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Size structure, reproduction, and growth of skipjack tuna (*Katsuwonus pelamis*) caught by the pole-and-line fleet in the southwest Atlantic

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ABSTRACT

Skipjack tuna (*Katsuwonus pelamis*) is one of the world's main fisheries resources. In Brazil, it is the most abundant tuna and sustains an important pole-and-line fishery in the southwest Atlantic. We systematically monitored landings of the pole-and-line fleet from January 2014 to May 2016 on fishing ports in Niterói (RJ) to evaluate the size structure of the catches, identify species reproductive patterns and to estimate growth, recruitment and mortality parameters on the southeastern Brazilian coast. Captured specimens of *K. pelamis* (n = 5650) ranged from 36.5 to 84.7 cm (fork length-FL, mean = 52.0 cm ± 7.0) and from 0.9 to 15.3 kg (total weight-TW, mean = 3.1 kg ± 1.6). There was a modal progression of sizes throughout the austral seasons, with smallest individuals entering in the spring, and larger individuals in the fall. The sex ratio was 1:1 (M:F), and reproductive indices indicated a period of greater reproductive activity between the spring and early summer, with spawning peaks in January. The length at maturity was estimated at 45.6 cm FL. The estimated von Bertalanffy growth parameters were $L_\infty = 90.1$ cm; $k = 0.24$ year^{-1}; $t_0 = -0.54$. Recruitment into the fishery occurs between 2 and 3 years of age. The total mortality, fishing mortality, natural mortality and exploitation rate were estimated at 1.42 year^{-1}, 0.95 year^{-1}, 0.47 year-1 and 0.67, respectively. Our results demonstrate changes in population parameters of skipjack tuna captured in southeastern Brazil. The reduction in the size structure of the fisheries, anticipation of length of first sexual maturation, small increase in the growth rate and the 30% increase in the exploitation rate indicate that, after 30 years of intense fishing activity, the Western Atlantic stock is under a high fishing pressure and must be monitored closely.

1. Introduction

Skipjack tuna (SKJ, *Katsuwonus pelamis*) is an economically valuable species worldwide subjected to intensive international trade for canning (Miyake et al., 2010; Grande et al., 2014). It is the most important species among tunas and tuna-like species, comprising 58.1% of the world's total volume landed in 2010 (FAO, 2018), supporting a growing global production in the last decades of above 3 million t/year (FAO, 2016). It is a cosmopolitan and migratory species, widely distributed throughout the world's tropical and subtropical oceans between 55°–60 °N and 45°–50 °S, but is mostly abundant in the equatorial region throughout the year (Matsumoto et al., 1984). Industrial fleets from different countries around the world exploit this fishery resource (Arrizabalaga et al., 2012; Grande et al., 2014).

In the southwest Atlantic, SKJ catches represent between 10 and 17.0% of global production (ICCAT, 2000). Despite SKJ being considered a resilient species (ICCAT, 2006) due to the high productivity and life history parameters (e.g., rapid growth and fecundity), it is

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classified as moderately vulnerable (Cheung et al., 2005, 2009). Recent assessments indicate that the southwestern Atlantic stock is close to reaching full exploitation status, with a maximum yield of about 30,000 t/year (ICCAT, 2011a).

In Brazil, the SKJ fishery production reached 18,000 t/year in the last decade (FAO, 2014). The pole-and-line fleet has been operating regularly on the resource since the 1980s in the south-southwestern Brazilian coast (23 °S - 34 °S) supplying the tuna canning industry (Almeida and Andrade, 2002; Andrade, 2006). However, since the mid-1990s, their catches have declined to below 15,000 t/year (ICCAT, 2017).

Reproduction, growth and mortality are life-history attributes that determine the dynamics and resilience of populations under fishing pressure. Population productivity is pivotal in sustainable fisheries management (Morgan et al., 2009), indicating the sustainable level of fishing mortality that can be exerted and the population's ability to recover from a state of overfishing. We investigated SKJ population parameters in the southeastern Brazilian coast, evaluating the size-structure of the catches, patterns of reproductive dynamics and mortality parameters for the species. Our results provide updated information on the SKJ population attributes in the southwestern Atlantic that may be used for productivity assessments and management of the stock.

2. Materials and methods

2.1. Sampling data and measurements

Between January 2014 and May 2016, 57 landings of the pole-and-line fleet were sampled at the main port used by the fleet in the State of Rio de Janeiro, Niterói. The fishing area for SKJ is located in the southeastern Brazilian coast, between 20°30'0" S and 25°30'0" S, and the isobaths of 50 and 3000 m deep (Fig. 1). The date-of-catch at the fishing grounds were obtained through interviews with skippers or consultations of the on-board maps. At each monitored landing, individuals randomly sampled during discharges were measured and weighted. Sample size varied between landings aiming to measure as many individuals as possible. Individuals had their fork length measured (FL, cm, from the tip of the upper jaw to the caudal fin fork), with the standard approximation for the lower centimeter, and weighted (W, g). A sub-sample of 15 to 30 individuals were randomly sampled for laboratory processing, except in October 2015 because vessel production had already been sold.

The FL values were distributed in size classes of 5 cm and grouped by austral seasons: summer (January, February, March), fall (April, May, June), winter (July, August, September) and spring (October, November, December). The Kruskal-Wallis test was used to determine statistical differences in length frequency distributions between seasons. In addition, a modal progression analysis of the population structure of SKJ was performed using the Battacharya method, within the FiSAT II package (Gayanilo and Pauly, 1997). The analysis aims to identify and separate fish cohorts from the global length frequency distribution (Gayanilo et al., 1997).

2.2. Sex ratio, maturity and histological treatment

Sub-samples were transported to the laboratory. All gonads were weighed to the nearest 0.1 g. The gonads of each fish were evaluated for sex and maturity stage based on the macroscopic characteristics described by Brown-Peterson et al. (2011) and Grande et al. (2012). In each season, ovaries at different stages of maturation were selected to assess their microscopic anatomy and to validate the previous macroscopic classification. A portion of the collected ovaries was preserved in 10% formalin and later dehydrated, embedded in paraffin, sectioned to 5 μm thickness and stained with hematoxylin-eosin (Suvarna et al., 2012) for histological examination. Ovaries were then classified microscopically in different reproductive phases (Brown-Peterson et al., 2011) based on observations of the most advanced oocyte stage present in the gonad (West, 1990) and the presence of post ovulatory follicles (POF).

The sex ratios were verified between the different length classes and seasons of the year. Chi-square test (X^2) was used to evaluate the significant deviation from the expected 1:1 sex ratio.

2.3. Length-weight relationship

The length-weight relationship was estimated for males and females, expressed as $W = a.FL^b$, where: W is the weight, FL is the fork length, *a* and *b* correspond to parameters related to the type of fish growth. For each *b*, the Student's *t*-test was applied to test the hypothesis that the calculated value was equal to 3.0 (Zar, 1984). In addition, ANCOVA was used to detect any differences in the parameters of the length-weight relationship between males and females.

2.4. Spawning patterns

Three condition indices were estimated for females and males to identify spawning patterns: the gonadosomatic index (I_G), the hepatosomatic index (I_H) and the Allometric condition factor *K* (LeCren, 1951). I_G and I_H were calculated as the gonad or livermass, M_G and M_L respectively, divided by the eviscerated weight (M_E). *K'* was estimated as the M_E divided by FL raised to the third power. The *Delta K* (ΔK) was estimated as *K-K'*.

$$I_G = (M_G/M_E)*100$$

$$_{IH} = (M_L/M_E)*100$$

$$K = W/FL^b;\ K' = M_E/FL^b$$

Where W = weight; FL = fork length; *b* = allometric coefficient obtained from the length-weight relationship. The Kruskal-Wallis test was used to determine statistical differences in I_G, ΔK e I_H between months.

2.5. Length at maturity (L_{50})

The length at maturity (L_{50}) was estimated for males and females separately and also to grouped sexes through the curve relating the relative frequency of adults to the midpoint of the length classes, adjusted by equation: $Fr = 1\text{-}(e^{-aFLb})$, where (Fr) is the relative frequency of adult individuals, (e) is the base of the neperian logarithm, (*a* and *b*) coefficients estimated by the least squares method applied in the linear relationship obtained by the transformation of the variables involved and (FL) mean point of the fork length classes (Moresco and Bemvenuti, 2006).

