in that study were relatively small, these samples have been included in the present study, increasing the size range and spatial coverage, and thus the present study is considered to be more comprehensive than the previous study of growth of *S. zygaena* in the Atlantic Ocean. The parameters from the quadratic modified Dahl-Lea back-calculation method are slightly different from those determined by Coelho et al. (2011) for the eastern equatorial Atlantic. Both sexes from our study seem to grow to a larger size and at a higher rate than that previously described for the eastern equatorial Atlantic (Table IV). Liu & Tsai (2011), based on an unpublished Master's thesis from the north-western

Pacific Ocean, reported slightly higher growth coefficients than the present study for *S. zygaena* and similar L_{inf} ; using equation 2 to convert from TL to FL, the reported L_{inf} values are 279 cm for males and 292 cm for females (Table IV).

Other closely related species have already been studied, such as the scalloped hammerhead in the NW Atlantic Ocean and Gulf of Mexico (Piercy et al. 2007), off NE Taiwan (Chen et al. 1990), off the southern Brazilian coast (Kotas et al. 2011), off the east Australian coast (Harry et al. 2011) and in the eastern Indian Ocean (Drew et al. 2015). The growth coefficients estimated for that species ranged from a minimum of 0.05 year^{-1} for males and females from the southern Brazilian coast (Kotas et al. 2011) to 0.222 year^{-1} (males) and 0.249 year^{-1} (females) off NE Taiwan (Chen et al. 1990). However, this later study considered a bi-annual band deposition periodicity pattern, making the growth rates higher (Table IV). The great hammerhead has been studied in the NW Atlantic (Piercy et al. 2010), with k values of 0.11 year^{-1} and 0.16 year^{-1} for

