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PROGRESS REPORT FOR SRDCP ON THE ATLANTIC-WIDE STUDY ON THE AGE AND GROWTH OF SHORTFIN MAKO SHARK

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SUMMARY

The ICCAT Shark Research and Data Collection Program (SRDCP) aims to develop and coordinate science and science-related activities needed to support provision of sound scientific advice for the conservation and management of pelagic sharks in the Atlantic. This Program was developed in 2013-2014 by the Sharks Species Group, and framed within the 2015-2020 SCRS Strategic Plan. Within this Program, a specific study on the age and growth of shortfin mako in the Atlantic was developed, with the purpose of contributing to the 2017 ICCAT SMA stock assessment. In the paper, we provide an update of the project, including preliminary growth models for the North Atlantic Ocean.

KEYWORDS: Age and growth; Isurus oxyrinchus; Life history parameters; Shortfin mako.

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1. Background

In 2013 the ICCAT Shark Species Group developed the general guidelines of the *Shark Research and Data Collection Program (SRDCP)*, aimed at the development and coordination of science and science-related activities needed to support provision of sound scientific advice for the conservation and management of sharks in the Atlantic. During the 2014 inter-sessional meeting, the Sharks Working Group updated the SRDCP, which was framed within the 2015-2020 SCRS Strategic Plan. The initial 2-year implementation of this Research Program focuses on biological aspects, ecology and fisheries of shortfin mako shark that are relevant to the upcoming stock assessment of this important species.

Understanding the age structure and growth dynamics of a population is crucial for the application of biologically realistic stock assessment models and, ultimately, for effective conservation and management. Information on age and growth is often used to estimate natural mortality or total mortality, which are important components of stock assessment models, and in the calculation of population and demographic parameters such as population growth rates and generation times. Successful fisheries management thus requires precise and accurate age information to make informed decisions, and inaccurate age estimates can lead to serious errors in stock assessments and possibly to overexploitation (Campana, 2001).

Despite their importance, published age and growth studies of sharks are still scarce and only a few have provided validation of the ageing method used. Specifically for the shortfin mako (SMA, *Isurus oxyrinchus*), there are still uncertainties in the age and growth parameters. Some previous studies assumed that vertebral band deposition could be either 1 or 2 bands per year, both in the Atlantic and Pacific oceans (e.g. Bishop et al., 2006; Doño et al., 2015; Semba *et al*., 2009). Some recent studies in the Atlantic have validated a one-band pair per year periodicity based on bomb radiocarbon (Campana *et al*., 2002; Ardizzone *et al*., 2006) and oxytetracycline tagging (Natanson *et al*., 2006), while in the Pacific a two-band pair per year pattern was validated for juvenile specimens based on oxytetracycline tagging and a one band pair per year was validated for adults (Wells *et al*., 2013; Kinney et al. 2016). As such, the question of age validation for the shortfin mako shark still remains uncertain, but it seems possible that this species shifts from depositing two band pairs per year to one band pair per year after reaching maturity. Further, most of the previous studies carried out in the Atlantic have focused relatively small areas when the geographical range of the species is considered. As such, there is the need to carry out a new and large scale Atlantic wide study that covers a wide Atlantic area and can take into consideration different hypothesis in terms of band deposition patterns for this species.

Therefore, within the ICCAT SRDCP, a specific study for the age and growth of the shortfin mako in the Atlantic was developed. The purpose of the study is to conduct an Atlantic wide age and growth study for this species that can contribute to the 2017 ICCAT SMA stock assessment. The main deliverable and outcome expected for this project is one SCRS paper to be presented during the 2017 SMA stock assessment meeting with the final results. Submission to a peer-review journal is also envisioned pending agreement between all participants in the study.

In 2016, an update of the project was presented to the SCRS (Coelho et al., 2016). The objectives of this paper are now to present the current development status of this project and the preliminary growth models for the North Atlantic Ocean.

2. Methods

2.1 Sampling and processing

Samples were collected from commercial fishing vessels, sports fishing and research vessels from IPMA, NOAA and DINARA, respectively, over an Atlantic wide area (**Figure 1**). Specimens were measured for fork length (FL, cm), location, sex, maturity stage and other biological parameters were also collected. A section of four to eight vertebrae was extracted from the region below the base of the first dorsal fin and transported to the laboratories. In the laboratory, the covering connective tissue of the vertebrae was removed, and once cleaned; the vertebrae were stored in 70% ethanol. Vertebrae were then sectioned with two methodologies. The first method used by the NOAA- NEFSC laboratory uses a Ray Tech Gem Saw to section vertebrae, with a resulting section thickness of about 1 mm, and stored in 70% ethanol. Each section was photographed with a digital camera (model DSR12, Nikon Inc.) attached to a stereo microscope (model SMZ1500®[5] , Nikon, Inc.) using reflected light and image processing software (model NIS Elements, version 4.40, Nikon, Inc.). While the second method used by the other laboratories (IPMA, DINARA and NOAA-SEFSC) used a Buehler Isomet (Lake Bluff, IL) low-speed saw, using two blades spaced approximately 0.5 mm apart. One, or both sides, of the section from IPMA and DINARA samples were stained with crystal violet (Sigma-Aldrich Co., St. Louis, MO). Once dried, the sections were mounted onto microscope slides with Cytoseal 60 (Thermo Fisher Scientific Inc., Waltham, MA). Vertebral sections were digitally photographed under a dissecting microscope using transmitted white light. For both methods, vertebrae were cut sagittally and 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". Photographs were digitally enhanced using Adobe Photoshop to improve the contrast of the growth bands and minimize differences between the different methodologies (**Figure 2**).

