GROWTH AND MORTALITY RATES OF SKIPJACK TUNA KATSUWONUS PELAMIS IN THE SOUTHWEST ATLANTIC OCEAN

J. Benevenuti Soares¹, G. Marcel de Souza Corrêa¹, C. Monteiro-Neto¹, R. de Almeida Tubino^{1,2}, M. Rodrigues da Costa¹

SUMMARY

The skipjack tuna supports an important pole-and-line fishery in the Southwest Atlantic. Dorsal fin spines from 452 specimens collected between January 2014 and May 2016 (Period I) and January 2017 and August 2018 (Period II) were used for age determination. Age validation was carried out by analyzing the percentage variation of the edge type and the seasonal average of marginal increment. The formation of a translucent band occurred in late autumn and early winter for both periods. The growth parameters did not show differences between sexes in each period. Nevertheless, the mortality rates indicated differences in the exploitation rates between periods. For the Period I the exploitation rate was 0.35, while in Period II it ranged from 0.50 - 0.52. Our results show an increase in fishing effort on the species between the periods evaluated, indicating that the stock is at the 50% limit of its exploited biomass. Given the risks and uncertainties surrounding the assessment of stocks, we recommend further studies on the species and factors that may affect its production in biomass.

RÉSUMÉ

Le listao soutient une importante pêcherie de canne et moulinet dans l'Atlantique Sud-Ouest. Les épines de la nageoire dorsale de 452 spécimens collectés entre janvier 2014 et mai 2016 (période I) et entre janvier 2017 et août 2018 (période II) ont été utilisées pour déterminer l'âge. La validation de l'âge a été effectuée en analysant le pourcentage de variation du type de bord et la moyenne saisonnière de l'accroissement marginal. La formation d'un anneau translucide s'est produite à la fin de l'automne et au début de l'hiver pour les deux périodes. Les paramètres de croissance n'ont pas montré de différences entre les sexes à chaque période. Néanmoins, les taux de mortalité ont indiqué des différences dans les taux d'exploitation entre les périodes. Pour la période I, le taux d'exploitation était de 0,35, tandis que pour la période II, il était compris entre 0,50 et 0,52. Nos résultats montrent une augmentation de l'effort de pêche sur l'espèce entre les périodes évaluées, indiquant que le stock est à la limite de 50% de sa biomasse exploitée. Compte tenu des risques et des incertitudes qui entourent l'évaluation des stocks, nous recommandons de poursuivre les études sur l'espèce et les facteurs susceptibles d'affecter sa production en biomasse.

RESUMEN

El listado sostiene una importante pesquería de caña y línea en el Atlántico sudoccidental. Para la determinación de la edad se utilizaron las espinas de la aleta dorsal de 452 ejemplares recogidas entre enero de 2014 y mayo de 2016 (Periodo I) y enero de 2017 y agosto de 2018 (Periodo II). La validación de la edad se realizó analizando la variación porcentual del tipo de borde y la media estacional del incremento marginal. La formación de una banda translúcida se produjo a finales de otoño y principios de invierno para ambos períodos. Los parámetros de crecimiento no mostraron diferencias entre sexos en cada periodo. Sin embargo, las tasas de mortalidad indicaron diferencias en las tasas de explotación entre períodos. Para el periodo I la tasa de explotación fue de 0,35, mientras que en el periodo II osciló entre 0,50 y 0,52. Nuestros resultados muestran un aumento del esfuerzo pesquero sobre la especie entre los períodos evaluados, lo que indica que el stock se encuentra en el límite del 50% de su biomasa explotada. Dados los riesgos e incertidumbres que rodean la evaluación de los stocks, recomendamos que se realicen más estudios sobre la especie y los factores que pueden afectar a su producción en biomasa.

KEYWORDS

Age validation, Back-calculation, Dorsal fin spine, Fisheries management

¹ Laboratório de Biologia do Nécton e Ecologia Pesqueira, Departamento de Biologia Marinha, Universidade Federal Fluminense. Caixa Postal 100644, 24001-970, Niterói, RJ, Brazil. E-mail: marcusrc@id.uff.br; jubenevenuti@hotmail.com (Corresponding authors).

² Departamento de Biologia Animal, Universidade Federal Rural do Rio de Janeiro, Rodovia BR 465, Km 07, 23890-000, Seropédica, RJ, Brazil.

1. Introduction

Tunas are top open ocean predators of great ecological (Bornatowski *et al.* 2017), economic and social importance (FAO 2020). Due to the large catch volumes, the wide international trade, and their contribution for world's protein needs, commercial tuna fishing represents a significant part of the blue economy (Pew Charitable Trusts 2020). The combined landings of the seven species of tunas of global commercial importance (yellowfin, skipjack, bigeye, albacore, and Atlantic, Pacific, and southern bluefin tunas) reached their highest levels in 2018 at about 7.9 million tones (FAO 2020). The latest SOFIA estimated that in 2017, 33.3% of stocks were caught at biologically unsustainable levels (FAO 2020).

The skipjack tuna *Katsuwonus pelamis* is the most fished tuna in the world, ranking third among the top globally exploited species for the ninth consecutive year at 3.2 million tons (FAO, 2020). In the Southwest Atlantic Ocean, between 20°S (Rio de Janeiro, Brazil) and 34°S (border with Uruguay), the pole and line live bait fleet operates at the edge of the continental shelf, capturing mostly skipjack tuna, but also other pelagic resources (Madureira *et al.* 2017; Martins *et al.* 2020). Almost all production is destined to the canning industry supplying the Brazilian domestic market, while a small proportion is exported as frozen fish (Andrade 2006; Schmidt *et al.* 2019).

The annual production of skipjack tuna in the southwestern Atlantic has remained around 25.000 tons from 1979 until 2018 when a considerable fall in catches was observed (Cardoso *et al.* 2020). According with Madureira *et al.* (2020) these recent variations in fisheries productivity were probably associated with changing environmental and oceanographic conditions in the Southwest Atlantic. Nevertheless, fishermen and shipowners, faced with these limitations in catches, sought after alternative fishing methods including associated schools (Silva *et al.* 2019) and purse seine where the species is regarded as a secondary target for the purse seine sardine fleet (Normative Instruction n° 14/2020).

The lack of up-to-date information of the southwestern Atlantic skipjack tuna stocks has raised concerns about the introduction of additional fishing methods other than the pole and line (Cardoso *et al.* 2020). Market demand for tuna remains high, and tuna fishing fleets continue to have significant overcapacity (Pew Charitable Trusts 2020). While a recent effort was conducted to consolidate information about the sustainability of the skipjack tuna fishery in Brazil (Madureira and Monteiro-Neto 2020), it is increasingly necessary to collect scientific data to understand the status of fish stocks, especially for skipjack tuna in the southwestern Atlantic in which statistical records are limited for recent years (FAO 2020; Zamboni 2020).

Age, growth and mortality studies of fishery resources are important tools for providing life history parameters used for modeling the population dynamics of regularly exploited stocks such as the case of the skipjack tuna in the southwestern Atlantic. Nevertheless, age and growth studies for the skipjack tuna in the southwestern Atlantic are limited and distributed over a period of four decades (Vilela and Castello 1991; Andrade and Kinas 2004; Andrade *et al.* 2004; Garbin and Castello 2014; Soares *et al.* 2019; Costa *et al.* 2020).

Traditionally, aging methods are based on counting light and dark bands from otoliths (Campana and Thorrold 2001). However, otoliths from skipjack tuna, like most open ocean pelagic fishes, are very small and difficult to retrieve from their capsules. As a consequence, the use of otoliths for aging skipjack tuna limited. In fact, all of the above studies used light and dark bands marked in spines of the first dorsal fin (e.g., Garbin and Castello 2014; Soares *et al.* 2019; Costa *et al.* 2020). Nevertheless, none of these age estimates from hard part readings have been validated. The objectives of the present study were to estimate growth parameters, mortality rates in addition to providing robust evidence for validating the annual periodicity of growth ring formation in dorsal spines of *Katsuwonus pelamis* captured by the pole and line live bait fleet in the southwestern Atlantic.

