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ESTIMATION OF AGE AND GROWTH OF THE LONGBILL SPEARFISH (*TETRAPTURUS PFLUEGERI)* IN THE WESTERN ATLANTIC OCEAN

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SUMMARY

The age and growth of the longbill spearfish, Tetrapturus pfluegeri, was estimated using transversal cuts from the third spine of the anal fin. Also, the structure and periodicity of annuli formation were validated for this species. The samples used were collected in a large zone of the Western Atlantic between 25ºN and 40ºS, obtained on the artisanal gillnet and commercial longline fleets of Venezuela and commercial longline fleets from Brazil and Uruguay. This is the first growth estimates for the longbill spearfish and the results showed that the third spine of the anal fin in this species is suitable for age and growth studies. An annual periodicity in the formation of growth bands was observed and, like most of billfish species, was characterized by having very fast growth in the early years of life (k = 0.52 years-1, L∞ =175 cm and t0 = -1.26). No differences in growth rates between sexes were observed and the parameters estimated for the longbill spearfish were within the range of parameters reported for species within the same family in the Atlantic Ocean like white marlin and sailfish.

RÉSUMÉ

L'âge et la croissance des makaires bécunes (Tetrapturus pfluegeri) *ont été estimés à l'aide de coupes transversales de la troisième épine de la nageoire anale. En outre, la structure et la périodicité de la formation des anneaux ont été validées pour cette espèce. Les échantillons utilisés ont été recueillis dans une vaste zone de l'Atlantique occidental entre 25ºN et 40ºS, obtenus des flottilles artisanales opérant au filet maillant et des flottilles commerciales palangrières du Venezuela et des flottilles palangrières commerciales du Brésil et de l'Uruguay. Il s'agit des premières estimations de croissance pour le makaire bécune et les résultats ont montré que la troisième épine de la nageoire anale chez cette espèce est adéquate pour les études de l'âge et de croissance. Une périodicité annuelle dans la formation des anneaux de croissance a été observée et, comme la plupart des espèces d'istiophoridés, a été caractérisée par une croissance très rapide dans les premières années de vie (k = 0,52 années-1, L∞ = 175 cm et t0 =- 1,26). Aucune différence dans les taux de croissance entre les sexes n'a été observée et les paramètres estimés pour le makaire bécune se sont inscrits dans la gamme des paramètres signalés pour les espèces au sein de la même famille dans l'océan Atlantique, comme le makaire blanc et les voiliers.*

RESUMEN

Se estimó la edad y el crecimiento de la aguja picuda, Tetrapturus pfluegeri, *utilizando cortes transversales de la tercera espina de la aleta anal. Además, se validó, para esta especie, la estructura y periodicidad de la formación de anillos. Las muestras utilizadas se recogieron en una amplia zona del Atlántico occidental, entre 25ºN y 40ºS, obtenidas por las flotas de redes de enmalle artesanales y de palangre comercial de Venezuela y por las flotas de palangre comercial de Brasil y Uruguay. Esta es la primera estimación de crecimiento de la aguja picuda y los resultados demostraron que la tercera espina de la aleta anal en esta especie es*

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adecuada para estudios de edad y crecimiento. Se observó una periodicidad anual en la formación de bandas de crecimiento y, al igual que la mayoría de los istiofóridos, se caracterizaba por tener un crecimiento muy rápido en los primeros años de vida (k = 0,52 años-1, L∞ =175 cm y t0 = -1,26). No se observaron diferencias en las tasas de crecimiento entre sexos y los parámetros estimados para la aguja picuda se encontraban dentro del rango de parámetros comunicados para especies de la misma familia en el océano Atlántico, como la aguja blanca y el pez vela.

KEYWORDS

Longbill Spearfish, Age estimation, Spines, Von Bertalanffy growth model

1. Introduction

The longbill spearfish, *Tetrapturus pfluegeri* (Robins and De Sylva, 1963) is a highly migratory species widely distributed in tropical, subtropical, and temperate oceanic waters of the Atlantic Ocean, between 40º N and 40º S (Nakamura, 1985; Domingo *et al*., 2009). It is one of the smallest billfish species with a maximum reported size of 207 cm fork length (Coutinho *et al*., 2010). It is a top predator (Vaske Junior *et al*., 2004; Satoh *et al*., 2004) and a batch spawner that spawns in separate discrete events in tropical waters of both hemispheres (De Sylva and Breder, 1997). In the central South Atlantic Ocean, Ueyanagi *et al*. (1970) found a high concentration of spawning females and larvae from January to March between 10 º and 20 º S. However, in the Venezuela Basin, Arocha *et al*. (2007) found high concentrations of spawning females with high gonadal index and hydrated oocytes between June and August. The reproductive size of females was estimated at 150 cm fork length by Arocha *et al*. (2007) in the central North Atlantic, but results from Couthino *et al*. (2010) over the southwestern Atlantic suggest that females may reach maturity at lower sizes. There is still great uncertainty about the biology, ecology and life history parameters of the longbill spearfish since few studies have focused on this species.

