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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 north and south

hemispheres. Data from 304 specimens, caught between October 2009 and September 2014,

ranging in size from 126 to 253 cm fork length (FL), were analyzed. Growth models were fitted

using the 3-parameter von Bertalanffy growth function (VBGF) re-parameterised 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 model to describe growth in this species, with resulting growth

parameters of L_{inf} = 285 cm FL, $k = 0.09$ year^{-1} for males and L_{inf} = 293 cm FL, $k = 0.09$ year^{-1} for

females. Compared to 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 this species' management and conservation.

Keywords: Age and growth, Smooth hammerhead, Atlantic Ocean, vertebral band counts, back-

calculation, life history

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,b). 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 eleven

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.

118   **Methods**

119   *Sampling and processing*

120   All *Sphyrna zygaena* samples were obtained by Portuguese Institute for the Ocean and Atmosphere

121   (IPMA) observers on board Portuguese commercial longline vessels targeting swordfish in the

122   Atlantic Ocean. Vertebra collection started in October 2008, with a total of 304 *S. zygaena* sampled

123   over a period lasting until September 2014. As per ICCAT Recommendation 13-10 (ICCAT 2013),

124   samples were collected only from sharks that were dead at haulback when retrieving the longline

125   and were taken in the framework of a research project notified to the Scientific Committee for

126   Research and Statistics (ICCAT-SCRS) through the Shark Working Group (Coelho & Santos 2015;

127   Santos & Coelho 2015). Samples were collected over a wide Atlantic region (latitudes 22º N to 29º

128   S; longitudes 7º E to 43º W) (Fig. 1). Some of these samples (n=139) were used to estimate growth

129   curves for the eastern equatorial Atlantic Ocean in a previous study (Coelho et al. 2011). Since the

130   sample size and sample areas were limited, the aforementioned samples were also included in the

131   present study in order to model the growth of this species for a wider Atlantic area.

132   All specimens were measured on board for fork length (FL, cm) in a straight line to the nearest cm,

133   and the sex was determined. A section from 4 to 8 vertebrae was extracted from the region below

134   the anterior part of the first dorsal fin. All samples were kept frozen while on the vessels and during

135   transportation to the laboratory. In the laboratory, the covering connective tissue of the vertebrae

136   was first removed manually with scalpels, and then by soaking the vertebrae in 4–6% sodium

137   hypochlorite (commercial bleach) for 10 to 20 min, depending on size. Once cleaned, the vertebrae

138   were stored in 70% ethanol, and then air-dried for 24 h before mounting on a microscope slide

139   using thermoplastic cement or a synthetic polymer glue. Once mounted, the vertebrae were

140   sectioned sagittally with a Buehler Isomet (Lake Bluff, IL) low-speed saw, using two blades spaced

141   approximately 500 µm apart. The resulting section included the focus of the vertebra and the two

142   halves (one on each side of the focus), in a form typically called "bow-tie". Finally, the sections

143   were stained with crystal violet (Sigma-Aldrich Co., St. Louis, MO), found by Coelho et al. (2011)

144 to be the best band enhancement technique for this species, for a better visualization of the growth

145 band pairs (comprising one opaque and one translucent band). Once dried, the sections were

146 mounted onto microscope slides with Cytoseal 60 (Thermo Fisher Scientific Inc., Waltham, MA).

147 The visualization of the vertebral sections was carried out under a dissecting microscope using

148 transmitted white light (Fig. 2).

149 *Age estimation and comparison of age readings*

150 For training and consistency between readings taken by different readers, a set of vertebrae (n=139)

151 was independently read by three readers, on three separate occasions, in order to guarantee quality

152 control and precision. To prevent bias while counting the bands, the three readers had no knowledge

153 of the length or sex of each shark. After this step, the remaining sample (n=165) was then read three

154 times by the primary reader and only those vertebrae whose band counts were the same for at least

155 two of the three readings of the primary reader were accepted for the age and growth analysis. Each

156 reading was finalized before starting the next one to prevent reader familiarity with any particular

157 vertebra.