2.6. Growth, recruitment and mortality

The growth parameters were estimated based on the fish size data obtained in the landings sampling, considering a single theoretical year. The ELEFAN I routine of the FiSAT II package (Gayanilo and Pauly, 1997) was applied according with the von Bertalanffy equation (1938): $L = L_\infty(1\text{-}e^{-k(t-t0)})$, where L_∞ = asymptotic length (cm), k = growth coefficient (year^{-1}), t = age of the individual, and t_0 = age of fish at zero length. This last parameter was calculated using Pauly's empirical formula (Pauly, 1980): $\log(-t_0) = -0.3922 - 0.2752 \log L_\infty - 1.038 \log k$. The growth parameters (L_∞ and k) were used to determine the length converted catch curve, with the conversion of length classes into age intervals by the inverse growth equation of von Bertalanffy - VBGF (Sparre and Venema, 1992) to estimate total mortality (Z). The natural mortality coefficient (M) was obtained using the empirical formula proposed by Pauly (1980), which requires the growth parameters and the mean ambient temperature (T = 23.3 °C) in which the species is

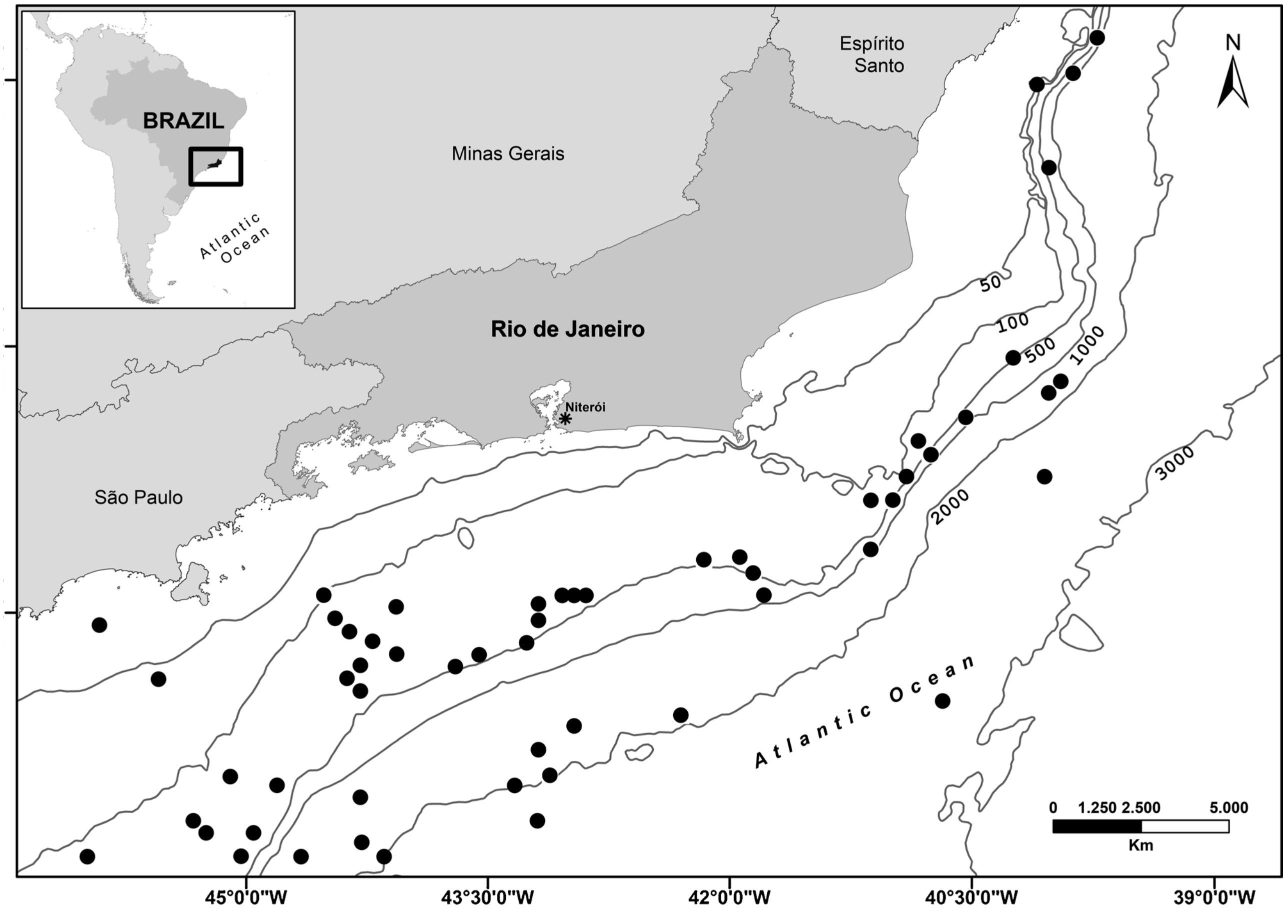

Fig. 1. Area with the main catch points of skipjack tuna caught by the pole-and-line fleet of southeastern Brazil during the sampling period between January 2014 and May 2016.

inserted: $\log(M) = -0.0066 - 0.279\log(L_\infty) + 0.6543\log(k) + 0.4634\log(T)$. The fishing mortality rate (F) was estimated from the equation: $F = Z - M$, whereas the Exploitation rate (E) was estimated by the equation: $E = F/Z$.

The recruitment pattern was also determined from the subroutine of the FISAT II package that reconstructs the recruitment pulses from a time series of length-frequency data, determining the number of pulses per year and the relative strength of each pulse. Growth parameters L_∞, k and t_0 were used as input data. By backward projection, along a trajectory defined by the VBGF of the frequencies onto the time axis of a time-series of samples, plots showing the seasonal patterns of recruitment into the fishery were obtained. Monthly length–frequency data of SKJ samples collected were pooled by months to create one theoretical year.

3. Results

3.1. Sample size and FL frequency

A total of 5650 individuals, ranging from 36.6 to 84.7 cm ($\bar{x} = 52.0 \pm 7.0$; median = 50.8), were sampled in 57 landings (Table 1). Size distribution presented a unimodal pattern centered in the 50.0 cm FL class (Fig. 2). Four hundred and nine fish had their gonads examined for sex and stage of maturation (37.7–84.7 cm; $\bar{x} = 51.5 \pm 7.8$).

Seasonal size distributions (Fig. 3) revealed a seasonal pattern [H (8, $n = 5650$) = 1315.971 $p = 0.000$], and a modal progression between summer and winter of 2014, and between summer and fall of 2015. The smallest individuals occurred in fall and spring of 2014/2015 (< 40.0 cm), whereas the largest fishes (> 71.0 cm) were observed in the fall and winter of 2014. Throughout the annual cycles, distinctive modes were observed. In the summer a unimodal and bimodal pattern with FL varying between 43.0 and 48.0 cm was evident. Increased sizes occurred in the fall with most frequent fork lengths between 50.0 and 52.0 cm. The winter of 2014 showed great variability between length classes with a prominent mode in 64.0 cm FL. In spring, a clear bimodal structure occurred in both years, with the first mode located at the 41.0 cm FL class, and the second at the 54.0 cm FL in 2014, and at the 51.0 cm FL in 2015 (Fig. 3).

The seasonal decomposition of length frequency distributions (FL) using the Battacharya routine showed a bimodal and trimodal pattern among all seasons of the years evaluated, indicating the presence of three age groups (Fig. 4). Up to 4 cohorts (C1, C2, C3 and C4) were identified along the successive seasons. C1 started in the summer 2014 (mean FL = 48.03 cm) progressing until the fall 2015 (mean FL = 67.34 cm); C2 started in the spring 2014 (mean FL = 54.41 cm) and progressed until the spring of the following year (mean FL = 66.00 cm); C3 started in the spring 2014 (average FL = 44.18 cm) and progressed until the summer 2016 (mean FL = 59.34 cm); and C4 started in the summer 2015 (mean FL = 43.62 cm) and progressed until the fall 2016 (Fig. 4). The observed increments between the beginning and the end of each cohort lasting five to six seasons were: C1 = 19.31 cm; C2 = 11.59 cm; C3 = 15.16; and C4 = 10.79 cm FL.

3.2. Sex ratio

Out of 409 processed fish, 53.1% were males (37.7–84.7 cm) and 46.9% were females (40.2–81.9 cm), generating a sexual ratio of 1:1

Table 1
Samples of the skipjack tuna (*K. pelamis*) collected from the landings of the pole-and-line fleet in Niterói, RJ, Brazil, between January 2014 and May 2016.