The longbill spearfish is caught as by-catch by different recreational, artisanal and industrial fisheries in the Atlantic Ocean (Arocha *et al*., 2007). However, there are no studies regarding the status of their populations; probably because it is the least commonly caught species among billfishes in the tuna and swordfish fisheries. Moreover, the catches of this species have been historically combined with those of sailfish in the International Commission for the Conservation of Atlantic Tunas (ICCAT) databases, although, efforts have been made to separate them with some catch estimates being presently available for this species (Anon, 2009, 2010). For management purposes ICCAT consider that there are two stocks for both sailfish and longbill spearfish in the Atlantic Ocean, one eastern and one western, despite there are no specific studies on stock structure for longbill spearfish (Graves and McDowell, 2003).

Stock assessments performed by ICCAT in the Atlantic Ocean, for white marlin, *Kajikia albidus*, and blue marlin, *Makaira nigricans*, indicated that these stocks are currently overfished (Anon., 2012, 2013) and that it is likely that the two stocks of sailfish are also overfished (Anon., 2010). However, ICCAT has repeatedly highlighted that these assessments have a high degree of uncertainty because of the lack of biological information and uncertainty in basic fishery data on catch and fishing effort (Anon., 2003, 2010, 2012, 2013). Age and growth studies are of particular relevance for stock assessments as they provide information for the estimation of mortality rates and stock productivity which are the basis of stock status evaluations (Haddon, 2001).

A comparative study between calcified structures (otoliths and fin spines) in the blue marlin showed that spines provided a more accurate estimation of age and are easier to collect than otoliths (Hill *et al*., 1989; Prince *et al*., 1988). Several studies have also used fin spines for age estimation in swordfish *Xiphias gladius* (Ehrhardt, 1992; Tserpes and Tsimenides, 1995; Sun *et al*., 2002; Arocha *et al*., 2003), black marlin *Makaira indica* (Speare, 2003), white marlin (Drew *et al*., 2007), striped marlin *Kajikia audax* (Melo-Barrera *et al*., 2003; Kopf *et al*., 2011) and sailfish *Istiophorus platypterus* (Hoolihan, 2006). However, no such studies have been done to date on the longbill spearfish. Therefore, the aim of this study was to provide the first growth estimates for this species in the western Atlantic Ocean. The study was specifically aimed to validate the structure and periodicity of annuli formation in anal fin spines, assigned the age to each individual, and to estimate sex specific growth curves.

2. Materials and methods

2.1 Samples collection

Spines from 497 longbill spearfish were collected by scientific observer's onboard longline vessels from Brazil, Uruguay and Venezuela fisheries, and also at landings sites of the longline and gillnet fleets from Venezuela. Samples were collected from a wide area of the western Atlantic Ocean between 22ºN and 36ºS during the period 2003-2011 (**Figure 1**). Although the study covered 9 years of sampling, inter-annual variations in growth were not considered due to low sample size obtained for each year.

To estimate the age and growth of sampled individuals, the third anal fin spine was removed after the species was identified visually and sex determined by gonadal examination (Drew *et al*. 2006a). Each specimen was measured to the nearest centimeter in a straight line from the tip of the lower jaw to the fork of the tail (Lower Jaw Fork Length - LJFL). The spines were stored on ice or frozen until laboratory processing.

2.2 Spines processing

At the laboratory, the excess of tissue was removed from each spine using a bath in warm water (less than 70ºC) and then dried in an oven at approximately 60ºC for 24 hours. Maximum condyle width (MCW) of each spine was measured to the nearest millimeter, and three transverse sections of 45 µm thick were cut at a level of 1/2 MCW (Drew *et al*., 2006a; Kopf *et al*., 2010) using a Buehler ISOMET low-speed saw with a diamond edged blade.

Digital images of the transversal sections were taken under transmitted light using a digital camera attached to a binocular microscope (Leica MZ7.5 and Olimpus SZ61) using magnifications from x1 to x4. Measurements were taken from the spine focus to the radius of the vascularized area and to each annulus radius - measured from the focus to the outer edge of each translucent zone. Also, the width of the marginal increment - defined as the distance between the last visible ring and the edge of the spine- were measured. Finally, the spine edge was classified as translucent or opaque following the criteria described by Kopf *et al*. (2010). Measurements were performed using the software Sigma Scan Pro 5.0 (Systat Software Inc, Richmond, CA, USA).

2.3 Analysis

To validate the third radius of the longbill spearfish anal fin as a suitable ageing structure the relationship between LJFL and the total spine radius was analyzed using a classical linear regression function (Zar, 2010). If this linear relationship exists it means that the spine grows proportionally with the size of the individual, demonstrating its growth.

