Regional Studies in Marine Science 76 (2024) 103623

Contents lists available at ScienceDirect

Regional Studies in Marine Science

journal homepage: www.elsevier.com/locate/rsma

Life-history updates and stock assessment of *Macrodon atricauda* (teleostei, sciaenidae) from southern Brazil

Eidi Kikuchi[a,b,*,1], Luis Gustavo Cardoso[b,2], Rodrigo Sant'Ana[c,3], Bruno L. Mourato[d,4], Maíra de Sousa Almeida[b], Manuel Haimovici[b,5]

[a] *Universidade Federal do Rio Grande, Instituto de Oceanografia, Programa de Pós-Graduação em Oceanografia Biológica, Universidade Federal do Rio Grande, Rio Grande, Brazil*

[b] *Universidade Federal do Rio Grande, Laboratório de Dinâmica Populacional Pesqueira, Instituto de Oceanografia, Caixa Postal 474, Avenida Itália Km 8, Rio Grande, RS CEP 96201-900, Brazil*

[c] *Universidade do Vale do Itajaí, Escola Politécnica, Laboratório de Estudos Marinhos Aplicados, Itajaí, Brazil*

[d] *Universidade Federal de São Paulo, Instituto do Mar, Santos, Brazil*

ARTICLE INFO

Keywords:
Age
Growth
Maturity
Overfished
Stock synthesis

ABSTRACT

The coastal demersal sciaenid fish *Macrodon atricauda* has been intensely fished since the 1950s along the southern Brazilian coast, resulting not only in decreasing abundance but also in long-term changes in its life history. Previous studies reported long-term increases in individual growth, size, and age at maturity. Using individual observed length-at-age, we did not observe the previously reported growth changes despite the increase in the mean length of older individuals from 1976 to 2023. These observed changes did not affect the estimation of the von Bertalanffy growth parameters, likely due to the species' faster growth at earlier ages and short lifespan. The length at first maturity remains smaller than the previous estimations from the 1970s but has not changed since the 2000s. The population dynamics assessed considering the updated life history parameter, including the size at maturity changes, showed that the species is not suffering from overfishing (*i.e.*, $F_{2019}/F_{MSY} = 0.17$). However, the spawning stock biomass was estimated at low levels (*i.e.*, $SSB_{2019}/SSB_{MSY} = 0.59$), indicating an overfished status highlighting the need for management action. The apparent stability of the life-history parameters observed for the species in the last four decades may be attributed to a combination of traits promoting resilience and recovery, including high fecundity, low age at maturity, fast individual growth, and a relatively short lifespan. In fact, despite decades of intense fishing, *M. atricauda* remains an important coastal demersal species in the landings of southern Brazil.

1. Introduction

Overfishing worldwide has triggered significant and lasting changes in the dynamics of marine fish populations (Hutchings, 2000; Kuparinen et al., 2016), primarily attributed to decreases in population density (Law, 2000; Saborido-Rey and Kjesbu, 2005; Pérez-Rodríguez et al., 2013; Haimovici and Cardoso, 2017). The decline of fish stock abundance resulting from biomass removal by fisheries leads to life history modifications as species adapt to changes in mortality and food availability (Dieckmann and Heino, 2007; Darimont et al., 2009). These changes can compromise the resilience of fish populations against environmental fluctuations and elevate the risk of commercial collapse (Longhurst, 2010; Marteinsdottir and Thorarinsson, 1998).

One such species significantly impacted by these trends is the southern king weakfish, *Macrodon atricauda* (Günther, 1880), which inhabits the shallow coastal waters (up to 60 m) in soft bottom areas

---

* Corresponding author at: Universidade Federal do Rio Grande, Instituto de Oceanografia, Programa de Pós-Graduação em Oceanografia Biológica, Universidade Federal do Rio Grande, Rio Grande, Brazil.

E-mail address: eidikikuchi@hotmail.com (E. Kikuchi).