158 In order to compare intra-reader ageing precision between the three readers both the coefficient of

159 variation (CV; Chang 1982) and the average percentage error (APE; Beamish & Fournier 1981)

160 were calculated and compared. The percentage of agreement (PA) among the primary reader

161 readings was also calculated. Bias plots were used to graphically assess the ageing accuracy

162 between the three readings (Campana 2001). Precision analysis was carried out using the R

163 language for statistical computing version 3.2.5 (R Core Team 2016), using the package "FSA"

164 (Ogle 2015).

165

166 *Growth modelling*

167 *Sphyrna zygaena* is a viviparous species; parturition time is estimated to be around December-

168 January in southern Brazilian waters (Vooren et al. 2005). As for other species the first growth band

169 is a birthmark, associated with an angle change along the *corpus calcareum* of sectioned vertebrae

170   (Goldman 2004) (Fig. 2). In order to verify the temporal periodicity of band formation in the

171   vertebral centra, an edge analysis and a marginal increment analysis was initially attempted.

172   However, due to the lack of captures for each month and for every estimated age class, it was not

173   possible to determine the periodicity of band formation. The deposition of a band pair (one

174   translucent and one opaque band) per year was assumed (see Discussion for details). Vertebrae

175   were aged accordingly in integer years.

176   Two models were used to describe this species' growth. The first model was the 3-parameter von

177   Bertalanffy growth function (VBGF) re-parameterised to estimate L_0 (size at birth) instead of t_0

178   (theoretical age at which the expected length is zero), as suggested by Calliet et al. (2006):

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

180   L_t = mean fork length at age t; L_{inf} = asymptotic maximum fork length for the model of average fork

181   length at age; k = growth coefficient; L_0 = fork length at birth.

182   A 2-parameter VBGF was also used, where L_0 was fixed to the maximum size at birth

183   described for this species. The maximum value of size at birth described for the species by Vooren

184   et al. (2005) is 55 cm total length (TL). Because size data in our study refers to FL we used the

185   conversion factor from Mas et al. (2014), to convert the size at birth from TL into FL:

186   FL = 0.78 × TL (size range: 114-330 cm TL) (2)

187   A likelihood ratio test (LRT), as defined by Kimura (1980) and recommended by Cerrato (1990),

188   was used to test the null hypotheses that there was no difference in growth parameters between

189   males and females, using the "fishmethods" package (Nelson 2014) in R (R Core Team 2016). The

190   LRT was also used to test differences between the present study sample and the sample in Coelho et

191   al. (2011).

192

193   *Back-calculation*

194   To account for the absence of the smaller individuals in the sample, lengths at ages prior to the ages

195   at capture were back-calculated from vertebral centra measurements. Back-calculation is a method

196   for describing the growth history of each individual sampled by estimating lengths at ages prior to

197   the ages at capture for each individual (Goldman 2004; see Francis 1990; Vigliola & Meekan 2009

198   for reviews). To obtain accurate parameter estimates from the growth models fitted to the resulting

199   back-calculated lengths at ages it is necessary to choose the appropriate relationship between the

200   vertebral radius (VR) and the specimen FL. Linear and quadratic models were used to describe the

201   FL-VR relationship, respectively:

202    $FL = a + b\text{VR}$ (3)

203    $FL = a + b\text{VR} + c\text{VR}^2$ (4)

204   For this analysis the vertebral sections of all specimens were micro-photographed, the distance from

205   the focus to each annulus and the vertebral radius were measured digitally using Image J software

206   (Abramoff et al. 2004) (Fig. 2). Distances were measured to the nearest 0.01 mm or 0.007 mm,

207   according to the dissecting microscope magnification used, as a straight line from the central focus

208   to the outer margin of the *corpus calcareum*. When measuring the distance to each annulus it was

209   assumed that a band pair constitutes one year of growth, therefore the measurements were made

210   from the outer edge of one translucent band to the outer edge of the next identifiable translucent

211   band. These measurements were made only in vertebrae with an accepted count of growth rings,

212   when two out of the three readings were the same. FL-VR models were fitted with a linear model in

213   R (R Core Team 2016) and goodness-of-fit compared with the Akaike Information Criterion value

214   (AIC) and the coefficient of determination (r^2), where the model with the lowest AIC and highest r^2

215   was considered the model that best fitted the data and described the FL-VR relationship.