2.2 Age estimation and comparison of age readings

To ensure that vertebral counts were consistent between laboratories, a three-laboratory inter-calibration study was done among researchers at the NOAA-NEFSC, NOAA-SEFSC, IPMA and DINARA (Anon., 2016). Digital images of 60 vertebrae were used as a reference set, criteria were discussed and readers counted the band pairs (consisting of one opaque and one translucent band) without prior knowledge of the FL of the samples. All counts were made using enhanced digital images although the actual samples were available if necessary. The final reference set consisted of 57 vertebrae (19 samples from each laboratory), with agreed ages between researchers and laboratories to ensure consistency between readers.

The North Atlantic sample reading was prioritized at this stage of the project because the stock assessment method to be used in the North stock will use age and growth parameters directly (stock synthesis) while in the south a production model will be used.

Based on the criteria from the inter-calibration, band pairs were counted once by three readers, for growth curve analysis the North Atlantic (latitude > 5 ºN). An annual deposition rate was assumed, based on validation studies in the Atlantic (Campana *et al*., 2002; Ardizzone *et al*., 2006; Natanson *et al*., 2006). Also, it was considered that immediately after the deposition of the birth mark and in the first few years, there are often smaller bands (shadow bands) deposited close together to the actual growth bands, and those are likely the ones that are considered in some studies as 2-bands per year in the smaller size classes. However, in larger specimens (larger vertebrae) those smaller bands deposited closely together after the birth mark tend to disappear (join together), and were not considered as growth marks in this study. This shadow bands were not counted during the age estimation process (**Figure 2**).

Inter-reader ageing precision was examined using both the coefficient of variation (CV; Chang 1982) and the average percentage error (APE; Beamish & Fournier 1981) which were calculated and compared. The percentage of agreement (PA) was also calculated. Bias plots were used to graphically assess the ageing accuracy between the three readers (Campana 2001). Precision analysis was carried out using the R language for statistical computing version 3.3.2 (R Core Team 2017), using the package 'FSA'(Ogle 2015).

2.3 Growth modelling

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) was fit to length at age data:

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

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.

Two variations of the model were used: 3-parameter calculation estimated L_{inf}, k and L_0 and 2-parameter method estimated L_{inf} and k and incorporated a fixed L_0. The length at birth described for the species by Mollet et al. (2000) is 70 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:

[5] Reference to Trade Names does not imply endorsement from NOAA Fisheries.

$$FL = 0.9286*TL-1.7101 \quad \text{(size range: 88 − 264 cm TL) (2)}$$

All of the growth equations were fit to the length and vertebral band count data using non-linear regression in R (R Core Team 2017). As a preliminary analysis, growth models were fit to vertebral band counts of individual readers, as well as to an accepted age when two out of the three band counts between readers agreed. Counts of vertebral band pairs were adjusted for the date of capture assuming a theoretical birthday of 1 March based on the beginning of the estimated period of parturition from Mollet et al. (2000). To assess model adequacy to the data, the Akaike information criterion value (AIC) and the Bayesian Information Criterion (BIC) values were calculated for each model.

A likelihood ratio test was used to test the null hypotheses that there was no difference in growth parameters between males and females, using the ‘fishmethods’ package (Nelson 2013). Plots were designed using library “ggplot2” (Wickham 2009).

3. Results and Discussion

3.1 Sample characteristics

A total of 721 sampled sharks (384 males, 332 females, five specimens with undetermined sex) were collected for this study from both the North and South Atlantic hemispheres (**Figure 1**). Females in the North ranged in size between 57 and 366 cm FL (mean ± SD: 175.7 ± 53.0 cm), while males ranged in size between 52 and 279 cm FL (mean ± SD: 167.3 ± 43.6 cm). In the South, females ranged in size between 92 and 330 cm FL (mean ± SD: 176.3 ± 39.6 cm), while males ranged in size between 81 and 250 cm FL (mean ± SD: 164.4 ± 35.4 cm) (**Figure 3**).

The sample length range seems to cover the size range of the species, the smallest free-swimming in this study was 52 cm FL, which is close to the reported size at birth by Mollet et al. (2000) of 63 cm FL. The maximum sizes for both males and females is also similar to the reported in other studies (Natanson et al., 2006; Barreto et al., 2016).

3.2 Age estimation and comparison of age readings

Inter-specific percentage agreement between the first and second, first and third, and second and third readers was 58%, 34% and 38%. A total of 73% of the vertebrae had at least two identical readings between all three readers. The CV between the three readers was 14.6% and the APE was 10.9%. Between the first and second, first and third, and second and third readers CV was 8.1%, 16.3%, 14.6%, respectively. No systematic bias was observed between the readings when comparing graphically the three readers using the age-bias plots (**Figure 4**).

Campana (2001) mentioned that most studies reporting shark ages based on vertebrae did so with CV values exceeding 10%. For the shortfin mako, CVs between 4 and 11% and APEs between 3% and 14% have been previously reported (Bishop et al., 2006; Natanson et al., 2006; Ribot-Carballal et al., 2005; Semba et al., 2009; Doño et al., 2015; Barreto et al., 2016). Reported values for this study fall on the higher range of the reported values for shortfin mako.

