

Population dynamics of *Scomberomorus brasiliensis* from a small-scale fishery off Southern Brazil

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ABSTRACT

Scomberomorus brasiliensis is the most important fish species of the small-scale fishery off the southwestern Atlantic north of the La Plata estuary. For management purposes, this study evaluated their reproductive biology, size, age and growth along the Paraná coast. Monthly samples (March 2018-June 2020) from the fishery comprised 933 specimens (413 males, 520 females), 210-779 mm fork length, corresponding to a size smaller than in the northern areas. It presented negative allometry ($b = 2.69159$, length-weight relationship). Specimens in all stages of maturity occurred during the study period, indicating spawning in the area from October to June, peaking from January to March. The gonad-length relationship was suitable to confirm this assessment. Individual fecundity varied between 34,484 and 390,786 oocytes. Maturity occurred at $L_{50} = 446.46$ mm, $t_{50} = 1.4$ years, and $L_{100} = 588.79$ mm, and $t_{100} = 2.3$ years. The growth parameters were $L^{\infty} = 771.68$ mm, $k = 0.65$ year⁻¹ and $t_0 = -0.102$ years, with cohorts aged from 0.5 to 6.5 years. *Scomberomorus brasiliensis* along the Paraná coast constitutes a self-sustaining group, not directly related to that from northeastern Brazil. This small-scale fishery is not currently negatively affecting stock level; it is essential to monitor these attributes to detect future changes or impacts.

Descriptors: Reproductive biology, Growth, Artisanal, Management, Southwestern Atlantic.

INTRODUCTION

Scombridae fishes are important pelagic fishery resources worldwide, including large (> 600 mm) and medium-sized (200 to 600 mm) species (Fréon et al., 2005). Tunas are typical large-sized oceanic scombrids (Pons et al., 2017; Collette and Graves, 2019), and *Scomber* species are medium-sized neritic ones. Spanish mackerel, king mackerel and Brazilian Spanish mackerel are vernacular names for *Scomberomorus* spp., which is a

medium-sized species (*sensu* Fréon et al., 2005) widely distributed in neritic and coastal areas, including the east coast of South America (Froese and Pauly, 2019). Three species have been recorded in Brazil: *S. regalis* (Bloch 1793), *S. cavalla* (Cuvier, 1829), and *S. brasiliensis* Collette, Russo & Zavala-Camin, 1978 (Figueiredo and Menezes, 2000; Fricke et al., 2020). Distributed from North and Central America, to South America, the southern limits of distribution of these species are different, ~23°50'S for *S. regalis*, ~26°10'S for *S. cavalla*, and ~34°S for *S. brasiliensis*, which is the most abundant (Figueiredo and Menezes, 2000; Collette et al., 2011). Until the 1970s, *S. brasiliensis* was confused with *S. maculatus* (Mitchill, 1815), a species

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restricted to the east coast of North America and the Gulf of Mexico (FAO, 1983).

The Brazilian Spanish mackerel is an important fishery resource mainly for the small-scale (artisanal) fishery (Fonteles-Filho, 1988; Batista and Fabrè, 2001; Nóbrega et al., 2009; Collette et al., 2011). According to the last reliable Brazilian fishery statistic (IBAMA, 2007), it is one of the most valuable fishery resources, attaining above average prices for commercialization in the fish production chain. In 2007, 8,873 tons of Brazilian Spanish mackerel were landed, 99.7% from the small-scale fishery. Higher landings (~94%) occur in northern and northeastern Brazil (~4°50'N to ~13°S), where *S. brasiliensis* is called “serra” in Portuguese and is targeted by a specific gillnet named “serreira” (Maia et al., 2015). In the southwestern Atlantic (22°S–34°S), it is named “sororoca” in Portuguese and 462 tons were landed in 2007 (IBAMA, 2007). From 2009 to 2011, the average annual production of 433.9 tons was an underestimated value (MPA, 2011) due to the progressive dismantling of fishery statistics promoted by deficient federal policies. There have been no national fishery statistics in Brazil since 2012; however, from 2016 this situation changed in some parts of southern Brazil owing to the commencement of the Fisheries Activity Monitoring Project. This project was demanded by an environmental agency (IBAMA) to the Petrobras oil company and was undertaken by researchers from different institutions. This project has provided a reliable source of data from both industrial and small-scale fisheries in the area between 22°S and 29°S.

The small-scale fishery is a common and well-developed activity throughout the Brazilian coast and is sometimes neglected and the victim of deficient policies similar to other fishery activities in Brazil (Oliveira and Silva, 2012; Isaac et al., 2013). Its importance is highlighted in the estuarine complexes and adjacent areas of the tropical and subtropical regions, including the Paraná coast (Chaves and Robert, 2003; Chaves and Silva, 2019). It is relatively short (~100 km in a straight line); however, it plays a significant role in fish populations, providing areas for reproduction, feeding, and growth, highlighting the Paranaguá Estuarine Complex and the Guaratuba Bay (Andrighetto-Filho et al., 2006; Lana and Bernardino, 2018).

The Paraná coast only presents a small-scale fishery (Andrighetto-Filho et al., 2006), comprising

approximately 5,000 artisanal fishers and an average landing of 2,573 tons per year (2017–2019) (PMAP, 2020). These recent data improved the previous lack of information reported by different authors (IBAMA/CEPSUL, 2000; Robert and Chaves, 2006; Mendonça and Miranda, 2008; Mendonça and Lucena, 2014; Chaves and Silva, 2019), and confirmed the importance of *S. brasiliensis* in the small-scale fishery of Paraná. During 2017–2019, the Brazilian Spanish mackerel occupied the third production position, with an average of 113 tons per year, after the shrimp *Xiphopennaeus kroyeri* (first) and the mollusk *Anomalocardia flexuosa* (second) (PMAP, 2020). Although it is landed the year-round, both as a target species and as by-catch (Chaves and Silva, 2019), higher frequencies are recorded during warmer months (October to March) (UNIVALI, 2013).

Despite the importance of *S. brasiliensis*, the amount and focus of available studies on its fishery and biology are heterogeneous. This species has been well studied in northeastern Brazil, where there is a single stock (Nóbrega et al., 2009; Isaac et al., 2013); however, in southern Brazil (22°S–34°S), including the Paraná coast, there are no studies. The species does not perform remarkable migrations like tunas, undergoing only seasonal and reproductive displacements (Collette et al., 1978, 2011; Batista and Fabrè, 2001). Therefore, it is reasonable that the individuals along the Paraná coast and adjacent areas caught by the small-scale fishery constitute a self-sustaining group (stock) not directly related to that from northeastern Brazil. Cadrin et al. (2014) defined stock as “an exploited fishery unit. A stock may be a single spawning component, a biological population, a metapopulation, or comprise portions of these units. For management purposes stocks are considered discrete units, and each stock can be exploited independently or catches can be assigned to the stock of origin”. Thus, patterns of size, age, and growth (Ximenes, 1981; Nóbrega and Lessa, 2009), reproductive biology (Silva et al., 2005; Lima et al., 2007; Lima et al., 2009), feeding (Menezes, 1970; Fonteles-Filho, 1988; Lopes et al., 2016), parasites (Alves and Luque, 2006; Eiras et al., 2014), and fisheries and management (Almeida et al., 2007; Brito and Furtado Júnior, 2010; Leão et al., 2018) described for this species in other areas cannot be assumed the same for management purposes along the Paraná coast (Moksness et al., 2013; Cadrin et al., 2014).