216   Goldman (2004) recommends that several proportional back-calculation methods should be

217   compared to examine the statistical and biological accuracy of back-calculated lengths relative to

218   vertebral sample data. Four different proportion methods were used (Table I) and compared with

219   our sample length at age data. The Dahl-Lea model assumes a direct proportion between fish length

220   and vertebral radius (see Vigliola & Meekan 2009); while the linear and quadratic Dahl-Lea models

221   use parameter estimates from the linear and quadratic fits that describe the FL-VR relationship,

222   respectively (Francis 1990). The size at birth Fraser-Lee model includes a biologically derived

223   intercept as the point of origin of back-calculations (Campana 1990).

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

225   Vertebral radii-at-birth (R_0) were averaged from all sectioned vertebrae to obtain a mean value. An

226   R_0 of 1.61 mm ± 0.31 standard deviation (SD) was estimated.

227   Biological accuracy was determined by plotting the sample mean length at age data against the

228   difference between mean back-calculated length at age and the sample mean length at age to

229   determine which method provides the best results (Goldman 2002). This plot shows which back-

230   calculation method most accurately reflects sample mean lengths at age (Goldman 2004). The 3-

231   parameter VBGF was then fitted to the back-calculated length data.

232   The FSA package (Ogle 2015) in R (R Core Team 2016) was used for the back-calculations. The

233   VBGF model was then fit using non-linear mixed effects models ('nlme', Pinheiro et al. 2016) in R

234   (R Core Team 2016), as suggested by Vigliola & Meekan (2009) due to the longitudinal nature of

235   the back-calculated data. A block variance-covariance structure was used to allow L_{inf} and k to be

236   correlated (Pinheiro & Bates 2000) and the convergence tolerance was set to 1^{-4}. For each model,

237   the parameters were estimated, as were the corresponding standard errors (SE) and the limits of the

238   95% confidence intervals (CI). Plots were created using 'ggplot2' (Wickham 2009).

239

240   **Results**

241   *Sample characteristics*

242   A total of 304 sampled sharks (175 males, 128 females, 1 specimen with undetermined sex) were

243   collected for this study (Fig. 3). From these individuals, 291 vertebra had at least two identical

244   readings and were considered to have valid age readings, thus were used for the age and growth

245   analysis. As the growth modelling was performed for the separate sexes the specimen with

246   undetermined sex was not included in this part of the analysis. Females ranged in size between 126

247   and 252 cm FL (mean ± SD: 193.5 ± 25.2 cm), while males ranged in size between 131 and 253 cm

248   FL (mean ± SD: 190.5 ± 22.5 cm).

249

250   *Age estimation and comparison of age readings*

251   Inter-specific percentage agreement between the first and second, first and third, and second and

252   third readings was 46%, 38% and 50%, respectively, demonstrating that vertebra can be read

253   consistently. A total of 95.7% of the vertebrae had at least two identical readings (97.8% within one

254   growth band) and thus were accepted for the growth modelling. The CV between the three readings

255   was 7.00% and the APE was 5.36%. A high agreement with no systematic bias was observed

256   between the readings when comparing graphically the three readings of the primary reader using the

257   age-bias plots (Fig. 4).

258

259   *Growth modelling*

260   Estimated ages of the analyzed specimens ranged from 3 to 24 years for females and from 4 to 25

261   years for males. The LRT showed significant differences between the samples used in Coelho et al.

262   (2011) and the remaining samples used in the present study (LRT: $\chi2 = 10.11$, df = 3, P = 0.02). The

263   LRT revealed significant differences between males and females (LRT: $\chi2 = 14.52$, df = 3, P =

264   0.002), therefore growth models were calculated for each sex.