3.3 Growth modelling

Estimated ages of the analysed specimens ranged from 0 to 28 years for females and from 0 to 27 years for males, which is in accordance with the maximum ages in other studies. The LRT revealed significant differences between males and females (LRT: $\chi^2 = 28.7$, df = 3, $P < 0.001$); therefore, growth models were calculated for each sex separately. Females exhibited lower growth coefficients (k) and higher asymptotic size (L_{inf}) than males. For the 3-parameter VBGF L_{inf} parameter estimates varied between 235 cm to 246 cm FL for males and 388 and 694 cm FL for females; k is between 0.11 to 0.13 $year^{-1}$ for males and 0.02 to 0.05 $year^{-1}$ for females. L_0 estimates varied between 75 and 100 cm for both sexes (**Table 1, Figure 5 and 6**). For the 2-parameter VBGF, L_{inf} estimates were lower than the estimates from the standard model, with estimates varying between

220 to 233 and 304 to 353 cm FL for males and females, respectively. Inversely, k estimates were higher, varying between 0.15 to 0.19 $year^{-1}$ and 0.06 and 0.09 $year^{-1}$ for males and females, respectively.

As a preliminary approach models were fit to each reader's individual count of the North Atlantic sample only, as well as to an agreed count (when two out of the three readers agreed). Male parameter estimates seem to be in accordance to the species maximum observed sizes, however, L_0 is slightly overestimated. The 3-parameter VBGF that seems to be more in accordance with the species biology for females is the model fit to Reader 1 age counts. Reader 2 and 3 estimated L_{inf} are highly overestimated, this can be caused by the small sample of very large females. Model convergence problems are also denoted by the large SE and CI, which could not be calculated for some of the fitted models. The difficulty to reach an asymptotic size estimate has been reported before for shortfin mako, especially for females, as large individuals are usually lacking in the sample (Doño et al., 2015). AIC and BIC values are higher in values were lower for the growth curves with estimated L_0, the AIC and BIC difference between growth models was greatest for females than for Males. Despite the higher AIC and BIC, when fitting a 2-parameter VBGF the model fit improves, especially for females, with more biologically realistic L_{inf} and k estimates.

A few studies have been published on age and growth of the shortfin mako in the Atlantic and Pacific Oceans (**Table 2**). The present study L_{inf} and k parameter estimates are similar to Natanson et al. (2006) and Semba et al. (2009). Regarding other studies the reported L_{inf} estimates are somewhat higher than the estimated in this study, while k estimates are lower (**Table 2**).

4. Project execution - progress

The list of milestones and deliverables originally developed in the project proposal and their current development status is provided in **Table 3**. Milestones 1 through 4 have been completed on due time. Furthermore, a "*Workshop on shortfin mako age reading and growth*" was held in the Narragansett Laboratory, NOAA Northeast Fisheries Science Center, Rhode Island (U.S.) in June 2016 to create the reference set of vertebrae for age reading. Milestones 6 and 7 are ongoing, and the progress presented in this document. The results presented here are preliminary growth curves on the North Atlantic sample. The final SCRS paper (Deliverable 8) will be prepared according to the proposed schedule in **Table 3.**

Given the stock assessment types that will be used in 2017 SMA assessment, the North Atlantic sample reading was prioritized at this stage as the method will be a Stock Synthesis that uses age and growth information directly. The South Atlantic samples will be read after this (during 2017).

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Table 1. Growth parameters for *Isurus oxyrinchus* (separate sexes) from the North Atlantic. The presented model is the re-parameterised von Bertalanffy growth function (VBGF). 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). "2out of 3" refers to growth curves estimated using data only when there was agreement in at least in 2 out of the 3 readers.