The translucent bands (annulus) were counted twice by the primary reader with an inter-reading period of three months and without any information of the specimen (i.e. size, sex or date of capture). A third reading was performed when no agreement occurred between the first and the second readings by the same reader. Some spines were discarded due to poor visibility of growth marks or because of disagreement between the three readings. The precision of annulus counts between the first and the second readings was assessed using the index of average percent error (IAPE, Beamish and Fournier, 1981) calculated as follow:

$$\mathrm{IAPE} = 100\ \frac{1}{\mathrm{N}} \sum_{j=1}^{\mathrm{N}} \left[\frac{1}{\mathrm{R}} \sum_{i=1}^{\mathrm{R}} \frac{\left| \mathrm{X}_{ij} - \mathrm{X}_{j} \right|}{\overline{\mathrm{X}}_{j}} \right]$$

Where, N is the number of aged fish, R is the number of times each fish was aged, Xij is the ith age determination of the jth fish and $\overline{\mathrm{X}}_j$ is the average age calculated for the jth fish.

Validation of the timing and periodicity of the opaque and translucent growth marks formation was evaluated using: 1) the proportion of edge type (opaque vs. translucent) as a function of month; and 2) the marginal increment ratio (MIR) calculated as:

$$\mathrm{MIR} = \frac{(\mathrm{R} - \mathrm{r}_{\mathrm{n}})}{(\mathrm{r}_{\mathrm{n}} - \mathrm{r}_{\mathrm{n-1}})}$$

Where, R is the total spine radius, rn is the radio of the last annulus and rn-1 is the ratio of the second last annulus (Hayashi, 1976). The MIR was also examined by month because annulus formation corresponds to the period in which this value is minimal.

2.4 Estimation of rings lost due to vascularization

Even though fin spines have advantages over otoliths on ageing billfish species because they provide a more accurate estimation of age and also because they are easier to collect (Hill *et al*., 1989; Prince *et al*., 1988), they suffer tissue loss due to vascularization. This process starts at the center of the spine (**Figure 2**) and as the spine grows, the area of vascularized tissue grows as well. Drew *et al*. (2006b) showed in white marlin specimens that the radius of the first visible ring in the smallest fish analyzed was less than the radius of vascularization in some of the larger fish. Hence, some rings could be partially obscured by vascularized tissue. Moreover, as animals grow the radius of vascularization tissue increases (Drew *et al*., 2006b).

We used the method proposed by Hill *et al.* (1989) to estimate the obscured rings in longbill spearfish due to vascularization. The first growth bands that are subsequently lost in larger individuals were estimated through the direct observation of growth marks in smaller/younger individuals, in which these rings were still visible. This method assumes that lost rings can be predicted by the radius of the spines and that available samples of young animals are representative of the population as a whole.

The final age estimation was based on the sum of total visible rings plus the rings obscured by vascularization and estimated by the Hill *et al*. (1989) method. Although some rings were able to be observed below the vascularization area, they were not taken into account because it could not be determined whether they were true or false rings. A ring was deemed to be a false rings whenever the translucent band did not extend into the cranial and caudal margins of the spine section (Speare 2003). Also, we assumed a ring was a false ring if the distance between two translucent annulus increased by more than 25% compared with the distance of the preceding (Kopf *et al*., 2011).

2.5 Growth model

We used the standard von Bertalanffy (1938) function to model the longbill spearfish growth in length. This model was fitted to the observed and back-calculated length at age. We decided to use also a back-calculation approach because there were few samples in the youngest age groups. The method developed by Ehrhardt (1992) was used to back-calculated LJFL at age. This method was applied to swordfish, *Xiphias gladius*, and was selected as the most parsimonious fit by Kopf *et al.* (2011) for striped marlin (*Kajikia audax*) compared with others classical back-calculation methods like Dahl–Lea (Lea, 1910) and Fraser –Lee (Francis, 1990). The equation used by Ehrhardt (1992) is described as:

$$\log LJFL_n = \log a + \left[\frac{\log S_n(\log LJFL - \log a)}{\log S}\right]$$

Where, LJFL is the observed length at capture, LJFLn is the length when annulus n was formed, S is the spine radius at capture, Sn the radius of the n annulus, and a is the intercept of the straight line fitted between LJFL and spine total radius.

Back-calculated lengths-at-age were compared to the observed lengths-at-age by using a two tail non-parametric Mann Whitney U-test, for sex-combined (also including unsexed specimens) and by sex (Zar, 2010). In addition, likelihood ratio tests (Kimura, 1980; Haddon, 2001) were performed to assess for differences in growth curves, comparing each sex specific model to the full model, assuming no differences in parameters between sexes. Statistical significance was set at 95% (α=0.05) for all test.