265   For the VBGF fit to the sample data, females exhibited lower growth coefficients (k values) and

266   higher asymptotic size (L_{inf}) than males. L_{inf} parameter estimates are 259.3 cm for males and 303.6

267   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

268   males and 99.1 cm for females (Table II, Fig.5). L_{inf} estimates from the model with fixed L_0 were

269   lower than the estimates from the standard model, with estimates of 237.6 cm and 251.8 cm for

270   males and females, respectively. Inversely, k estimates were higher, being 0.14 year^{-1} and 0.13 year^{-}

271   ^{1} for males and females, respectively. The model with fixed L_0 presented higher AIC than the model

272 with 3-parameters (Table II), indicating that the models with estimated L_0 better represented the

273 data.

274

275 *Back-calculation*

276 Of the 291 individuals with valid age readings only 287 individuals were included in the back-

277 calculation analysis, 125 males and 162 females, because it was not possible to measure the

278 distances from the focus to each annulus for some individuals.

279 There was a slight curvilinear relationship between VR and FL (Fig. 6). A linear regression gave a

280 significant fit to the data (FL=64.04+11.77×VR; r^2=0.86; AIC = 2054; P<0.001); however, the

281 quadratic equation produced a slightly better goodness-of-fit (FL=21.45+19.49×VR–0.34×VR^2;

282 r^2=0.86; AIC = 2048; P<0.001). Nonetheless, it was still necessary to compare the back-calculated

283 data with the mean sample length at age to check if the slightly better statistical fit of the quadratic

284 equation translated into better biological accuracy for modelling growth.

285 Lee's phenomenon, the tendency for older aged fish lengths at previous ages to underestimate

286 sample mean length of fish of that age class (see Ricker 1969) was observed in individual back-

287 calculated lengths. This is apparent in the mean back-calculated lengths of smaller length classes

288 particularly for the Dahl-Lea and size at birth modified Fraser-Lee models. For the linear modified

289 Dahl-Lea model the mean back-calculated lengths were, overall, very similar to the mean sample

290 length at age data with males and females within 14 and 13 cm for males and females, respectively.

291 Likewise the quadratic Dahl-Lea provided similar back-calculated lengths to the mean length at age,

292 especially for males and females larger than 165 cm FL (Fig. 7).

293 For all back-calculated methods the female VBGF estimates had higher L_{inf} than males and similar k

294 estimates. Between VBGF models, fit to the different back-calculation methods, L_0 estimates varied

295 from 29 to 83 cm for males and 29 to 84 cm for females (Table III). L_{inf} estimates varied from

296 436.33 cm to 284.58 cm for males, and 461.31 cm to 293.94 cm for females. Although similar,

297 estimates of k varied inversely from L_{inf}, where the quadratic Dahl-Lea had the highest k estimate

298 for both sexes (Fig. 8).

299

300 **Discussion**

301 The fact that age precision is highly influenced by species and the nature of the structure being read

302 makes it difficult to establish target levels of precision indexes such as the CV and APE. Campana

303 (2001) suggested 7.6% as a reference level for CV and 5.5% for APE, but mentioned that most

304 studies reporting shark ages based on vertebrae did so with CV values exceeding 10%. In this study,

305 values for intra-reader precision of 7.00 % CV and 5.36 % APE were determined, which taken

306 together with the age bias plots, indicates that our age estimates were consistent and seem adequate

307 for this species.

308 Although no age validation was carried out in the present study, previous studies on other

309 hammerhead shark species have discussed this issue, with different criteria and results. For the

310 scalloped hammerhead, Chen et al. (1990) assumed that two pairs of bands per year were being

311 deposited in the NW Pacific (Taiwan), while Piercy et al. (2007) assumed a pattern of one pair of

312 bands per year in the NW Atlantic. For the great hammerhead shark, *Sphyrna mokarran* (Rüppell,

313 1837), Passerotti et al. (2010) validated the annual deposition pattern of the growth bands with the

314 bomb radiocarbon technique, demonstrating that indeed one band pair was being deposited

315 annually. For the bonnethead (*Sphyrna tiburo*) in the Gulf of Mexico and western North Atlantic,

316 Parsons (1993) and Frazier et al. (2014) also validated the periodicity of growth band deposition as

317 one pair of bands per year by analysing vertebrae of specimens marked with oxytetracycline. As

318 such, our assumption of the deposition of one band per year in *Sphyrna zygaena* seems to be valid,

319 but a confirmation of this annual pattern is still lacking for this species and future work should

320 address this issue.