Sex	Reader	Model	AIC	BIC	Parameter	Estimate	SE	95% CI Lower	95% CI Upper
Males	Reader 1	VBGF	1693	1706	L_{inf}	245.8	8.5	230.1	266.8
					k	0.12	0.01	0.09	0.15
					L_0	78.1	4.7	68.3	87.4
		VBGF L_0=63 cm	1700	1710	L_{inf}	233.7	5.9	222.2	247.2
					k	0.16	0.01	0.13	0.18
	Reader 2	VBGF	1632	1645	L_{inf}	244.6	8.2	229.4	264.5
					k	0.11	0.01	0.09	0.14
					L0	80.2	4.1	71.9	88.3
		VBGF L_0=63 cm	1646	1655	L_{inf}	230.9	5.6	219.7	243.9
					k	0.15	0.01	0.13	0.18
	Reader 3	VBGF	1702	1715	L_{inf}	235.2	7.2	221.6	253.5
					k	0.13	0.02	0.10	0.17
					L_0	85.4	4.3	76.2	94.2
		VBGF L_0=63 cm	1721	1731	L_{inf}	219.9	4.54	210.5	230.7
					k	0.19	0.01	0.17	0.23
	2 out of 3	VBGF	1239	1251	L_{inf}	237.5	9.5	220.3	260.8
					k	0.13	0.02	0.10	0.17
					L_0	74.7	4.5	65.5	83.6
		VBGF L_0=63 cm	1243	1252	L_{inf}	226.5	6.8	213.4	242.4
					k	0.16	0.01	0.14	0.19
Females	Reader 1	VBGF	1585	1597	L_{inf}	388.4	46.5	318.3	574.2
					k	0.05	0.01	0.02	0.07
					L_0	88.4	5.3	77.2	99.1
		VBGF L_0=63 cm	1601	1611	L_{inf}	304.2	14.5	276.5	341.2
					k	0.09	0.008	0.07	0.11
	Reader 2	VBGF	1422	1435	L_{inf}	597.7	164.2	409.7	3136.5
					k	0.02	0.008	0.004	0.04
					L_0	88.8	4.22	79.8	97.4
		VBGF L_0=63 cm	1448	1458	L_{inf}	339.6	21.4	300.0	398.4
					k	0.07	0.007	0.05	0.08
	Reader 3	VBGF	1541	1554	L_{inf}	693.8	23.0	445.7	-
					k	0.02	0.008	0	0.04
					L_0	99.5	3.9	91.1	107.6
		VBGF L_0=63 cm	1596	1605	L_{inf}	319.3	16.7	285.9	365.7
					k	0.08	0.008	0.06	0.10
	2 out of 3	VBGF	1109	1120	L_{inf}	548.6	130.0	387.4	1654.6
					k	0.03	0.01	0.007	0.05
					L_0	85.4	4.6	75.7	94.8
		VBGF L_0=63 cm	1126	1134	L_{inf}	352.9	25.7	306.3	425.2
					k	0.06	0.008	0.05	0.08

Table 2. Growth parameters for *Isurus oxyrinchus* from previosuly published studies. TL = total length (cm), PCL= Pre-caudal length (cm), FL = Fork length (cm), OTBFL = over the body fork length (cm), VBGF = von Bertallanfy growth model, GOM = 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.

Ocean	Area	Periodicity	Measurment	Growth model	Parameters	Sex			Reference
						Male	Female	Combined	
Pacific	New Zeland	Annual	FL	VBGF*	L_{inf}	302.16	820.1		Bishop et al., 2006
					K	0.0524	0.013		
					t_0	-9.04	-11.3		
	Western coast of Baja California Sur, Mexico	Annual	TL	VBGF	L_{inf}			411	Ribot-Carballal et al., 2005
					K			0.05	
					t_0			-4.7	
	Western and Central North Pacific Ocean	Annual	PCL	VBGF	L_{inf}	171.3	248.6		Semba et al., 2009
					K	0.156	0.09		
					L_0	60	60		
	South-Eastern Pacific off Chile	Annual	FL	VBGF	L_{inf}	296.60	325.29		Cerna & Lincadeo, 2009
					K	0.087	0.076		
					t_0	-3.58	-3.18		
Atlantic	North Atlantic	Annual	OTBFL	VBGF (males) GOM (females)	L_{inf}	253	366		Natanson et al., 2006
					K	0.125	0.087		
					L_0	72	88		
	Western and Central Atlantic	Annual	FL	VBGF	L_{inf}	328.74	407.66		Barreto et al., 2016
					K	0.08	0.04		
					t_0	-4.47	-7		
		Biannual			L_{inf}	340.2	441.64		
					K	0.14	0.07		
					t_0	-2.75	-3.98		
		Biannual/ Annual**			L_{inf}	291.57	309.79		
					K	0.2	0.13		
					t_0	-2.38	-3.27		
Indian	South-west Indian Ocean	Annual	FL	VBGF	L_{inf}			285	Groeneveld et al., 2014
					K			0.113	
					L_0			90	

Note: *A Schnute model was considered to best fit the data; VBGF is presented for comparison purposes. **A bi-annual growth band deposition was considered until 5 years old, after that an annual periodicity was considered.

Table 3: List of milestones and deliverables (some originally planned and some additional) with the respective expected completion dates, for the shortfin mako age and growth study. The differences in the original and currently expected delivery dates are related with the fact that the shortfin mako Atlantic stock assessment has been postponed to 2017.

Item	Type[6]	Name	Description	Expected date	Status
1	M	Project leader initial contact	E-mail to national scientists calling for participation in the project with SMA samples	31-Mar-15	Completed on 31-Mar-2015
2	M	Compilation of information on vertebrae	Summary table with SMA vertebrae currently available	5-May-15	Completed on 5-May-2015[7]
3[8]	D	SCRS paper	A SCRS paper describing the project status is prepared and presented to the ICCAT Sharks-WG	Additional deliverable originally not planned (	completed on 18-Apr 2016 (WG sharks meeting)
4	M	Vertebrae processing	Vertebrae are processed and digital images are uploaded to an ICCAT online repository	30-Dec-16	Completed on 30-Dec-16
5	D	SCRS paper	A SCRS paper describing the project status is prepared and presented to the ICCAT Sharks-WG (SMA data preparatory meeting)	Additional deliverable originally not planned	Completed at the SMA data preparatory meeting (this paper)
6	M	Age estimates	Ages are estimated by at least 1 scientist from each participating laboratory	31-Apr-17	Ongoing
7	M	Data analysis	Growth models are finished	31-Jun-17[9]	Ongoing
8	D	SCRS paper	A final SCRS paper is prepared and presented to the ICCAT Sharks-WG (SMA stock assessment meeting)	2017 ICCAT SMA stock assessment meeting	Not started yet

[6]: M=milestone; D=deliverable

[7]: This refers to the initial compilation of vertebrae already in the national laboratories in different processing stages. Summary tables will be periodically updated as more samples are collected and processed during the project.