3. Results

A total of 416 fin-spines were aged; 16% were excluded from growth analysis due to: 1) spines that were broken during the cutting process, 2) spines discarded because no consensus among readings was reached (see below, % IAPE) and 3) rings that were not readable in any of the three cuts made. We found that some individuals ranging in size between 124 and 184 cm LJFL, showed unreadable or not visible marks in their spines. Therefore, it was impossible to distinguish, in the smaller individuals, if the absence of visible annulus was due to a real absence of ring formation (age 0) or due to very poor visibility of marks. Therefore, no age 0 longbill spearfish were identified in the study.

The length of the 416 longbill spearfish aged ranged from 110 to 202 cm LJFL (**Figure 3**) with a mean size of 167 cm (± 0.65 standard error, SE). A total of 397 individuals were sexed; males were significantly larger than females (U = 15622, P < 0.01) presenting a mean size of 169 cm (± 0.77 SE, n=229) and 165 cm (± 1.08 SE, n=168), respectively. A linear relationship between LJFL and spine radius was observed (R^2 = 0.31, P < 0.01) indicating that these spines were suitable structures for age determination (**Figure 4**).

Both the proportion of edge type and the MIR analysis indicated an annual periodicity in ring formation. The higher proportion of translucent edges and the smallest MIR occurred in September. The MIR increased progressively after this month, reaching its largest values in March (**Figure 5**).

The IAPE estimated between the first two independent readings was 11 % for the entire sample. The number of visible rings in spine sections ranged between 1 and 5 (**Figure 6A**); however, assigned ages using the Hill's method ranged from 1 to 7, with the majority of individuals falling in the third and fourth year age classes (**Figure 6B**).

Statistical differences were found between the observed and back-calculated mean length at age for the entire sample (sex combined and unsexed individuals, W=82114, P<0.01) and for males (W=22594, P<0.01) and females (W=13725, P<0.01). Back-calculated lengths at age were lower than the observed length at age, particularly at younger ages (**Table 1**).

The von Bertalanffy growth model estimated a set of parameters of L∞= 175 cm LJFL, k=0.74 years-1 and t0=-0.99 years for the observed length at age data and combined sexes. The back-calculated length at age von Bertalanffy growth curve also for combined sexes showed the same L∞ estimate but a lower value for t0 and k (**Table 2**). Particularly, the differences between observed and back-calculated estimations were greater in the estimated von Bertalanffy parameters for males than for females (**Figure 7**). In all cases (males, females and sex combined) the estimated standard errors of L∞ were greater for the back-calculated data than the observed data but lower for t0 and k (**Table 2**).

Likelihood ratio test indicated no significant differences in growth by sex for the observed length at age in any of the parameters (PL∞=0.777, Pk=0.277, Pto=0.380). The back-calculation method also showed the same patterns, with the differences not being statistically significant for any of the curves by sex compared to the full model (PL∞=0.273, Pk=0.167, Pto=0.258). In spite of this, **Table 2** and **Figure 7** present all parameter estimates because this is the first estimation of growth parameters for the longbill spearfish.

4. Discussion

This is the first estimation of age and growth in the longbill spearfish worldwide. The analysis of accuracy of ring counts (IAPE) was 11.2 % and was within the range observed for species of the same genus. IAPE calculated here was less than the 20 % reported by Drew and Die (2008) for white marlin but higher than that reported in several other studies: 9.8 % for striped marlin (Kopf *et al*., 2011), 5.2 % for swordfish (Sun *et al*., 2002) and 4.8 % for sailfish (Hoolihan, 2006). A large proportion of the spines analyzed presented false rings, doubles or triples, and these marks could sometimes cause disagreement between readings. However, the third spine of the anal fin was suitable in terms of readability to be used in age and growth studies for the longbill spearfish.

A yearly periodicity of ring formation was indirectly validated for this species as has been recorded for other billfish species such as blue marlin (Hill *et al*. 1989), white marlin (Drew *et al*., 2007), black marlin (Speare, 2003), striped marlin (Kopf *et al*. 2011), sailfish (Jolley 1974) and swordfish (Ehrhardt, 1992), as well as in other large pelagic species like tunas (*Thunnus obesus*, Sun *et al*., 2001; Duarte-Neto *et al*., 2012). The MIR suggested that a single annulus is formed each year around September, which matches the end of the spawning period observed in the Venezuela Basin (Arocha *et al.*, 2007). Other studies in billfish species found that ring formation match with the spawning activity in sailfish (Chiang *et al*., 2004), swordfish (De Martini *et al*., 2007) and striped marlin (Kopf *et al*., 2011). However, as it has been suggested by others authors (Sun *et al*. 2002, Chiang *et al*. 2004), this coincidence should exists only if the reproduction season is associated with ring formation. Nevertheless, these marks were also presented in immature individuals, which makes this hypothesis unlikely. Migration patterns or other environmental factors could cause ring formation in the longbill spearfish however this hypothesis are beyond the scope of this study.