Year	Month	Landings	Fish measured	Fork Length (cm)		Weight (kg)		Sub-sampled
				Min-Max	Average (SD)	Min-Max	Average (SD)	
2014	January	3	316	42.3–70.4	50.5 (± 5.0)	1.2–8.6	2.9 (± 1.1)	22
	February	4	407	39.3–63.9	53.4 (± 4.3)	1.2–6.1	3.4 (± 0.9)	29
	March	3	295	44.0–70.8	55.8 (± 6.4)	1.5–8.5	3.9 (± 1.5)	30
	April	6	327	46.0–72.9	58.0 (± 6.0)	1.8–8.2	4.4 (± 1.6)	40
	May	4	230	36.5–84.7	51.3 (± 7.1)	0.9–15.3	2.9 (± 1.7)	28
	July	1	98	47.3–76.8	62.3 (± 6.9)	2.0–10.7	5.5 (± 2.0)	9
	August	1	101	46.1–82.1	66.6 (± 8.8)	1.9–13.3	7.1 (± 2.9)	11
	October	3	288	41.2–66.3	56.8 (± 4.3)	1.4–6.8	4.1 (± 1.1)	9
	November	2	220	38.1–60.7	48.1 (± 6.2)	1.1–5.3	2.4 (± 1.1)	10
	December	3	333	39.6–66.0	49.8 (± 5.8)	1.2–6.6	2.7 (± 1.1)	41
2015	January	3	398	38.2–64.9	48.7 (± 3.8)	0.9–5.9	2.4 (± 0.7)	16
	February	2	261	39.5–63.8	4.6 (± 4.7)	1.0–5.7	2.1 (± 7.9)	19
	March	2	255	38.2–61.0	46.2 (± 4.6)	1.0–5.5	2.0 (± 0.8)	25
	April	1	133	41.3–60.4	50.2 (± 3.9)	1.3–4.5	2.6 (± 0.6)	10
	May	3	286	36.5–75.6	58.2 (± 8.3)	1.0–10.4	4.8 (± 2.3)	15
	June	3	133	38.0–70.8	52.2 (± 6.7)	1.1–7.8	3.1 (± 1.5)	15
	October	1	116	41.7–67.9	51.4 (± 4.6)	1.5–7.4	2.9 (± 1.0)	-
	November	3	193	38.0–68.3	49.4 (± 6.2)	1.0–7.6	2.5 (± 1.1)	20
	December	2	415	39.5–71.0	50.7 (± 5.6)	1.1–8.2	2.7 (± 1.0)	10
2016	January	1	368	41.9–65.9	48.8 (± 3.1)	1.4 – 6.1	2.4 (± 0.5)	11
	February	2	216	40.7–62.8	49.9 (± 3.6)	1.1–5.3	2.5 (± 0.7)	10
	March	2	202	40.6–63.5	47.8 (± 4.7)	1.1–5.6	2.2 (± 0.8)	20
	May	2	59	40.5–60.0	52.1 (± 3.9)	1.3–4.9	3.1 (± 0.8)	9
Total		57	5650	36.5–84.7	52.0 (± 7.0)	0.9–15.3	3.1 (± 1.6)	409

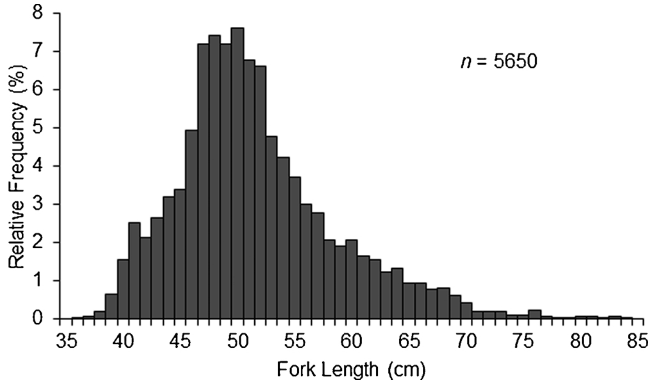

Fig. 2. Fork length (FL) relative frequency distributions for skipjack tuna caught by the pole-and-line fleet in southeastern Brazil during the sampling period.

(M:F) ($\chi^2 = 0.37$). Males predominated in most of the size classes, except for classes of 55 and 65 cm FL in which there was a significant predominance of females ($\chi^2 > 3.84$). Above 70 cm FL, males predominated. The seasonal distribution of sexual proportions did not show a regular pattern.

3.3. *Length–weight relationship*

The analysis of covariance (ANCOVA) applied to length-weight relationship parameters for separated sexes indicated significant differences ($r^2 = 0.96$, F = 10 df = 1 $p < 0.001$), showing a faster growth for males. The *t*-test revealed no significant differences in the "*b*" value between sexes for allometry coefficients (females, $t = 7.53$; $p < 0.01$) and (males, $t = 9.82$; $p < 0.01$). The overall length-weight relationship equation ($n = 5650$) was $W = 0.004FL^{3.4184}$ ($r^2 = 0.96$), for females $W = 0.005FL^{3.352}$ ($r^2 = 0.96$) and for males $W = 0.004FL^{3.416}$ ($r^2 = 0.90$).

3.4. *Spawning period*

Histological sections made from ovaries of 30 females (45–75 cm FL) allowed the identification of different stages of oocyte development confirming the macroscopic classification. At the spawning capable stage, we identified oocytes at all stages of development without a dominant cell population, corroborating the asynchronous pattern of oocyte development. Mature individuals occurred throughout spring and summer, and immature in all the seasons, except winter (Fig. 5).

The values of the gonadosomatic index (I_G) confirmed the seasonal reproductive pattern observed in the analysis of the histological sections. During the sampling period, the I_G varied between 0.02 and 8.53 ($\bar{x} \pm SE = 1.63 \pm 1.57$). Significant differences were observed in the monthly values of I_G [H (21, $n = 409$) = 284.0152; $p = 0.000$]. The highest I_G means were recorded between spring and early summer, corresponding to months of higher reproductive activity. The spawning peaks were always recorded in early summer (Jan/2014: $\bar{x} = 3.74 \pm 1.07$; Jan/2015: $\bar{x} = 4.62 \pm 1.85$; Jan/2016: $\bar{x} = 4.56 \pm 1.38$) (Fig. 6a), indicating a well-marked seasonal pattern. The lowest I_G values were observed in the fall when gonads were at rest (Fig. 6).

The monthly variation of ΔK values followed the same pattern observed for the I_G, thus strengthening the recognition of reproductive peaks (Fig. 6b). The I_H values also showed significant variation ($p < 0.05$) between months [H (21, $n = 409$) = 97.58838; $p = 0.000$]. However, the observed pattern was not consistent with the typical energy transfer dynamics during the reproductive period (Fig. 6c).

3.5. *Length at maturity (L_{50})*

The estimated length at which 50% of the female population reached maturity was 43.2 cm FL. The male population reached maturity at 46.2 cm, and grouped sexes at 45.6 cm (Fig. 7). The L_{75} and L_{100} values for the grouped sexes were estimated at 49.1 cm and 63.3 cm, respectively. Out of the total individuals measured, 15.0% were below the L_{50}.