2. Material and methods

2.1 Sampling

Between January 2014 and May 2016 (Period I) and January 2017 and August 2018 (Period II), samples of skipjack tuna were obtained regularly from landings of the pole-and-line live-bait commercial fleet. Landings occurred at the ports located in the municipality of Niterói, in the state of Rio de Janeiro, Brazil. This fleet operates mainly off the coast of Rio de Janeiro and neighboring states, between 20°30′0′′S and 25°30′0′′S (**Figure 1**). Juvenile Brazilian sardinella (*Sardinella brasiliensis*) is used as the predominant and preferred live bait. However, other species such as the Argentine anchovy (*Engraulis anchoita*), Atlantic anchoveta (*Cetengraulis edentulus*) and the false herring (*Harengula clupeola*) may be used at different times and locations (IBAMA 2009; Soares *et al.* 2019; Madureira *et al.* 2020).

The South Brazil Shelf Large Marine Ecosystem (SBSLME) extends roughly over the entire continental shelf off southeastern South America, including the Brazilian southwest. In this region, fishery resources are highly productive, supported by great continental freshwater inflow and the coastal upwelling resulting from the South Atlantic Central Water (SACW) and Brazil Currents along the coast (Madureira *et al.* 2020).

For each of the monitored landings, a fish sample was randomly separated for later sex identification and removal of spines. Individuals had their fork length measured (FL, cm), with the standard approximation for the lower centimeter (ICCAT 2016). Gonad macroscopic characteristics of each fish was evaluated for sex determination. For size structure analysis, the length frequencies were separated by sex and grouped in size classes of 2 cm. To verify possible differences between sexes, the Kruskal-Wallis test was applied (p < 0.05).

2.2 Relationship between fork length and spine radius

In order to determine the relationship between fish fork length and spine radius, two fits by least-squares minimization algorithm were performed for pairs of values, following two regression functions:

- Linear regression: $FL = a + bR$	(1)
- Power regression: $FL = cR^d$; $FL' = c' + dR'$	(2)

where: FL = fork length (cm); *a*, *b*, *c*, *d* = parameters of the regression functions; R = spine radius (mm); FL'= ln(FL); $c' = \ln(c)$.

2.3 Age estimation

For estimating age, the first spine of the first dorsal fin of 452 specimens was removed along with the joint condyle and stored in 70% alcohol. After 48-72 h, the spines were removed, cleaned and dried in open air. Cross-sections of dried spines were taken at 2 cm of the spine length above the condyle, and embedded in polyester resin. Further sections 0.80 mm thick were taken nearest to the condyle as possible using a low-speed IsoMET Buehler saw.

Sliced 0.8 mm sections were mounted on glass slides using the synthetic resin ENTELLANTM and viewed with transmitted light in a binocular stereoscopic microscope connected to an image capture system. Cross-sections of the spines show a central vascularized region and an alternating sequence of opaque (OP) and translucent (TR) bands. Each pair of one opaque band and one translucent band corresponds to one year of growth (annulus). Age was estimated by counting the translucent bands. The cross-sections were read blindly at different times by two independent readers and annuli were counted without knowing the length of the individuals. Using an image analysis software (ImageJ), measurements of both, the diameter of the spine (horizontal distance between the outer edges, measured on the line of the caudal concavity) (Vilela and Castello 1991), and of the annuli diameters (measured from the outer edge of each translucent band to the opposite edge of the cross-section) (Antoine *et al.* 1983) were obtained (**Figure 2**). Measurements of the spine radius and spine radius of each annulus were also taken.

2.4 Precision and validation of the ageing method

The variability between the two readings was assessed, considering the coefficient of variation (CV) (Chang 1982) and the average percentage error (APE) (Beamish and Fournier 1981):

$$CVj = 100\% \times \frac{\sqrt{\sum_{i=1}^{R} \frac{(Xij-Xj)^2}{R-1}}}{Xj}$$

where CV_j is the reading precision estimate for the *j*th fish, *Xij* is the *i*th reading of the *j*th fish, *Xj* is the mean reading estimate of the *j*th fish, and *R* is the number of readings.

$$APEj = \frac{1}{R} \sum_{i=1}^{R} \frac{|NAi - NAj|}{NAj} \times 100\%$$

where *R* is the number of readings *R*; *NAi* is the number of annuli in the *i*th reading; *NAj* is the average number of annuli.

To confirm the periodicity and the time of formation of the translucent bands, the type of edge (translucent TR or opaque OP) was identified in all cross-sections. Their respective percentages were calculated by seasons considering the entire sample set. The seasons were defined as summer (December, January, February), autumn (March, April, May), winter (June, July, August) and spring (September, October, November). For both periods, the monthly data between years were grouped to improve the consistency of the analysis. The periodicity of formation of the annulus was considered the one with the highest percentage of occurrence of translucent bands. Additionally, the marginal increment ratio (MIR) analysis was performed for all individuals, according to Skomal (1990):

$$MIR = (SD - D_n)/(D_n - D_{n-1})$$

where *SD* is the spine diameter, D_n is the diameter of the last complete TR band and D_{n-1} is the diameter of the penultimate complete TR band. The value of the marginal increment varies between zero and one and the smallest values indicate the time of formation of the annulus.

After validating the periodicity and the time of the annulus formation, the annuli were considered ages, thus allowing access to the age structure of the captured population. A fork age-length key was constructed for males and for females composed of the relative percentage of individuals at each age by fork length class. Furthermore, an age *vs.* length table was constructed to present the age distribution by fork length classes by sex and grouped data.

2.5 Back-calculated lengths

We considered both, the Fraser-Lee (Lee 1920) and the "body proportional hypotheses" (BPH or SPH) (Whitney and Carlander 1956) to back-calculate lengths:

- Fraser-Lee equation: $FL_i = a + (FL a) (R_i/R)$ (3)
- Body Proportional Hypothesis (BPH): $FL_i = FL(a + bR_i)/(a + bR)$ (4)

where FL_i = fork length when spine radius was R_i (cm); FL = fork length (cm); R_i = spine radius of the *i*th annulus of the spine (mm); R = spine radius (mm); a, b = parameters of the linear regression (1); when the power regression was used, FL', c, d and R' from (2) instead of FL, a, b and R were used in (3) and (4).

2.6 Growth and mortality rates

The data on the average length at age, obtained through the spine readings, was used to provide first estimates of growth parameters (seeds) using the Ford-Walford method (Walford 1946). These estimates were fine-tuned using the Levenberg-Marquardt algorithm (Transtrum and Sethna 2012) for the whole dataset, and finally adjusted to the logistic growth curve of von Bertalanffy (1938):

$$L_i = L_{\infty} [1 - e^{-k(t-t0)}]$$

where L_i is the average length at age, L_{∞} is the asymptotic length, k is the growth coefficient, t is the age and t_0 is the theoretical age at length zero.

New estimates of L_{∞} , k and t_0 were obtained from the structure in observed data and back calculated lengths. Thus, it was possible to describe the growth of *K. pelamis* based on the adjustment of data on observed lengths and back calculated by age for group sex, males and females. The performance growth index (ϕ) was estimated according to the Pauly and Munro (1984) equation: $\phi = \log k + 2 \log L_{\infty}$. Furthermore, we used a likelihood ratio test ($\alpha =$ 0.05) to compare growth curve parameters between separate and grouped sexes (Cerrato 1990; Aubone and Wöhler 2000). Estimates of k, L_{∞} and t_0 for grouped sexes were used to determine the catch curve, based on the conversion of length classes into age intervals by the von Bertalanffy inverse growth equation (Sparre and Venema 1992) for the estimate of total mortality (Z). The average Natural Mortality coefficient (M) was estimated from the "Natural Mortality" app via The Barefoot Ecologist's Toolbox website (http://barefootecologist.com.au) (Cope, 2020). Inputs for estimating M were: k, L_{∞} , and t_0 observing a life span of eight years. The Fishing Mortality rate (F) was estimated from the equation: F = Z-M, while the Exploitation rate (E) was estimated by the equation: E = F/Z. Stock status was evaluated by comparing estimates of the fishing mortality rate with target ($F_{opt} = 0.5$ M) and limit ($F_{limit} = 2/3$ M) biological reference points (Patterson 1992).