321 The observed growth curves of both sexes were similar until age 10, after which males exhibited a

322 considerable reduction in the growth rate, while females showed a straighter growth curve, with a

323   less acute reduction in the growth rate than males and at a later age. This difference in growth

324   between sexes as also described for other shark species (e.g. Kotas et al. 1993; Parsons 1993; Piercy

325   et al. 2007; Frazier et al. 2014; Drew et al. 2015).

326   Newborn *S. zygaena* must have a very high growth rate in the early years (our youngest individual

327   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

328   43 cm). As this size/age range is not represented in our dataset, it might be the reason the growth

329   model is not able to estimate L_0 as low as the observed size at birth. The estimated L_0 values from

330   the growth curves fitted to the sample data (90-100 cm) are much higher than the values reported by

331   Vooren et al. (2005), i.e. between 38 and 43 cm FL. By overestimating L_0 the model estimates of k

332   and L_{inf} will also be biased. Also, when setting L_0 to 43 cm FL, k estimates are forced to be higher,

333   as to explain the rapid increase in size in the first few years. As k and L_{inf} are inversely correlated

334   this makes L_{inf} estimates to be lower than expected. Back-calculation was used to complete the gap

335   by calculating length at ages prior to the ages at capture based on the relationship between fork

336   length and vertebral radii.

337   Lee's phenomenon was observed in individual data and resulted in an underestimation of mean

338   back-calculated length at age regarding the observed mean length at age in some age classes. This

339   phenomenon describes the apparent change in back-calculated growth rates with increasing age,

340   which can occur as a result of length-dependent mortality, non representative sampling, use of the

341   wrong back-calculation equation, or ageing errors (see Ricker 1969; Duncan 1980). Both modified

342   Dahl-Lea equations were more accurate in representing the mean length at age than the standard

343   Dahl-Lea or the size at birth Fraser-Lee. Besides not representing the mean back-calculated lengths

344   at age the Dahl-Lea and the size at birth modified Fraser-Lee L_{inf} estimates are very high compared

345   to the largest observed individuals in our dataset for each sex.

346   The linear modified Dahl-Lea equation was the best predictor of length at ages prior to capture,

347   however L_0 estimates fit to this data were much higher than the values previously reported for this

348   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 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. In comparisons of 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 thesis from the north-eastern 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 for males is 279 cm 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

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

375 ranged from a minimum of 0.05 year^{-1} for males and females from the southern Brazilian coast

376 (Kotas et al. 2011) to 0.222 year^{-1} (males) and 0.249 year^{-1} (females) off NE Taiwan (Chen et al.

377 1990). However, this later study considered a bi-annual band deposition periodicity pattern, making

378 the growth rates higher (Table IV). The great hammerhead has been studied in the NW Atlantic

379 (Piercy et al. 2010), with k values of 0.11 year^{-1} and 0.16 year^{-1} for females and males, respectively;

380 and off eastern Australia (Harry et al. 2011) with estimated growth coefficients of 0.08 year^{-1} for the

381 combined sexes. Even though no direct comparison can be made between different species, the

382 values that were estimated for *S. zygaena* in the present study seem to fall in the low to middle of

383 these ranges presented previously for *S. lewini* and *S. mokarran*.

384 Accurate age information is vital for obtaining quality estimates of growth that are essential for

385 successful and sustainable fisheries management. The growth parameters estimated and presented in

386 this study support the hypothesis that this species, like other elasmobranchs, requires conservative

387 management due to its slow growth and subsequent susceptibility to overexploitation (Musick

388 2004). Future work on this species should be focused on validation of band deposition and

389 obtaining vertebrae from younger specimens. Although further work is needed, this study adds to

390 the knowledge of the vital life-history parameters of smooth hammerhead sharks. The growth

391 parameters estimated from the quadratic modified Dahl-Lea VBGF are recommended for future

392 use, and can now be incorporated into stock assessment models to allow more robust science based

393 fishery management and conservation initiatives.