[1] https://orcid.org/0000-0002-9940-9767

[2] https://orcid.org/0000-0003-1026-0853

[3] https://orcid.org/0000-0003-2252-6014

[4] https://orcid.org/0000-0001-8405-3983

[5] https://orcid.org/0000-0003-1741-8182

https://doi.org/10.1016/j.rsma.2024.103623
Received 29 February 2024; Received in revised form 4 June 2024; Accepted 5 June 2024

from Espírito Santo state (Brazil) to northern Argentina. Genetic studies have identified five distinct populations of *M. atricauda*, with the largest occurring between the La Plata River estuary and Cape Santa Marta Grande in southern Brazil (Rodrigues et al., 2014), hereafter called southern Brazil. Since the late 1950s, this region has been a significant focus of industrial bottom pair-trawl fisheries (Haimovici, 1998; Valentini et al., 1991; Yamaguti and Moraes, 1965; Yesaki and Bager, 1975), resulting in long-term changes in population parameters for several sciaenid species (Miranda and Haimovici, 2007; Alves et al., 2020; Haimovici et al., 2021, 2022), including *M. atricauda* (Haimovici and Cardoso, 2017).

Decades of intense marine industrial fishing in southern Brazil have led to a decline in the abundance of the entire demersal fish community on the continental shelf (Haimovici, 1998; Haimovici and Cardoso, 2017). This decrease in abundance has reduced competition for benthic prey and potentially increased food availability for sciaenid species in the area (Cardoso and Haimovici, 2016). Consequently, it has been inferred that changes in the growth and maturity patterns of the main sciaenid stocks in the region, including *Cynoscion guatucupa*, *Cynoscion jamaicensis, M. atricauda*, *Micropogonias furnieri*, and *Umbrina canosai*, have occurred as a density-dependent response to both intra- and interspecific competition resulting from the overall decline in demersal fish biomass along southern Brazil (Miranda and Haimovici, 2007; Cardoso and Haimovici, 2016; Alves et al., 2020; Haimovici et al., 2021, 2022). Despite their distinct life cycles, these sciaenid species exhibit relative resilience compared to other fish families, attributed to their high fecundity and phenotypic plasticity in adapting to decreasing population densities (Haimovici and Cardoso, 2017; Haimovici et al., 2021, 2022).

Specifically, former investigations into the long-term effects of fishing on *M. atricauda's* life history reported growth increases between 1977 and 2009 (Cardoso and Haimovici, 2011) and a reduction in age and size at first maturity from 1976 to 2011 (Cardoso and Haimovici, 2014). To delve deeper into the impact of fishing on *M. atricauda*, Cardoso and Haimovici (2015) analyzed various population indicators between the 1950s and the 2000s, including catch per unit effort (CPUE), age composition, total mortality, and exploitation rate. Over these five decades, this study evidenced a reduction of the CPUE by nearly 50 %, a truncation of the age composition, an increase in the total mortality of almost 280 %, and a substantial reduction in total biomass by nearly 67 %. Despite this catastrophic scenario, the stock did not collapse, remaining among one of the most landed demersal resources in southern Brazil (Cardoso et al., 2022; Perez and Sant'Ana, 2022a, 2022b).

Life-history parameters are essential input values for assessing the fish stock status and establishing reference points, which, in turn, are critical for sustainable fisheries management (Sagarese et al., 2015; Chrysafi and Kuparinen, 2016). Given that harvest-induced life history changes are likely to intensify (Audzijonyte et al., 2016), our objective in this study was to update the growth and maturity parameters of *M. atricauda* stock from southern Brazil and perform an assessment with these updated parameters to generate potentially useful information for future management.

2. Methods

2.1. Data source

Macrodon atricauda was sampled from commercial bottom trawlers and bottom gillnets landed in Rio Grande from 2016 to 2023 between latitudes 30'S and 34°40'S. The samplings involved measuring total length (TL, mm) and total weight (TW, g), determining the sex, extracting sagittae otoliths for age estimations, and collecting gonads for maturity analysis. For the temporal comparative analysis, data on age and growth for earlier periods (1977–2009) were obtained from Cardoso and Haimovici (2011), while information on maturation covering the years 1976–2011 was extracted from Cardoso and Haimovici (2014).

