

AN APPROACH TO AGE AND GROWTH OF SOUTH ATLANTIC SWORDFISH (*XIPHIAS GLADIUS*) STOCK

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SUMMARY

A first growth function was estimated for the South Atlantic swordfish stock. A total of 406 anal fins were collected from 2006 to 2013. Fins were classified into three types and the most common, type A, was selected. Biometric relationships among several ray section measurements and lower jaw fork length were analysed. A detailed methodological description for swordfish age interpretation has been developed. Inconclusive results have been obtained when indirect validation test, as edge type and marginal increment ratio analysis, were applied. Mean size at age and growth parameters were estimated using the Standard Von Bertalanffy growth model (VBGM) ($L_{\infty} = 358.7$, $k = 0.092$, $t_0 = -1.929$), which showed the best fit in comparison with other VBGMs.

RÉSUMÉ

Une première fonction de croissance a été estimée pour le stock d'espardon de l'Atlantique Sud. Un total de 406 nageoires anales ont été prélevées de 2006 à 2013. Les nageoires ont été classées en trois types et le type le plus commun, le type A, a été sélectionné. On a analysé les relations biométriques entre plusieurs mesures de sections de raies et la longueur maxillaire inférieur-fourche. Une description méthodologique détaillée a été mise au point afin d'interpréter l'âge de l'espardon. Des résultats non concluants ont été obtenus lorsqu'un test de validation indirect, comme analyse de type bordure et du taux de croissance marginal, a été appliqué. La taille moyenne par âge et les paramètres de croissance ont été estimés à l'aide du modèle de croissance standard Von Bertalanffy (VBGM) ($L_{\infty} = 358,7$, $k = 0,092$, $t_0 = -1,929$), qui ont montré le meilleur ajustement par rapport aux autres VBGM.

RESUMEN

Una primera función de crecimiento ha sido estimada para el stock de pez espada del Atlántico sur. Un total de 406 aletas anales se recogieron entre 2006 y 2013. Las aletas se clasificaron en tres tipos y fue seleccionado el más común, tipo A. Se analizaron varias relaciones biométricas entre varias medidas de la sección del radio espinoso y la longitud desde la mandíbula inferior a la horquilla. Se ha desarrollado una descripción detallada de la metodología de la interpretación de la edad del pez espada. No se han obtenido resultados concluyentes al aplicar pruebas de validación indirecta, como el tipo de borde y el análisis del incremento marginal. Se estimaron las tallas medias por edad y los parámetros de crecimiento utilizando el modelo de crecimiento estándar de Von Bertalanffy (VBGM) ($L_{\infty} = 358,7$; $k = 0,092$, $t_0 = -1,929$). Este modelo mostró el mejor ajuste en comparación con otros VBGM.

KEYWORDS

Swordfish, South Atlantic Ocean, Age interpretation, Growth curves

1. Introduction

Swordfish (*Xiphias gladius*, L. 1758) is a worldwide fish distributed species, mainly occurring in temperate, subtropical and intertropical waters. Swordfish has been fished by ancestral fishing communities in coastal areas using harpoon, hooks and nets (Ellis, 2013; Neilson *et al.* 2013). However, its worldwide commercial importance has been increased since 1980's and their captures reached to its highest level around 1995 in the South Atlantic stock (ICCAT, 2012).

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The International Commission for the Conservation of Atlantic Tunas (ICCAT) is the multilateral regional fishery organization responsible for the conservation of tunas and tuna-like species in the Atlantic Ocean and its adjacent seas. During the last three decades, the ICCAT has been assessing the two Atlantic swordfish stocks over the 5°N boundary, based on historical fishing data as well as new data and studies carried out recently (ICCAT, 2007; ICCAT, 2012). The low probability of migration between both Atlantic stocks units has been suggested from conventional tagging-recapture data (ICCAT, 2007) and recent pop-up satellite results (Abascal *et al.*, *in press*; Neilson *et al.*, 2009, 2013). Moreover, it is believed that the genetic mixing of the swordfish from both stocks is very low, and this genetic isolation should be enough to detect significant genetic difference between both Atlantic stock units. Some studies have already confirmed such genetic difference among both Atlantic swordfish stocks and the Mediterranean stock (e.g. Alvarado Bremer *et al.*, 1996, Alvarado Bremer *et al.*, 2005, Kasapidis *et al.*, 2007a); however, some genetic studies are pointing out that the stock boundary of the Atlantic swordfish could be different from the established one (Chow *et al.*, 2007).

Research on the South Atlantic swordfish stock has been in general more limited than the North one (Neilson *et al.* 2013). Some of the reasons have been addressed to the lack of an ICCAT research programs in these areas as well as the shorter historical fishery activity and countries involved (Mejuto *et al.*, *in press.*). For instance, Spanish surface longline fishery started its South Atlantic activity in 1986 (ICCAT, 2012), but the fishery observer programs have been recently established to provide information for basic data and biological studies.

Information on age and growth of swordfish is an important factor to assessing stock trends and has been used in the stock assessment of ICCAT fisheries. Several of the growth swordfish studies have been carried out in North Atlantic waters (Berkeley and Houde, 1983; Riehl, 1984; Ehrhardt *et al.*, 1996; Esteves *et al.*, 1995; Arocha *et al.*, 2003, Kasapidis *et al.*, 2007b, Kasapidis *et al.*, 2008), but growth studies for the South Atlantic Swordfish stock have not yet carried out. Fin rays have been used in many different marine and freshwater fish species for this kind of studies, as they are the easiest structures to collect and process instead other calcified structures such as otoliths; indeed, otoliths in swordfish and tuna are very small and delicate (Beamish, 1981). Some studies have been carried out in other stocks of swordfish using anal fin rays (e.g. Berkeley and Houde, 1983; Tsimenides and Tserpes, 1989; Sun *et al.*, 2002; DeMartini *et al.*, 2007) and billfishes (e.g. Kopf *et al.*, 2010; Kopf *et al.*, 2011).

The aim of this study is to identify methodological difficulties on the age interpretation of the South Atlantic stock of swordfish using anal fin ray sections and propose some solutions, and to obtain a preliminary growth equation based on these calcified structures.