3. Results

3.1 Fork length distribution

Individuals collected in Period I ranged in size from 37.7 to 82.2 cm FL, and Period II from 33.5 to 83.0 cm FL. No differences in size structure were found between the sexes to both periods [KW test: H (1.225) =1.835 p = 0.1755]. Males in Period I (n = 122) ranged in size from 37.7 to 82.2 cm FL, with the mode in the 46.0 cm class. Females (n = 103) ranged in size between 40.2 to 81.9 cm FL, and modes occurring in the 48.0 and 50.0 cm FL classes. In Period II males (n = 124) ranged between 36.5 to 83.0 cm FL, with modes at 40.0, 50.0, and 58.0 cm FL classes, whereas females (n = 103) ranged 33.5 to 78.0 cm FL, and presented modes at the of 42.0, 48.0, and 52.0-54.0 cm FL classes (**Figure 3**).

3.2 Annuli counting

The annuli counting in both periods showed little variability and good consistency between readings. Readings in Period I presented an average coefficient of variation CV = 4.97% and average percent error APE = 7.02\%, and in Period 2 CV = 8.0% and APE = 6.0% (**Figure 4**).

3.3 Periodicity and time of annuli formation

Age validation performed for the most frequent ages (3 and 4) and all individuals sampled of both periods, indicated the formation of a TR band in late autumn and early winter (**Figure 5**). However, there were interannual differences in edge dominance in Period I. The dominance of translucent edges in 2014 occurred in April, whereas in 2015 and 2016, in June and May, respectively. During Period II this dominance was well marked in the winter months. The highest percentage of opaque edges occurred in the transition period from spring to summer in Period I, and summer in Period II (**Figure 5**).

3.4 Age structure

The counts of the translucent bands of the first spine of the dorsal fin provided estimated ages from 1 to 8 years in both periods. A fork age-length key, for a males and females, was constructed for periods (**supplementary material S1**). Both keys show the relative percentage of individuals at each age by fork length class (FL) per period.

3.5 Relationship between fish fork length and spine radius

The mean back-calculated length for each age was estimated using the linear function, which presented a slightly higher adjustment in relation to the power function, using Fraser-Lee and BPH back-calculation equations. The Fraser-Lee equation was chosen since it presented the smallest differences in relation to the lengths observed for males, females and grouped sexes.

The relationship between the spine radius (R) and fork length (FL) was estimated for both periods. Both regression functions were significant and showed little difference in the values of the determination coefficients (r^2). The linear function showed a better fit compared to the power function. However, the variability of the spine radius values showed the same trend in both functions, *i.e.*, it increases with fish length.

Linear regression – Period I: FL = 22.734 + (17.272R).

 $(r^2 = 0.7911, p < 0.001)$

Linear regression – Period II: FL = 15.249 + (22.63R). ($r^2 = 0.8973$, p < 0.001) Mean fork lengths-at-age and back-calculated mean overall fork lengths-at-age for *K. pelamis* were computed for males, females and overall specimens (**Table 1**). Both estimates are close mainly when the data are grouped, indicating a good consistency of the back-calculation method.

3.6 Growth and mortality rates

The estimated growth parameters considering all the curves suggest a similar type of growth increment for the skipjack tuna, with the same value of performance growth index (ϕ) (ranging between 2.9 to 3.1), and a fast early growth from the negative values of t₀ (**Table 2**). Comparisons of growth parameters between sexes and overall showed no significant differences according to the likelihood ratio test (*p*> 0.05) (**supplementary material S2**; **Figure 6**).

All mortality estimates and reference values were generated from observed and back-calculated growth parameters (**Table 3**). The calculated exploitation rate to observed and back-calculated data, that maintains the spawning stock biomass at 50% of the virgin spawning biomass was less than expected for Period I and the same as expected for Period II (E=0.50). The simulations with age-dependent M (natural mortality – Toolbox) (Cope 2020) associated with fishing mortality per age, reflect the current Z rate experienced by the stock, showing that Z obtained from the sample mean length and von Bertalanffy growth parameters is a good predictor for data-poor stocks (**Figure 7**). Subtle differences between observed and back calculated data were observed.

4. Discussion

Spines in *K. pelamis* have clear growth zones that provided reproducible counts with a level of precision comparable to other tunas. To ensure an accurate validation, the counting accuracy between readers with reasonable values of APE and CV was considered, as well as the correct classification of the edges attributed by each reader to their counts associated with the size of the edge of the translucent bands of each reading (MIR). Using the edge percentage in the 90s, Vilela and Castello (1991) found a higher incidence of TR edge between February to July and OP edge in September, December and January. Andrade *et al.* (2004) identified a trend for TR edge to be deposited between May and October, while OP edges were dominant in the summer. These observations corroborate the pattern of TR edge formation observed in the present study, reinforcing that the period of annuli formation occurs between the end of autumn (May) and the beginning of winter (June). Regardless of the fact that the methods used (MIR and percentage of the edge type) are indirect, both converged in the validation of a single annulus per year formation for the skipjack tuna in the southwestern Atlantic, off the Brazilian coast.

Increments in rigid structures, through the deposition of calcium carbonate with different opacities throughout the year, occur because of the combination of both endogenous and exogenous factors including temperature, food availability, changes in photoperiod and reproduction (Wright et al. 1991; Green et al. 2009). The pattern of annual deposition of an opaque band during the austral spring and summer found in the present study may be related with reproductive events. Soares et al. (2019) identified spawning peaks in early summer off the Brazilian coast, indicating a well-marked seasonal reproductive pattern. Grande et al. (2014) suggested that skipjack tuna reproduces more actively under conditions of higher primary productivity and large prey aggregates. During the maturation process, the recruitment of oocytes is activated through a continuous supply of energy from the liver, which acts as an energy buffer (Grande 2013). This income breeder strategy, which allows oocytes to be provisioned using the energy acquired from food, triggers variations in energy allocation between growth and reproductive phases (Druon et al. 2017). Thus, skipjack reproductive events may reflect temporal inconsistencies in the development of otoliths (Sardenne et al. 2015). In addition, it indicates that the annulus formation is governed by physiological mechanisms associated with the environmental conditions of the area occupied by the species. These same authors also observed significant variations in the formation of the first annulus and the length of the individuals (20, 36 and 45 cm FL at three, six, and nine months, respectively). This indicates that growth is very fast in the first year of life, when they also reach the size of first sexual maturation according to Soares et al. (2019) for the study area.

The minimization of the sources of errors in the determination of ages occurs by comparing the counting of the annulus (Campana 2001), regardless of the type of rigid structure, *i.e.*, otoliths, or spines. Several authors have observed that the spines of the skipjack tuna show the absence of a systematic pattern in the deposition of the bands, that is, they have identified a variety of thicknesses of the growth zones in the cross-sections (Cayré 1979;

Antoine et al. 1982; Vilela and Castello 1991). Antoine et al. (1982) interpret this variability as an opportunistic strategy associated with the growth of skipjack, just as Cayré (1981) related this discontinuity to the reproduction of the species. Our results of verification and validation of readings showed CV and APE values within the expected for two independent readings, indicating good accuracy. At the most representative/initial ages, we observed an increasing pattern of annulus thickness, different from the postulate above. This can be explained by the sampling carried out in the same school, where the growth zones can be different or equal from one fish to another, and may be an indicator of individual growth variability (Antoine et al. 1983) and/or of the same cohort. The skipjack tuna is considered the fastest growing species of all tuna (Murua et al. 2017). Regarding the studies carried out in the Eastern and Western Atlantic Ocean, the growth curves for skipjack obtained from different methodologies (length frequency analysis/modal progression, mark-recapture, analysis of rigid structures) have shown high variability (Batts 1972; Cayré 1979; Antoine et al. 1982; Cayré et al. 1986). Such inconsistency may be related to differences in the specific growth of each stock or to differences related to the methodology and/or sampling strategy of each study (Murua et al. 2017). It is observed that in general, skipjack tunas caught in the Western Atlantic Ocean reach a L_{∞} higher than those caught in the Eastern Atlantic (Vilela and Castello 1991; Matsuura and Andrade 2000). Murua et al. (2017) compiled several studies carried out in the Atlantic Ocean and observed that L_{∞} values vary between 58 and 112 cm FL and k values vary between 0.15 and 2.96 year⁻¹. Nevertheless, our results differ from other areas, probably due to the different environmental conditions in which the fish were captured, since the growth constant k is related to the metabolic rate of the fish, which varies with temperature (Sparre and Venema 1998). Another assumption is that fish with an intertropical distribution tend to grow faster and become mature earlier than fish that are distributed in subtropical zones (Froese and Binohlan 2003). Thus, the estimates raised here corroborate the ecogeographic pattern described in the literature for tuna, in which fish tend to be larger at higher latitudes (Pauly 1981).