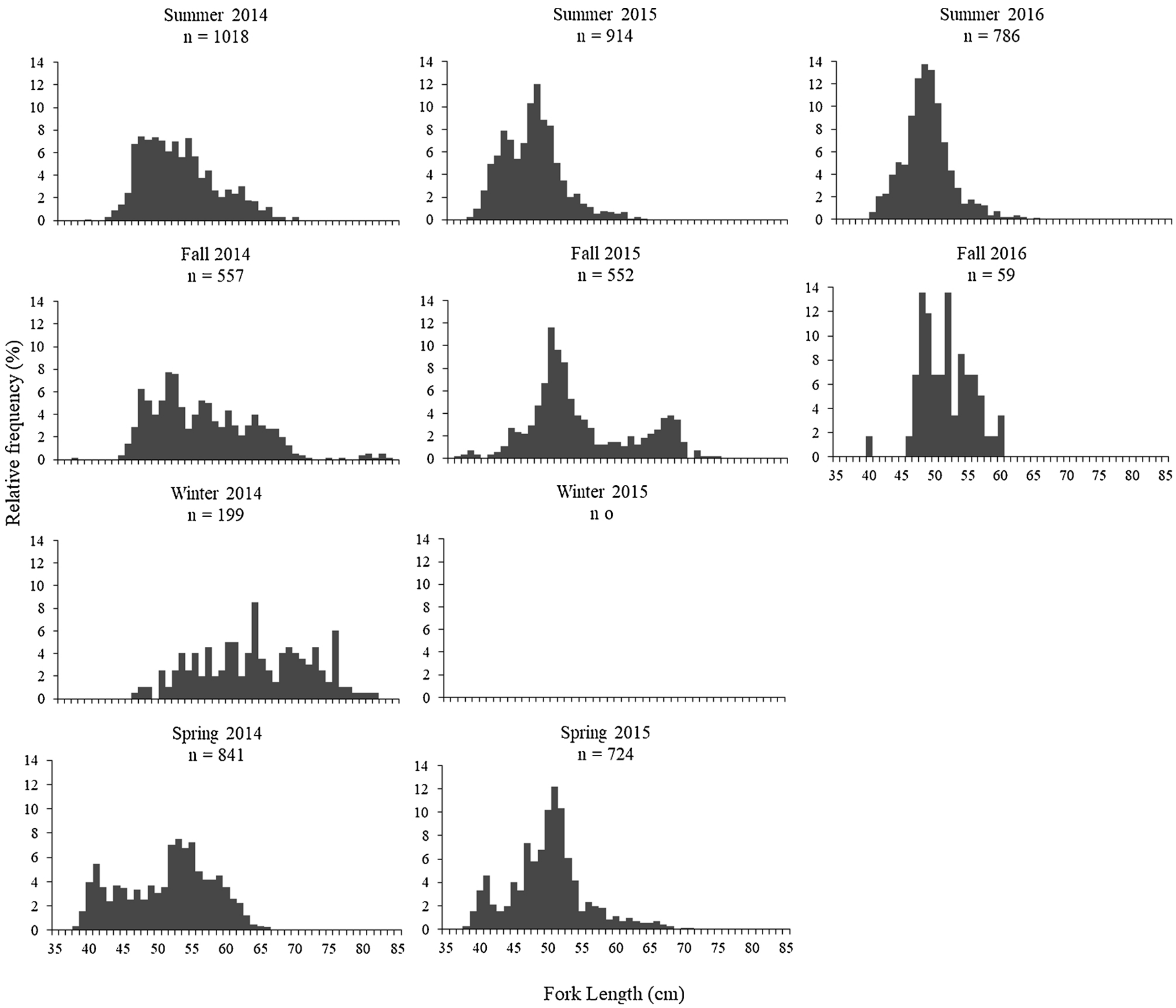

Fig. 3. Fork length (cm) seasonal distributions of skipjack tuna caught in southeastern Brazil during the sampling period.

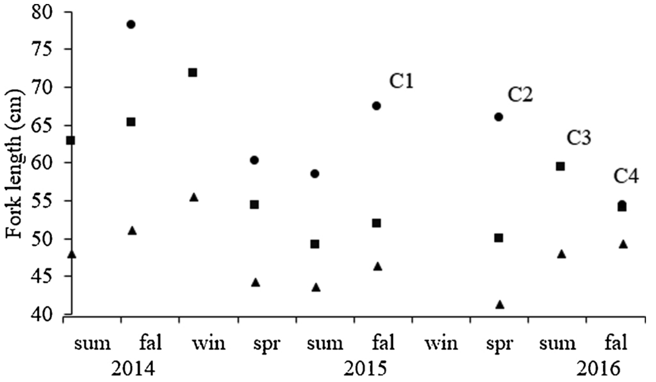

Fig. 4. Modal progression of four cohorts by seasons,using the Battacharya routine. Each symbol refers to an age group.

3.6. Recruitment patterns

The analysis of the recruitment pattern of the SKJ, simulated for a theoretical year, evidenced two peaks of recruitment: one in May, representing 18.3%, and another weaker (10.8%) in October (Fig. 8).

3.7. Growth and mortality

The growth parameters were estimated in: L_∞ = 90.1 cm, k = 0.24 yr^{-1} and t_0 = -0.54. The linearized catch curve based on the age composition data for the theoretical year, representing two and a half year cycles, showed a total recruitment age for the fishery between 2 and 3 years (Fig. 9). From this regression, Z was estimated at 1.42 yr^{-1}. The fishing mortality F was 0.95. The natural mortality (M), estimated by Pauly's method (Pauly, 1980) presented a rate of 0.47 yr^{-1}. The calculated E rate was 0.67.

4. Discussion

The unimodal behavior of fork length recorded in the SKJ catches of the pole-and-line fleet in southeastern Brazil confirms the selectivity of this fishing modality. On the other hand, the analysis of length frequency distributions by seasons of the year showed a multimodal progression, with the presence of up to three age groups. This mode displacement shows a cohort substitution, suggesting a constant entry of smaller individuals into the fishing grounds, mainly in fall and spring. No data were available during the winters of 2015 and 2016 due to landings prohibitions on the fishery for Brazilian sardine (*Sardinella brasiliensis*), which is used as bait by the pole-and-line SKJ fleet (IBAMA, 2009).

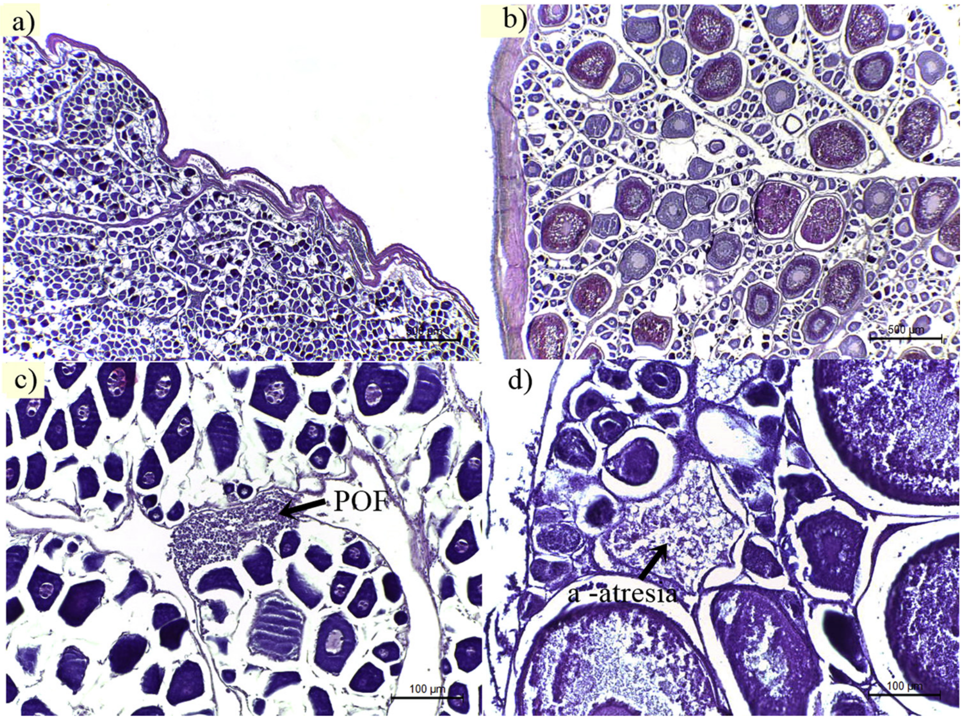

Fig. 5. Histological sections of ovaries of skipjack tuna at different stages of development: (a) immature (May/2016); (b) spawning capable (January/2014); (c) regressing, postovulatory follicle (POF) present (August/2014); (d) Regenerating, α-atresia present (January/2015).

The size distributions reported in the 1980s by Vilela and Castello (1993) for the south-southeastern region of Brazil presented a mode at the 55 cm FL class, and for the years 2002–2004, the smallest mode found for the southern region was 51 cm (Garbin and Castello, 2014). The length structure observed in this work presented a mode at the class of 50 cm, indicating some stability in the catches in the past ten years. The length distributions recorded in the present study indicated an increase in the frequency of smaller individuals and the decrease in the frequency of larger fish in the last ten years, a fact also observed for the southern region by Garbin and Castello (2014).

When comparing the fork length values recorded by different authors for the southeastern region of Brazil, it is possible to observe that the size amplitudes recorded in this study are similar to those recorded in previous periods. The size distributions registered in the 1980s by Jablonski and Matsuura (1985) in landings in Rio de Janeiro presented individuals between 34 and 82 cm FL (average of 58.3 cm). Menezes et al. (2010) followed commercial discharges of SKJ captured in the same area during the year 2007 and recorded average lengths of 59.4 cm (41.1–85.6 cm). Even though the available amplitudes are similar, we observed a decrease in the order of five centimeters in the mean fork length in the present study (52.0 cm). This size reduction reinforces the observed trend reported by Garbin and Castello (2014).