Considering this scenario, it is possible to establish the following premises: (i) *S. brasiliensis* is the most important fish species for the small-scale fishery along the Paraná coast; (ii) the small-scale fishery is an important, essential and complex activity whose management requires relevant information regarding fisheries resources; and (iii) population dynamics parameters are intrinsic for each stock and subsidize proper management measures. Therefore, the present study aimed to estimate the population parameters of *S. brasiliensis* along the Paraná coast, verifying which population component was accessed by the fishing activity. Techniques

for investigating reproductive biology, size, age and growth were applied, considering the hypothesis that the self-sustaining group along the Paraná coast had its own biological patterns.

METHODS

SAMPLING AND DATA ACQUISITION

Scomberomorus brasiliensis samples were obtained from small-scale fishery landings at the Fishery Market of Matinhos (FMM), Paraná coast, southern Brazil (25°49'S, 48°32'W) (Figure 1). Catches

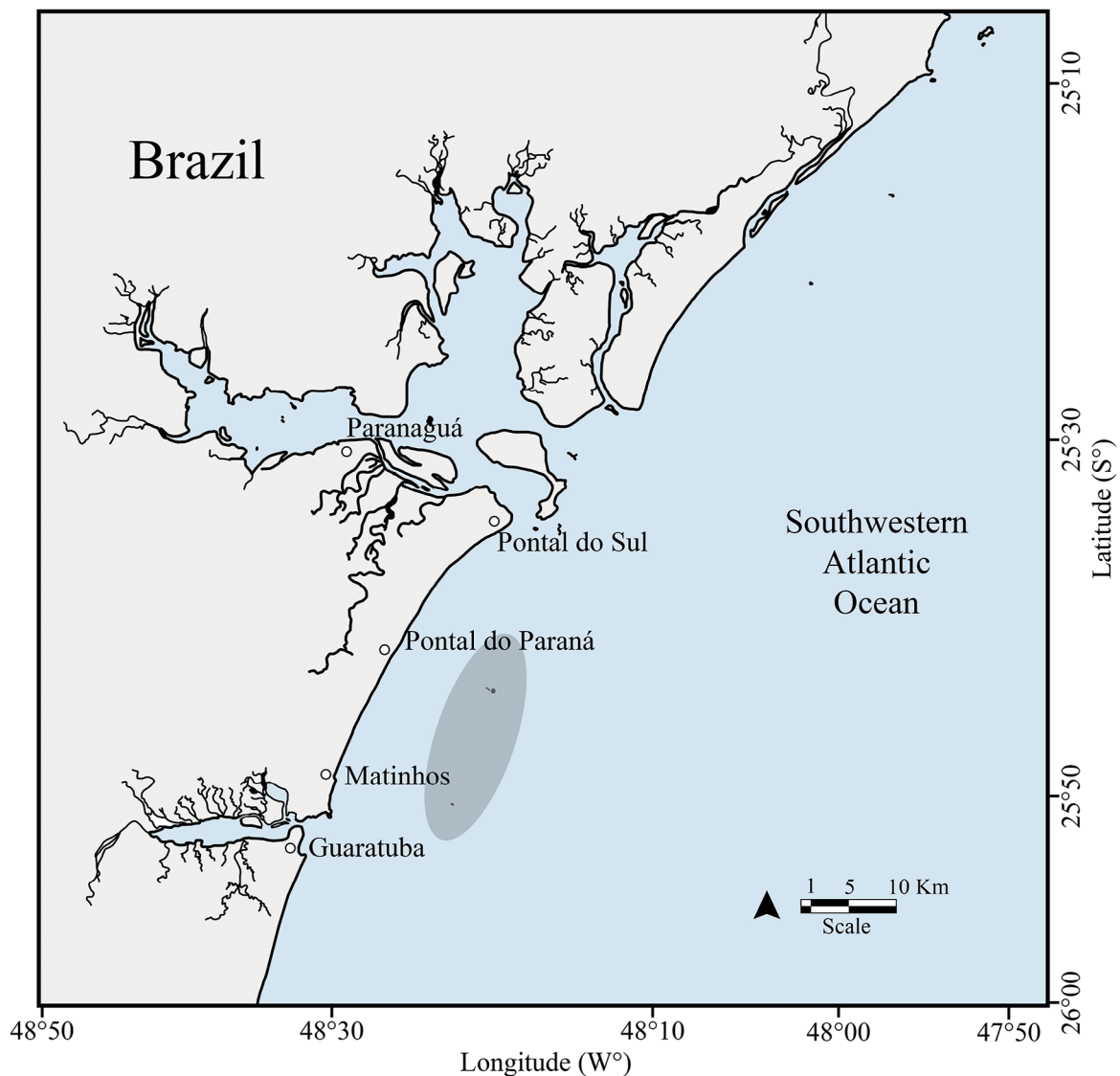


Figure 1. Paraná coast (southern Brazil) showing Matinhos (fishery landing site), Paranaguá Estuarine Complex and Guaratuba Bay. In grey the main fishing area of *Scomberomorus brasiliensis* by small-scale fishery.

usually occurred with gillnets of varying mesh sizes (from 50 mm to 400 mm, usually 70 mm to 170 mm mesh), 2–3.5 km of extension, varied soak time (usually 20–30 h), with local modalities named “fundeio” and “caceio” in Portuguese (Chaves and Robert, 2003; Andriquetto et al., 2006; Afonso and Chaves, 2021). FMM is the centre of the landings and processing of fishery resources in coastal adjacent areas up to 40 m in depth. As a gross estimate, fishing occurs in a surface area of 2,000 km² and a volume of 40,000 km³ of the neritic region, corresponding to the inner continental shelf. The inner shelf is characterized by the coastal water, a water mass with salinities less than 35 and varying temperatures, limited by the bottom temperature boundary, an intersection between the mixed coastal waters and subsurface cold-water intrusions (< 18°C) that seasonally occur at the mid and outer shelf (Piola et al., 2018). During the study period, the atmospheric temperature in this region varied from 10.0°C (August 2019) to 38.5°C (January 2020) (DHN/Marinha do Brasil, 2021). The average values of sea surface temperature are available in the Supplementary Material, characterizing the seasons (summer = January, February, and March; autumn = April, May, and June; winter = July, August, and September; and spring = October, November, and December).

Biological samples were obtained monthly at FMM from March 2018 to June 2020, comprising

biometry and gonads of 933 *S. brasiliensis* specimens (Table 1), with limited numbers in some months due to non-capture. Specimens were measured for total length (TL, mm) and fork length (FL, mm) and, whenever possible, total weight (TW, g) depending on immediate filleting. Sex (male and female) and maturity were identified based on visual inspection of the gonads (Vazzoler, 1996; Brown-Peterson et al., 2011) as follows: immature (A), developing (B), spawning capable (C), spawning capable with pre-ovulatory hydration (Ch) only for females, and regressing (D). Morphological details of gonad features in each developmental phase are described in the Supplementary Material. From December 2018, gonad weight (GW, g) was recorded.

For fecundity estimates, between December 2018 and February 2019 the left and right ovaries of 42 individuals, previously fixed in 10% formalin, were separated and weighed, and a medial, small portion of each was obtained and weighed too. The two dry portions were mechanically dissociated, aiming to identify, under a stereomicroscope, the vitellogenic oocytes recognized by their opacity, resulting from yolk deposition (Vazzoler, 1996; Brown-Peterson et al., 2011). The opaque oocytes were counted, and the number found in each portion was extrapolated for the total ovary weight. The total number of oocytes in both ovaries was summed, constituting the individual fecundity (F).

Table 1. *Scomberomorus brasiliensis*: number of individuals (N), range of fork length (FL, mm) by sex and month landed at Fishery Market of Matinhos, southern Brazil (zero indicates no samples available due to non-capture).