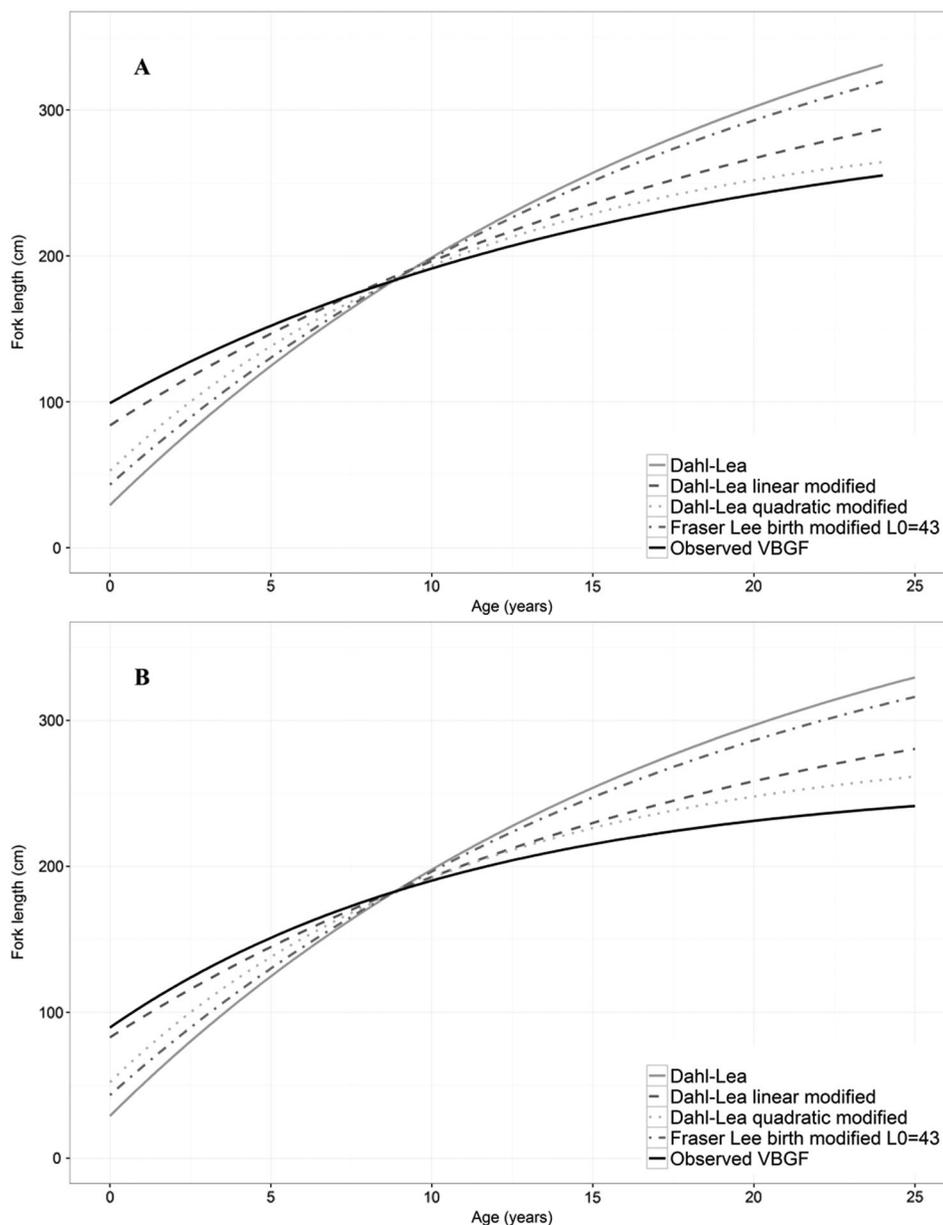


Figure 8. von Bertalanffy growth curves for *Sphyrna zygaena* for (A) females and (B) males. Fitting to individual observed data and four back-calculation models: Dahl-Lea, linear modified Dahl-Lea, quadratic modified Dahl-Lea and Fraser-Lee size at birth modified (with biologically derived intercept at 43 cm fork length).

females and males, respectively; and off eastern Australia (Harry et al. 2011) with estimated growth coefficients of 0.08 year^{-1} for the combined sexes. Even though no direct comparison can be made between different species, the values that were estimated for *S. zygaena* in the present study seem to fall in the low to middle of the ranges presented previously for *S. lewini* and *S. mokarran*.

Accurate age information is vital for obtaining quality estimates of growth that are essential for successful and sustainable fisheries management. The growth parameters estimated and presented in this study support the hypothesis that this species, like

other elasmobranchs, requires conservative management due to its slow growth and subsequent susceptibility to overexploitation (Musick 2004). Future work on this species should be focused on validation of band deposition and obtaining vertebrae from younger specimens. Although further work is needed, this study adds to our knowledge of the vital life-history parameters of smooth hammerhead sharks. The growth parameters estimated from the quadratic modified Dahl-Lea VBGF are recommended for future use, and can now be incorporated into stock assessment models to allow more robust science-based fishery management and conservation initiatives.

Table IV. Growth parameters for *Sphyrna zygaena*, *S. lewini* and *S. mokarran* from previously published studies. FL = fork length (cm), TL = total length (cm), STL = stretched total length (cm), VBGF = von Bertalanffy growth model, VBGF L_0 = re-parameterized von Bertalanffy growth function, GOM = Gompertz growth function, GOM L_0 = re-parameterized Gompertz growth function, L_{inf} = asymptotic maximum length (cm fork length), k = growth coefficient (year^{-1}), L_0 = size at birth (cm fork length), t_0 = theoretical age at which the expected length is zero.

Species	Ocean	Area	Periodicity	Measurement	Growth model	Parameters	Sex			Reference
							Female	Male	Combined	
<i>S. zygaena</i>	Atlantic	Atlantic Ocean wide area	Annual	FL	VBGF L_0^a	L_{inf} k L_0	293.9 0.09 52.7	284.6 0.09 52.4	288.2 0.09 52.4	Present study
	Atlantic	Eastern Equatorial Atlantic	Annual	FL	VBGF ^b	L_{inf} k t_0	285.2 0.07 -7.3	271.8 0.06 -9.4	277.7 0.06 -8.3	Coelho et al. (2011)
	Pacific	NE Taiwan waters	-	TL	VBGF	L_{inf} k t_0	375.2 0.11 -1.31	358.8 0.13 -0.72		Liu & Tsai (2011)
<i>S. lewini</i>	Pacific	NE coast of Taiwan	Biannual	TL	VBGF ^b	L_{inf} k t_0	319.7 0.25 -0.75	320.6 0.22 -0.75		Chen et al. (1990)
	Pacific	Southern coast of Sinaloa, México	Biannual	TL	VBGF ^a	L_{inf} k t_0	376 0.1 -1.16	364 0.12 -1.18		Anislado-Tolentino et al. (2008)
	Pacific	East coast of Australia	Annual	STL	VBGF L_0^b	L_{inf} k L_0			330.5 0.08 58.2	Harry et al. (2011)
	Atlantic	NW Atlantic and Gulf of Mexico	Annual	FL	VBGF ^b	L_{inf} k t_0	233.1 0.09 -2.22	214.8 0.13 -1.62	219.8 0.12 -1.84	Piercy et al. (2007)
	Atlantic	Southern Brazilian coast	Annual	TL	VBGF L_0^a	L_{inf} k L_0	300 0.05 51	266 0.05 47		Kotas et al. (2011)
	Indian	Indonesian waters	Annual	TL	GOM L_0^b	L_{inf} k L_0^c	289.6 0.16 50	259.8 0.16 56.8	289.6 0.16 50	Drew et al. (2015)
<i>S. mokarran</i>	Atlantic	NW Atlantic and Gulf of Mexico	Annual	FL	VBGF ^b	L_{inf} k t_0	307.8 0.11 -2.86	246.2 0.16 -1.99	-	Piercy et al. (2010)
	Pacific	East coast of Australia	Annual	STL	VBGF L_0^b	L_{inf} k L_0^c			402.7 0.08 70	Harry et al. (2011)

Note: ^aBack-calculated data. ^bObserved data. ^cFixed L_0 .

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