The sex ratio close to 1:1 was also observed in a previous study in the southeastern region of Brazil (Vilela and Castello, 1993). Nevertheless, Jablonksi et al. (1984) and Cayré and Farrugio (1986) identified a global sex ratio significantly in favor of males in the same region. Although in the present study the predominance of males in classes above 70 cm FL was not significant, a similar pattern in favor of males in the larger length classes was also observed for the species captured in other oceans. Stéquert and Ramcharrun (1996) and Timohina and Romanov (1996) identified a predominance of males in larger size fishes in the Indian Ocean. According to Timohina and Romanov (1996), as the fish grow older, the proportion of females in the population is reduced, a phenomenon observed when tunas reach a length of around 70 cm. In size groups over 86 cm fork length, females were completely absent (Timohina and Romanov, 1996).

The relative growth parameters a and b were compared between two regions of the southwestern Atlantic. Estimates of both parameters are dependent upon each other in such a way that the variation in one is reflected on the other (Andrade and Campos, 2002). The coefficient of allometry obtained in the general length-weight relationship (n = 5650), when compared to those obtained for the southeast (Amorim et al., 1981; Menezes et al., 2010) and southern regions of Brazil (Vilela and Castello, 1991; Andrade and Campos, 2002), indicated positive allometric growth for the SKJ during the last 30 years. The coefficient a is related to body shape and was slightly lower than those reported previously in 1980s-1990s. Such variations may be attributed to a combination of one or more factors: *i*) number of specimens examined; *ii*) fishing grounds; *iii*) health; *iv*) sex; *v*) gonadal maturity; *vi*) differences in the observed length ranges of the specimens (Hossain et al., 2014). Garbin and Castello (2014) observed variations in these parameters for over three decades, where fish of the same size presented higher weights compared with previous periods. Thus, the estimates of a and b can be related to ecological processes in time and space, between stocks and even between areas.

The histological analysis confirmed the occurrence of immature individuals in different seasons, indicating the presence of recruits in the fishing grounds. This is the first evidence that the reproduction of the SKJ in tropical areas occurs continuously throughout the year. Nevertheless, the I_G showed a reproductive peak in the summer. These results corroborate with Andrade and Santos (2004) and with the first results obtained in the southwestern Atlantic in the 1980s (Goldberg and Au, 1986; Matsuura, 1986). In addition, such continuous spawning can be justified by the opportunistic spawning behavior of the species, where spawning occurs whenever favorable conditions to reproduction are present (Cayré and Farrugio, 1986).

Previous studies in the south-southwestern Brazilian coast (Cayré and Farrugio, 1986; Goldberg and Au, 1986) indicated that the reproduction of SKJ begins between December and March, with a reproductive peak in January-February, corroborating with the larger averages of I_G recorded for the present study. Studies in the Indian Ocean (Stéquert and Ramcharrun, 1996; Timohina and Romanov,

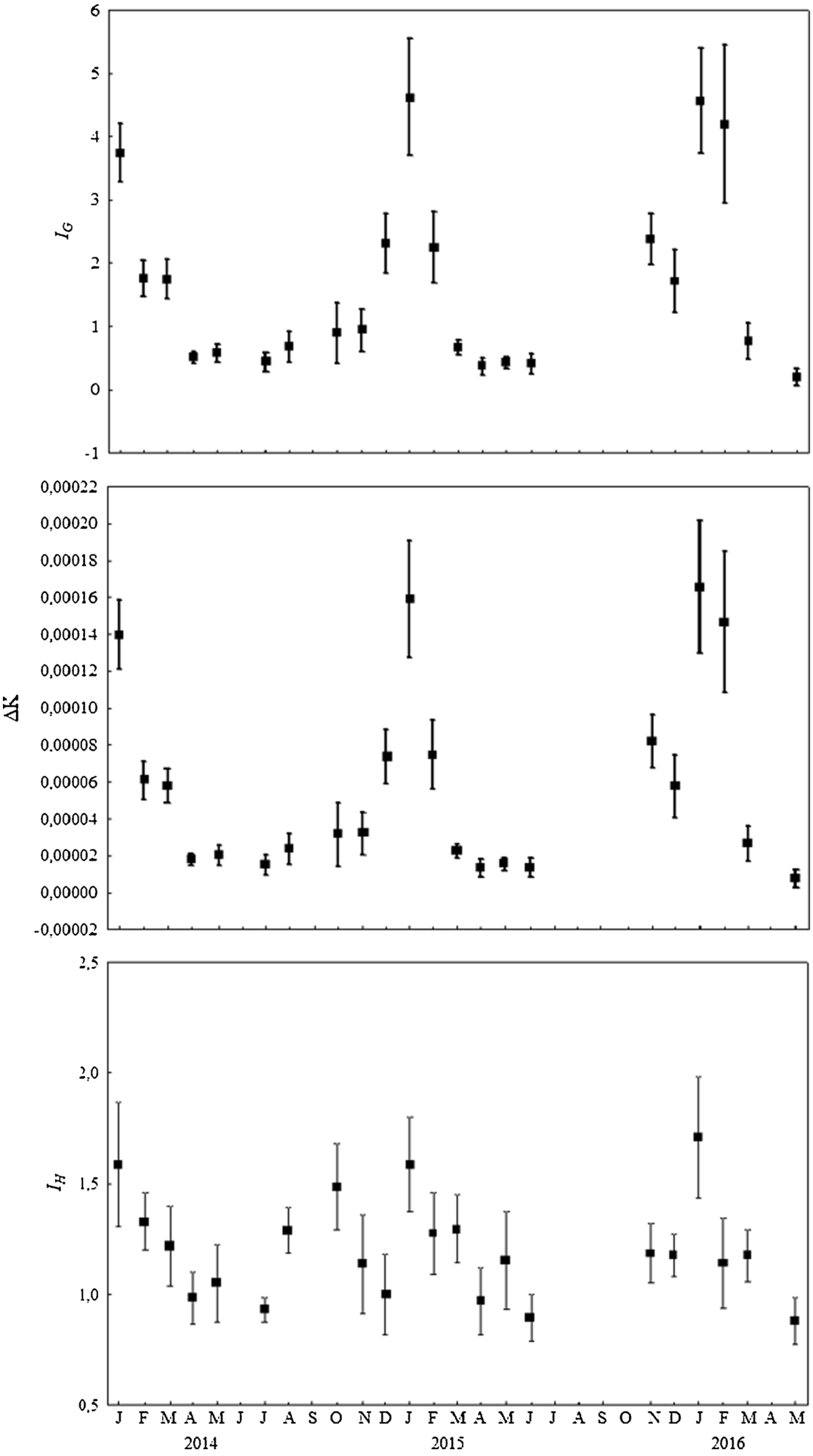

Fig. 6. Monthly variation (mean ± SE) in the gonadosomatic index (a), *Delta K* (b) and hepatosomatic index (c) for the skipjack tuna during the sampling period.

1996; Grande et al., 2014) identified two reproductive peaks between November and March (northeast monsoon) and from June to July (southeast monsoon). In the Pacific, no reproductive peaks were identified (Schaefer, 2001).

The asynchronous pattern of oocyte development observed in the present study, based on histological slide analysis, confirmed the pattern already registered in other studies for the species (Stéquert et al., 2001; Grande et al., 2014). For Grande et al. (2016), this pattern of oocyte development masks the temporal variability of condition indices and biochemical constituents. Grande et al. (2014) suggested that SKJ reproduces more actively in conditions of higher primary productivity and large aggregates of prey. Both attributes may contribute to increased energy supply, and therefore, increase reproductive capacity in response to the high metabolic rate of the species. For Grande et al. (2016) and Druon et al. (2017), SKJ should be considered an income breeder, *i.e.*, support their reproductive efforts through a concurrent intake of food during the breeding season, regardless of energy storage.

The estimates of length at maturity generated in the present study

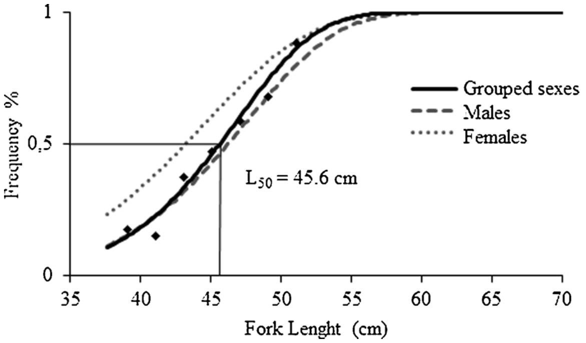

Fig. 7. Logistic regression model for the estimated proportion of mature skipjack tuna females(dotted line), males (dashed line) and grouped sexes (solid line) classified using histological staging system.