[8]: This deliverable was not originally planned. However, due to the postponement of the SMA stock assessment to 2017, a progress reports was provided in 2016 as a SCRS paper to the Sharks Working Group.

[9]: The date provided is tentative, and can be altered depending on the schedule for the SMA stock assessment session in 2017

Figures

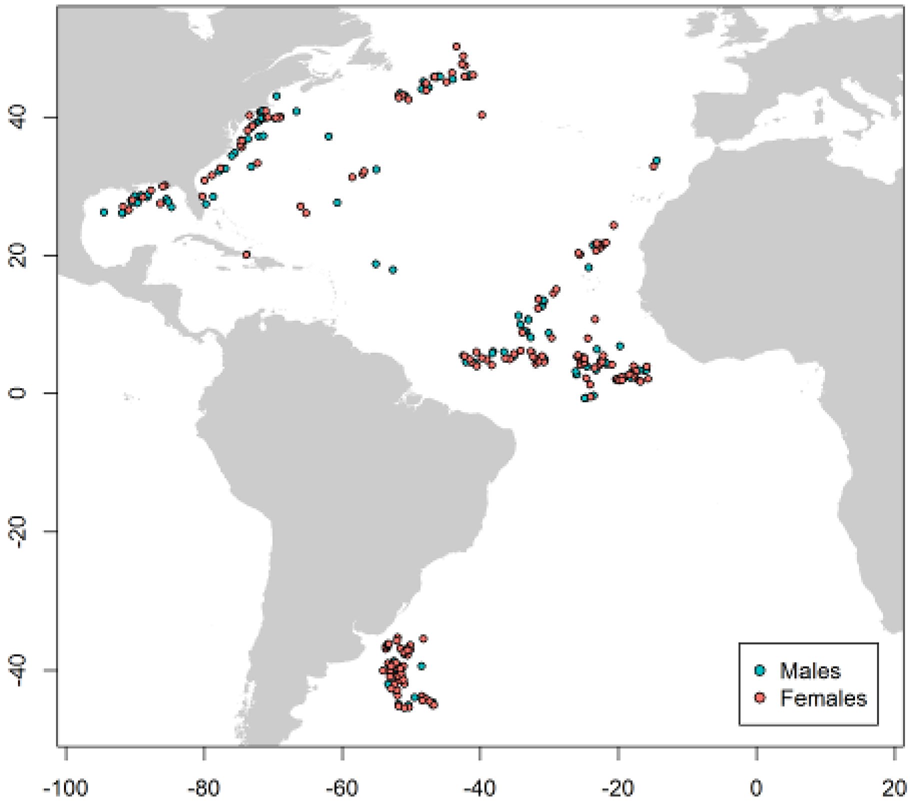

Figure 1. Map with the location of the SMA vertebrae samples currently available for the age and growth study.