2.2. Growth

For the current period age estimations, 568 sagittae otoliths (381 females and 187 males) were embedded in a transparent polyester resin and sectioned (0.2–0.3 mm) transversally through the nucleus with a low-speed precision saw (Isomet Buehler Ltd) and mounted on histology slides with synthetic resin (Entellan, Merck). Images of otolith sections were captured using a stereoscopic microscope at 10× magnification by a camera with a 2048 × 1536 pixels per inch resolution. Two readers independently counted alternate opaque and translucent bands. If counts differed, otoliths were counted again by both readers and discarded from further analyzes if the difference persisted.

Growth analyses conducted for earlier periods (i.e., 1977–1979, 1984–1986, 1997–1998, and 2006–2009) used mean back-calculated lengths-at-age within a von Bertalanffy growth model (Cardoso and Haimovici, 2011). Therefore, the same methodology was applied in estimating growth for the current period (2016–2023). For that, the distance between the otolith nucleus and the end of each opaque band (Fig. 1) was measured with ImageJ 1.47 (www.imagej.nih.gov). Then, back-calculated lengths-at-age were computed using the proportional hypothesis (Francis, 1990) through the same regression parameters obtained by Cardoso and Haimovici (2011). Thus, individual total length at the time of the formation of the *i*th opaque band was back-calculated as:

$$\text{females}: \quad TL_i = (TL * (\ln(R_i) + 1.829))/\ln(R) + 1.829$$

$$\text{males}: \quad TL_i = (TL * (\ln(R_i) + 1.919))/\ln(R) + 1.919$$

where R_i is the distance from the nucleus to the end of the *i*th opaque band, and R is the distance from the nucleus to the inner edge on the sections of the otoliths.

Nevertheless, beyond the inherent subjectivity in determining measurements for each opaque band across different readers and periods, a growth model based only on the back-calculated mean lengths-at-age leads to the omission of crucial variability inherent in the individual data. In this way, growth for all analyzed periods (*i.e.*, 1977–1979, 1984–1986, 1997–1998, 2006–2009, and 2016–2023) was also described from individual observed lengths-at-age. Moreover, Cardoso and Haimovici (2011) showed that there are no variations in the length of *M. atricauda* during the first year of age across the periods; therefore, to enhance the precision of growth model adjustments, 20 juveniles under one year of age with daily growth increments calculated by Almeida (2010), were integrated into each model for each period analyzed.

The fit of the models to the data was performed with a Bayesian approach (Kinas and Andrade, 2010). The age-at-length data were assumed as log-normally distributed: $y_i = \log N(\mu_i, \sigma^2)$, where y_i is the length distribution with an average expected length at an age class *i* with variance σ^2. A logarithmic version of the von Bertalanffy equation was used for computational convenience:

$$\mu_i = \log(L_\infty) + \log(1^{-k(i-t_o)})$$

Uninformative priors were constructed:

$$p(\log L_\infty) \sim dN(0, 0.001) \quad I \quad (-10, \quad 10)$$

$$p(\log k) \sim dN(0, 0.001) \quad I \quad (-5, \quad 5)$$

$$p(\log t_0) \quad \sim dU(- \quad 3, \quad 0)$$

The posterior distributions of each period (obtained *via* the stochastic Monte Carlo Markov Chain process) were used to compare the estimates of the growth parameters across time. After 10,000 burn-in runs, every second value of the remaining 20,000 was retained, resulting in a final sample of 10000 in the posterior distribution (Kinas and Andrade, 2010). The posterior distribution of each estimated parameter (log L_∞,