Back-calculation estimated size at age was significantly smaller than those observed, indicating the presence of the phenomenon described by Rosa Lee in 1912 in which the back-calculated lengths from older fish tend to be lower than the observed. There are several hypotheses that may explain this phenomenon: 1) sampling bias and therefore under-representation of individuals from the lower end of the age distribution, 2) problems or lack of relationship between size of spine and size of individuals and 3) an age dependent natural and/or fishing mortality (Ricker, 1969; 1979). In the present study, the selectivity due to a fishery dependent sampling could have resulted in an overestimation of the average size observed at early ages. The smallest longbill spearfish sampled in this study was 110 cm LJFL. Therefore, bias sampling may have occurred for young fish where only the largest individuals of each age group being included in the samples (Anon, 2010; Kopf *et al*., 2011). In addition, the high variability observed in the relationship between individual fork length and spines radius may also have affected the differences between observed and back-calculated length at age.

If we accept the hypothesis of bias sampling, back-calculated parameters estimated from the von Bertalanffy growth curve would be more realistic than the calculations from the observed sample, attributed to an underrepresentation of the lower end of the length distribution. The differences found in the k and t_0 growth parameters estimated from the observed sample between males and females are probably due to the fact that most of individuals <150 cm LJFL were females, hence younger male classes were underrepresented in the sample. This is the likely reason why we found the greatest differences in growth parameters between observed and back-calculated length at age for males (**Table 2**). It is important to remind the reader, however, that according to our data, differences in growth parameters of males and females were not statistically significant.

Longbill spearfish, like most of billfish species, was characterized by having very fast growth in the yearly years of life. This species reaches 110 cm LJFL in the first year of life, more than half of their average maximum size (L_∞). Since this is the first study of longbill spearfish growth, the estimated parameters can only be compared with other closely related species. This species presented similar estimated growth rate as the striped marlin in the Pacific Ocean (k~0.5; Kopf *et al.*, 2011), or white marlin in the Atlantic (k~0.4; Drew and Die 2008), but higher than the reported values for sailfish in waters off eastern Taiwan (k~0.1; Cheng *et al*., 2004). However, the estimated parameters for the longbill spearfish were among the reported values for species within the same family.

Ortiz *et al.* (2003) reported the recapture of a marked individual of longbill spearfish after being at liberty for 5 years. In the present study we estimated that the longbill spearfish could achieve at least 7 years old. This maximum age is less than that reported for larger sized billfish species such as the white marlin (15 years; Anon, 2010) but similar to striped marlin (8 years; Kopf *et al*., 2011). Probably, the longbill spearfish can reach older ages and the observed maximum age is not a representation of maximum longevity. Maybe, older individuals do occur in the region but are not as vulnerable to the fisheries as smaller age classes, or simply were not present in the area during our sampling.

Age and growth estimations in marlins is quite complicated and it was particularly complex for the longbill spearfish due to difficulties associated with: 1) sampling methods (fisheries dependent data, limited number of samples and constrained length distribution), 2) spines reading and interpretation (associated with visualization and identification of true and false increments), 3) estimation of annulus obscured due to vascularization processes, 4) validation of annulus formation and 5) variability observed in the relationship between spine radius and individual fork length. In the present study the last point is particularly important because the estimation of ring lost due to vascularization and back-calculation techniques rely on this relationship, so it is important that future studies consider other structures, rather than anal spines, to be compared with these estimations.

Despite this, we found that the third radius of the anal fin was suitable for age estimation in this species. The sampling effort and cooperation among countries (Venezuela, Brazil and Uruguay) allowed us to cover a wide range in the distribution of this species and a sufficient sample size which is very difficult for this specie because is the least common among billfishes in the Atlantic. Moreover, this effort was very important to validate the annual periodicity of ring formation because we could obtained samples from all month along the year.

The present study lays the foundation for the development of better estimates of age and growth in the longbill spearfish. Also, it provides relevant information regarding life history parameters of this species that may be used in future stock assessments and fisheries management.

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Table 1. Longbill spearfish observed and back-calculated mean length at age for the total sample (sex combined and unsexed), males and females. N: number of individuals sampled; Min.: minimum length at age; Max.: maximum length at age.

		Observed				Back-calculated		
	Age	N	Mean length	Min.	Max.	Mean length	Min.	Max.
Total	1	16	131	110	147	120	93	156
	2	71	161	123	180	143	110	172
	3	160	167	140	184	156	128	183
	4	107	171	143	188	162	127	183
	5	46	173	157	188	168	143	185
	6	14	183	170	202	177	161	193
	7	2	179	178	180	177	176	178
Males	1	5	133	123	147	122	96	156
	2	37	160	132	180	145	116	172
	3	88	167	148	184	157	128	183
	4	67	171	148	185	164	144	183
	5	26	173	158	184	167	143	182
	6	6	178	170	194	173	161	186
Females	1	8	131	110	147	120	93	140
	2	31	157	123	174	142	110	170
	3	68	164	140	180	155	128	180
	4	37	167	143	188	160	127	182
	5	16	173	160	188	169	151	185
	6	7	184	170	202	181	168	193
	7	1	180	180	180	178	178	178

Table 2. Observed and back-calculated estimation of coefficients from the von Bertalanffy growth model for the longbill spearfish. SE=Standard Error.