A measure commonly used to describe and compare intraspecific and interspecific growth patterns is the use of the growth performance index (ϕ), which uses the growth parameters *k* and L_{∞} obtained from the von Bertalanffy growth function (Munro and Pauly 1983). Although skipjack has the lowest growth performance index (ϕ) among all tuna (Murua *et al.* 2017), comparisons between the values of ϕ generated in the present study with others performed in the Southwest Atlantic Ocean, which also used the first spine of the beautiful-striped dorsal fin as a research element, were similar (Vilela and Castello 1991; Andrade *et al.* 2004; Garbin and Castello 2014). Likewise, Batts (1972) recorded equivalent values for the northwestern Atlantic Ocean. Thus, despite the small differences in values of L_{∞} and *k* (methodological or not), the ϕ values maintained a proportionality, indicating a good consistency in the adjustment of parameters, as well as similar life histories.

Studies considering back-calculation are opportune when it comes to estimating growth parameters as they allow confirmation of whether or not there is a proportional relationship between the thorn radius and the length of the fish. If there is such a relationship, this function allows predicting ages according to lengths, as well as estimating ages in lengths rarely observed, regardless of the type of sampling effort (Francis 1990). This situation applies mainly to large pelagic migratory fish. Due to the selectivity of some fishing gear that is restricted to the collection of specimens within a narrow and/or wide size distribution (Landa *et al.* 2015). In the case of skipjack fishing carried out in southeastern Brazil, essentially by the pole-and-line fleet, the dependence on the availability of the bait *Sardinella brasiliensis*, gives a seasonal character due to the closure of the main bait (IBAMA 2009). In addition to the size of the bait, the size of the hooks is also important for defining the population stratum to be captured. In this case, back-calculation estimates play a relevant role for species of commercial importance whose catches occur in a range of size limited by allowable fishing equipment, reducing the effect of selectivity on the estimates of length classes not recorded during catches.

Another limiting factor for understanding the growth of tunas and the like is the vascularization of the core of the dorsal fin spines, which can lead to underestimation of ages. The first increments are the most vulnerable to this action, since they are likely to disappear as the fish increases in size and age (Kopf *et al.* 2010). Some authors claim that in some tunas the resorption of the central portion of the first spine of the dorsal begins to occur from two years of age (Compeán-Jimenez and Bard 1983; Rodríguez-Marín *et al.* 2007; Luque *et al.* 2014). Therefore, defining the measurements of the first annulus is essential to ensure that the estimated ages along the spine section are accurate. In this context, the application of the back-calculation method can provide indispensable information for a detailed and accurate age estimate, providing a continuous sequence of lengths to fit an accurate growth curve (Campana 2001; Landa *et al.* 2015), generating values of L_{∞} and *k* less biased.

The variation between the observed and mean back-calculated lengths was consistent when comparing the variability of sizes recorded within each age. The smallest difference between observed FL vs back-calculated lengths was registered at age 5 (0.29 cm) and the largest, at age 4 for males (6.87 cm). This indicates that the method is capable of generating reliable estimates, with acceptable margin of error. Our FL estimates based on the

back-calculation model were similar to those obtained by Garbin and Castello (2014). These authors evaluated changes in the structure in size and growth of skipjack tuna caught between different periods (1984-1986 and 2004-2009) off the south of Brazil, the southern limit of the species distribution. Among other similarities, we can highlight the growth parameters that presented identical performance indexes, suggesting the presence of a single stock unit for the South Atlantic. However, to confirm this hypothesis, further studies regarding the reproduction and feeding processes of this species in the study area are necessary. Since 2006, the International Commission for the Conservation of Atlantic Tunas (ICCAT) has reported the presence of a single stock of skipjack tuna for the western Atlantic Ocean for fisheries management purposes. This assumption does not disregard the different studies carried out in this region, and it is plausible that there are differences both in the structure in size and in the parameters of growth over time and space, *i.e.*, in tropical, subtropical and temperate areas of the South Atlantic. Another finding associated with the application of the back-calculation methodology for estimating the size of individuals is their degree of certainty (r^2). Thus, it is clear that this tool translates into a valuable source of information that can minimize the effect of selective sampling bias for lengths/ages little represented in the samples, reducing the uncertainties in the assessment of stocks.

The linearized catch curve based on length composition data showed a recruitment age for the fishery between 2-3 years. According to Soares *et al.* (2019) females and males mature with 43.2 and 46.2 cm TL, respectively, which corresponds to ages between 1-3 years. These mortality results are inferior to the reported values proposed by Garbin and Castello (2014) in the southwestern Atlantic for the 80s and early 2000s. The differences observed in the Z values can be explained by the fishing effort and area of operation of the fleets in the south and southeast of Brazil. The data from Garbin and Castello (2014) were obtained from the landings of the pole-and-line fleet in the south of Brazil, whose vessels are larger than those of the fleet in the southeast (Rio de Janeiro) (Martins *et al.* 2020). In addition, Coletto *et al.* (2021) observed that the species present seasonal movement patterns, which justifies changes in the structure in size of the skipjack between the south and southeast regions of Brazil.

The specified precautionary target F_{opt} and F_{limit} values, applied as biological reference points, demonstrated to be good limits for the assessment of this stock, given the current stock re-building and resource conservation management objectives. For Period I (2014-2016) the fishing mortality (F= 0.15 year⁻¹; 0.14 year⁻¹) was slightly higher than the optimum level (F_{opt} = 0.14 year⁻¹; 0.13 year⁻¹), but under the limit (F_{limit} = 0.19 year⁻¹; 0.17 year⁻¹) of the biological reference point. The results also concluded that the fishing mortality was below the limit, corroborating with the exploitation rate (E = 0.35), indicating that in Period I the exploitation rate kept the spawning stock within the acceptable 50% limit of stock biomass. On the other hand, the exploitation rate obtained for Period II, ranging between 0.50 - 0.52, points towards an increase in fishing effort on the species, placing the stock at its 50% limit of exploited biomass. Most recently, Cardoso *et al.* (2020) using the skipjack tuna length composition from two fishing seasons (2017-2018 and 2018-2019), estimated the fraction of the remaining reproductive potential to be at 47.0% of the virgin biomass. Regardless of the fact that the availability of the stock to the fishery may be highly dependent on regional oceanographic conditions, and that the year 2018 was considered "atypical" due to low availability of the skipjack tuna on fishing grounds (Martins *et al.* 2020), our results of the exploitation rate calculated from growth estimates, nearly matched those obtained by Cardoso *et al.* (2020).

It is important to note that all primary data were obtained from the fleet based in Rio de Janeiro, whose fishing area does not entirely overlap the area of the fleet in the southern region of Brazil. Using the three mortality estimates we calculated the rate of exploitation (E) for the recent dataset (2017-2018). Our result (E=0.5) considers as a limiting expectation of death by fishing in a given cohort (Pauly 1983). We also remind that, this validity as a management decision tool can be compromised by variations in recruitment and availability between the years. Thus, such an estimate should be used only as a preliminary indication of the fishery's operating status. From the results presented here, it is recommended not to stimulate the increase of the fishing effort mainly of skipjack smaller than the length of first sexual maturation defined for the Southwest Atlantic Ocean.