	2018				2019				2020			
	Males		Females		Males		Females		Males		Females	
	N	FL range	N	FL range	N	FL range	N	FL range	N	FL range	N	FL range
January					2	546-558	33	558-718	30	450-530	22	470-570
February					2	460-500	10	500-670	6	440-570	8	480-580
March	33	310-510	36	282-555	0	-	0	-	20	210-570	19	490-570
April	20	420-550	14	480-550	5	320-510	3	460-710	18	370-540	22	480-600
May	10	514-600	13	545-673	0	-	0	-	29	490-600	6	460-600
June	11	462-560	7	479-571	23	400-701	25	440-730	13	550-610	29	510-630
July	36	497-617	36	479-778	21	430-740	49	440-690				
August	10	576-692	10	582-667	10	480-680	37	430-660				
September	0	-	0	-	17	430-670	34	400-710				
October	0	-	0	-	21	440-600	26	400-760				
November	0	-	0	-	34	460-630	26	450-660				
December	18	510-693	22	485-779	24	420-570	33	430-610				

DATA ANALYSIS

The results are presented based on FL data. Regressions between TL and FL were fitted for males and females together and separate, allowing for conversions. Linear models were adjusted by the iterative least squares method with the Levenberg–Marquardt algorithm and 9,999 iterations (Motulsky and Christopoulos, 2003). Residual analysis was performed and outliers ($|Z| > 1.96$) were removed. The models were re-adjusted, and regressions for each sex were compared with an analysis of covariance (Zar, 2010). The length–weight relationship was fitted for males and females together (Froese, 2006), and using the iterative method. A t -test was applied to verify the isometric pattern ($\beta = 3$) of the coefficient b value. All statistical procedures were performed with $\alpha = 0.05$.

The spawning period was verified based on the overall monthly distribution of gonad developmental phases (Lowerre-Barbieri et al., 2011). For a detailed diagnosis, monthly frequencies of females and males in reproductive activity (combined frequency of C+Ch+D) were tested using a heterogeneity chi-square test (Zar, 2010). The gonad–length relationship ($\text{GLR} = \text{GW} / \text{FL} \times 100$) was individually estimated from December 2018, helping the spawning period diagnostic. Because of the GLR dependence on FL, the size effect was removed by calculating $\text{GLR}' = \text{GLR} \times (\text{FL}_0 / \text{FL})^b$, where the reference values for standardization were $\text{FL}_0 = 516.05$ mm (average FL), and $b = 3.0208$ from the model $\text{GLR} = a\text{FL}^b$ (Lombarte and Leonart, 1993). Then, a confidence interval plot (95% t -distribution) of GLR' values by sex and gonad developmental phase was created to ascertain the representativeness of gonad maturity. After checking, individual values were graphically analyzed: (i) a dot-plot by sex, gonad maturity and month was used to investigate individual variations, and (ii) a confidence interval plot was used to analyze averages (excluding immature individuals) by sex and month. Monthly averages of GLR' were tested using a one-way analysis of variance, and assumptions were tested and confirmed in the residual analysis. The variance inflation factor was used to detect extreme averages with multicollinearity, considering a cut-off value of 5 (Zuur et al., 2009; Legendre and Legendre, 2012). A *post-hoc* Tukey test was applied to detect differences among monthly averages.

Individual fecundity (y) was evaluated by fitting linear models between FL and gonad weight (x) by the aforementioned iterative method. The average length at first maturity (L_{50}) was estimated based on a logistic model (Haddon, 2011), in which the frequencies of adult females (P) were plotted against the bottom limit of length classes (L) following the formula $P = 1 / [1 + e^{-r(L-L_{50})}]$. Previously, two approaches were verified: one considering C + Ch + D as adults, and the other with B + C + Ch + D as adults, the former being inadequate due to the mix between individuals for the first time as developing and recurrent ones. The non-linear iterative least squares method with the Levenberg–Marquardt algorithm and 9,999 iterations was applied to fit the model (Motulsky and Christopoulos, 2003). Based on the model, the length at which all individuals could reproduce (L_{100}) was estimated.

The von Bertalanffy growth model (VBGM) parameters were estimated. After simulations, the maximum theoretical length (L_{∞}) was calculated using the Powell-Wetherall method and the growth rate (k) with the Shepherd length composition analysis (SLCA) (Isaac, 1990), considering fine adjustments in the routine introduced by Gayanilo et al. (2005). The theoretical age at zero length (t_0) was estimated using the Pauly formula (Pauly, 1984). The instantaneous growth rate ($G = [(\ln \text{FL}_2 - \ln \text{FL}_1) / (t_2 - t_1)] \times 100$) was calculated, and for age zero approximated values were $\text{FL}_1 = 5$ mm (based on Jenkins et al., 1984; Shoji et al., 2002) and $t_2 = 0.5$ years. Based on the growth parameters, an inverse VBGM was used to estimate the average age at first maturity (t_{50}) and the age at which all individuals could reproduce (t_{100}).

RESULTS

The 933 individuals of *S. brasiliensis* comprised 413 males (range of 210–740 mm FL), and 520 females (range of 282–779 mm FL) (Table 1). The FL–TL relationships did not show significant differences between males and females ($F = 0.88$; $p = 0.35$), thus ensuring representativeness for the grouped model (Table 2). The length–weight relationship (Table 2, and Figure in the Supplementary Material) presented negative allometry ($t = -3.86$; $p = 0.000172$).

Specimens from all maturity stages were found, although with varying proportions during the study period. Juveniles (immature, A) of *S. brasiliensis* were

Table 2. *Scomberomorus brasiliensis*: summary of regressions involving total length (TL), fork length (FL), weight (TW), individual fecundity (Fi), gonad weight (GW), and proportion of adult females (P) for individuals landed at Fishery Market of Matinhos, southern Brazil, years 2018-2020 (*a* and *b* - regression coefficients; in the logistic model $r = a$ and $L_{50} = b$, SE - standard error, N - number of data, F - regression statistics, *p* - probability, r^2 - coefficient of determination).

Model	<i>a</i>	SE _{<i>a</i>}	<i>b</i>	SE _{<i>b</i>}	n	F	<i>p</i>	r^2
FL = <i>a</i> + <i>b</i> TL								
males+females	-13.17	3.56	0.87805	0.00587	674	22393.55	< 0.001	0.971
males	-10.03	5.09	0.87339	0.00863	288	10247.27	< 0.001	0.973
females	-17.14	5.14	0.88399	0.00832	387	11293.90	< 0.001	0.967
TW = <i>a</i> FL ^{<i>b</i>}	0.0000537775	0.0000275	2.69159	0.0798774	49	91.55	< 0.001	0.971
Fi = <i>a</i> + <i>b</i> FL	-806,174.00	129,607.00	1,784.00	246	38	52.63	< 0.001	0.594
Fi = <i>a</i> + <i>b</i> GW	-13,803.00	10,572.00	5,385.00	352	39	234.61	< 0.001	0.864
$P = 1 / [1 + e^{-r(L-L_{50})}]$	0.03229	0.00439	446.47	4.470	13	54.63	< 0.001	---

constant and frequent between June and October 2019 (autumn and winter). Individuals in the developing (B) phase occurred in all months of the year, and from April (beginning of autumn) and August (winter) their frequencies were higher than 30% over the two years (Figure 2).