	L_∞	SE	t_0	SE	k	SE
Total						
Observed Age 1–7	175	1.14	-0.99	0.25	0.74	0.08
Back-calculated Age 1–7	175	2.48	-1.26	0.20	0.52	0.05
Males						
Observed Age 1–6	174	1.16	-0.66	0.32	0.92	0.14
Back-calculated Age 1–6	173	2.90	-1.12	0.20	0.58	0.08
Females						
Observed Age 1–7	181	3.68	-2.23	0.70	0.44	0.10
Back-calculated Age 1–7	179	5.20	-1.67	0.40	0.42	0.08

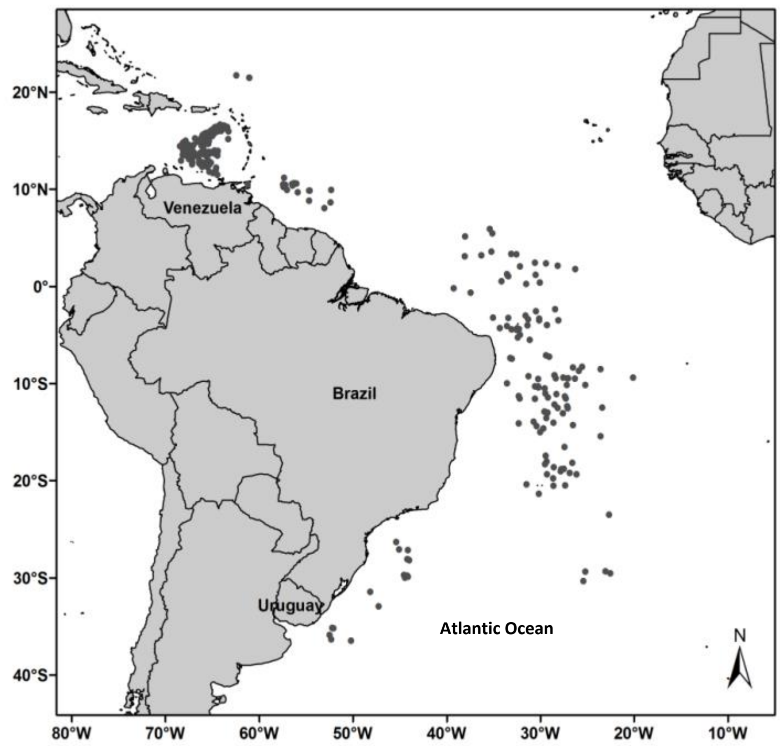

Figure 1. Study area in the Western Atlantic Ocean, indicating the locations were the longbill spearfish anal fin spines were collected (grey dots).

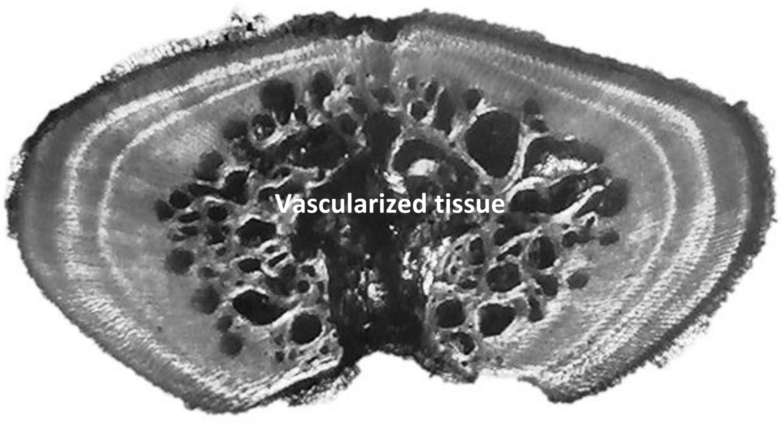

Figure 2. Anal fin spine transverse cut at a half of the maximum condyle width from a longbill spearfish.

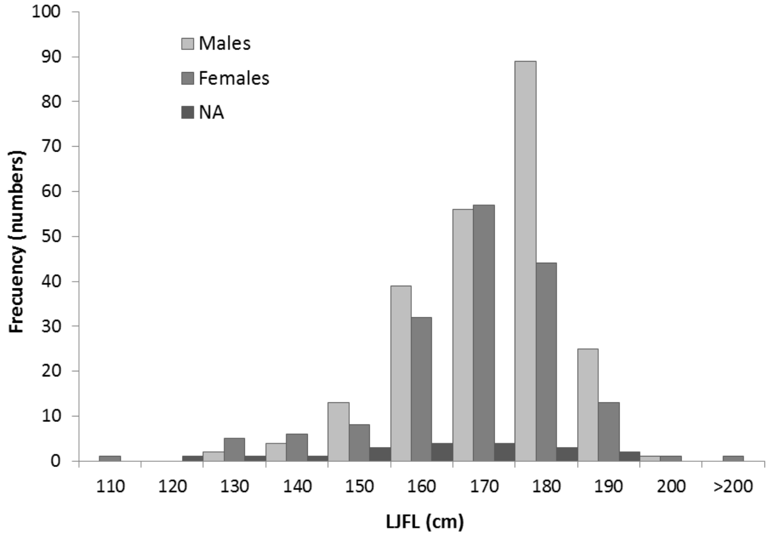

Figure 3. Length frequency distribution of longbill spearfish aged by sex. NA: Sex information is not available.