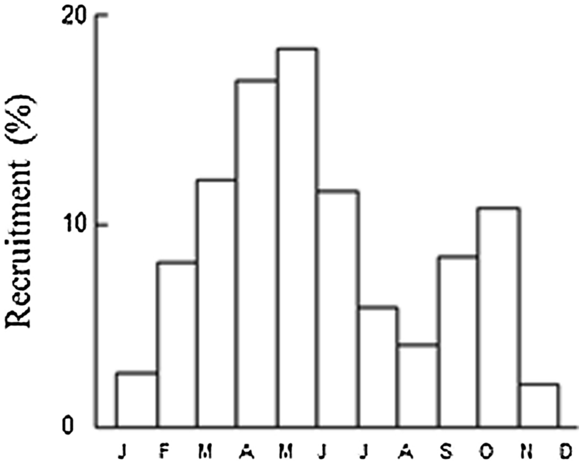

Fig. 8. Recruitment pattern for skipjack tuna caught in southeastern Brazil using a theoretical year.

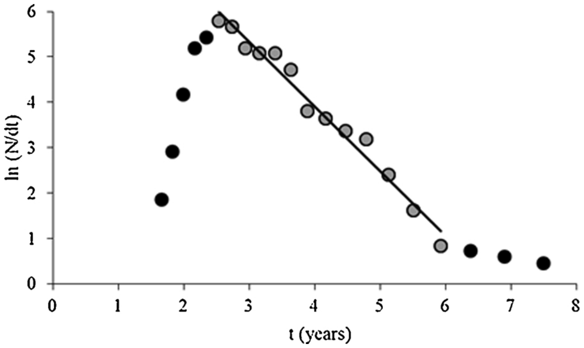

Fig. 9. Catch curve for skipjack tuna caught in southeastern Brazil. The slope of the regressed line (b) is an estimator of total mortality rate (Z).

are lower than those established by Vilela and Castello (1993) in the southwestern Atlantic (52 cm FL for females and 51 cm for males) and Goldberg and Au (1986) in Rio de Janeiro, where the smallest sexually mature specimen was identified at 51 cm FL. Both works only made use of macroscopic analysis of gonads for the estimates. However, the L_{50} values in the present study were close to the values found by Cayré and Farrugio (1986) for the whole Atlantic Ocean (females: 42 cm and males: 45 cm) and Cayré (1981) on the eastern side of the Atlantic (females: 44 cm and males: 46 cm), which also made microscopic analysis. The first authors used histology, and the second ones, oocyte distribution. In other regions, such as the Pacific Ocean, Schaefer and Orange (1956) identified the smallest mature specimen at 50 cm FL. In two studies from the Indian Ocean, Timohina and Romanov (1986) identified that 50% of the females reached sexual maturity at 43 cm and males at 40 cm, while for Stéquert and Ramcharrun (1996) females reached maturity at 41–42 cm and males at 42–43 cm.

The use of different methodologies to classify maturation stages, such as macroscopic scales (Schaefer and Orange, 1956; Goldberg and Au, 1986; Vilela and Castello, 1993), oocyte diameter distributions (Cayré, 1981), and histological analysis (Cayré and Farrugio, 1986; Timohina and Romanov, 1986; Stéquert and Ramcharrun, 1996), allow the generation of different estimates of L_{50}, even for the same region. In this sense, the histological analysis performed in the present study provided greater safety in determining the gonadal maturation stage and the spawning periods. We do not discard the hypothesis that the smallest length at maturity recorded here represents an anticipation of the length at maturity for the SKJ population. This might indicate a strategy of adaptation to environmental changes and fishery pressure for population balance recovery (Barbieri et al., 2004).

The identification of two annual recruitment peaks corroborates with the pattern found by Andrade and Santos (2004). It should be noted that the peak of recruitment observed in the fall coincides with the period in which the pole-and-line fleet in the southwestern Atlantic decreases its performance. This fact may contribute to the entry of young recruits into the fishery. Jablonksi et al. (1984) raised the hypothesis of a reproductive migration along the south-southwestern Brazilian coast, which may be justified by the fact that few specimens are found in a pre-spawning stage in the southern most range of the stock distribution (Vilela and Castello, 1993). In the present study, where captures occurred towards the northern range of the geographical distribution, spawning capable individuals were identified.

During winter and early spring (May - October/November), the cooler waters from the Malvinas Current move over the shelf waters towards the North, displacing SKJ schools to lower latitudes (Castello, 2000). At the end of spring, warm waters of the Brazil Current progress southwards into the region of the Subtropical Convergence, merging with the cold Malvinas Current. This water movement allows the return of the schools to its southernmost range until early fall (Castello and Habiaga, 1989; Castello, 2000). Matsuura (1986) identified areas suitable for massive spawning in the North and northeastern Brazil, especially off the Abrolhos archipelago (17.9 °S). Thus, it is possible that spawning of SKJ is occurring over this migratory movement across latitudes in the southwestern Atlantic. Matsuura (1982) reported the close relationship between the occurrence of SKJ larvae and water temperatures above 24 °C in the Brazil Current (Matsuura, 1986). After spawning on the northeastern coast of Brazil, SKJ schools move southward, influenced mainly by the Brazil Current (Matsuura and Andrade, 2000; Castro et al., 2006).

Tuna species exhibit asymptotic growth ranging from 75 cm FL (SKJ) to 400 cm FL (Atlantic bluefin tuna), with different growth rates ranging from 0.95 yr^{-1} (SKJ) and 0.05 yr-1 (Atlantic bluefin tuna) (Murua et al., 2017). Thus, SKJ is considered the fastest growing species of all tunas. Similarly, fish in the Western Atlantic Ocean reach a L_∞ higher than in the Eastern Atlantic (Matsuura and Andrade, 2000). Overall, the estimated L_∞ values range between 80 and 112 cm and the k values range between 0.15 and 0.6 yr^{-1} in the Atlantic Ocean. Pacific SKJ growth rates are higher than those recorded for the Atlantic and Indian Oceans. In addition, the Atlantic SKJ also reaches larger asymptotic sizes but with a slower growth rate than the Indian Ocean (Murua et al., 2017).

Comparing the values of SKJ performance indices (ϕ), based on modal progression analysis, we observed that there are differences between stocks in the Western Atlantic, Eastern Atlantic, Pacific and Indian Oceans. In the Atlantic Ocean, values of ϕ range from 2.9 to 3.5 (Vilela and Castello, 1991; Andrade et al., 2004; Garbin and Castello, 2014), whereas values of ϕ for SKJ captured in other oceans ranged from 3.4 to 3.8 (Brock, 1954; Joseph and Calkins, 1969; Marcille and Stéquert, 1976; Hafiz, 1985; Koya et al., 2012). One possible explanation for such differences may be related to the fact that tuna growth undergoes different stanzas of growth rates (Murua et al., 2017). These stanzas have been linked to: *i*) changes in habitat use through different life history stages (Hearn and Polacheck, 2003), *ii*) sexual maturation (Eveson et al., 2015) and *iii*) changes in prey as fish size/age increases.

The growth parameters obtained for the present study revealed a higher L_∞ value (90.1 cm FL) compared to the values calculated for the 1980s (87.1 cm FL) and 2004 (66.9 cm FL) obtained by Vilela and Castello (1991) and Garbin and Castello (2014), respectively. The growth rate was similar to the one obtained in 2004 (0.24 yr^{-1}) but slightly higher when compared to 1984–1986 (0.22 yr^{-1}).

In studies conducted in the 1980s, the fishing mortality coefficient was estimated around F = 0.75 (Jablonski and Matsuura, 1985; Vilela and Castello, 1993), while in the present study, F = 0.95. Regarding the rate of exploitation (E), the current rate showed a significant increase in catches compared to previous decades (Jablonksi and Matsuura, 1985; Vilela and Castello, 1993). Despite the use of different methodologies, the present values are much higher than those estimated by Andrade (2006), which could represent an increase in catches. The exploitation rate of less than 0.35 in the early 2000s indicated a sustainable exploitation of SKJ.

The estimated exploitation rate in the present study (E = 0.67) in addition to those estimated for the southern region in the period 2004–2009 are all higher than 0.5 (Garbin and Castello, 2014), suggesting that the exploitation level is above the biological recovery capacity. The results obtained in the present study demonstrated that, after 30 years, the exploitation rate for the current catches of SKJ in the southwestern Atlantic increased by 30% when compared to the rate of E during the period of 1980–1983 (Vilela and Castello, 1993). In addition, Ruffino et al. (2016) stated that, according to recent stock assessments published by ICCAT, there are indications that the West Atlantic unit is close to the full exploitation status. These estimates were based on a conservative maximum sustainable yield of around 30,000 t per year (ICCAT, 2011a). According to ICCAT (2011b), the Brazilian pole-and-line fleet is currently accounting for about 75% of the catches for the West Atlantic stock. Recently, ICCAT has proposed a subdivision of the current East and West Atlantic stocks into smaller and more homogeneous units (ICCAT, 2018). The data presented here may provide additional information for defining future management subunits.