2. Material and methods

2.1 Fish sampling

Data and biological samples of swordfish caught by Spanish commercial pelagic surface longline vessels operating in South Atlantic Ocean were collected within the observer program from 2006 to 2013 (**Figure 1**). A total of 406 swordfish anal fins were collected on board by scientific observers. Lower jaw fork length (LJFL) and sex were recorded from each specimen, an additional data such as date; geographic location and sea surface temperature were also gathered. Anal fins were removed taking care not to cut the condyle base of the rays. Fins were kept frozen (-21°C) inside labelled plastic bags for further analysis.

2.2 Anal fin processing

Anal fins were boiled to remove the flesh, and remains were removed carefully with a piece of a paper or a cloth. Some fins were rejected because they were damaged during on board finning. This practice can spoil the condyle base of the spiny ray and makes the fin useless.

The three first rays were stored in paper bags in a cool and dry area until the cutting process. Due to anatomic differences between specimens, anal fins were classified in three different categories based on the morphology of these first three rays (**Figure 2**):

- 1) Type A; they were the most common ones, with a short first ray, a medium length and not branched second one and a third ray larger than the other two and branched.
- 2) Type B; first and second rays were small and not branched, while the third one was larger and branched
- 3) Type C; first ray was medium length and not branched, while second and third ray were longer and branched.

Frequency occurrence of each morphology type was examined by sex and LJFL group (<100cm; 100cm \geq <150cm; \geq 150cm). A Fisher exact test was used to probe differences in frequency between groups.

Fin ray section preparation methodology was based on Valeiras *et al.* (2008). Two cross sections of the second ray of the anal fin (hereafter spine) were performed; the section location of the first one was done at an equal distance to a half of the width of the condyle base ($d/2$) (Ehrhardt *et al.*, 1996), and the second one at an equal distance of the width of the condyle base (d) (Riehl, 1984) (**Figure 3**). Following Ehrhardt *et al.* (1996) methodology, transversal sections of 0.45 – 0.50 mm thick were obtained using a linear precision saw ISOMET 5000 with a diamond blade (Series 15HC). For small swordfish measuring less than 90cm of LJFL, several spines were previously embedded in a matrix of polyester resin and sectioned together following Ruiz *et al.* (2005) methodology. Both types of sections were cleaned in ethanol 70% to remove residuals, and were left in trays to dry during two hours. Sections were mounted in glass microscope slides with Eukkit mounting medium and cover with a slide to avoid oxidation.

2.3 Biometry

Measurements of whole rays and ray sections, not damaged during the fins processing, were explored in relation to LJFL and sex of individuals. It was assumed an allometric relationship function to describe the bivariate scatterplot for every log-transformed pair of values. The function was estimated using the Standardised Major Axistest (SMA) using the smatr3 package (Warton *et al.*, 2012) with R software statistical program (R Core Team, 2013). Slope's equality was tested using Likelihood Ratio statistic test (Warton and Weber, 2002). Also, isometric relationship was tested for all relationships (slopes equal to 1 would indicate an isometric relationship) (Warton *et al.*, 2006).

Measurements description is shown in **Figure 3** and **Figure 4**. It was necessary to establish a benchmark (focus) in the ray section lobe to make the measurements. Focus was defined as the line which connects the two innermost ends of the lobes of the structure. A second perpendicular line was drawn from the focus, which was used to take all measurements (**Figure 4**). Not previously defined calcified structure measurements in the bibliography were established:

- Pre-growth structure. Distance between the focus and the area where the growth process start.
- Inner resorption distance. Distance between the focus and the end of the vascularised area, where the growth tissue starts to be visible.
- Vascularisation. It was quantified as the inner resorption minus the pre-growth structure distance.
- Adjusted annulus radius. It was obtained as annulus radius minus the pre-growth structure distance.

To test whether the assumption of Panfili *et al.* (2002) was fulfilled, the size of the spine mark was assumed to be the same as the size of the spine at the time that the mark was formed indicating no degeneration of the calcified structure; differences by age were checked in vascularisation and adjusted measurement of the presumed first annulus. Kolmogorov-Smirnov test was applied to prove normally distributed data followed by an ANOVA or Kruskal-Wallis test if normality assumption was not fulfilled.

2.4 Age interpretation

In order to standardize age interpretation, several methodological decisions were adopted: section location was established using the width of the condyle base (d) and left lobe of the ray section was selected (**Figure 3**). All age interpretations have been done using digital images. Images of the spine sections were taken using a Nikon DS-5M camera with a 0.5X reducing lens attached to a Nikon SMZ 1500 stereo microscope with an objective 0.5X. Calibration (1.5x), resolution (2560x1920), and exposure settings were also pre-set. The measurements of the spine sections were taken using the NIS-ELEMENTS D 3.0. software package. Images were taken under transmitted light. Width and height of the section, maximum width of the lobe and translucent bands, pre-growth structure and inner resorption distances were recorded.

Ehrhardt *et al.* (1996) age interpretation criterion was used: one broad opaque band followed by a narrow translucent band was considered one year. A year was counted at the edge of the lobe when the translucent band was fully formed, which means that a consecutive opaque band was beginning to be seen. When multiple annuli and disappearance of the first annulus in older fish appeared, careful interpretation was carried out to assess the age classes. Two readers read independently the whole set of samples; when readers disagree on the interpreted age, a third read was performed by both readers, and the sample was rejected when disagreement persisted.

Two methods were used to identify the age one annulus:

1. Distribution pattern of annuli. Assuming that distance between annual marks must be similar in consecutive years, the distance of visible annuli was extrapolated to the vascularised area where annuli were obscured.
2. Age one annulus distance. In accordance with other studies, fish of 80-105 cm LJFL were identified as possibly being one year old (e.g. Berkley & Houde, 1983, Riehl, 1984, Restrepo, 1990, Arocha *et al.*, 2003). Annuli of these specimens were measured and the obtained mean radio of age one (± 2 SD) was used to identify the interpreted age of first visible annulus.

When any inconsistency between both methods appeared, distribution pattern was primarily used. If more than 3 presumed ages were estimated within the vascularised area, the spine was removed from the analysis.