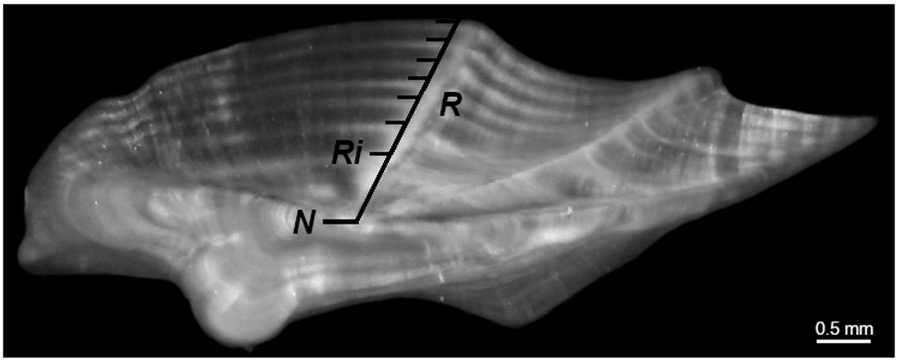

Fig. 1. Thin section examined with reflected light of a seven-year-old male (TL: 387 mm) *Macrodon atricauda* sampled in February/2020 in southern Brazil. Black bars indicate the end of each opaque band. N: nucleus; Ri: the distance from the nucleus to the end of each opaque band; R: the distance from the nucleus to the inner edge. Opaque bands can be seen as white bands, whereas translucent ones can be seen as dark bands.

log k, log t_0) provided an easy way to compare the results among periods. All statistics in this study were run by R version 3.6.1. The MCMC was performed by *OpenBUGS*, using the libraries *R2WinBUGS* (Sturtz et al., 2005) and *BRugs* (Thomas et al., 2006).

2.3. Sexual maturation

Sexual maturity stages were identified using a macroscopic maturation scale applied to 1708 gonads sampled from 2016 to 2023, comprising 1002 females and 706 males. The gonads extracted were classified into seven stages: virginal (I), early maturing (II), maturing (III), advanced maturing (IV), spawning (V), recovering (VI), and spawned (VII) (Haimovici and Cousin, 1989). To avoid misidentification between mature and recovering stages, only specimens collected during the reproductive peak, specifically between November and March (Cardoso and Haimovici, 2014), were chosen for estimating maturation ogives.

The maturity stages and the mean gonadosomatic index (GSI = 100 × gonad weight (g)/total weight (g) were used as a criterion to discriminate immature from mature specimens. Females in stage III or above with GSI ≥ 2 and males in stage III or above with GSI ≥ 0.8 were considered mature (Cardoso and Haimovici, 2014).

For comparative purposes, the length at first sexual maturity (L_{50}) estimated for 2016–2023 followed the same protocol and criteria established by Cardoso and Haimovici (2014), who had previously determined the L_{50} for *M. atricauda* during earlier periods (*i.e.*, 1976–1980, 1983–1988, 1997–1998, and 2008–2011) with a Bayesian approach with a logistic model (Kinas and Andrade, 2010). The total number (*ni*) and number of mature individuals (*yi*) were calculated for each sex in 10-mm length classes (*i*). Where *Θi* expresses the probability that an individual in a length class was sexually mature and was assumed to follow a binomial distribution *Bin* (*ni*, *Θi*). Data were fitted to a logistic model defined by the *logit* link function, which transforms the parameter *Θi*, restricted to the interval [0,1] to a binomial distribution m between − ∞ and + ∞ (Kinas and Andrade, 2010):

$$mi = \quad g \quad (\Theta i) \quad = \log(\Theta i \quad /1 \quad - \Theta i)$$

$$mi = \beta 0 \quad + \beta 1.Xi$$

where *mi* is the probability of maturity for each *Xi* at each length class.

Length at maturity was defined as $L_{50} = -\beta 0/\beta 1$. The posterior distribution $p\ (\beta 0,\ \beta 1|D)$ was obtained using MCMC to compare the overlap of distributions and thereby avoid further statistical analyses (Kinas and Andrade, 2010). The MCMC was performed by *OpenBUGS*, using the libraries *R2WinBUGS* (Sturtz et al., 2005) and *BRugs* (Thomas et al., 2006).

The age at first sexual maturity (A_{50}) was then calculated for each sex and period by converting the currently estimated L_{50} and the earlier values estimated by Cardoso and Haimovici (2014). For this, the L_{50} and the growth parameters estimated in each period through the individual observed lengths-at-age were used in a von Bertalanffy inverse function, as stated below:

$$A_{50} = \frac{1}{k}\ln\left(\frac{L_\infty - \quad L_{50}}{L_\infty - \quad t_0}\right)$$

2.4. Population dynamics

The status of the *M. atricauda* stock from Brazil was assessed using the Stock Synthesis Data-limited Tool framework (SS-DL tool; Cope, 2020) based on the Stock Synthesis likelihood-based statistical catch-at-age modeling package (Methot and Wetzel, 2013). In addition to incorporating input data related to fishing sources, such as catches, length compositions, and abundance indices, this model is based on pre-specified life history parameters, including growth (L_∞, k, and t_0), natural mortality (M), females length at maturity (L_{50}), length-weight relationship, and recruitment parameters (steepness and log of initial recruitment).