Few studies have been conclusive to date regarding the validation and periodicity of annulus formation for *K*. *pelamis* in southwestern Brazil. In this context, this study represents the first detailed analysis of the growth of *K*. *pelamis* carried out after a period of ten years for the Southwest Atlantic, the first focused on catches made exclusively in southeast Brazil. This work provides updated information on the validation and periodicity of annulus formation (one per year). We also emphasize that the counting of annulus in spines corresponds to a satisfactory method for assessing their age and that, when associated with the use of multiple models for estimating growth parameters, they generate robust and appropriate values to describe the growth of the species. The model derived from the back-calculation was considered a good predictor of the spine *vs* fork length/age ratio, corroborating the growth estimates of *K. pelamis*. In this sense, results generated have the potential to improve the management of this resource, as long as there is continuity of research based on monitoring programs with systematic sampling of the species and its catches in the South Atlantic.

Supplementary material

Table S1. Fork age-length key (class 2 cm) of males and females of *Katsuwonus pelamis* for both periods: Period I: 2014-2016, Period II: 2017-2018. Relative percentage (%) of individuals at each age by fork length class.

Table S2. Comparisons of the von Bertalanffy growth parameters for both periods according to the likelihood ratio test between sexes obtained by fitting growth curves.

Acknowledgements

We thank Professor Jorge P. Castello and Dr. André Martins Vaz-dos-Santos for all the dedication in passing on knowledge. All of these teachings were fundamental during this journey. We also thank the trainees and staff from ECOPESCA-UFF and FIPERJ. Research supported by FAPERJ (Grant # E-26/112.613/2012) and CNPq (Grant # 406249/2012-1), and more recently Bonito Project has supported this work. Bonito Project has resource support from the Commitment of Conduct Adjustment Agreement, signed by Chevron Brasil with the Federal Public Ministry, with implementation of the Brazilian Biodiversity Fund – Funbio. J. B. Soares holds a Master's degree scholarship from CAPES, C. Monteiro-Neto a Research Productivity Fellowship from CNPq (Grant # 305292/2016-1), and R. A. Tubino a post-doctoral fellowship PNPD-CAPES.

References

- Andrade, H.A., Kinas, P.G. 2004. Estimation of birthdates and catch-at-age using length frequency analysis (LFA) with application for skipjack tuna (*Katsuwonus pelamis*) caught in the Southwest Atlantic. ICES Journal of Marine Science, 61, 798-811. https://doi.org/10.1016/j.icesjms.2004.03.002
- Andrade, H.A. 2006. Diagnóstico do estoque e orientações para o ordenamento da pesca de Katsuwonus pelamis (Linnaeus, 1758). In Rossi-Wongtschowski C.L.D.B., Ávila-da-Silva A.O., Cergole M.C. (Eds) Análise das principais pescarias comerciais da região Sudeste-Sul do Brasil: dinâmica populacional das espécies em explotação II. Série documentos Revizee: Score Sul. São Paulo: Instituto Oceanográfico USP.
- Andrade, H.A., Abreu-Silva, J.L., Duarte-Pereira, M. 2004. Crescimento do bonito-listrado (*Katsuwonus pelamis*) e um método para a correção de vícios decorrentes da vascularização central dos espinhos das nadadeiras dorsais. Notas técnicas da FACIMAR, 8, 83-93. https://doi.org/10.14210/bjast.v8n1.p83-93
- Antoine, L., Cayré, M., Mendoza, J. 1982. Etude de la croissance du listao (*Katsuwonus pelamis*) de L'Atlantique au moyen des rayons de la nageoires dorsale. Mise au point d'une methodologie Resultats preliminaires. Collective Volumes of Scientific Papers ICCAT, 17(1), 195-208.
- Antoine, L., Mendoza, J., Cayré, M. 1983. Progress of age and growth assessment of Atlantic skipjack tuna, Euthynus pelamis, from dorsal fin spine. NOAA Technical Report, 8, 91-97.
- Aubone, A., Wöhler, O.C. 2000. Aplicación del método de máxima verosimilitud a la estimación de parámetros y comparación de curvas de crecimiento de von Bertalanffy. Mar del Plata: INIDEP Informe Técnico 37.
- Batts, B.S. 1972. Sexual maturity, fecundity and sex ratios of the skipjack tuna Katsuwonus pelamis (Linnaeus), in North Carolina waters. Transactions of the American Fisheries Society, 10, 626-637. https://doi.org/10.1577/1548-8659(1972)101<626:SMFASR>2.0.CO;2
- Bard, F.X. 1986. Croissance du listao dans l'Atlantique Est. In: Symons P.E.K., Miyake P.M., Sakagawa G.T. (eds) Proceedings of ICCAT conference on the international skipjack year program. Madrid: ICCAT.
- Beamish, R.J., Fournier, D.A. 1981. A method for comparing the precision of a set of age determinations. Canadian Journal of Fisheries and Aquatic Sciences, 38, 982-983. https://doi.org/10.1139/f81-132
- Bornatowski, H., Angelini, R., Coll, M., Barreto, R.R.P., Amorim, A.F. 2017. Ecological role and historical trends of large pelagic predators in a subtropical marine ecosystem of the South Atlantic. Reviews in Fish Biology and Fisheries, 28, 241-259. https://doi.org/10.1007/s11160-017-9492-z
- Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology, 2, 197-242. https://doi.org/10.1111/j.1095-8649.2001.tb00127.x
- Campana, S.E., Thorrold, S.R. 2001. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? Canadian Journal of Fisheries and Aquatic Sciences, 58, 30-38. https://doi.org/10.1139/f00-177
- Cardoso, L.G., Castello, J.P., Costa, M.R., Tubino, R.A., Monteiro-Neto, C., Madureira, L. 2020. Stock assessment of skipjack tuna in the Southwest Atlantic. In Madureira, L., Monteiro-Neto, C. (Orgs.) Sustainability of Skipjack Tuna Fishery in Brazil. Jundiaí SP: Paco.
- Cayré, R. 1979. Determination de d'age de listaos, *Katsuwonus pelamis* debarques a Dakar, note preliminarie. Collective Volumes of Scientific Papers ICCAT, 8(1), 196-200.
- Cayré, R. 1981. Maturite sexuelle, fecondite et sex ratio du listao (*Katsuwonus pelamis* L.) des cotes d'Afrique del L'Ouest (20°N-0°N) etudies a partir des debarquements thoniers (1977 a 1979), au port de Dakar, Senegal. Collective Volumes of Scientific Papers ICCAT, 15(1), 135-149.
- Cayre, P., Fonteneau, A., Veira, M.H.S. 1986. Analyse dês données de marquages et recaptures de listao (*Katsuwonus pelamis*) réalisés par le Sénégal et la République du Cap-Vert. In: Symons, P.E.K., Miyake, P.M., Sakagawa, G.T. (eds) Proceedings of ICCAT conference on the international skipjack year program. Madrid: ICCAT.
- Cerrato, R.M. 1990. Interpretable Statistical Tests for Growth Comparisons using Parameters in the von Bertalanffy Equation. Canadian Journal of Fisheries and Aquatic Sciences, 47(7), 1416-1426. https://doi.org/10.1139/f90-160