2.5 Indirect validation

In order to determine when the translucent and opaque bands were formed, edge type frequency occurrence and marginal increment ratio (MIR) were analyzed monthly. Edge was considered translucent when a translucent band appeared in more than 50% of the lobe edge, otherwise was called opaque. MIR was estimated for each spine using the equation from Esteves *et al.*, (1995):

$$\text{MIR} = (S - S_n) / (S_n - S_{n-1}),$$

where, S was the spine radius; S_n was the distance from the ray focus to the translucent band n, and S_{n-1} was the distance from ray focus to translucent band n-1.

2.6 Growth parameters

Growth parameters have been calculated for combined sexes and by sex using non-linear least square method. Data were fitted to three von Bertalanffy growth models (VBGM): (1) von Bertalanffy standard model (von Bertalanffy, 1938), and (2) two version of the generalized von Bertalanffy model: Chapman's VB (Chapman, 1961) and Richards' VB (Richards, 1959).

Standard VB model: $L_t = L_\infty(1 - e^{-k(t-t_0)})$

Chapman's VB model: $L_t = [L_\infty^{(1-\delta)} - (L_\infty^{(1-\delta)} - l_0^{(1-\delta)})e^{-k(1-\delta)t}]^{1/(1-\delta)}$

Richards' VB model: $L_t = L_\infty(1 - e^{-k(1-m)(t-t_0)})^{1/1-m}$

where, L_t was the length (LJFL) at age t, L_∞ the asymptotic length, k the growth coefficient, t_0 the theoretical age at zero length, l_0 the theoretical length at zero age, m and δ the fitted fourth function parameters.

Some assumptions were set in order to analyse the growth parameters:

- 1) Birth date: South Atlantic Ocean swordfish spawns during the whole year (Neilson *et al.*, 2013) and therefore age was considered to be the interpreted age plus 0.5.
- 2) Age 0 samples: fish under 65cm were not captured due to the gear selectivity. This issue implies that a bias in length at age 0 will occur, thus we decided not to use this age class.

To assess the best fitted model, Akaike Criterion Statistics (AIC) (Cerna *et al.*, 2009) was used:

$$\text{AIC} = -2 \log(L) + 2p$$

where, L was the residual sum of squares at the maximum goodness-of-fit and p the number of free parameters in the model.

3. Results

3.1 Study Area, samples and anal fins classification

Swordfish anal fins from 156 males, 248 females and 2 undetermined sex (n=406) were collected from 2006 to 2013 (**Table 1**). Sampling geographical location by size range is shown in **Figure 1**. A total of 398 fin rays were used for describing the fin type. Type A was classified in 94.47% of the samples, 4.78% as type C, and only 0.75% as type B. No fin type differences have been detected between sexes (p-value= 0.61), but a significant difference was found in range sizes (p-value= 0.045) with B and C types being more frequent in specimens ≥ 150 cm LJFL.

3.2 Biometry

No differences between sexes were found in the most of the relationships between LJFL and spine measurements, except with the maximum width of the spine lobe and vascularisation (**Table 2**). All measurements showed a significant result with the slope, indicating that the assumption of allometric relationship was true. The r squared value showed strong correlation between spine measurements: maximum diameter, width and height of the section and lobe maximum width, versus LJFL.

3.3 Age interpretation

A total of 312 sexed anal fins of southern Atlantic swordfish were analysed from 2006 to 2013 for ageing. The LJFL of the aged individuals, ranged from 67 to 217 cm in males and from 66 to 309 cm in females. Fish ages ranged from 0 to 14 years old and the mean lengths by age were calculated for both males and females. **Table 3** shows mean length at age, standard error and length range by sex. Length at age 0 was calculated, although this estimation is biased as explained in the “growth parameters” section 2.6.

Checking for differences by age in the vascularisation and mean adjusted radius of the presumed age one annulus, the Kolmogorov-Smirnov test showed no normal distribution of both measurements, and Kruskal-Wallis test showed a significant increase in vascularisation ($d.f.= 8$, $\chi^2= 89.87$, $P < 0.001$) and mean adjusted radius of the presumed age one ($d.f.= 8$, $\chi^2= 46.69$, $P < 0.001$) with increasing age (**Figure 5**).

3.4 Indirect validation

A total of 309 edges of spine sections (126 males and 181 females) were analysed for the monthly proportion of edge type and MIR. Opaque edge proportion and MIR throughout the year are shown in **Figure 6**. Although we could not obtain samples from austral winter, the highest values of the opaque edge proportion were found in the first quarter, with a maximum in March and a minimum in July. MIR showed no clear trend for the sampled months.

3.5 Growth parameters

Growth parameters were calculated from 312 sex combined samples. Growth parameters, residual sum of squares and AIC values showed similar results for Chapman's and Richard's VBGMs, while standard VBGm presented a lower maximum size, a quicker growth rate and the lower value of AIC (**Table 4**). A comparison of present findings with the growth curves accepted by ICCAT is shown in **Figure 7**. **Growth model comparison of the North Atlantic (Restrepo, 1990; Arocha et al., 2003) and the South Atlantic Ocean (present study) for swordfish (ages shown are based on sampling over 5 specimens).**Figure 7.

4. Discussion

The identification of the second anal fin ray is a matter of concern in swordfish ageing studies because most of the publications do not present a detailed description of the type of anal fin or select a different ray according to the morphology of the fin (Berkeley and Houde, 1983; Riehl, 1984; Vanpouille et al., 2001). Berkeley and Houde (1983) and Riehl (1984) used the ray morphology instead of the anal fin type, choosing the second ray when they found an anal fin similar to our type A, and the first ray when was similar to our type C. On the other hand, Vanpouille et al. (2001) used the second ray of four different anal fin morphologies, but one of their

morphologies was not found in the present study. We found that most of the anal fins displayed a type A morphology; therefore, we suggest the use of this type A anal fin to standardize the methodology and to reduce the variability on the spine measurements and age interpretation for this species.