5. Conclusion

The results obtained in the present study allow the comparison between different fishing and biological parameters of the SKJ with previous work produced for the southwestern Atlantic. The size structure revealed a reduction in the frequency of larger fish and the entry of individuals with smaller fork length in the fishery. The decrease in L_{50} suggests an anticipation of the length at maturity. Regarding the relative growth, it was also identified a change in the length-weight relation since the 80's. Regarding the growth parameters, a small increase in the growth rate was observed. All these aspects indicate that the share of the SKJ stock captured in southeastern Brazil has been showing changes in its population structure. Such changes may be related to the intense exploitation activity of SKJ, which occurs for more than 30 years, not only in the studied area but also in larger latitudes. Treating the SKJ fishery in a condition of stability can be an erroneous decision, as this is not consistent with the observed changes in population structure and growth rates observed in this study.

Finally, the results presented in this study show the importance of maintaining a continuous program of information gathering about the size of the captured individuals, as well as biological elements for breeding and growth studies, especially in the boundaries of the pole-and-line fleet in southeastern Brazil. We also suggest the expansion of studies that could clarify the patterns of displacement of individuals and eventual correlations with water mass characteristics, such as satellite monitoring, mark-recapture experiments. In addition, novel approaches including otolith microchemistry studies can reveal correlation patterns throughout the life history of these individuals and maintain up-to-date information on Western Atlantic SKJ population characteristics, contributing to responsible and sustainable fisheries.

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References

Almeida, L.R., Andrade, H.A., 2002. Comparação entre a eficiência de captura das frotas de vara e isca-viva e de cerco na pescaria do bonito listrado (*Katsuwonus pelamis*): análise preliminar. Notas Téc. Facimar 6, 59–64.

Amorim, A.F., Antunes, S.A., Arfelli, C.A., 1981. Relationships of *Katsuwonus pelamis* Linnaeus, 1758, caught in the south and southeast of Brazil: length-weight and gilled/gutted weight-weight. Col. Vol. Sci. Pap. ICCAT 15 (1), 129–134.

Andrade, H.A., 2006. Análise das principais pescarias comerciais da região Sudeste-Sul do Brasil: dinâmica populacional das espécies em explotação II. Série documentos Revizee: Score Sul. Instituto Oceanográfico, USP, São Paulo 96 p.

Andrade, H.A., Campos, R.O., 2002. Allometry coefficient variations of the length-weight relationship of skipjack tuna (*Katsuwonus pelamis*) caught in the southwest South Atlantic. Fish. Res. 55, 307–312.

Andrade, H.A., Santos, J.A.T., 2004. Seasonal trends in the recruitment of skipjack tuna (*Katsuwonus pelamis*) to the fishing ground in the southwest Atlantic. Fish. Res. 66, 185–194.

Arrizabalaga, H., Murua, H., Majkowski, J., 2012. Global status of tuna stocks: summary sheets. Rev. Invest. Mar. 18, 9.

Barbieri, G., Salles, F.A., Cestarolli, M.A., Teixeira-Filho, A.R., 2004. Estratégias reprodutivas do dourado, *Salminus maxillosus* e do curimbatá, *Prochilodus lineatus* no Rio Mogi Guaçu, Estado de São Paulo, com ênfase nos parâmetros matemáticos da dinâmica populacional. Acta Sci. Biol. Sci. Maringá 26 (2), 169–174.

Brock, V.E., 1954. Some aspects of the biology of the aku (*Katsuwonus pelamis*) in the Hawaiian Islands. Pac. Sci. 8, 94–104.

Brown-Peterson, N.J., Wyanski, D.M., Saborido-Rey, F., Macewicz, B.J., Lowerre-Barbieri, S.K., 2011. A standardized terminology for describing reproductive development in fishes. Mar. Coast. Fish.: Dynam. Manage. Ecosyst. Sci. 3 (1), 52–70.

Castello, J.P., 2000. Síntese sobre distribuição, abundância, potencial pesqueiro e biologia do bonito-listrado *(Katsuwonus pelamis*). Análise/Refinamento dos Dados Pretéritos Sobre Prospecção Pesqueira. Avaliação do Potencial Sustentável de Recursos Vivos na Zona Econômica Exclusiva MMA – REVIZEE. Rio Grande, p.13.

Castello, J.P., Habiaga, R.P., 1989. The skipjack tuna fishery in Southern Brazil. Col. Vol. Sci. Pap. ICCAT 30 (1), 6–19.

Castro, B.M., Lorenzzetti, J.A., Silveira, I.C.A., Miranda, L.B., 2006. Estrutra termohalina e circulação na região entre o Cabo de São Tomé (RJ) e o Chuí (RS). In: Rossi-Wongtschowski, C.L.D.B., Madureira, L.S.P. (Eds.), O ambiente oceanográfico da plataforma continental e do talude na região sudeste-sul do Brasil. EDUSP, São Paulo, pp. 359–446.

Cayré, R., 1981. Maturite sexuelle, fecondite et sex ratio du listao *(Katsuwonus pelamis*) 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. Col. Vol. Sci. Pap. ICCAT 15 (1), 135–149.

Cayré, P., Farrugio, H., 1986. Biologie de la reproduction du listao *(Katsuwonus pelamis)* del ocean Atlantique. In: Symmons, P.E.K., Miyake, P.M., Sahagawa, G.T. (Eds.), Proc. ICCAT Conf. Int. Skipjack Year Program, Int. Comm. Conser. Atl. Tunas, pp. 252–272 Madrid, Spain.

Cheung, W.W.L., Pitcher, T.J., Pauly, D., 2005. A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. Biol. Conserv. 124, 97–111.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., Pauly, D., 2009. Projecting global marine biodiversity impacts under climate change scenarios. Fish Fish. 10, 235–251.

Druon, J.N., 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. Front. Mar. Sci. 4https://doi.org/10.3389/fmars.2017.00315. article 315.

Eveson, J.P., Million, J., Sardenne, F., Le Croizier, G., 2015. Estimating growth of tropical tunas in the Indian Ocean using tag-recapture data and otolith-based age estimates. Fish Res. 163, 58–68.

FAO, 2014. The State of World Fisheries and Aquaculture 2014. Rome, 223 pp.. .

FAO, 2016. The State of World Fisheries and Aquaculture 2016. Contributing to Food

Security and Nutrition for All. Rome, 200 pp.. .

FAO, 2018. Fishery Statistical Collections. Global Tuna Catches by Stock. (Accessed 18 May 2018). http://www.fao.org/fishery/statistics/tuna-catches/en.

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. Lat. Am. J. Aquat. Res. 42 (3), 534–546.

Gayanilo, F.C., Strome, T., Pauly, D., 1997. Toward a generic trawl survey database management system. In: In: Silvestre, G., Pauly, D. (Eds.), Status and Management of Tropical Coastal Fisheries in Asia. ICLARM Conf. Proc. 53. pp. 116–132 208p.

The FAO-ICLARM Stock Assessment Tools (FiSAT). In: Gayanilo, F.C., Pauly, D. (Eds.), Reference Manual. FAO Comp. Inform. Ser. (Fisheries), No. 8, 202 pp.

Goldberg, S.R., Au, D.W.K., 1986. The spawning of skipjack tuna from Southeastern Brazil as determined from histological examination of ovaries. Proc. ICCAT Intl. Skipjack Yr. Prog. 1, 277–284.

Grande, M., Murua, H., Zudaire, I., Korta, M., 2012. Oocyte development and fecundity type of the skipjack, *Katsuwonus pelamis*, in the Western Indian Ocean. J. Sea Res. 73, 117–125.

Grande, M., Murua, H., Zudaire, I., Gõni, N., Bodin, N., 2014. Reproductive timing and reproductive capacity of the skipjack tuna (*Katsuwonus pelamis*) in the western Indian Ocean. Fish. Res. 156, 14–22.

Grande, M., Murua, H., Zudaire, I., Arsenault-Pernet, E.J., Pernet, F., Bodin, N., 2016. Energy allocation strategy of skipjack tuna *Katsuwonus pelamis* during their reproductive cycle. J. Fish Biol. 89, 2434–2448. https://doi.org/10.1111/jfb.13125.