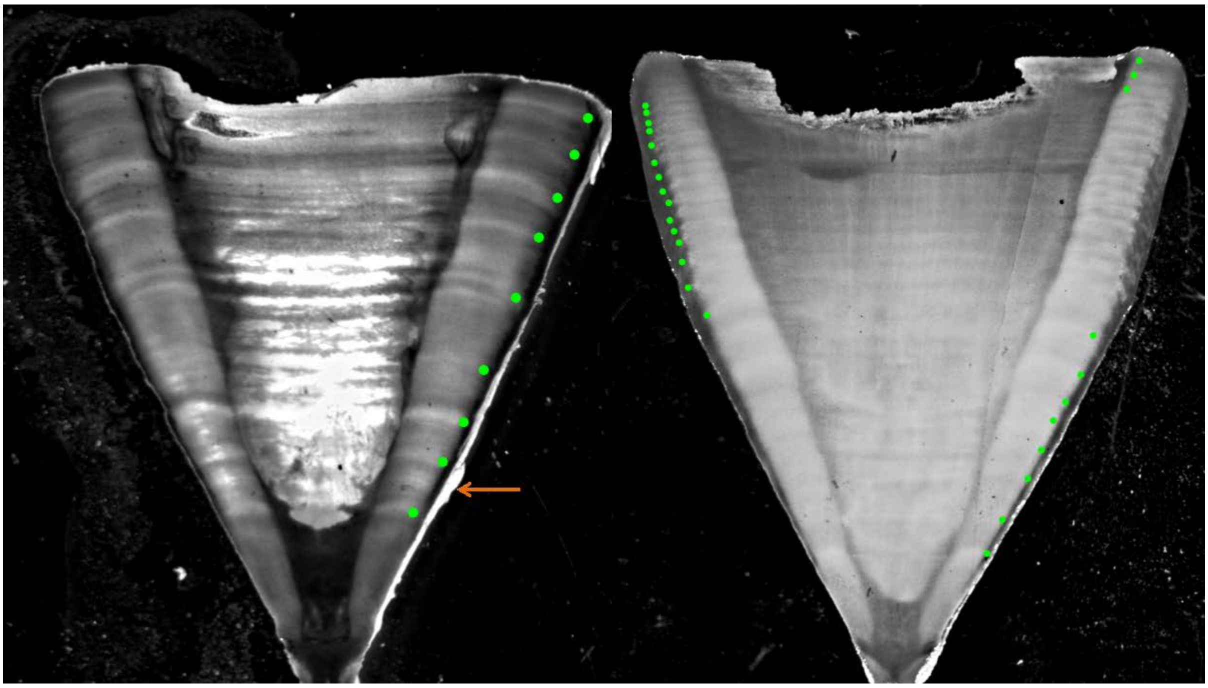

Figure 2. Example of edited microphotograph of a vertebral section of male shortfin mako (*Isurus oxyrinchus*). On the left a specimen of 205 cm fork length (FL) with an agreed band count of 8 years. On the right a specimen of 235 cm FL with an agreed band count of 25 years. The first green point represents the birth mark.The orange arrow signals a “shadow band”.

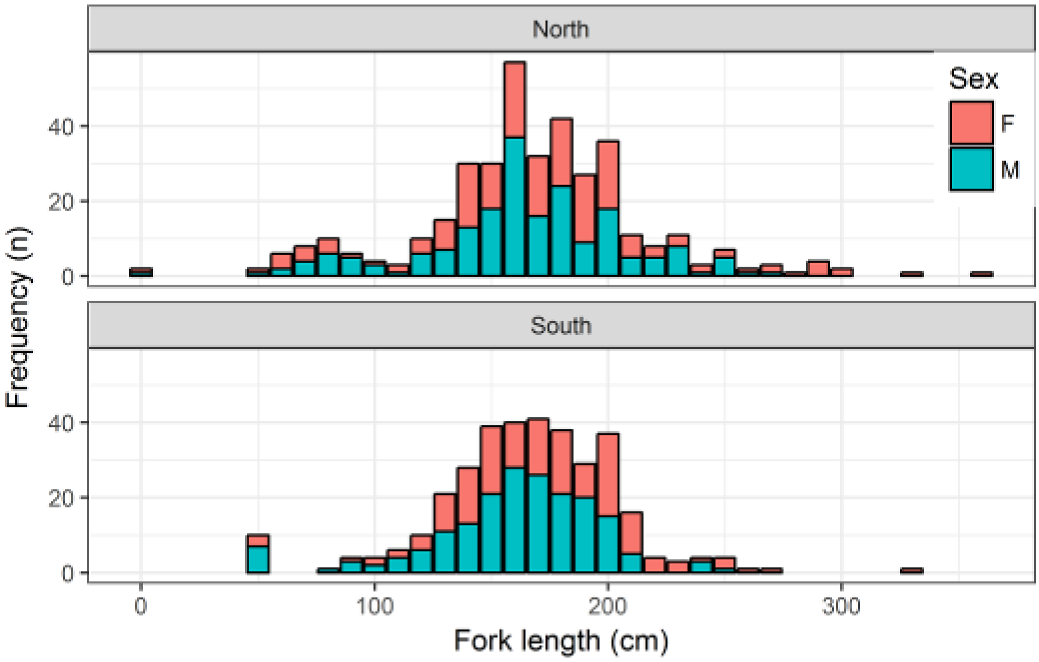

Figure 3. Size (fork length, in cm) frequency distribution of male (n = 334) and female (n = 332) SMA samples currently available for the age and growth study, for the north and south Atlantic (separated at the 5ºN).