The spine sectioning location criterion, and therefore ray section measurements, varies according to different studies. Berkeley and Houde (1983) indicated that the reference location was the “spine flare”; Ehrhardt *et al.* (1996) performed the sectioning at half of the maximum width of the ray condyle base, while Riehl (1984) and Valeiras *et al.* (2008) carried out the cut at the maximum width of this distance. Our findings show that the use of this third sectioning location might give better results on the growth studies using swordfish anal fin rays. A unique reference height should be settled to standardize the different studies on ageing using these structures. For example, Kopf *et al.* (2010) delimited the optimum location between $\frac{1}{4}$ and 1 condyle width for striped marlin; however, a more restricted area should be defined for swordfish spines to avoid annuli measurement differences.

Another matter of concern for spine growth analysis and identification of first annulus is the focus definition. Two main approaches have been applied: the convergence of the striations of the first annulus of one of the lobes (Esteves *et al.*, 1995; Ehrhardt *et al.*, 1996) and the half width of the section formed by the two lobes (Kopf *et al.*, 2010). The first criterion is not easily identifiable and open to subjectivity; the second one depends on the preparation of the spine, because according to the boiling time the structure formed by the two lobes changes due to the inner matrix deterioration. In order to obtain reproducible results, an enhanced criterion should be set. The criterion applied in this study is considered easy to apply, even for readers with low experience. However, further studies on the identification of the focus should be carried out; because the present paper focus location may be influencing our results showing that mean radius of the presumed age one annulus varies between age groups. This result prevent using back-calculation, since not all the assumptions to apply this method are been satisfied (Panfili *et al.*, 2002).

The appearance of vascularisation in the inner part of the lobe of the fin ray was first described by Berkley and Houde (1983). These authors indicated that one or two first annuli might be reabsorbed due to the vascularisation of the area during the growth of the fish. Present results showed that vascularisation increased when fish length and age increase. This issue has been pointed out in different studies (e.g. Tsimenides and Tserpes, 1984; Tserpes and Tsimenides, 1995; Vanpouille *et al.*, 2001; Sun *et al.*, 2002), however, these authors assert that the identification of age one annulus can be resolved with an experienced reader. Tserpes and Tsimenides (1995) and Cerna (2009) apply the measurements of first annuli of young individuals without vascularisation to estimate the annulus that have “disappeared” in the vascularised area of older specimens. The results in this study showed that presumed age one adjusted radius increases with age, although this increase is not so high to invalidate its utilization. Taking all this arguments into account, a combined method using the distribution pattern of annuli and a measurement approach could be used to identify age one annulus for specimens older than 4 years old.

Validation analysis is essential in direct ageing studies (Campana, 2001). In the present study, the periodicity of growth increment formation has been assessed by two methods, monthly formation of edge type and MIR. Opaque edge showed a general trend to reduce its proportion from January to July with higher proportion of the opaque edge appearing in austral summer and consequently translucent edge might be formed in austral winter. The formation of a translucent band in winter has also been observed by other authors for this species from the northern hemisphere (Berkley and Houde, 1983; Tsimenides and Tserpes, 1989; Ehrhardt *et al.*, 1996) and the southern hemisphere (Young *et al.*, 2004); by contrast Cerna (2009) found the opposite pattern. We found that MIR results showed no clear trend with a flat pattern, although the lack of samples, in late austral winter, prevents further conclusions. The formation of rings have been assumed as a response of the habitat or/and the physiological processes due to the swordfish behaviour and its environment (Tsimenides and Tserpes, 1989; Ehrhardt *et al.*, 1996, Sun *et al.*, 2002; Cerna, 2009). This species is reproductively active in some warm areas throughout the year, or with marked peaks of spawning in different months and areas, and with a complex migratory behaviour according to sex and sexual maturity (Mejuto *et al.*, 1998; Mejuto, 2007; Neilson *et al.*, 2013). All this facts seemed to affect monthly growth, hindering a clear temporal seasonal pattern in the MIR in this specie. Results of both analyses were not conclusive and further studies covering all months of the year are needed. In order to obtain an alternative approach to the validation of this calcified structure, tagging-recapture techniques should be applied in the South Atlantic area.

Growth parameters have been calculated with both sexes combined. The three VBGMs tested in the present paper are the most commonly ones used to fit the swordfish growth. The Standard VBGM was the better fitting model for our data set. Cerna (2009) also found that the standard VBGM was the most suitable one. However, Sun *et al.* (2002) and DeMartini *et al.* (2007) used standard and Richard's VBGMs, but they did not find significant differences between both models. On the other hand, Arocha *et al.* (2003) indicated that Chapman's VBGM was the most statistically appropriate one to fit his samples.

A short number of samples has hampered progress in growth estimations by sex. These estimations by sex were neither statistically robust nor of biological sense. Further efforts will be focused on getting more samples to carry out growth analysis by sex. In the present study, growth curve is close to the growth curves currently used by ICCAT (ICCAT, 2013) for the Atlantic for swordfish up to 5 years or 180 cm LJFL. For bigger specimens there is an increasing divergence among the curves. Restrepo (1990) found a low L_{∞} since it is lower than sampled individuals from our study and regularly observed in the Atlantic fisheries. Conversely, Arocha *et al.*, (2003) obtained a very high L_{∞} for their combined curve, but more conservative growth parameters by sex.

In order to standardize swordfish direct ageing using the anal fin, we suggest the following recommendations: type A anal fin should be used and the second ray must be selected; the maximum ray width ("d") should be selected for the sectioning location. We recommend using the "focus" as described previously, since we believe it is easy to locate and the "growth pattern" must be taken into account to identify age one annulus. Additionally we recommend making a bigger sampling effort to collect large swordfish specimens (> 150 cm LJFL). Further studies must be addressed to get a growth function by sex and fully standardize the ageing methodology for this species.

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Table 1. Number of swordfish anal fins collected between 2006 and 2013. Lower jaw fork length (LJFL) range and mean length is given in cm; N is the sample size.