Hafiz, A., 1985. Skipjack fishery in the Maldives. IPTP Coll. Vol. Work. Docs. 1, 1–20.

Hearn, W.S., Polacheck, T., 2003. Estimating long-term growth rate changes of southern bluefin tuna (*Thunnus maccoyii*) from two periods of tag-return data. Fish Bull. 101 (1), 58–74.

Hossain, M.Y., Rahman, M.M., Ahmed, F., Ahmed, Z.F., Ohtomi, J., 2014. Length–weight and length–length relationships and form factor of three threatened fishes from the Ganges River (NW Bangladesh). J. Appl. Ichthyol. 30, 221–224. https://doi.org/10.1111/jai.12251.

IBAMA, 2009. Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis.Instrução Normativa IBAMA Nº 16, de 22 de maio de 2009. (accessed 3 May 2018). http://www.icmbio.gov.br/cepsul/images/stories/legislacao/Instrucao_normativa/2009/in_ibama_16_2009_retificada_defesosardinhaverdadeira_sc_rj_rev_p_ibama_68_2003.pdf.

ICCAT, 2000. International commission for the conservation of Atlantic tunas. Detailed report on skipjack tuna. SCRS/99/21 LI, 132–220.

ICCAT, 2006. International Commission for the Conservation of Atlantic Tuna 2006-2009. Manual, International Commission for the Conservation of Atlantic Tuna Publications (Accessed 24 October 2012. http://www.iccat.int/en/ICCATManual.htm.

ICCAT, 2011a. International Commission for the Conservation of Atlantic Tunas – Report of the Standing Committee on Research and Statistics (SCRS). 2-3p. .

ICCAT, 2011b. International Commission for the Conservation of Atlantic Tunas – Report 2010–2011 (I). Executive Summary Skipjack Tuna SKJ.

ICCAT, 2017. International commission for the conservation of Atlantic Tunas – the current edition provides the catch and other statistics series starting in 1950 up to 2015. Statis. Bull. 43 (2).

ICCAT, 2018. International Commission for the Conservation of Atlantic Tunas –Report for Biennial Period, 2016-17. Part I 2 2017.

Jablonksi, S., Braile, A.A., Romo, C.M., Teixeira, M.S., 1984. Sexual maturity and sex-ratios of the skipjack tuna, *Katsuwonus pelamis* (Linnaeus), from Southeastern Brazil. SCRS/83/49 ICAAT. Coll. Vol. Sci. Pps. 20 (1), 217–233.

Jablonski, S., Matsuura, Y., 1985. Estimate of exploitation rates and population size of skipjack tuna off the southeastern coast of Brazil. Bol Inst. Oceanogr., S Paulo 33 (1), 29–38.

Joseph, J., Calkins, T.P., 1969. Population dynamics of the skipjack tuna *Katsuwonus pelamis* of the Eastern Pacific Ocean. Bull. Int. Am. Trop. Tuna Comm. 13 (1) 273p.

Koya, K.P.S., Joshi, K.K., Abdussamad, E.M., Rohit, P., Sivadas, M., Kuriakose, S., Ghosh, S., Koya, M., Dhokia, H.K., Prakasan, D., KunhiKoya, V.A., Sebastine, M., 2012. Fishery, biology and stock structure of skipjack tuna, *Katsuwonus pelamis* (Linnaeus, 1758) exploited from Indian waters. Indian J. Fish. 59 (2), 39–47.

LeCren, E.D., 1951. The length-weight relationship and seasonal cycle in gonad weight and conditions in the perch Perca fluviatilis. J. Anim. Ecol. 20 (2), 201–219.

Marcille, J., Stéquert, B., 1976. Croissance des jeunes albacores (*Thunnus albacares*) et patudos (*Thunnus obesus*) de la côte nord-ouest de Madagascar. Cah ORSTOM, SérOcéanogr XIV, pp 153–162.

Matsumoto, W.M., Skillman, R.A., Dizon, A., 1984. Synopsis of Biological Data on Skipjack Tuna, Katsuwonus Pelamis. U.S, The National Marine Fisheries Service. Spec. Rep. Fish 695.

Matsuura, Y., 1982. Distribution and abundance of skipjack (*Katsuwonus pelamis*) larvae in Eastern Brazil waters. Col. Vol. Pap. ICCAT 17 (1), 211–213.

Matsuura, Y., 1986. Distribution and abundance of skipjack larvae off the coasts of Brazil. Proc. ICCAT Intl. Skipjack Yr. Prop. 1, 285–289.

Matsuura, Y., Andrade, H.A., 2000. Synopsis on biology of skipjack tuna population and related environmental conditions in Brazilian waters. Col. Vol. Sci. Pap., ICCAT 51 (1), 395–400.

Menezes, A.A.S., Santos, R.A., Lin, C.F., Vianna, M., Neves, L.F., 2010. Caracterização das capturas comerciais do bonito-listrado, *Katsuwonus pelamis*, desembarcado em 2007 no Rio de Janeiro, Brasil. Rev. CEPSUL – Biodivers. Conservação Marinha 1 (1), 29–42.

Miyake, M., Guillotreau, P., Sun, C.H., Ishimura, G., 2010. Recent developments in the-tuna industry: stocks, fisheries, management, processing, trade and markets. FAO Fish. Tech. Pap. 543, 125.

Moresco, A., Bemvenuti, M.A., 2006. Biologia reprodutiva do peixe-rei *Odontesthes argentinensis* (Valenciennes) (Atherinopsidae) da região marinha costeira do sul do Brasil. Rev. Bras. Zool. 23 (4), 1168–1174.

Morgan, M.J., Murua, H., Kraus, G., Lambert, Y., Marteinsdo´ttir, G., Marshall, C.T., O'Brien, L., Tomkiewicz, J., 2009. The evaluation of reference points and stock productivity in the context of alternative indices of stock reproductive potential. Can. J. Fish. Aquatic Sci. 66, 404–414.

Murua, H., Rodriguez-Marin, 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. Rev. Fish. Biol. Fish. https://doi.org/10.1007/s11160-017-9474-1.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer. 39 (2), 175–192.

Ruffino, M.L., Lima, L.H., Sant'Ana, R., 2016. Situação e tendências da pesca marítima no Brasil e o papel dos subsídios. São Paulo - SP, 2016: WWF-Brasil. 76 p. .

Schaefer, K.M., 2001. Assessment of skipjack tuna (*Katsuwonus pelamis*) spawning activity in the eastern Pacific Ocean. Fish. Bull. 99, 343–350.

Schaefer, M.B., Orange, C.J., 1956. Studies of the sexual development and spawning of yellowfin tuna (*Neothunnus macropterus*) and skipjack (*Katsuwonus pelamis*) in three areas of the eastern Pacific Ocean, by examination of gonads. Inter-american tropical tuna commission. Bull. – Boletin 1 (6).

Sparre, P., Venema, S.C., 1992. Introduction to tropical fish stock assessment. Part 1: manual. FAO Fish. Tech. Pap. 306 (1) 337 pp.

Stéquert, B., Ramcharrun, R., 1996. La reproduction du listao (*Katsuwonus pelamis*) dans le bassin ouest de l'océan Indien. Aqunr. Living Krsour. Y 235–247.

Stéquert, B., Nunez Rodriguez, J., Cuisset, B., Le Menn, F., 2001. Gonadosomatic index and seasonal variations of plasma sex steroids in skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnu salbacares*) from the western Indian Ocean. Aquat. Living Resour. 14, 313–318.

Suvarna, K.S., Layton, C., Bancroft, J.D., 2012. Bancroft's Theory and Practice of Histological Techniques E-Book. USA. Elsevier Health Sciences, pp. 114–119.

Timohina, O.I., Romanov, E.V., 1996. Characteristics of ovogenesis and some data on maturation and spawning of skipjack tuna, *Katsuwonus pelamis* (Linnaeus, 1758), from the western part of the equatorial zone of the Indian Ocean. Indian Ocean Tuna Comission 24.

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 Sec. A.

Vilela, M.J.A., Castello, J.P., 1993. Dinamica poblacional del barrilete (*Katsuwonus pelamis*) explotado en la region sudeste-sur del Brasil en el periodo 1980-1986. Frente Maritimo 14, 111–124 Sec. A.

von Bertalanffy, L., 1938. A quantitative theory of organic growth. Hum. Bio1. 10, 181–213.

West, G., 1990. Methods of assessing ovarian development in fishes: a review. Aust. J. Mar. Freshw. Res. 41, 199–222.

Zar, J.H., 1984. Biostatical Analysis, second edition. Prentice-Hall, Inc., Englewood Cliffs, New Jersey 718 p.