Landing of *M. atricauda* was obtained from reports from the Rio Grande Fisheries Research Center (CEPERG, 1945–2011), bulletins of industrial fisheries landed in the Rio Grande do Sul State (FURG-MPA, 2012–2018; FURG-SEMA, 2020) and Santa Catarina State (CEPSUL, 1978–1999; PMAP-UNIVALI, 2000–2019). Landings for the main fishing fleets that operate in the study area were combined into two fleets: bottom trawling (pair, otter, and double-rig trawling) and artisanal fishing, covering the period between 1945 and 2019 (Fig. 2**a**).

The length composition dataset of this species is available from the long-term sampling program conducted by the Oceanography Institute from the Federal University of Rio Grande (IO-FURG) since 1976 (Haimovici, 1998; Cardoso et al., 2022). Between 1977 and 2019, 183,335 individuals were measured from the tips of the snout to the end of the extended caudal fin for pair bottom trawling activity (Fig. 2**b**). Only one year of length composition was available for the artisanal fleet, with 166 individuals measured. Despite this fleet's limited representation of length compositions, this information is crucial for estimating selectivity. The length compositions were defined in 2 cm TL bins for both fleets. Lengths were not sexed; thus, all compositions available for the population modeling were treated as unsexed. The effective sample sizes were equal to the *ln* (number of observations) to reduce the effect of pseudo-replication in sampling and decrease the weight of length data in the overall model likelihood.

Two standardized abundance indices were available for the bottom trawling fleet (Cardoso et al., 2022): one referring to pair bottom trawling activity for the period between 1977 and 2019 and the other for double-rig bottom trawling between 1994 and 2018 (Fig. 2**c**). The pair bottom trawl abundance index was broken into two temporal blocks