Scomberomorus brasiliensis specimens in reproductive activity (C + Ch + D) presented more than 30% of the frequency between November and December (end of spring) up to February 2019 (summer) and June 2020 (winter) (Figure 3a). There were differences between sexes and years ($\chi^2 = 50.30$, $p = 2.65 \times 10^{-6}$) due to the predominance of females. This predominance was remarkable in January 2019 ($\chi^2 = 24.40$, $p = 7.43 \times 10^{-7}$), April 2019 ($\chi^2 = 4.00$, $p = 0.0455$), January 2020 ($\chi^2 = 7.20$, $p = 0.0073$), April 2020 ($\chi^2 = 15.21$, $p = 9.61 \times 10^{-5}$) and June 2020 ($\chi^2 = 14.23$, $p = 0.0002$), evidencing a recurrent pattern. Detailing the frequency of females, during the summer of 2019 and summer–autumn of 2020 there was a gradual decrease of spawning capable individuals (C + Ch) and an increase of repressing ones (D) (Figure 3b).

The gonad–length relationship (after size-effect removal) varied significantly among the gonad developmental phases (Figure 4 and referential values in the Supplementary Material). Higher individual values were

recorded during the summer and autumn for both sexes (Figure 5a and 5c), related to reproductive activity. Average values of GLR' (Figure 5b and 5d) presented significant variation among months for both females ($F = 13.78$; $p < 0.001$) and males ($F = 9.96$; $p < 0.001$). Increases in GLR' indicated periods of intense reproductive activity. Alternate patterns of increases and decreases presented differences ($p < 0.05$ from Tukey tests, cf. Supplementary Material), although sequential values of these “sets” of high and low values did not differ, indicating homogeneity during intense and non-intense periods of reproductive activity.

Individual fecundity varied between 34,484 (410 mm FL) and 390,786 oocytes (650 mm FL), progressively increasing in relation to FL and ovary weight (Figure 6 and Table 2). The first maturity corresponded to an average length of 446.46 mm FL (Figure 7, Table 2), corresponding to $t_{50} = 1.4$ years, and based on the model, $L_{100} = 588.79$ mm FL and $t_{100} = 2.3$ years.

The estimated growth parameters were $L_{\infty} = 771.68$ mm, $k = 0.65$ year⁻¹, and $t_0 = -0.102$ years (Figure 8). The score function plot revealed a single peak corresponding to the estimated *k* value, ensuring its representativeness. *Scomberomorus brasiliensis* individuals presented ages from 0.5 to 6.5 years, predominating individuals of 1 year (32%), 1.5 years (45%) and 2 years (16%). The instantaneous growth

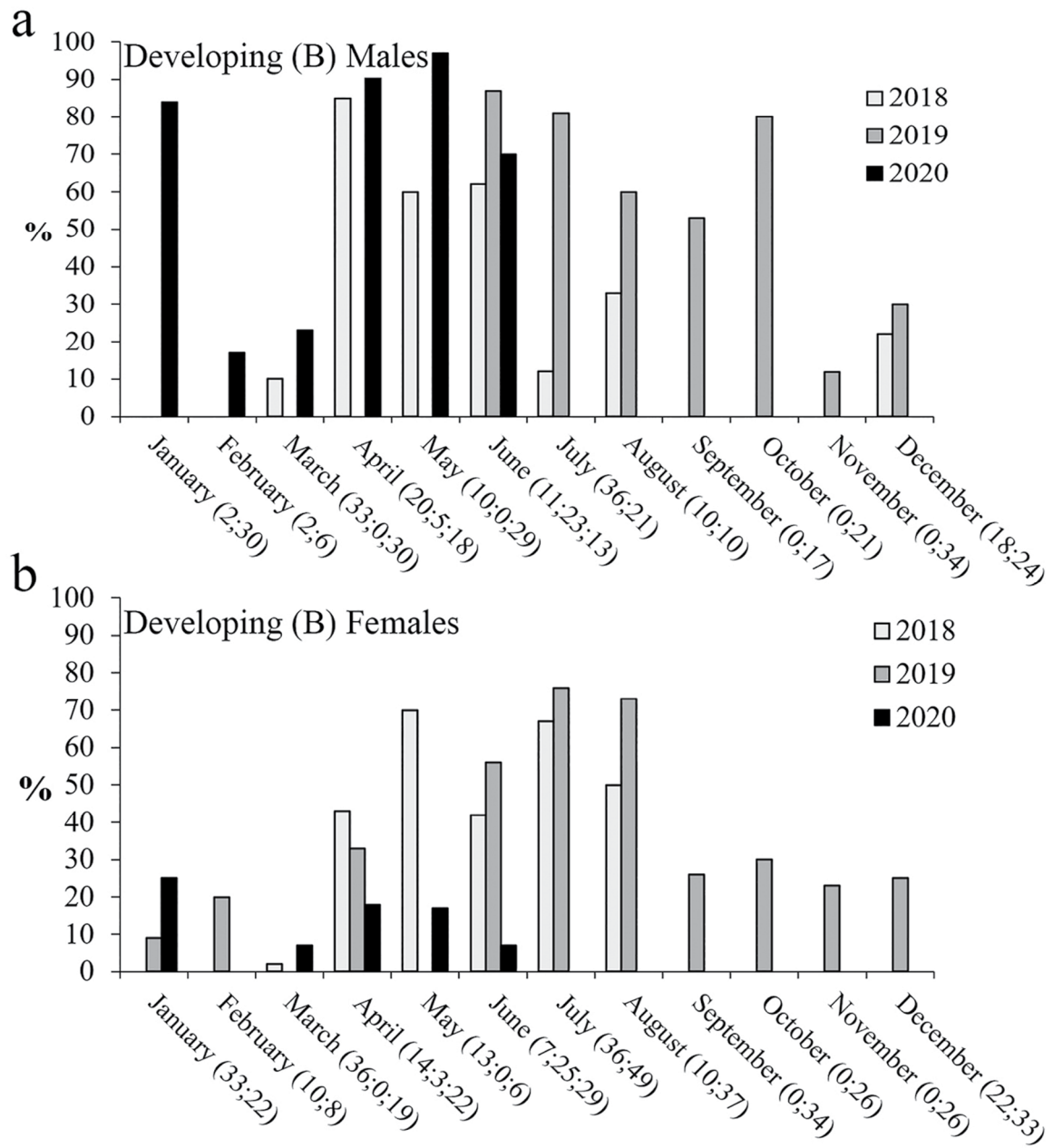


Figure 2. *Scomberomorus brasiliensis*: developing proportion of (a) males and (b) females (number of individuals by year into parenthesis, respectively).

rate evidenced a rapid growth up to 2.5 years, corresponding to 629 mm FL, which then decreased significantly (Figure 8).

DISCUSSION

Biological sampling of fish landings is crucial for understanding the population strata accessed by

fishing activity, information that subsidizes stock assessment and proper management measures (Cadima et al., 2005; Murie et al., 2012). The practical sample unit in the present study was the FMM, the focal point of a small-scale fishery, and sampling effort comprised the size range available of *S. brasiliensis*, similar to the procedures described by Batista and