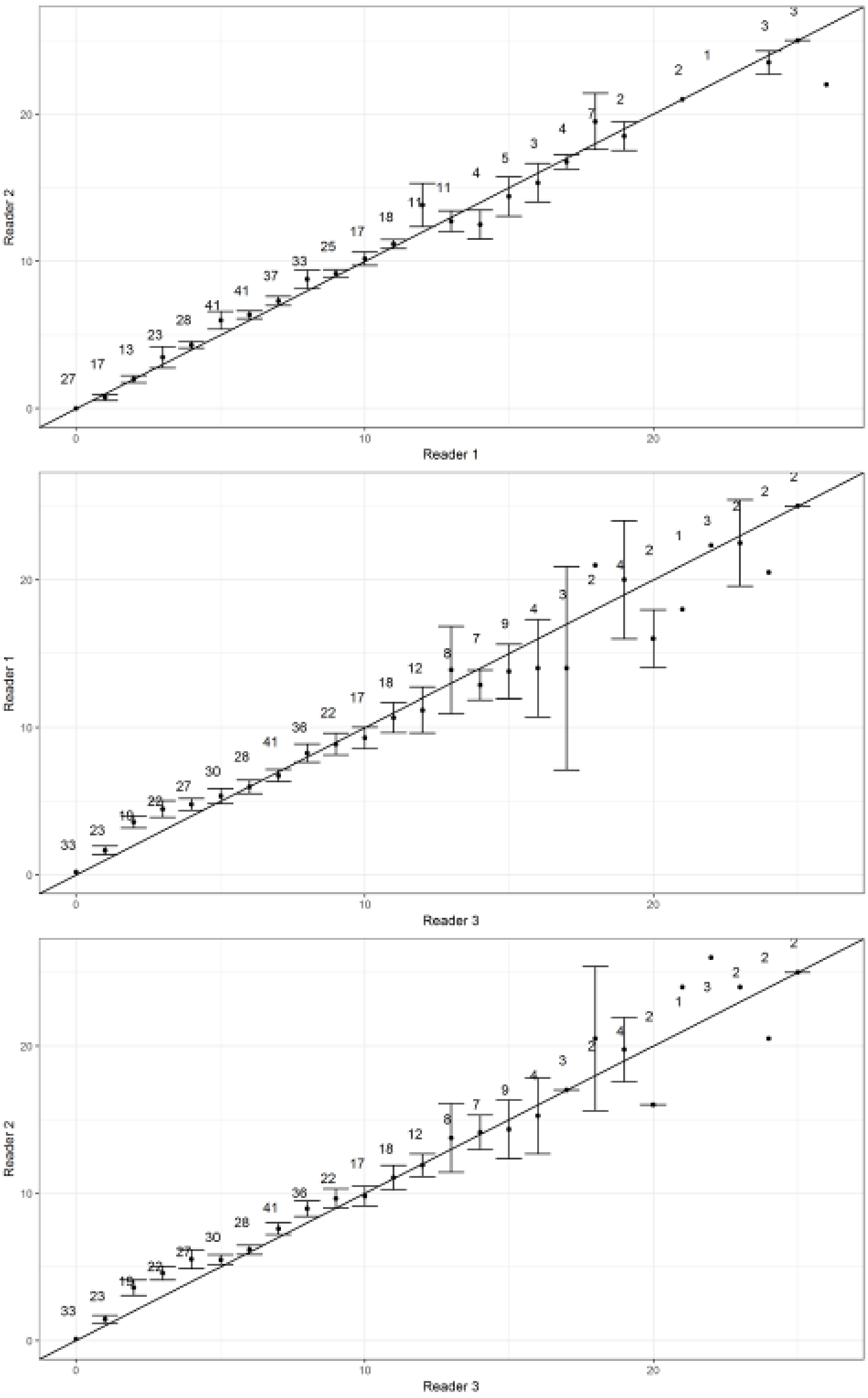

Figure 4. Age–bias plots of pairwise age comparisons between readers based on examination of *Isusur oxyrinchus* vertebrae. Numbers represent number of samples. and dots with error bars represent the mean counts of reading (± 95% confidence intervals) relative to the accepted age. The diagonal line indicates a one-to-one relationship.