- Chang, W.Y.B. 1982. A statistical method for evaluating the reproducibility of age determination. Canadian Journal of Fisheries and Aquatic Sciences, 39, 1208-1210. https://doi.org/10.1139/f82-158
- Coletto, J.L., Botta, S., Fischer, L.G., Newsomee, S.D., Madureira, L.S.P. 2021. Isotope-based inferences of skipjack tuna feeding ecology and movement in the southwestern Atlantic Ocean. Marine Environmental Research, 165, p. 105246. https://doi.org/10.1016/j.marenvres.2020.105246
- Compeán-Jimenez, G., Bard, F.X. 1983. Growth increments on dorsal spines of eastern Atlantic bluefin tuna, Thunnus thynnus, and their possible relation to migration patterns. NOAA Technical Report NMFS, 8, 77-86.
- Cope, J.M. 2020. The Natural Mortality. From https://github.com/shcaba/Natural-Mortality-Tool
- Costa, M.R., Tubino, R.A., Castello, J.P., Mello, V.S., Soares, J.B., Marcel, G., Almeida, P.R.C., Coletto, J.L., Monteiro-Neto, C. 2020. Knowledge about the skipjack tuna life cycle in the Southwest Atlantic. In Madureira, L., Monteiro-Neto, C. (Orgs.) Sustainability of Skipjack Tuna Fishery in Brazil. Jundiaí SP: Paco.
- Druon, J., Chassot, E., Murua, H., Lopez, J. 2017. Skipjack Tuna availability for purse seine fisheries is driven by suitable feeding habitat dynamics in the Atlantic and Indian Oceans. Frontiers in Marine Science, 4, Article 315. https://doi.org/10.3389/fmars.2017.00315
- FAO. 2020. The State Of World Fisheries and Aquaculture 2020 Sustainability In Action. Rome: FAO. https://doi.org/10.4060/ca9229en
- Francis, R.I.C.C. 1990. Back-calculation of fish length: a critical review. Journal of Fish Biology, 36, 883-902. https://doi.org/10.1111/j.1095-8649.1990.tb05636.x
- Froese, R., Binohlan, C. 2003. Simple methods to obtain preliminary growth estimated for fish. Journal of Applied Ichthyology, 19, 376-379. https://doi.org/10.1111/j.1439-0426.2003.00490.x
- Garbin T., Castello J.P. 2014. Changes in population structure and growth of skipjack tuna, Katsuwonus pelamis during 30 years of exploitation in the southwestern Atlantic. Latin American Journal of Aquatic Research, 42(3), 534-546.
- Grande, M. 2013. The reproductive biology, condition and feeding ecology of the skipjack, Katsuwonus pelamis in: The Western Indian Ocean. Ph.D. thesis, Universidad del Pais Vascos, 260 pp.
- Grande, M., Murua, H., Zudaire, I., Goñi N., Bodin N. 2014. Reproductive timing and reproductive capacity of the skipjack tuna (Katsuwonus pelamis) in the western Indian Ocean. Fisheries Research, 156, 14-22. https://doi.org/10.1016/j.fishres.2014.04.011
- Green, B.S., Mapstone, B., Carlos, G., Begg, G.A. 2009. Tropical Fish Otoliths: Information for Assessment, Management and Ecology. New York: Springer.
- IBAMA. 2009. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. From https://www.icmbio.gov.br/cepsul/images/stories/legislacao/Instrucao_normativa/2009/in_ibama_15_2009 _refiticada_defesosardinhaverdadeira_sc_rj_rev_p_96_1997_68_2003_in_128_2006.pdf
- ICCAT. 2016. 2006-2016. ICCAT Manual. International Commission for the Conservation of Atlantic Tuna. In: ICCAT Publications on-line.
- Kopf, R.K., Drew, K., Humphreys, R.L.Jr. 2010. Age estimation of billfishes (Kajikia spp.) using fin spine crosssections: the need for an international code of practice. Aquatic Living Resources, 23, 13-23. https://doi.org/10.1051/alr/2009045
- Landa, J., Rodríguez-Marín, E., Luque, P.L., Ruiz, M., Quelle, P. 2015. Growth of bluefin tuna (Thunnus thynnus) in the North-eastern Atlantic and Mediterranean based on back-calculation of dorsal fin spine annuli. Fisheries Research, 170, 190-198. https://doi.org/10.1016/j.fishres.2015.06.002
- Lee, R.M. 1920. A review of the methods of age and growth determination by means of scales. Fisheries Investigation Lond. Ser., 2 (4), 32 (2).
- Luque, P.L., Rodríguez-Marín, E., Ruiz, M., Quelle, P., Macias, D., Urbina, J.M.O. 2014. Direct ageing of *Thunnus thynnus* from the east Atlantic and western Mediterranean using dorsal fin spines. Journal of Fish Biology, 84, 1876-1903. https://doi.org/10.1111/jfb.12406

Madureira, L., Monteiro-Neto, C. 2020. Sustainability of Skipjack Tuna Fishery in Brazil. Jundiaí SP: Paco.

- Madureira, L., Coletto, J., Pinho, M., Weigert, S.C., Varela, C.M., Campello, M.E.S., Llopart, A. 2017. Skipjack (*Katsuwonus pelamis*) fishery improvement project: From satellite and 3D oceanographic models to acoustics, towards predator-prey landscapes. RIO Acoustics 2017 IEEE/OES Acoustics in Underwater Geosciencies Symposium. 10.1109/RIOAcoustics.2017.8349755.
- Madureira, L., Azevedo, J.L., Brum, A., Coletto, J., Pinho, M., Varela, C. 2020. The oceanographic dynamics of the skipjack tuna fishing area in the Southwest Atlantic. In Madureira, L., Monteiro-Neto, C. (Orgs.) Sustainability of Skipjack Tuna Fishery in Brazil. Jundiaí SP: Paco.
- Martins, R.R.M., Silva, F.G., Soares, J.B., Monteiro-Neto, C., Costa, M.R., Tubino, R.A., Madureira, L., Castello, J.P. 2020. Pole and live bait fleet dynamics in the Southwest Atlantic. In Madureira, L., Monteiro-Neto, C. (Orgs.) Sustainability of Skipjack Tuna Fishery in Brazil. Jundiaí SP: Paco.
- Matsuura, Y., Andrade, H.A. 2000. Synopsis on biology of skipjack tuna population and related environmental conditions in Brazilian waters. Collective Volumes of Scientific Papers ICCAT, 51(1), 395-400.
- Munro, J.L., Pauly, D. 1983. A Simple Method for Comparing Growth of Fishes and Invertebrates. ICLARM Fishbyte, 1, 5-6.
- Murua, H., Rodríguez-Marín, E., Neilson, J.D., Farley, J.H., Juan-Jordá, M.J. 2017. Fast versus slow growing tuna species: age, growth, and implications for population dynamics and fisheries management. Reviews in Fish Biology and Fisheries, 27, 733-773.
- Patterson, K. 1992. Fisheries for small pelagic species: an empirical approach to management targets. Reviews in Fish Biology and Fisheries, 2, 321±338.
- Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Berichte der Deutschen Wissenschaftlichen Kommission fur Meeresforschung, 28, 251-282.
- Pauly, D. 1983. Some simple methods for the assessment of tropical fish stocks. FAO Fisheries Technical Paper, 234, 52p.
- Pauly, D., Munro, J.L. 1984. Once more on the comparison of growth in fishes and Invertebrates. ICLARM Fishbyte, 2(1), 1-21.
- PEW CHARITABLE TRUSTS. 2020. Netting Billions 2020: A Global Tuna Valuation. From: https://www.pewtrusts.org/en/research-and-analysis/reports/2020/10/netting-billions-2020-a-global-tuna-valuation?utm_campaign=conservation_intf_oceans_tuna_nttbll20____&utm_source=facebook_environ ment&utm_medium=social&utm_content=report_sciencebased____linkcard_&utm_term=___solution
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada, Number 191.
- Rodríguez-Marín E., Clear N., Cort J.L., Megalofonou, P., Neilson, J.D., Neves dos Santos, M., Olafsdottir, D., Rodriguez-Cabello, C., Ruiz, M., Valeiras, J. 2007. Report of the 2006 ICCAT Workshop for bluefin tuna direct ageing. Collective Volumes of Scientific Papers ICCAT, 60(4), 1349-1392.
- Sardenne, F., Dortel, E., Croizier, G.L., Million, J., Labonne, M., Leroy, B., Bodin, N., Chassot, E. 2015. Determining the age of tropical tunas in the Indian Ocean from otolith microstructures. Fisheries Research, 163, 44-57. https://doi.org/10.1016/j.fishres.2014.03.008
- Schmidt, J.O., Bograd, S.J., Arrizabalaga, H., Azevedo, J.L., Barbeaux, S.J., Barth, J.A., Boyer, T., Brodie, S., Cárdenas, J.J., Cross, S., Druon, J., Fransson, A., Hartog, J., Hazen, E.L., Hobday, A., Jacox, M., Karstensen, J., Kupschus, S., Lopez, J., Madureira, L., Martinelli, F.J.E., Miloslavich, P., Santos, C.P., Scales, K., Speich, S., Sullivan, M.B., Szoboszlai, A., Tommasi, D., Wallace, D., Zador, S., Zawislak, P.A. 2019. Future ocean observations to connect climate, fisheries and marine ecosystems. Frontiers in Marine Science, 6, 550. https://doi.org/10.3389/fmars.2019.00550
- Silva, G.B., Hazin, H.G., Hazin, F.H.V., Travassos, P. 2019. The tuna fisheries on 'associated school' in Brazil: description and trends. Collective Volumes of Scientific Papers ICCAT, 75, 1924-1934.
- Skomal, G.B. 1990. Age and growth of the blue shark, Prionace glauca, in the North Atlantic. M.S. thesis, Univ. Rhode Island, pp. 1-82.