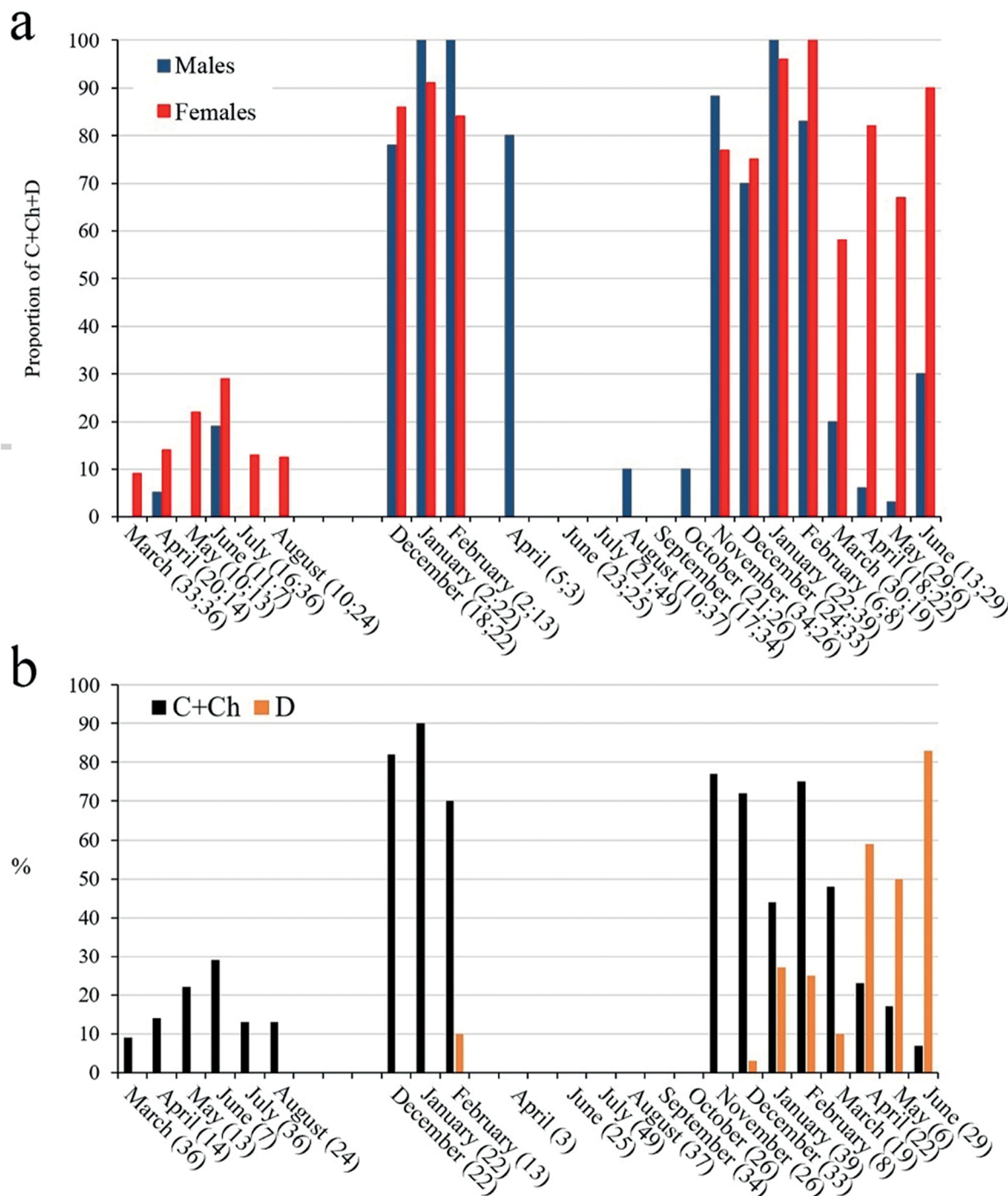


Figure 3. *Scomberomorus brasiliensis*: (a) monthly proportion of reproductive activity (C+Ch+D) individuals by sex (number of males and females into parenthesis, respectively), (b) monthly proportion of reproductive activity (C+Ch and D) females (number of individuals into parenthesis) (no samples available from September to November 2018, nor in March and May 2019).

Fabrè (2001). Thus, the population parameters of *S. brasiliensis* along the Paraná coast were properly estimated, revealing that the small-scale fishery caught mainly adults at and just after the first maturity.

The range of observed FLs was influenced by gillnet selectivity, explaining the low incidence of individuals less than 300 mm FL and larger than 700 mm FL. In the Caribbean Sea and the northern

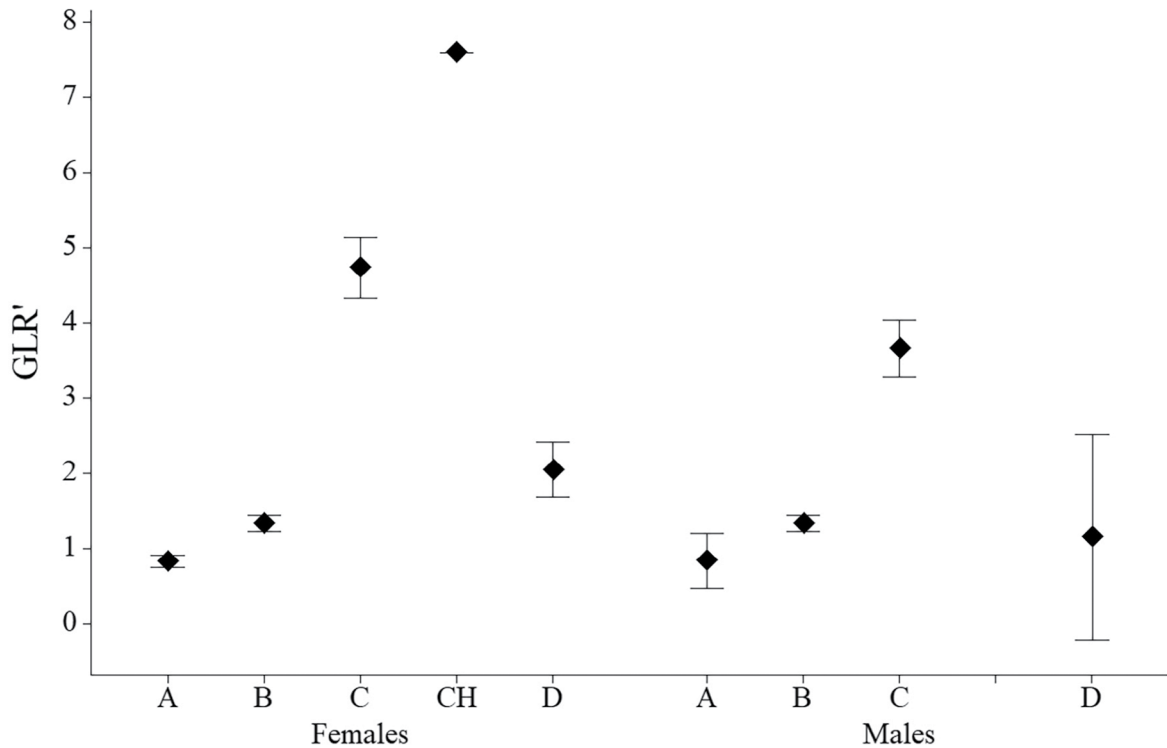


Figure 4. *Scomberomorus brasiliensis*: average values and confidence intervals (95% *t*-distribution) of gonad-length relationship (GLR') by sex and gonad developmental phase.

and northeastern Brazil, maximum lengths recorded were larger than 900 mm FL (Froese and Pauly, 2019) and attained a 1360 mm FL (Nóbrega et al., 2009), which does not occur in the small-scale fishery of Paraná. These individuals either cannot occur at this latitude or are not accessed by the fishing activity. The former has support; otherwise, larger individuals would be common in other small-scale fisheries and in the industrial fishery that occurs in adjacent areas far from the coast, which has not happened either historically (Andriguetto et al., 2006; IBAMA, 2007) or recently (PMAP, 2020). However, *S. brasiliensis* along the Paraná coast is caught mainly by gillnets (Chaves and Robert, 2003), and 99% came from this fishing gear during 2017–2019 (PMAP, 2020). Therefore, the samples in the present study well represented the adults of the area, in view of the different mesh sizes of gillnets and fishing gears used in the Paraná coast and adjacent areas (Andriguetto et al., 2006), even under selectivity effects (Hubert et al., 2012).