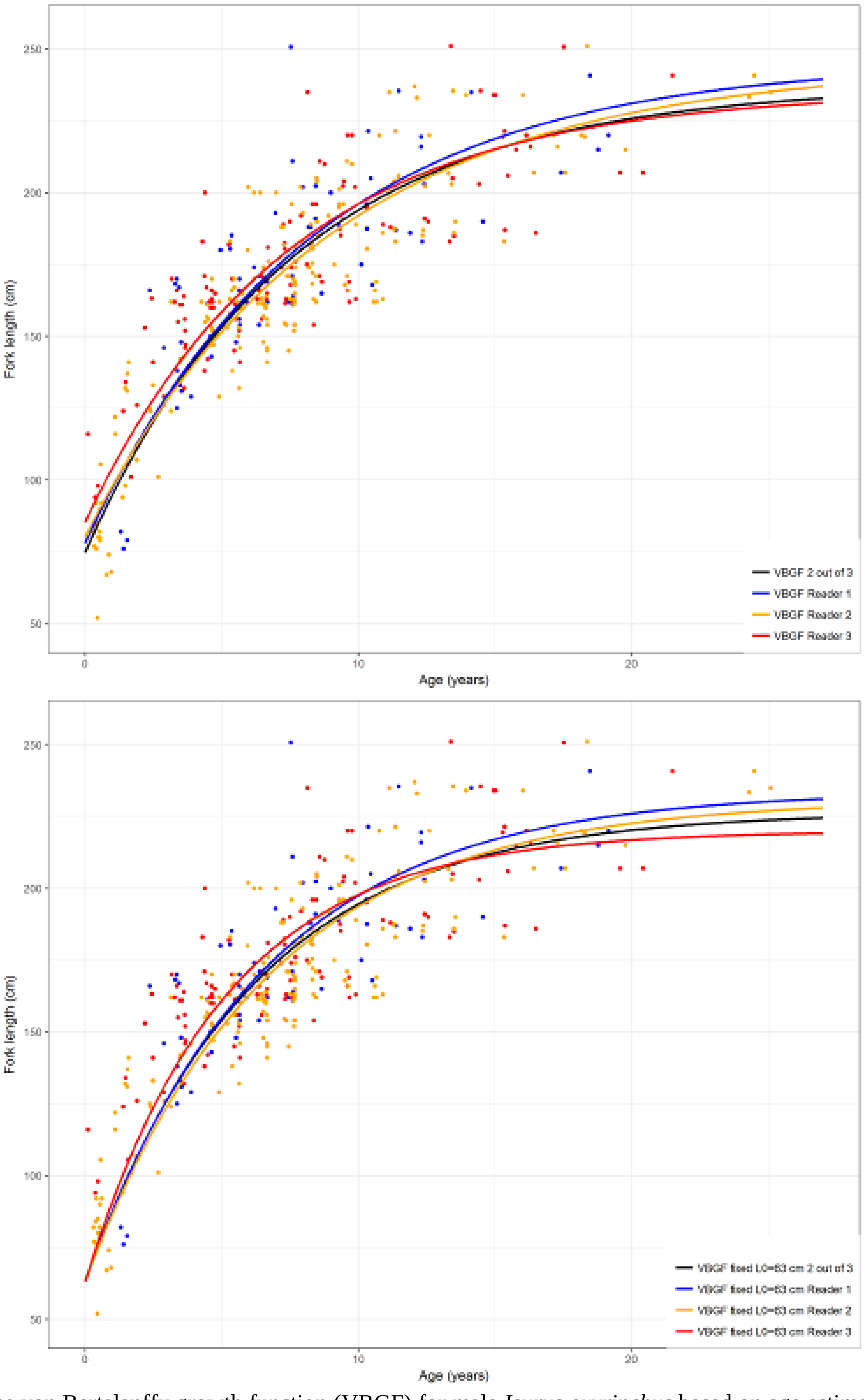

Figure 5. The von Bertalanffy growth function (VBGF) for male *Isurus oxyrinchus* based on age estimations by vertebrae growth marks. Circles represent observed data and line represents in the upper panel the 3-parameter VBGF and in the lower panel the VBGFwith fixed L_0= 63 cm FL.

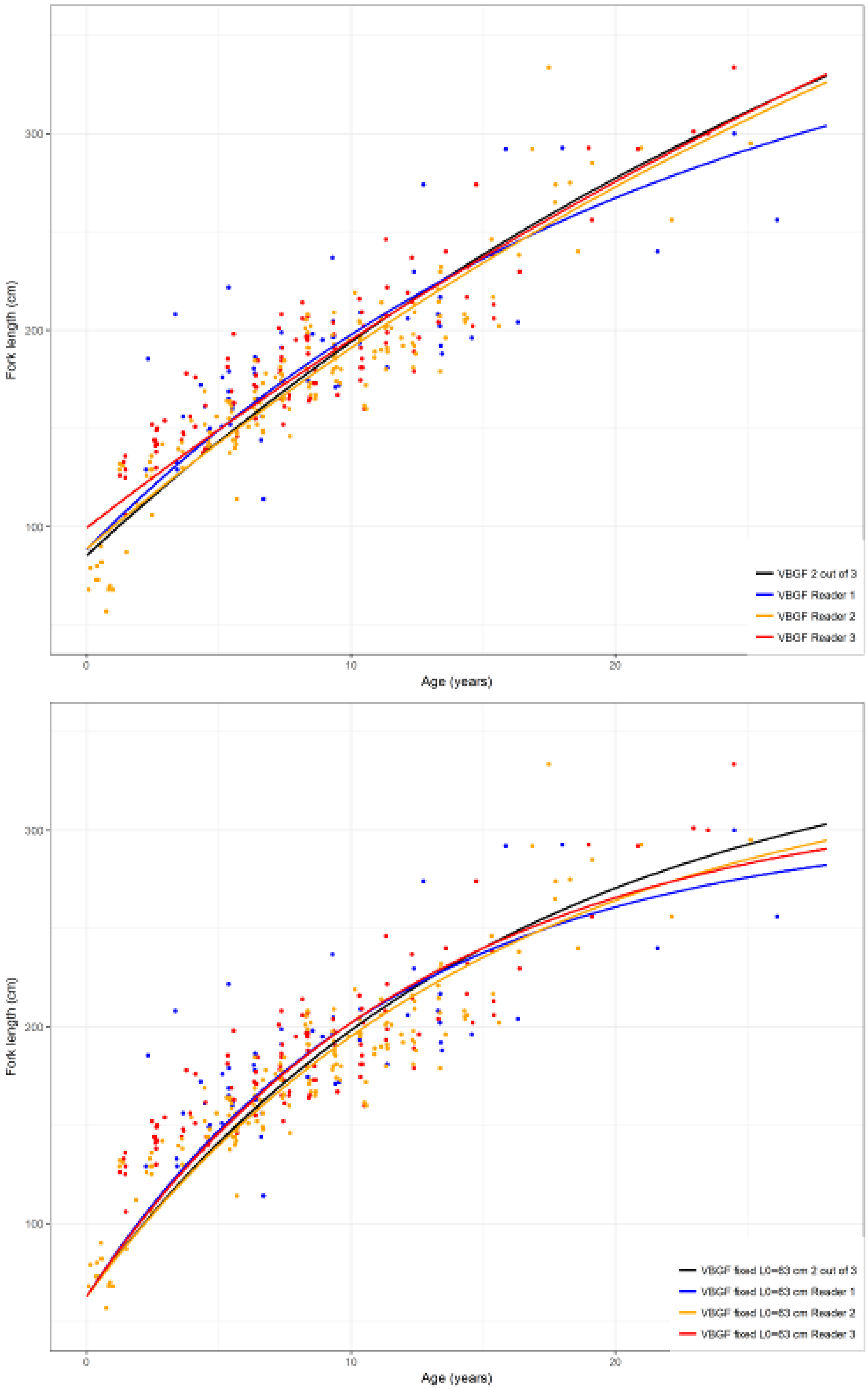

Figure 6. The von Bertalanffy growth function (VBGF) for female *Isurus oxyrinchus* based on age estimations by vertebrae growth marks. Circles represent observed data and line represents in the upper panel the 3-parameter VBGF and in the lower panel the VBGFwith fixed L_0= 63 cm FL.