394

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539 Table I - Summary of the four back-calculation models examined in this study: Dahl-Lea (see

540 Vigliola & Meekan 2009), Linear modified Dahl-Lea (Francis 1990), Quadratic modified Dahl-

541 Lea (Francis 1990), and size at birth modified Fraser-Lee (Campana 1990).

Back calculation models	
Dahl-Lea	$L_i = (VR_i / VR_c)L_c$
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	$L_i = L_c + (VR_i - VR_c)[(L_c - L_0)/ (VR_c - VR_0)]$

542 Note: L fish length; VR vertebral radius; L_0 fish length at birth; L_i length at age i; L_c length at

543 capture; VR_0 vertebral radius at birth; VR_i radius at age i; VR_c radius at capture.

544   Table II - Growth parameters for *Sphyrna zygaena* (sexes separate) from the Atlantic, fitted with

545   individual observed data. The presented models is the re-parameterised von Bertalanffy growth

546   function (VBGF) and the VBGF with fixed L_0 at 43 cm fork length (FL). For each model,

547   parameters are presented with the respective standard errors (SE) and 95% confidence intervals

548   (CI). L_{inf} = asymptotic maximum length (cm FL), k = growth coefficient (year^{-1}), L_0 = size at birth

549   (cm FL).

550

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
			L_0	89.6	8.5	71.2	105.00
	VBGF L_0=43	1152	L_{inf}	237.57	2.72	232.26	243.28
			k	0.14	0.005	0.14	0.15
Females	VBGF	927	L_{inf}	303.6	24.2	270.6	385.1
			k	0.06	0.01	0.03	0.09
			L_0	99.1	9.00	80.2	115.2
	VBGF L_0=43	949	L_{inf}	251.81	4.45	243.23	261.46
			k	0.13	0.006	0.12	0.14

551 Table III - Growth parameters for *Sphyrna zygaena* (separate sexes) from the Atlantic, fitted with

552 back-calculated length at age data. The presented model is the re-parameterised von Bertalanffy

553 growth function (VBGF). For each back-calculation model parameters are presented with the

554 respective standard errors (SE) and 95% confidence intervals (CI). L_{inf} = asymptotic maximum

555 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	42.23	44.26
		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

556 Table IV - Growth parameters for *Sphyrna zygaena*, *S. lewini* and *S. mokarran* from previosuly published studies. FL = Fork length (cm), TL = total

557 length (cm), STL = stretched total length (cm), VBGF = von Bertallanfy growth model, VBGF L_0 = re-parameterised von Bertallanfy growth

558 function, GOM = Gompertz growth function, GOM L_0 = re-parameterised Gompertz growth function, L_{inf} = asymptotic maximum length (cm fork

559 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	Measurment	Growth model	Parameters	Female	Male	Combined	Reference
S. zygaena	Atlantic	Atlantic Ocean wide area	Annual	FL	VBGF L_0*	L_{inf}	293.9	284.6	288.2	Present study
						k	0.09	0.09	0.09	
						L_0	52.7	52.2	52.4	
	Atlantic	Eastern Equatorial Atlantic	Annual	FL	VBGF**	L_{inf}	285.2	271.8	277.7	Coelho *et al.* 2011
						k	0.07	0.06	0.06	
						t_0	-7.3	-9.4	-8.3	
	Pacific	NE Taiwan waters	-	TL	VBGF	L_{inf}	375.2	358.8		Liu & Tsai 2011
						k	0.11	0.13		
						t_0	-1.31	-0.72		
S. lewini	Pacific	NE coast of Taiwan	Biannual	TL	VBGF**	L_{inf}	319.7	320.6		Chen *et al.* 1990
						k	0.25	0.22		
						t_0	-0.75	-0.75		
	Pacific	Southern coast of Sinaloa, México	Biannual	TL	VBGF*	L_{inf}	376	364		Anislado-Tolentino *et al.* 2008
						k	0.1	0.12		
						t_0	-1.16	-1.18		
	Pacific	East coast of Australia	Annual	STL	VBGF L_0**	L_{inf}			330.5	Harry *et al.* 2011
						k			0.08	
						L_0			58.2	
	Atlantic	NW Atlantic and Gulf of Mexico	Annual	FL	VBGF**	L_{inf}	233.1	214.8	219.8	Piercy *et al.* 2007
						k	0.09	0.13	0.12	
						t_0	-2.22	-1.62	-1.84	
	Atlantic	Southern Brazilian coast	Annual	TL	VBGF	L_{inf}	300	266		Kotas *et al.*