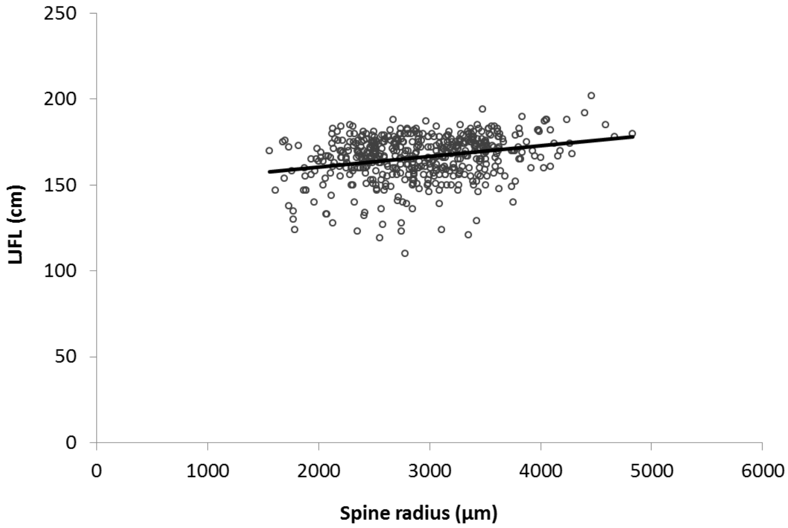

Figure 4. Relationship between spine radius (in μm) and longbill spearfish length (LJFL in cm).

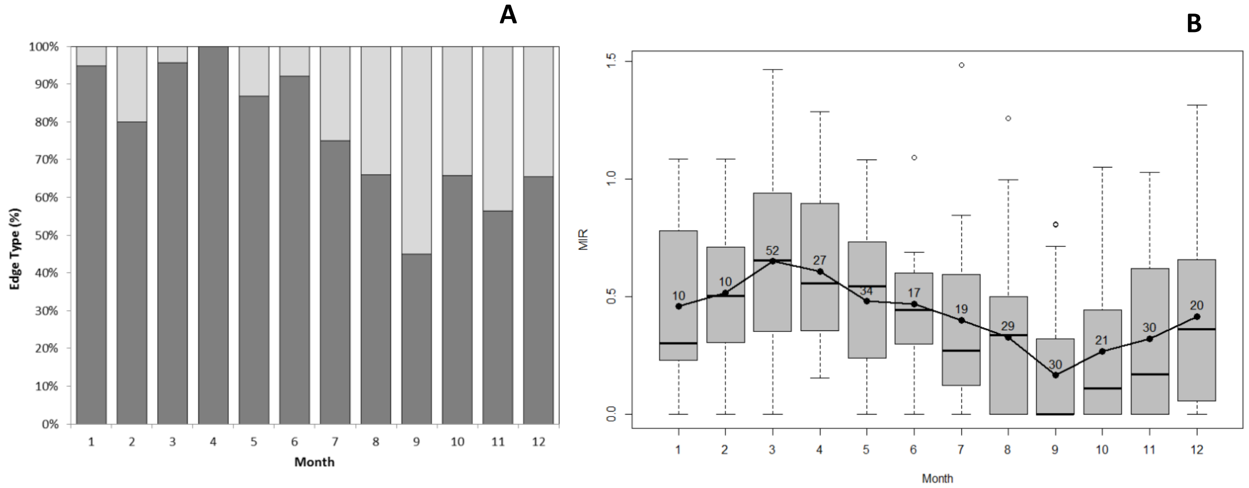

Figure 5. **A**: Percentages of edge type (dark grey: opaque; and light grey: translucent). **B**: Marginal increment ratio (MIR) by month of the longbill spearfish in the western Atlantic Ocean between 2003 and 2011. The number in each box represent the sample size per month.