<i>Month</i>	<i>Males</i>			<i>Females</i>			<i>Undetermined</i>			<i>Total</i>		
	<i>N</i>	<i>Mean LJFL</i>	<i>LJFL range</i>	<i>N</i>	<i>Mean LJFL</i>	<i>LJFL range</i>	<i>N</i>	<i>Mean LJFL</i>	<i>LJFL range</i>	<i>N</i>	<i>Mean LJFL</i>	<i>LJFL range</i>
1	29	143.4	85-213	84	201.9	78-309				113	186.8	78-309
2	21	139.1	84-217	35	206.5	68-288				56	181.2	68-288
3	4	118.5	81-187	23	189.7	87-268				27	179.2	81-268
4	35	137.3	85-190	30	160.8	90-255				65	148.2	85-255
5	10	153.2	103-205	13	164.3	80-235				23	159.5	80-235
6	11	133.6	87-210	18	127.4	67-225	1	62.0		30	127.5	62-225
7	16	100.4	67-137	9	94.4	66-132	1	71.0		26	97.2	66-137
11	14	139.7	108-170	13	168.4	103-262				27	153.5	103-262
12	16	123.9	76-201	23	177.9	73-269				39	155.8	73-269
Total	156	133.9	67-217	248	181.2	66-309	2	66.5	62-71	406	162.5	62-309

Table 2. Analysis of second anal fin ray biometry by sex. Spine measurements are displayed as column headings. Sample size (N), parameters of the allometric function ($Y=aX^b$, where Y represents LJFL and X the different measurements) and statistical significance are shown.

Spine measurements	Maximum diameter (d)	Width section	Height section	Maximum width of lobe		Pre-Growth structure	Vascularisation	
				Males	Females		Males	Females
N(male,female)	127, 185	102, 172	102, 172	127	186	91, 134	115	154
<i>H₀: slopes are equal between sexes</i>								
L	0.728	0.154	0.058		4.375	1.108		8.565
df	1	1	1		1	1		1
p-value	.	.	.		**	.		***
<i>H₀: common slope not different from 1</i>								
L	19.7	347.5	350.9	$r_{rf}(b)=0.929$	$r_{rf}(b)=0.944$	101	$r_{rf}(b)=0.742$	$r_{rf}(b)=0.547$
df	2	2	2	125	184	2	113	152
p-value	****	****	****	****	****	****	****	****
a(elevation)	-1.335	-2.336	-2.412	-3.545	-3.308	-4.019	-4.680	-3.733
(95% Conf. interval)	(-1.387,-1.283)	(-2.440,-2.232)	(-2.503,-2.320)	(-3.741, -3.349)	(-3.434,-3.182)	(-4.453,-3.585)	(-5.263,-4.096)	(-4.147,-3.319)
b(slope)	1.211	1.545	1.499	1.913	1.798	1.771	2.077	1.591
(95% Conf. Interval)	(1.188,1.236)	(1.499,1.593)	(1.458,1.541)	(1.821, 2.009)	(1.742,1.856)	(1.584,1.981)	(1.816,2.374)	(1.414,1,790)
r squared	0.968	0.935	0.946	0.923	0.953	0.278	0.481	0.457
p-value	****	****	****	****	****	****	****	****

Signif. codes: 0 '*****' 0.001 '****' 0.01 '***' 0.05 '**' 0.1 '.' 1

L: Likelihood Ratio

$r_{rf}(b)$: Correlation between residual and axis scores when these variables are calculated using a slope of b=1

Table 3. Mean and length range (LJFL cm) and number (N) of samples by ages; Std. Error is the length standard error

Age	Males				Females				Combined			
	N	Mean LJFL	LJFL range	Std. Error	N	Mean LJFL	LJFL range	Std. Error	N	Mean LJFL	LJFL range	Std. Error
0	13	81.9	67-96	7.94	21	81.1	66-96	9.59	34	81.4	66-96	8.88
1	39	97.5	80-125	10.00	23	97.6	87-126	9.21	62	97.5	80-126	9.64
2	23	116.7	95-140	12.75	20	122.6	95-150	14.03	43	119.4	95-150	13.53
3	17	134.8	118-155	11.44	8	142.8	127-175	15.80	25	137.3	118-175	13.21
4	12	164.3	145-188	13.33	7	161.3	135-195	22.65	19	163.2	135-195	16.78
5	9	179.0	143-209	19.60	17	180.0	139-209	22.60	26	179.7	139-209	21.21
6	3	184.3	171-202	15.95	21	200.1	165-217	15.53	24	198.1	165-217	16.13
7	6	199.8	180-213	10.80	18	209.1	177-221	10.18	24	206.8	177-221	10.89
8	4	208.5	201-217	7.72	19	218.2	201-247	11.56	23	216.5	201-247	11.48
9					14	231.9	220-249	8.37	14	231.9	220-249	8.37
10					6	246.2	231-264	11.48	6	246.2	231-264	11.48
11					5	261.4	241-288	21.94	5	261.4	241-288	21.94
12					1	250.0	250-250		1	250.0	250-250	
13					3	269.0	260-280	10.15	3	269.0	260-280	10.15
14					3	286.3	269-309	20.53	3	286.3	269-309	20.53
Total	126	127.1	67-217	38.95	186	170.9	66-309	60.21	314	152.6	62-309	57.08

Table 4. Growth parameters, sum of residual squares (RSS) and Criterion Statistics (AIC) values are given for the three VB fitted models.

	Standard VB model			Chapman's VB model			Richards' VB model		
	St. Error	CI 95%		St. Error	CI 95%		St. Error	CI 95%	
Linf	358.65	21.24	316.8 - 400.4	371.02	73.24	226.8 - 515.2	371.02	73.27	226.7 - 515.2
k	0.092	0.011	0.071 - 0.113	0.073	0.086	-0.096 - 0.243	0.073	0.086	-0.096 - 0.243
T0 / L0	-1.929	0.216	-2.354 - 1.503	56.652	9.972	37.0 - 76.2	-1.615	1.525	-4.618 - 1.387
δ / m				-0.112	0.579	-1.252 - 1.028	-0.112	0.579	-1.252 - 1.027
N parameters	3			4			4		
N samples	278			278			278		
RSS	52385.71			52377.75			52377.74		
AIC	-3.44			-1.44			-1.44		