Size structure influences the sex-ratio. Data from the present study showed that *S. brasiliensis* females were larger than males, similar to that in northeastern

Brazil (Nóbrega and Lessa, 2009; Maia et al., 2015). This dimorphism was not evidenced in the relative growth pattern (FL–TL relationship), only in the predominance of females (0.8:1, males:females), which varied compared to other studies. In northeastern Brazil, in coastal areas between 04°39'S and 06°29'S, the sex-ratios observed were 1.1:1 ($n = 145$) in a beach (from beach trawls) (Lima et al., 2007), and 2:1 (Oliveira et al., 2015), from joining samples from various beaches and omitting the number of individuals analyzed. The former represents a local proportion between males and females; however, the latter cannot be considered owing to the lack of information. In contrast, Nóbrega and Lessa (2009) found a sex ratio of 1.4:1, sampling a large area of the continental shelf (02°30'S–13°S, macro-scale study), evidencing different patterns of *S. brasiliensis* from northeastern Brazil compared to the Paraná coast.

Length–weight relationships also present intrinsic patterns related to biological and methodological aspects (Froese, 2006). Biological aspects include stock-population identity and density-dependent processes related to population dynamics (McBride,

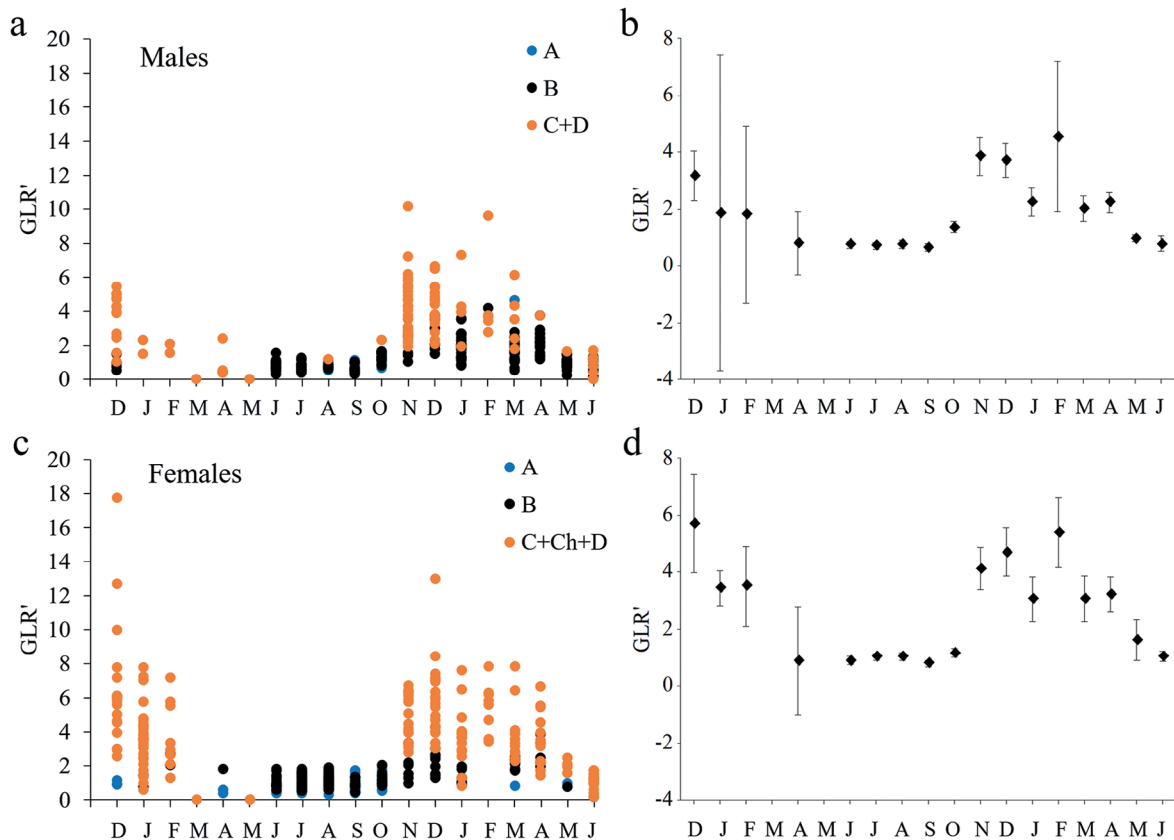


Figure 5. *Scomberomorus brasiliensis*: individual values of gonad-length relationship by gonad developmental phase for males (a) and females (c) and average values and confidence intervals (95% *t*-distribution) of gonad-length relationship (GLR') for males (b) and females (d) excluding immature individuals.

2014). Methodological aspects are related to the size range analyzed, number of fishes, and model adjustments (*i.e.* algorithm used, linear vs. non-linear procedure, checking of assumptions). Thus, although direct comparisons among different studies require caution, some insights emerge. The *b* coefficient of the Caribbean Sea and northeastern Brazil ranged between 2.800 and 3.264, mean 2.97 ($n = 9$) (Silva et al., 2005; Tagliafico et al., 2015; Froese and Pauly, 2019), suggesting a conservative pattern of negative allometry also detected in the present results. In *S. brasiliensis*, these *b* values (< 3) were closely related to their elongated body shape, which predominates growth in length (Froese, 2006).

A remarkable diagnostic herein presented is the spawning of *S. brasiliensis* on the inner continental shelf of the Paraná coast, reinforcing the group identity in the area. In northeastern Brazil, there are two

proposals, a high migratory pattern based on seasonal absences in some areas (Batista and Fabrè, 2001), and small-scale displacements in large areas (Colette et al., 2011). Both do not apply for the Paraná coast, where there is a continuous landing of individuals with 400–600 mm FL throughout the year, indicating the stock permanency in the area and small-scale fishery availability. Regarding the spawning period of *S. brasiliensis* on the Paraná coast (beginning in the spring, peaking in the summer, and finishing in the autumn), it was similar to historical records in northeastern Brazil (Gesteira and Mesquita, 1976). Nonetheless, more recent data from that area indicate spawning peaks in the summer and autumn (March to June), corresponding to the rainy season in that region (Lima et al., 2007) and matched with a higher abundance of *S. brasiliensis* (Brito and Furtado Júnior, 2010).