Species	Ocean	Location				Parameter				Reference
					L_0*	k	0.05	0.05		2011
						L_0	51	47		
	Indian	Indonisean waters	Annual	TL	GOM L_0**	L_{inf}	289.6	259.8	289.6	Drew *et al.* 2015
						k	0.16	0.16	0.16	
					L_0***	50	56.8	50	
S. mokarran	Atlantic	NW Atlantic and Gulf of Mexico	Annual	FL	VBGF**	L_{inf}	307.8	246.2		Piercy *et al.* 2010
						k	0.11	0.16		
						t_0	-2.86	-1.99		
	Pacific	East coast of Australia	Annual	STL	VBGF L_0**	L_{inf}			402.7	Harry *et al.* 2011
						k			0.08	
					L_0***			70	

560 Note: * Back-calculated data; **Observed data; ***Fixed L_0

561   Fig. 1 - Map of the Atlantic areas with the location of the *Sphyrna zygaena* samples. Dark circles

562   represent males and grey circles represent females.

563   Fig. 2 - Microphotograph of a vertebral section of *Sphyrna zygaena* from a female specimen with

564   182 cm fork length. with the identification of the birth mark (b) and the estimated 8 growth bands.

565   Fig. 3 - Size (fork length. in cm) frequency distribution of male (n = 175) and female (n = 128)

566   *Sphyrna zygaena* caught in the Atlantic Ocean and used for this study.

567   Fig. 4 - Age–bias plots of pairwise age comparisons between A) reading 1. B) reading 2 and C)

568   reading 3 and the final accepted count of growth band pairs (when two out of the three readings

569   agreed) carried out by the primary reader based on examination of *Sphyrna zygaena* vertebrae.

570   Numbers represent number of samples. and dots with error bars represent the mean counts of

571   reading (± 95% confidence intervals) relative to the accepted age. The diagonal line indicates a

572   one-to-one relationship.

573   Fig. 5 - The von Bertalanffy growth function (VBGF) for *Sphyrna zygaena* based on age

574   estimations by vertebrae growth marks. Circles represent observed data and line represents VBGF,

575   dashed line represents VBGF with fixed L_0 (43 cm fork length). Black represents males and grey

576   represents females.

577   Fig. 6 - Relationship between fork length (cm) and vertebrae centrum radius (mm) for *Sphyrna*

578   *zygaena*. Dots represent individual observations. Solid line represents linear regression where: FL =

579   64.04+11.77×VR. Dashed line represents quadratic regression where: FL= 21.45+19.49×VR-

580   0.34×VR^2. FL= Fork length; VR= Vertebral radius.

581   Fig. 7 - Mean deviation. from mean sampled fork length of four proportional back-calculation

582   methods for A) female and B) male *Sphyrna zygaena*. Data points represent mean back-calculated

583   lengths at age for each model. A point on the x-axis (black horizontal line) would represent zero

584   deviation from the sample mean length at age.

585   Fig. 8 - von Bertalanffy growth curves for *Sphyrna zygaena* for A) females and B) males. Fitting to

586   individual observed data and 4 back-calculation models: Dahl-Lea. Dahl-Lea linear modified. Dahl-

587   Lea quadratic modified and Fraser-Lee size at birth modified (with biologically derived intercept at

588   43 cm fork length).