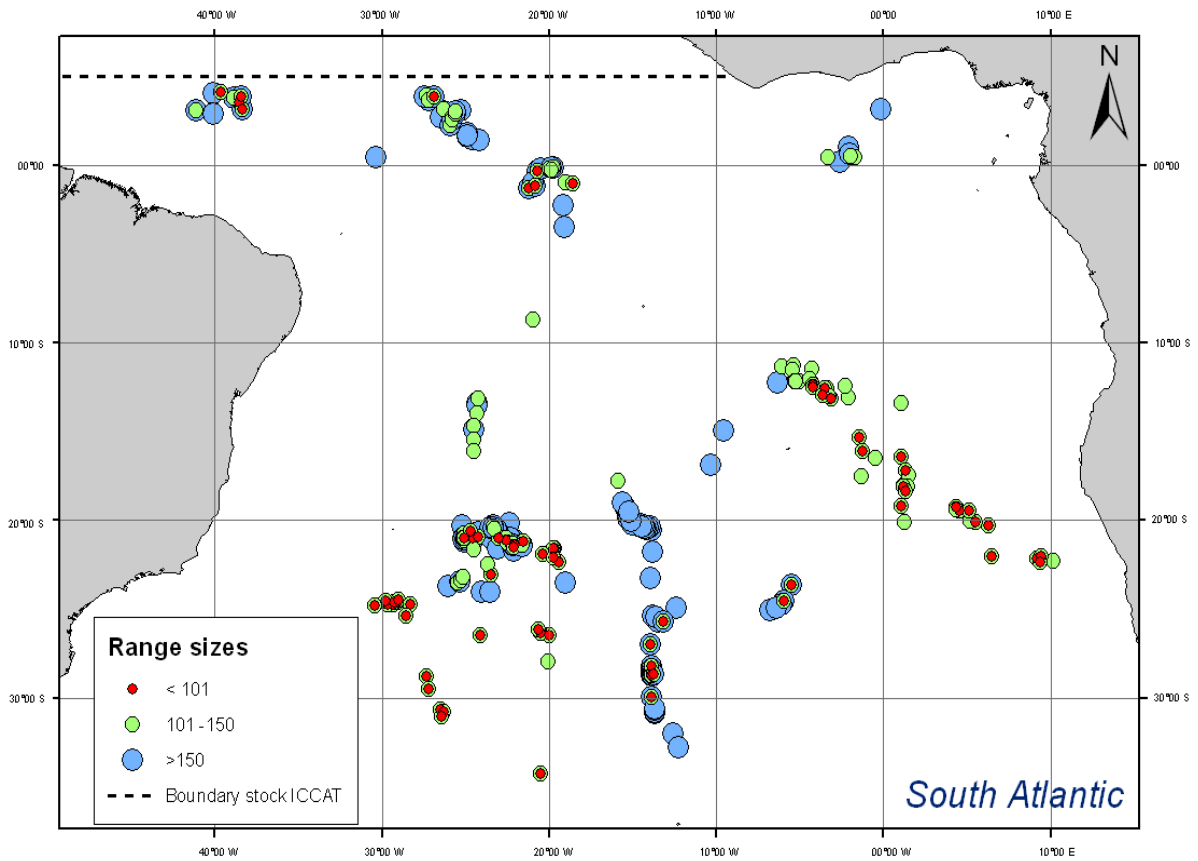


Figure 1. Geographical distribution of the samples by size range.

	1 ^{re} épine petite épine	2 ^e épine épine(s) moyenne(s)	3 ^e épine épine digitée
A			
C	?		
B			

Figure 2. Fin type configuration according to the first three radii by order of frequency appearance (Adapted from Vampuille *et al.*, 2001).

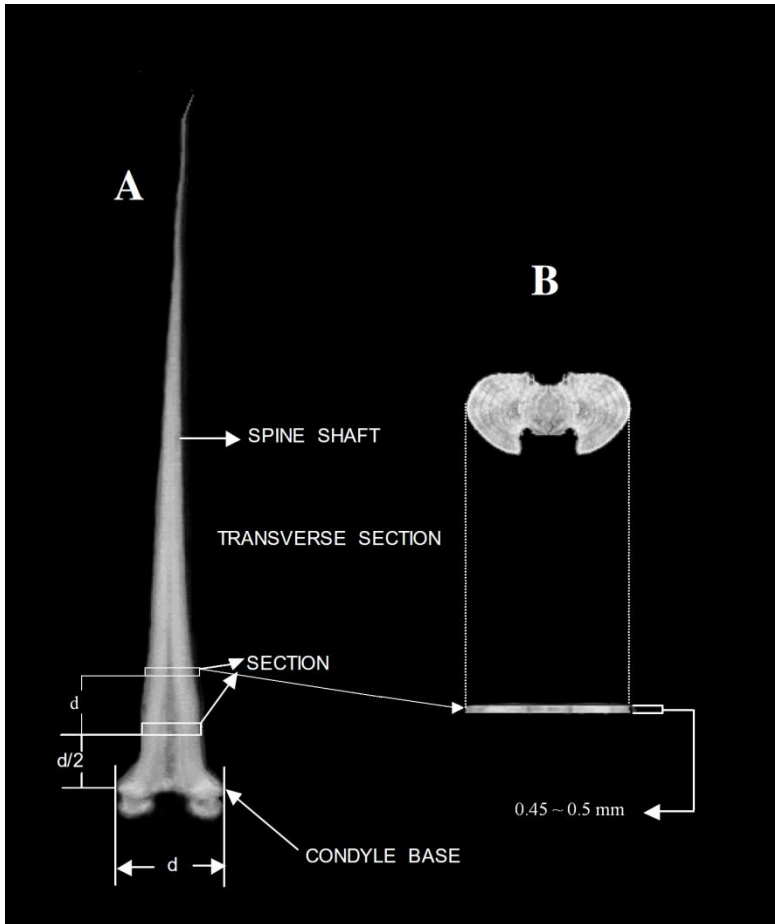


Figure 3. A: Second anal fin ray of a swordfish, showing the maximum diameter of the condyle base (d). **B:** Cross section of the fin ray at distance d (Adapted from Sun *et al.*, 2002).