- Soares, J.B., Monteiro-Neto, C., Costa, M.R., Martins, R.R.M., Vieira, F.C.S., Andrade-Tubino, M.F., Bastos, A.L., Tubino, R.A. 2019. Size structure, reproduction, and growth of skipjack tuna (Katsuwonus pelamis) caught by the pole-and-line fleet in the southwest Atlantic. Fisheries Research, 212, 136-145. https://doi.org/10.1016/j.fishres.2018.12.011
- Sparre, P., Venema, S.C. 1992. Introduction to Tropical Fish Stock Assessment. Part 1. Manual, FAO Fisheries Technical Paper 306. No. 1. Rome: FAO.
- Sparre, P., Venema, S.C. 1998. Introduction to tropical fish stock assessment, Part I: Manual. Rome: FAO.
- Transtrum, M.K., Sethna, J.P. 2012. Improvements to the Levenberg–Marquardt algorithm for nonlinear least-squares minimization. arXiv e-prints. From: https://arxiv.org/pdf/1201.5885.pdf
- Vilela, M.J.A., Castello, J.P. 1991. Estudio de la edad y del crescimiento del barrilete (*Katsuwonus pelamis*) en la region Sur y Sudeste de Brasil. Frente Maritimo, 9, 29-35.
- Von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquires on growth laws II). Human Biology 10, Wayne State University Press, pp 181–213.
- Walford, L.A. 1946. A new graphic method of describing the growth of animals. The Biological bulletin by Marine Biological Laboratory, 90, 141-147.
- Whitney, R.R., Carlander, K.D. 1956. Interpretation of body-scale regression for computing body length of fish. Journal of Wildlife Management, 2, 1-27. https://doi.org/10.2307/3797243
- Wright, P.J., Rowe, D., Thorpe, J.E. 1991. Daily growth increments in the otoliths of Atlantic salmon parr, Salmo salar L., and the influence of environmental factors on their periodicity. Journal of Fish Biology, 39, 103-113. https://doi.org/10.1111/j.1095-8649.1991.tb04345.x
- Zamboni, A. 2020. Auditoria da pesca Brasil 2020: uma avaliação integrada da governança, da situação dos estoques e das pescarias. Brasília: Oceana Brasil, pp. 1-62. https://brasil.oceana.org/pt-br/relatorios/auditoria-da-pesca-brasil-2020

Period I									
Estimated	Mea	n observed FL	. (cm)	Back-	Back-calculated mean FL (cm)				
age group	Males	Females	Overall	Males	Females	Overall	n		
1	43.14	42.75	42.76	38.27	40.26	39.18	9		
2	47.35	47.14	47.14	43.50	41.87	42.95	28		
3	51.00	49.53	49.46	46.23	45.07	45.80	61		
4	53.95	52.01	51.61	47.08	49.73	48.29	59		
5	55.54	54.39	53.50	53.32	53.15	53.21	39		
6	56.23	55.25	54.45	56.70	58.50	57.55	21		
7	60.64	71.37	64.28	60.29	68.81	65.41	5		
8	67.31	60.91	65.71	65.82	59.69	63.78	3		
			Period II						
Estimated	Mea	n observed FL	. (cm)	Back-					
age group	Males	Females	Overall	Males	Females	Overall	n		
1	41.25	44.67	43.30	36.94	40.28	38.90	5		
2	45.65	46.91	46.25	42.58	43.93	43.21	48		
3	48.76	48.46	48.62	46.98	46.54	46.77	71		
4	54.87	53.31	54.06	52.28	51.92	52.09	56		
5	59.87	56.42	58.88	57.57	55.70	57.04	21		
6	68.70	70.14	69.33	66.00	67.99	66.87	16		
7	75.70	71.00	75.11	72.94	69.00	72.12	8		
8	79.00	78.00	78.50	78.38	72.60	75.47	2		

Table 1. Mean observed fork lengths-at-age, FL (cm), and back-calculated mean overall fork lengths-at-age for *K. pelamis* sampled in the Southwest Atlantic.

Table 2. Growth parameters and performance index estimated for *K. pelamis* in the Southwest Atlantic Ocean.

		Observed		Back-calculated				
Period I	Females	Males	Grouped	Females	Males	Grouped		
L_{∞} (cm)	82.23	64.67	72.83	87.34	66.37	76.67		
k (year ⁻¹)	0.13	0.25	0.17	0.11	0.21	0.14		
t_0	-3.72	-2.65	-3.07	-3.17	-2.51	-3.00		
φ	2.94	3.02	2.96	2.92	2.97	2.92		
Period II								
L_{∞} (cm)	97.00	90.80	94.80	98.08	92.60	94.30		
k (year ⁻¹)	0.12	0.17	0.15	0.13	0.16	0.14		
t_0	-2.88	-1.52	-2.10	-2.18	-1.49	-1.95		
φ	3.05	3.15	3.13	3.10	3.14	3.10		

Table 3. Values of natural mortality rates (M), fishing mortality (F) total mortality (Z), stock exploitation status (E) and reference points for *K. pelamis* captured by the tuna fleet in the Southeast region of Brazil.

		Period I	Period II			
Estimates	Observed	Back-calculated	Observed	Back-calculated		
Ζ	0.43	0.40	0.50	0.48		
М	0.28	0.26	0.25	0.23		
F	0.15	0.14	0.25	0.25		
E	0.35	0.35	0.50	0.52		
F_{opt}	0.14	0.13	0.13	0.12		
$\mathbf{F}_{\text{limit}}$	0.19	0.17	0.17	0.15		



Figure 1. Area of operation of the pole-and-line fleet in southeastern Brazil (highlighted) during the study periods (Period I: 2014-2016, Period II: 2017-2018).



Figure 2. Cross-section of first dorsal spine of *Katsuwonus pelamis* (53.5 cm FL) showing the spine diameter and spine radius. D1 and R1 represent the measurement of the diameter and radius of the first annulus, consecutively.



Figure 3. Fork length (classes of 2 cm) distributions of *K. pelamis* caught in the Southwest Atlantic during the sampling periods: (a) Period I: 2014-2016, (b) Period II: 2017-2018.



Figure 4. Age-bias graph for the pairwise age comparison of *K. pelamis* spines from counts by the first and second reader. Each error bar represents the 95% confidence interval over the mean age assigned. 1:1 equivalence (dotted line) is also indicated. Numbers represent the quantity of spines read by age for both periods: (a) Period I: 2014-2016, (b) Period II: 2017-2018.



Figure 5. Seasonal variation of the frequencies of opaque (OP) and translucent (TR) edges for all age groups of *K. pelamis* in the Southwest Atlantic. Seasonal variation of mean marginal increment (MIR, mm), with number of individuals sampled in each period: (a) Period I: 2014-2016, (b) Period II: 2017-2018.



Figure 6. Growth curves to *K. pelamis* caught in the Southwest Atlantic. Observed (A, C) and back-calculated (B, D) lengths data for the grouped sexes for both periods: Period I: 2014-2016, Period II: 2017-2018. Red trend lines represent the parameters for grouped sexes, black dotted line prediction interval, and green dotted line confidence interval.