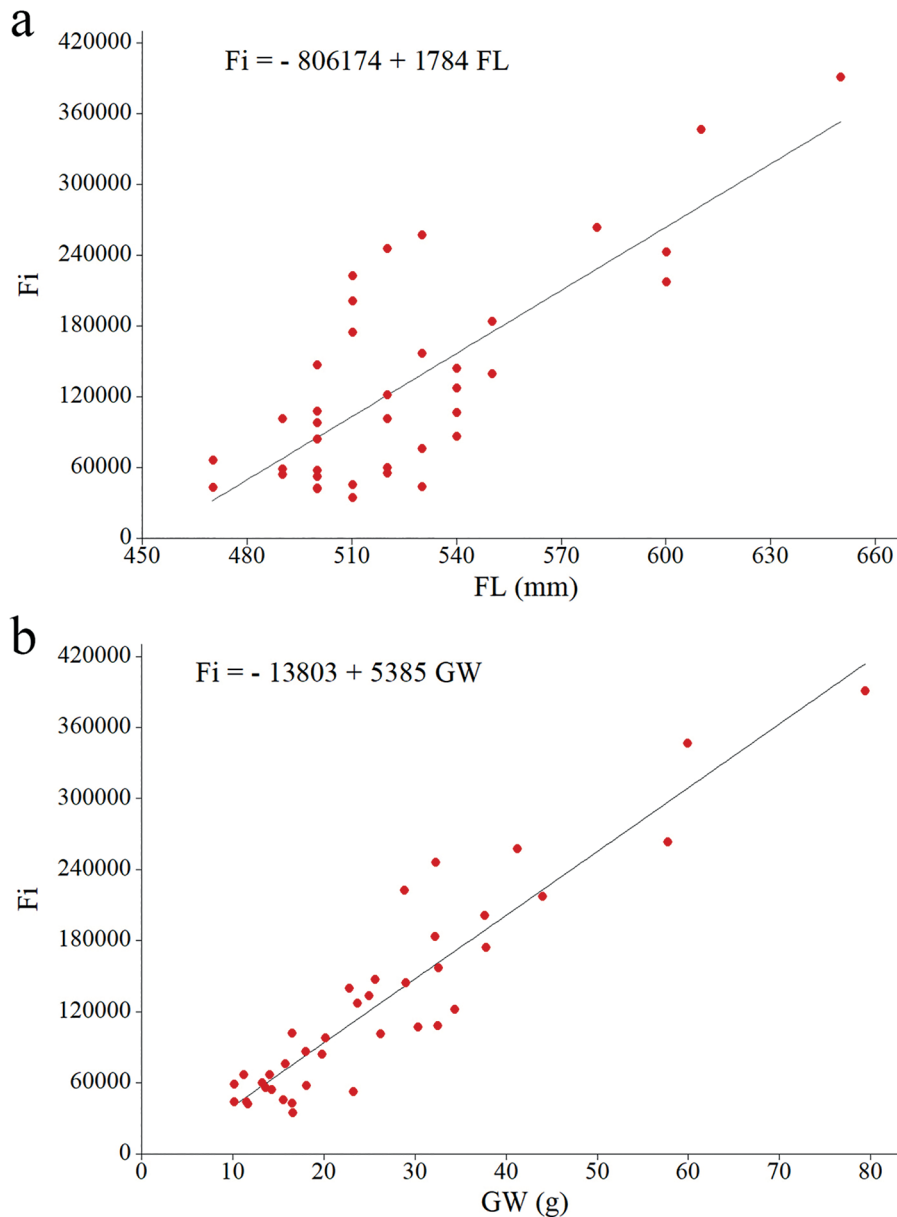


Figure 6. *Scomberomorus brasiliensis*: regressions between individual fecundity (F_i) and (a) fork length and (b) gonad weight (see also Table 2).

A methodological highlight deserves attention, the efficient use of the gonad–length relationship for spawning period diagnosis. Because of the difficulty in sampling weight data from small-scale fisheries, it was impossible to use the gonadosomatic relationship, *i.e.*, the proportion between the gonad and total body weights (Brown-Peterson et al., 2011). Thus, the gonad index ($GI = GW / FL^b$, b from the length–weight relationship), more often referred to as the gonad condition factor (Vazzoler, 1996), is a good indicator

of reproductive activity, mainly for spawning periods (West, 1990; Lowerre-Barbieri et al., 2011). The GI denominator implies an estimated value (FL^b), and it can be calculated using the expected total weight (aFL^b), becoming the gonadosomatic relationship. Simulated values can be a source of bias, and thus this approach was disregarded. Initially, the size-dependence of the GLR values constituted a problem (West, 1990), which was easily solved adopting a size-effect removal procedure (Lombarte and Lleonart,

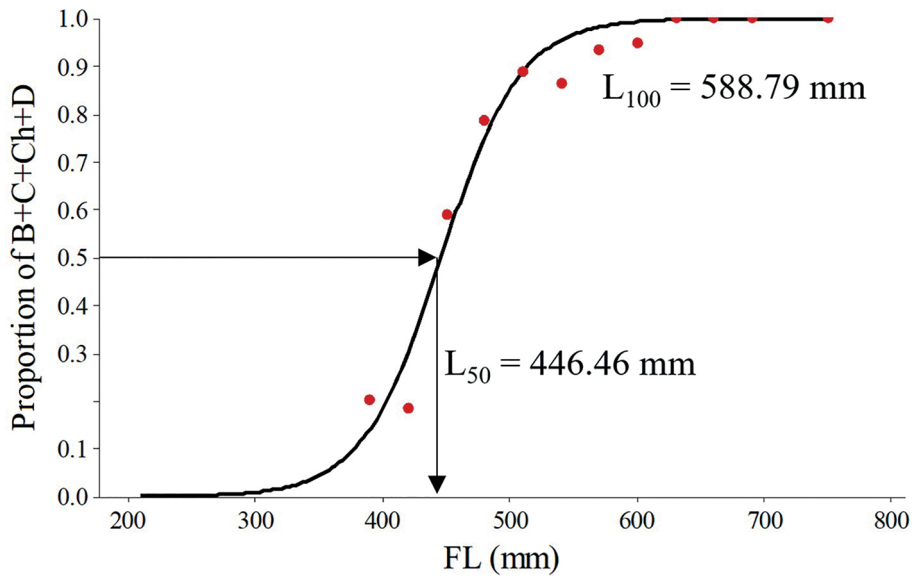


Figure 7. *Scomberomorus brasiliensis*: mature ogive of females representing average length of first maturity (L_{50}) and the length at which all individuals can reproduce (L_{100}) (see also Table 2).

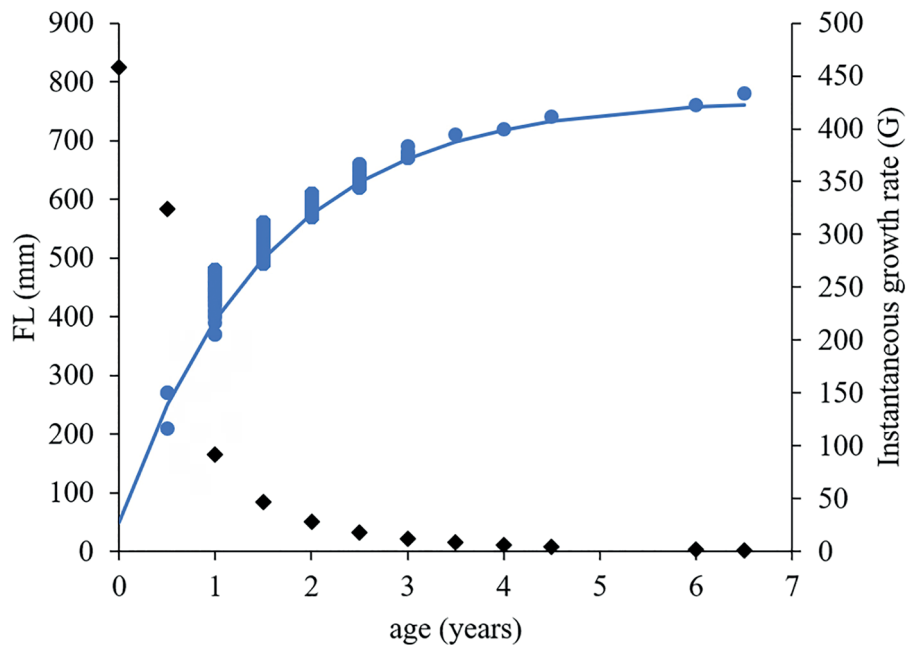


Figure 8. *Scomberomorus brasiliensis*: von Bertalanffy growth curve ($L_{\infty} = 771.68$ mm, $k = 0.65$ year⁻¹ and $t_0 = -0.102$ year) and fork lengths by age in blue. Black points indicate instantaneous growth rate (G).

1993), efficient for GLR based on the present findings. Thus, the gonad morphological attributes and volume evaluated with the gonad-length relationship indicated an extensive spawning period at the inner continental shelf of *S. brasiliensis*.