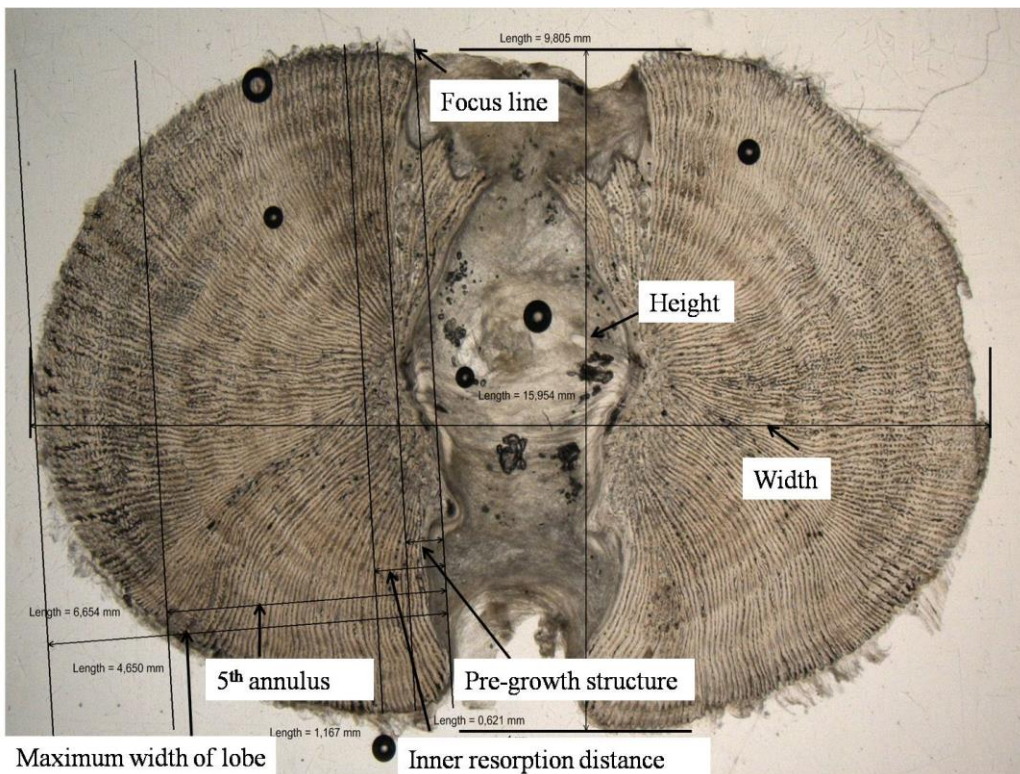


Figure 4. Ray transverse section and description of measurements of the second anal fin ray of the swordfish.

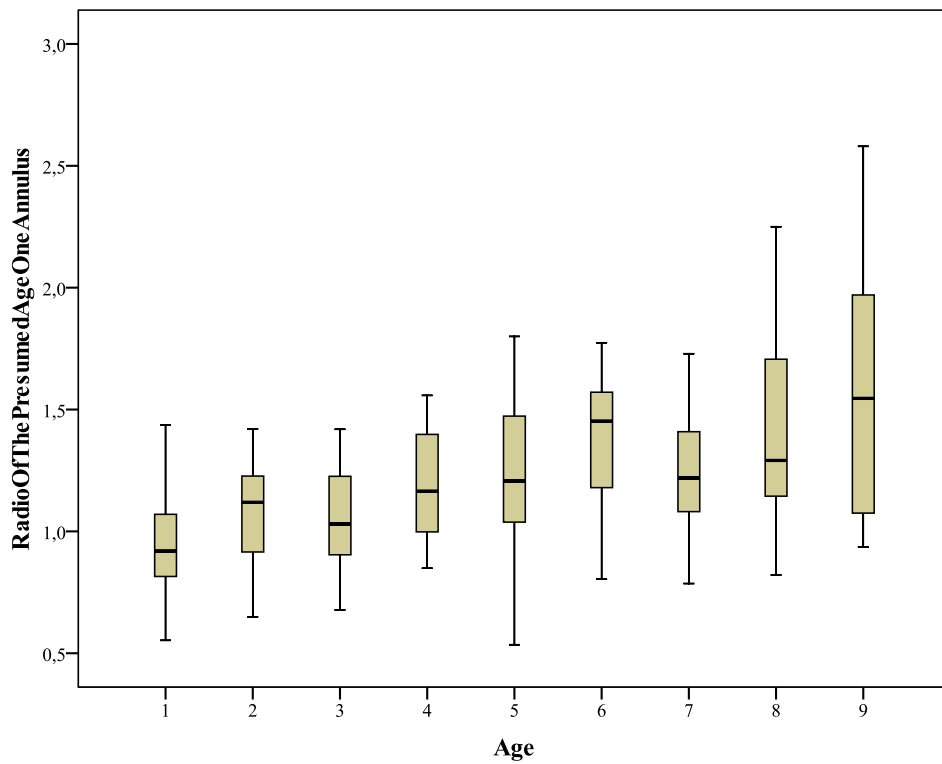
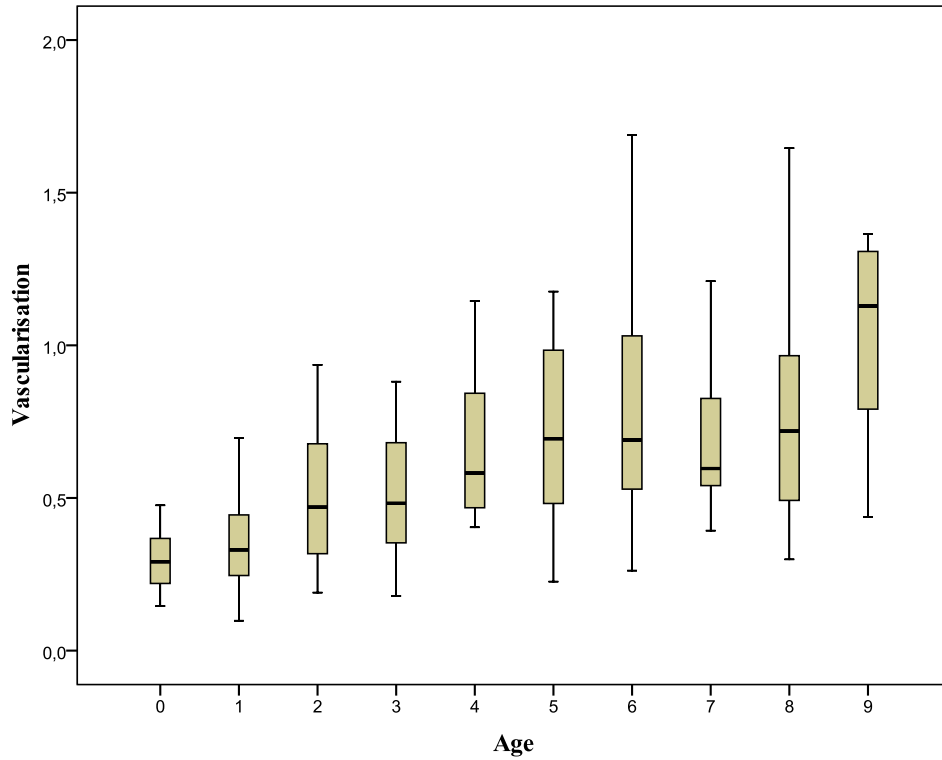