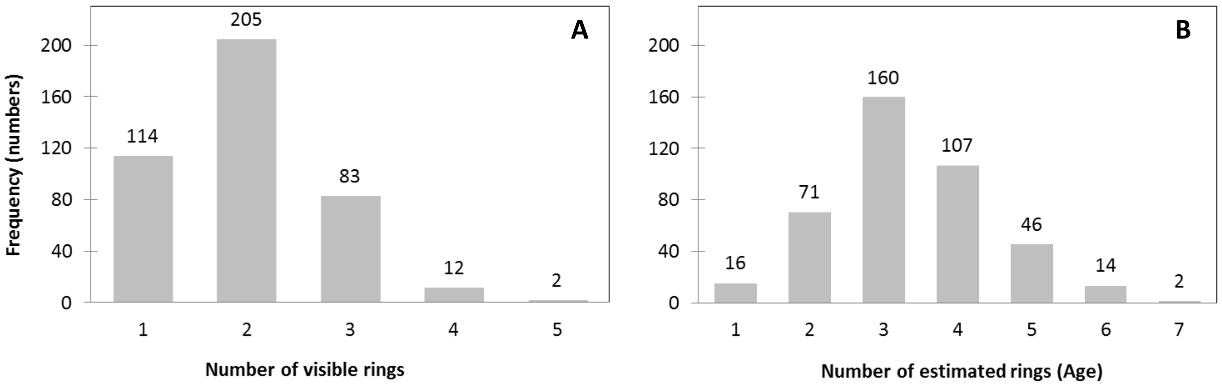

Figure 6. A: Distribution of visible ring counts; and B: assigned ages using Hill's (1989) method. The numbers above the bars correspond to the sample size by category.

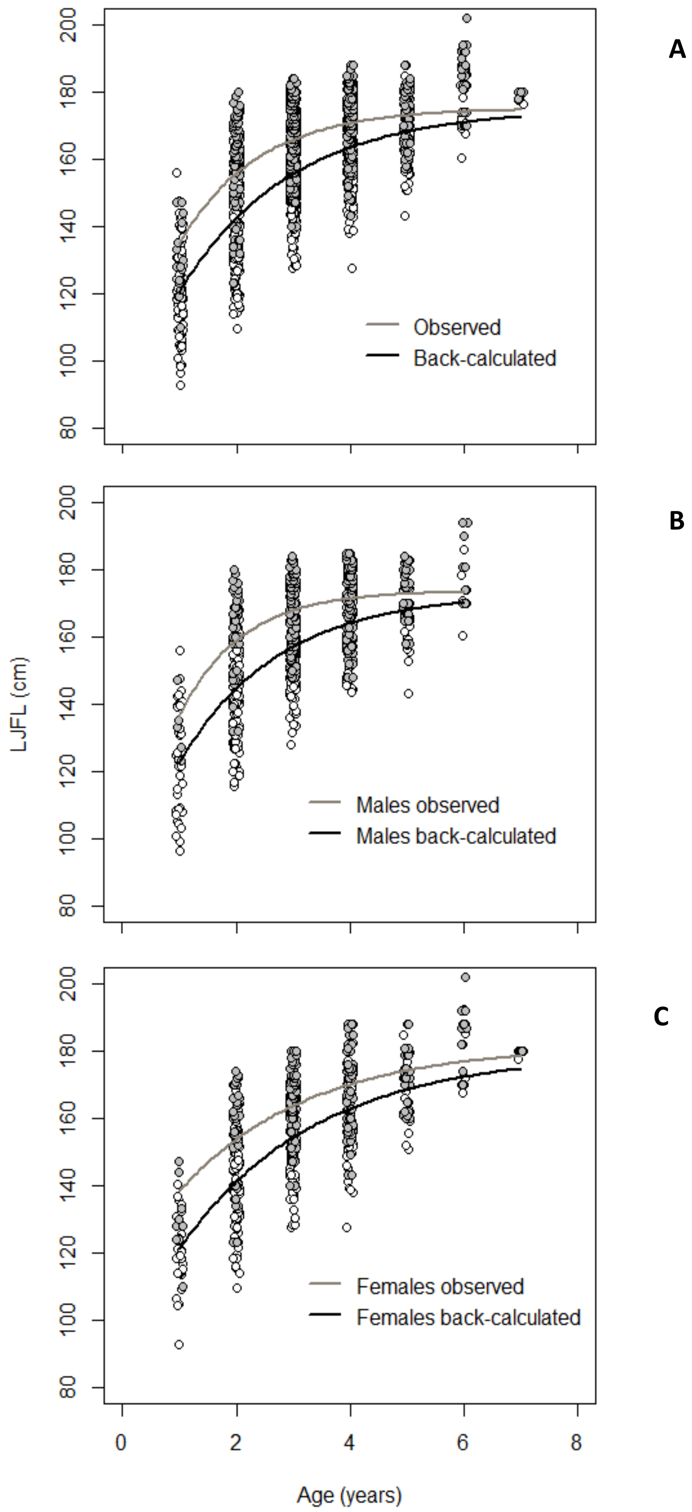

Figure 7. Length-at-age of the longbill spearfish and associated Von Bertalanffy growth model fits for **A**: the total sample (sex combined); **B**: Males; and **C**: Females. White circles, back calculated, grey circles, observed.