Fecundity is an important component of reproductive strategies, operating on a spatial scale related to spawning and nursery areas, and enhancing the reproductive resilience of a stock (Lowerre-Barbieri et al., 2017). For *S. brasiliensis*, fecundity was higher

in heavier gonads and larger individuals, as expected. In northeastern Brazil, other estimates include a fecundity of 2,204,000 oocytes, and 350–790 mm FL, which were directly proportional to size, age and weight (Gesteira, 1972), and 871,523 oocytes, and 350–790 mm FL (Lima et al., 2007). More than the features of each stock, differences in relation to the Paraná coast (34,484–390,786, 410–650 mm FL) can be related to period, areas, and the criteria for counting oocytes. The fecundity results are the first referential for southern Brazil, showing the importance of larger and older females in the stock maintenance and other biological and environmental factors (Lowerre-Barbieri et al., 2017).

The average length at first maturity is a tool for stock management, and is usually a referential for establishing minimum legal sizes (Lowerre-Barbieri, 2009). The current estimate for *S. brasiliensis* (446.46 mm FL corresponding to 524.44 mm TL) was similar to that in most cases in northeastern Brazil. These other estimates include 410 mm FL (Gesteira and Mesquita, 1976), 419 mm FL (Nóbrega et al., 2009), 410 mm FL (Lima et al., 2009), and 400 mm FL (Maia et al., 2015). These reveal a conservative pattern for the species in Brazil. In northeastern Brazil, there is an exception of 280 mm TL, which is a reduction in size due to overfishing (Lima et al., 2007). This last situation highlights the limitations of estimating catches of larger individuals or the use of L_{50} values to restrict catches as management measures (Chaves, 2012). Especially for *S. brasiliensis*, larger females have a remarkable contribution to the reproductive success, ensuring egg availability. We refine this diagnostic with age and growth information below.

In northeastern Brazil, previous age and growth parameters of *S. brasiliensis* included values of $L_{\infty} = 1067$ mm FL and $k = 0.16$ year⁻¹ (otolith analysis, Ximenes, 1981), $L_{\infty} = 1360$ mm FL and $k = 0.29$ year⁻¹ (modal progression analysis, Gonçalves et al., 2003), and $L_{\infty} = 957$ mm FL, $k = 0.15$ year⁻¹, and $t_0 = -0.212$ years (otolith analysis, Nóbrega and Lessa, 2009). In these studies, age groups varied between one and eight years, matching the present findings. In contrast, the maximum theoretical length ($L_{\infty} = 771.68$ mm) was lower and the growth rate ($k = 0.65$ year⁻¹) was higher than the other estimates. Differences in the results might be due to factors such as the methods applied, size structure with a predominance of juveniles

in previous studies, time and area, once the analysis herein applied was properly conducted.

The Powell-Wetherall method is more accurate to estimate L_{∞} in species that present prolonged spawning and recruitment, a trend that increases the individual variability of growth; in this situation, SLCA method is more accurate for estimating k values (Isaac, 1990). These features apply to *S. brasiliensis*, and their reproductive biology sustains the present findings regarding age and growth. In the modal progression analysis (SLCA), a new cohort appeared in January, matching the spawning peak identified here. Different cohorts were identified, despite some overlap in the interval of 400–600 mm FL (modal progression in Supplementary Material). Other elements can affect growth parameter estimation via modal progression analysis. Some species present schools structured by size, not by age (Murie et al., 2012). This probably does not apply to the present samples because, in addition to the absence of larger specimens of *S. brasiliensis* in other fisheries in the area, schools are more typical for juveniles (Maia et al., 2005; Nóbrega and Lessa, 2009), and were not numerous in the present study where adults predominated. Regarding the environmental conditions affecting fish growth, considering the heterogeneity of the inner shelf of the Paraná coast (e.g., water mass, estuaries, and temperatures), it is reasonable to hypothesize that there was growth adaptation for local thermal conditions, resulting in individuals that grow faster than in low latitudes (Yamahira and Conover, 2002). This could explain the higher growth rate value compared to the northeastern Brazil estimates, a question that remains open for future studies.

Thus, the age structure and growth parameters of *S. brasiliensis* along the Paraná coast reflect its population structure, where it is smaller and grows faster than the stock in northeastern Brazil. Current data on age and growth are robust and suitable, and can reflect the high biological productivity and shelters of the Paraná coast, including its two estuaries (Lana and Bernardino, 2018), which are areas favorable for fish growth as well as spawning, nursery, and feeding. These population patterns have resemblance with the congeneric *S. queenslandicus*, a species that occurs in northern Australia in the same latitude as that of the Paraná coast whose patterns are similar to *S. brasiliensis*, an example that reinforces the

results obtained. *Scomberomorus queenslandicus* is relatively small (L_{∞} range = 628–651 mm), grows fast (k range = 0.59–0.71 year⁻¹) and presents small displacements, with a number of stocks (Begg et al., 1997; Begg & Sellin, 1998).

Current findings and discussions attained the objectives and confirmed the hypothesis, *i.e.*, along the Paraná coast *S. brasiliensis* has its own biological patterns in terms of size, reproductive biology, age, and growth, constituting a self-sustaining group for management purposes (a stock *sensu* Cadrin et al., 2014), which is not directly related to that from northeastern Brazil. Based on this, recommendations can be proposed and must be considered in future strategic management planning (Isaac et al., 2013). Juveniles are being preserved, considering their absence in the catches, as are the larger and older individuals, mainly females. A point that deserves attention is the predominance of individuals at one year of age and in first maturity at the landings. If there is a reduction in the resource availability, size reduction, earlier maturation, and other indicators of overfishing, it is recommended a legal-size range for catches, based on the maturity and age structure are provide (Chaves, 2012). Period restrictions of *S. brasiliensis* fishing would be desirable only if larger and older females become constant at landings during spawning periods. It is strongly recommended that all measures enforced emerge from participative management, involving all stakeholders, actors, and processes (Almeida et al., 2007; Mourão et al., 2014), considering the fishing complexity along the Paraná coast (Andriguetto-Filho et al., 2006). For non-English readers, a Portuguese version of this paragraph is available in the Supplementary Material.

CONCLUSIONS

The importance of *S. brasiliensis* for the small-scale fishery along the Paraná coast is undeniable, and the present study provided relevant information regarding the population dynamic parameters of this species. The small-scale fishery accesses mainly “young adults”, *i.e.*, individuals between 400- and 650 mm FL, 1–2.5 years old, in the first maturity stage or just after this stage. Allied to the spawning period and area and growth parameters estimated, they constitute a first referential, standardizing the methods applied to monitor the species in the area. Future changes

in these attributes could reliably indicate impacts due to fishing activity or other factors. These biological indicators are essential for proper management (McBride, 2014), highlighting that small-scale fishery is “our best hope for sustainable utilization of coastal resources” (Pauly, 2006).

Further studies focusing on the *S. brasiliensis* stock along the Paraná coast must expand the present analyses. These could comprise: (i) histological analysis of gonads and oocyte diameter concerning the gonad-length relationship, providing additional information regarding the maturation process (West, 1990; Lowerre-Barbieri et al., 2011); (ii) otolith analysis (and/or other calcified structures) to refine age and growth estimates (Vaz-dos-Santos, 2015); (iii) inspection of eggs and larvae in the area (Lowerre-Barbieri et al., 2017); and (iv) an accurate definition of stock limits and connectivity level among groups in the species distribution area (Cadrin et al., 2014).

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AUTHOR CONTRIBUTIONS

P.T.C.C.: Conceptualization; Data curation; Formal Analysis; Funding acquisition; Investigation; Methodology; Resources; Supervision; Visualization; Writing - original draft; Writing - review & editing;

P.O.B.: Formal analysis; Investigation; Visualization; Writing - review & editing;

A.M.V.S.: Formal analysis; Methodology; Validation; Visualization; Writing - original draft; Writing - review & editing.

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