Figure 5. Box-plot showing the relationship between the vascularisation (cm) (upper) and the radius of the first annulus (cm) (lower) versus age (number of annuli) for South Atlantic swordfish. The superior limit of the boxes is the third quartile and the inferior the first quartile. The horizontal bar represents the median and the vertical bar indicates minimum and maximum values of the radius.

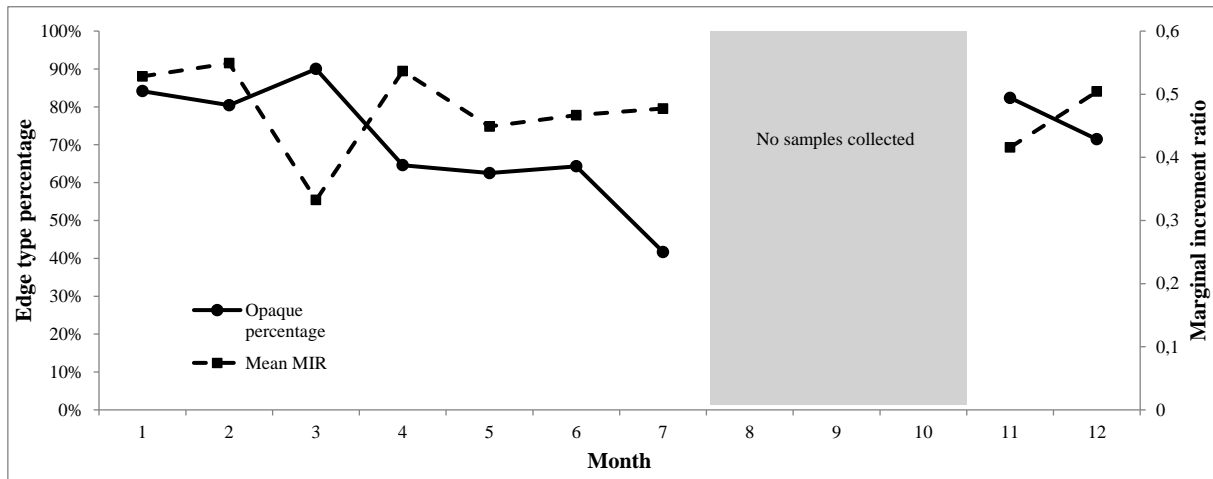


Figure 6. Opaque edge percentage (solid line) and marginal increment ratio (MIR) values (discontinuous line), for both sex combined throughout the year.

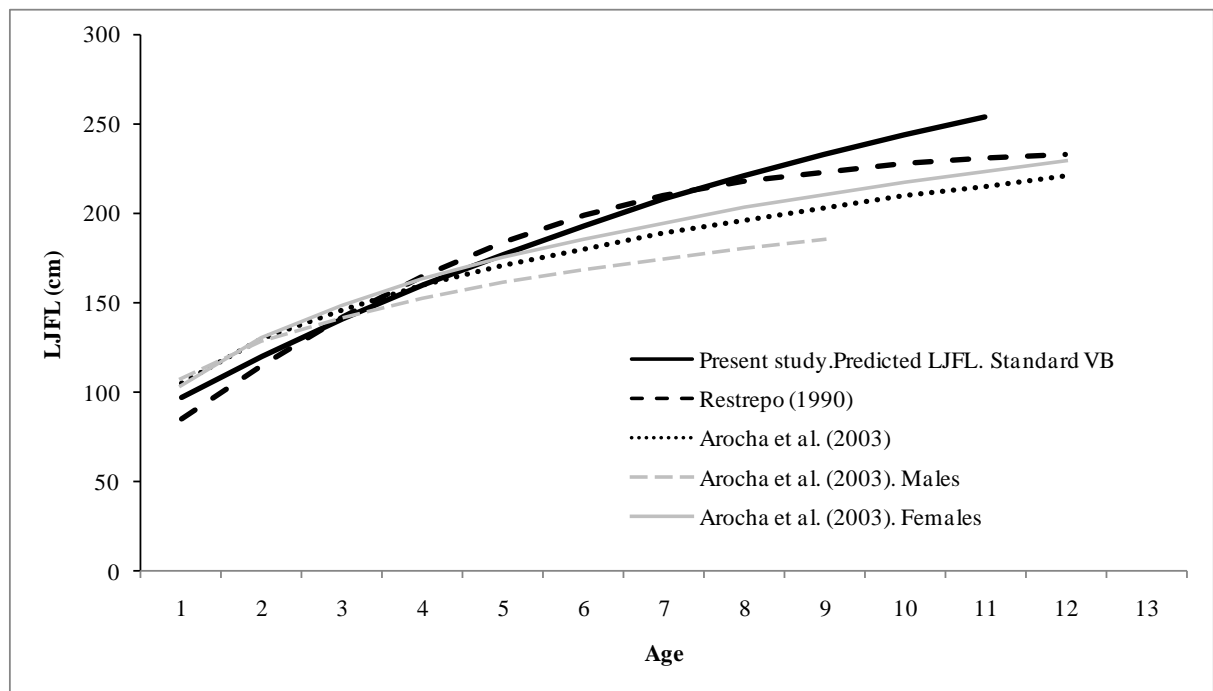


Figure 7. Growth model comparison of the North Atlantic (Restrepo, 1990; Arocha *et al.*, 2003) and the South Atlantic Ocean (present study) for swordfish (ages shown are based on sampling over 5 specimens).