Figure 7. Relationship between natural (M) and fishing mortality (F) rates by age, based on Z estimated from the linearized catch curve for both periods. Solid line observed data and dotted line back calculate data.

Supplementary Material

			PERI		MALES				
FL Classes	1	2	3	Age (y	ears) 5	6	7	8	Tota
36	100.0	4	5		3	U	/	0	1
38	50.0	50.0							2
30 70	50.0	50.0	25.0	25					1
40	71	21.4	23.0 57.1	14.3					-
42	167	21. 4 /1.7	25.0	14.3					12
46	10.7	41.7	23.0 47.8	39.1	87	43			23
40		77	30.8	53.8	0.7 7 7	ч.5			13
50		83	41 7	25.0	167			83	12
52		27.3	18.2	18.2	9.1	273		0.5	11
54		1/1.3	14.3	28.6	12.0	27.5			7
56		14.5	14.5	20.0 50.0	$\frac{12.9}{25.0}$	25.0			4
58				50.0	25.0	20.0 50.0			2
60			50.0	50.0		50.0	50.0		$\frac{1}{2}$
62			14.3		12.9	12 9	50.0		7
6 <u>4</u>		50.0	14.5	50.0	72.7	72.7			2
66		50.0		50.0		100.0			1
68						50.0	50.0		2
70			100.0			50.0	50.0		1
72			100.0		100.0				1
82					100.0			100.0	1
Total	5	18	38	32	14	11	2	2	122
			PERIO	DI-FI	EMALES	S			
FL Classes				Age (y	ears)				Tota
(cm)	1	2	3	4	5	6	7	8	1012
40		16.7	50.0	33.3					6
42	36.4	27.3	27.3		9.1				11
44		33.3	44.4	11.1	11.1				9
46		11.1	55.6	22.2	11.1				9
48		9.1	18.2	45.5	27.3				11
50		9.1	36.4	27.3	18.2	9.1			11
50					10.2				
52			11.1	22.2	55.6	11.1			9
52 54			11.1 14.3	22.2 57.1	55.6 14.3	11.1 14.3			9 7
52 54 56			11.1 14.3	22.2 57.1 60.0	55.6 14.3 30.0	11.1 14.3 10.0			9 7 10
52 54 56 58			11.1 14.3	22.2 57.1 60.0	55.6 14.3 30.0 60.0	11.1 14.3 10.0 40.0			9 7 10 5
52 54 56 58 60			11.1 14.3	22.2 57.1 60.0 40.0	55.6 14.3 30.0 60.0 40.0	11.1 14.3 10.0 40.0		20.0	9 7 10 5 5
52 54 56 58 60 62			11.1 14.3	22.2 57.1 60.0 40.0	55.6 14.3 30.0 60.0 40.0 100.0	11.1 14.3 10.0 40.0		20.0	9 7 10 5 5 2
52 54 56 58 60 62 64			11.1 14.3	22.2 57.1 60.0 40.0	55.6 14.3 30.0 60.0 40.0 100.0 33.3	11.1 14.3 10.0 40.0 33.3	33.3	20.0	9 7 10 5 5 2 3
52 54 56 58 60 62 64 66			11.1 14.3	22.2 57.1 60.0 40.0	55.6 14.3 30.0 60.0 40.0 100.0 33.3	11.1 14.3 10.0 40.0 33.3 50.0	33.3 50.0	20.0	9 7 10 5 5 2 3 2
52 54 56 58 60 62 64 66 68			11.1 14.3	22.2 57.1 60.0 40.0	55.6 14.3 30.0 60.0 40.0 100.0 33.3	11.1 14.3 10.0 40.0 33.3 50.0 100.0	33.3 50.0	20.0	9 7 10 5 5 2 3 2 1
52 54 56 58 60 62 64 66 68 70			11.1 14.3	22.2 57.1 60.0 40.0	55.6 14.3 30.0 60.0 40.0 100.0 33.3	11.1 14.3 10.0 40.0 33.3 50.0 100.0 100.0	33.3 50.0	20.0	9 7 10 5 5 2 3 2 1 1
52 54 56 58 60 62 64 66 68 70 80			11.1 14.3	22.2 57.1 60.0 40.0	55.6 14.3 30.0 60.0 40.0 100.0 33.3	11.1 14.3 10.0 40.0 33.3 50.0 100.0 100.0	33.3 50.0 100.0	20.0	9 7 10 5 5 2 3 2 1 1 1

Table S1. Fork age-length key (class 2 cm) of males and females of *Katsuwonus pelamis* for both periods: Period I: 2014-2016, Period II: 2017-2018. Relative percentage (%) of individuals at each age by fork length class.

PERIOD II - MALES									
FL Classes				Age (ye	ears)				Total
(cm)	1	2	3	4	5	6	7	8	Total
36			100.0						1
38		33.3		33.3	33.3				3
40	7.1	42.9	35.7	14.3					14
42	9.1	54.5	36.4						11
44		60.0		40.0					5
46		12.5	62.5	12.5	12.5				8
48		11.1	55.6	33.3					9
50		20.0	46.7	20.0	13.3				15
52		14.3	71.4	14.3					7
54		16.7	33.3	16.7	33.3				6
56		25.0	25.0	50.0					4
58		14.3	14.3	42.9	28.6				7
60		11.5	33.3	33.3	33.3				3
62			20.0	20.0	20.0	40.0			5
64			20.0	40.0	20.0 40.0	20.0			5
66				75.0	25.0	20.0			3 4
68				75.0	25.0	100.0			2
70					33.3	33.3	33 3		23
70				167	167	167	50.0		5
74				10.7	10.7	10.7	50.0		0
74						50.0	50.0		1
70						50.0	50.0	50.0	2
/0							100.0	30.0	2 1
04 Total	2	25	20	27	15	0	7	1	124
10181	4	25	JO	<u> </u>	15 7 M A I E	9	/	1	124
EL Classes			ILKIU		ore)	0			
rL Classes	1	2	2	Age (ye	5 5	6	7	0	Total
<u>((iii)</u> 32	1	4	100.0	4	3	U	/	0	1
32		22.2	22.2	22.2					1
38 40		33.3	33.3 71.4	33.3 29.6					07
40	22.2	22.2	/1.4	28.6					/
42	22.2	33.3	11.1	33.3					9
44		50.0	50.0	00.1					4
46		38.5	30.8	23.1	7.7				13
48	6.3	43.8	37.5	6.3	6.3				16
50		25.0		75.0					4
52		25.0	25.0	37.5		12.5			8
54		12.5	75.0		12.5				8
56			33.3	33.3	33.3				3
58			50.0	50.0					4
60				100.0					3
62					100.0				1
64			33.3	66.7					3
66					100.0				1
					100.0				
68				100.0	10010				2
68 70				100.0 33.3	10010	50.0	16.7		2 6
68 70 72				100.0 33.3	10010	50.0 100.0	16.7		2 6 1
68 70 72 74				100.0 33.3	10010	50.0 100.0 100.0	16.7		2 6 1 1
68 70 72 74 78				100.0 33.3	10010	50.0 100.0 100.0 50.0	16.7	50.0	2 6 1 1 2

Period I									
Observed lengths Back-calculation									
Comparison	X^2	Р	X2	р	H0				
Female vs. Male									
	L_{∞}	13.798	0.00	105.02	0.00	Reject*			
	Κ	272.29	0.00	284.00	0.00	Reject*			
	t_0	57.43	0.00	89.59	0.00	Reject*			
Period II									
		Observed 1	lengths	Back-calculation					
Comparison		X^2	р	X2	р	H0			
Female vs. Male									
	L_{∞}	37.30	0.00	3.44	0.00	Reject*			
	k	148.99	0.00	69.63	0.00	Reject*			
	t_0	122.42	0.00	13.59	0.00	Reject*			

Table S2. Comparisons of the von Bertalanffy growth parameters for both periods (Period I: 2014-2016, Period II: 2017-2018) according to the likelihood ratio test between sexes obtained by fitting growth curves.

* Test result was the same for both.