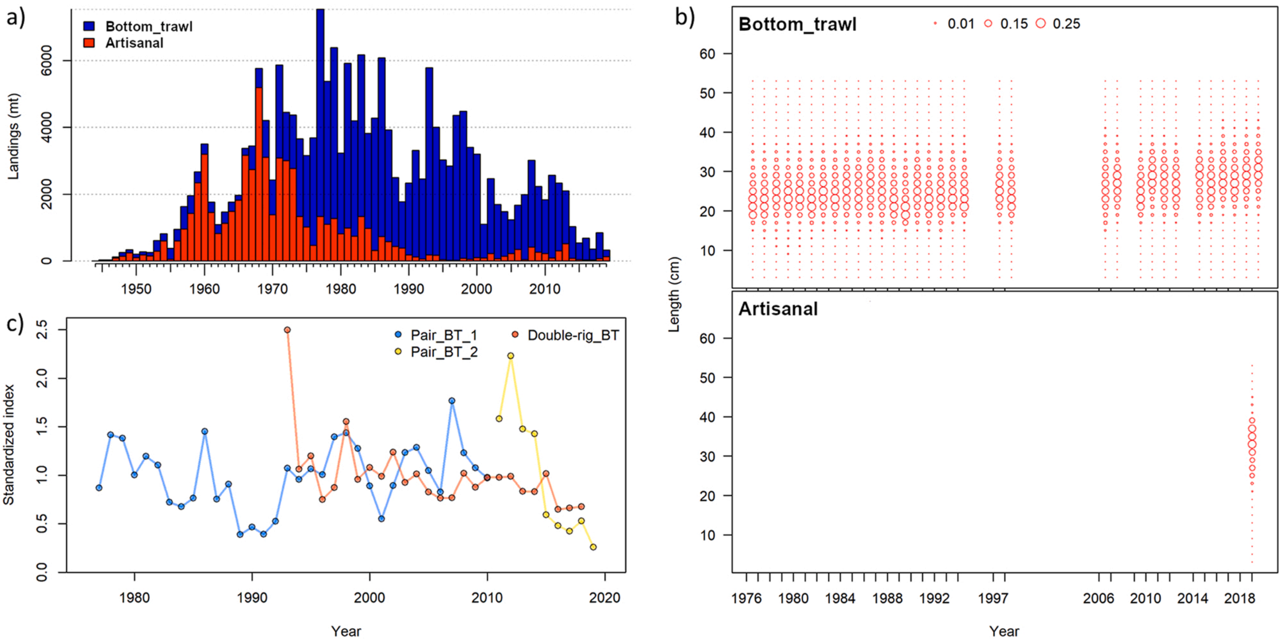

Fig. 2. a) Total landings of *Macrodon atricauda* by the fishing fleets employing bottom trawling (including pair, otter, and double-rig trawling) and artisanal fishing in southern Brazil from 1945 to 2019. b) Length composition data for pair bottom trawl and artisanal fishing fleets. Red bubbles indicate the proportion of each length bin in each year. c) Standardized catch per unit of effort for the pair bottom trawling fleet broken in two time-blocks and the double-rig bottom trawling fleet. All these data were primarily compiled by Cardoso et al. (2022).

since, from 2010 onwards, this fleet began to operate in deeper waters and capture larger fish, as observed in Fig. 2**b**.

Based on the data availability, the model was set up to reconstruct the historical spawning stock biomass (SSB) until 2019 for one area, two fleets, and two sexes. Concerning the life-history parameters, the growth and maturity estimates derived from this study were used as inputs for the model. Natural morality was estimated for each sex through the empirical estimation ($M = 4.118k^{0.73}\ L_{\infty}^{-0.33}$) proposed by Then et al. (2015). Length-weight parameters were obtained for pooled sexes from Cardoso and Haimovici (2011) (*i.e.*, $TW = 1.36 \times 10^{-4} \times TL^{3.33}$), and the weight-fecundity relationship assumed was proportional to a length-weight relationship (*i.e.*, eggs = aTL^{b}). Steepness was set at 0.61, corresponding to the value estimated for species using the *FishLife* package (Thorson et al., 2023). A standard Beverton-Holt stock--recruitment relationship was assumed with a log of initial recruitment (ln R0) estimated internally through maximum likelihood estimation (MLE). Deviations from the stock-recruit relationship were assumed only when length composition data were available (*i.e.*, from 1977 to 2019). Selectivity was freely estimated by the model, assuming an initial logistic model (asymptotic selectivity) for the bottom trawling fishery and a double-normal distribution for the artisanal fishing.

Model convergence was assessed using the Carvalho et al. (2021) flow chart. The first diagnostic was whether the Hessian matrix (matrix of second derivatives of the likelihood concerning the parameters) was positive and definite. The second diagnostic ensured joint residual plots were randomly distributed. The third diagnostic was a retrospective analysis with five-year retrospective peels. Diagnostic tests for Stock Synthesis were performed with the *ss3diags* (Carvalho et al., 2021) and *r4ss* packages (Taylor et al., 2021).

3. Results

3.1. Growth

Overall, 568 specimens (381 females and 187 males) measuring from 153 mm to 472 mm, collected between 2016 and 2023, had otolith sections examined for aging. Of these specimens, 29 females and 21 males had no discernible growth bands in the otolith sections and were discarded. For the remaining, the identification and measurement of opaque bands exhibited consistency for both sexes, as evidenced by the back-calculated mean length-at-age closely aligning with the observed mean length-at-age (Table 1). The oldest females were six years old, while the oldest male was seven years old.

For the temporal comparisons, 1566 fishes previously aged by Cardoso and Haimovici (2011) grouped across four distinct periods (1977–1979, n: 280; 1984–1986, n: 270; 1997–1998, n: 328; 2006–2009, n: 688) were used to reconstruct growth curves based on the observed individual lengths-at-age. In the first analyzed period (1977–1979), the credibility intervals of the growth curve, estimated using the observed lengths, did not completely overlap with the back-calculated mean length-at-age curve estimated by Cardoso and Haimovici (2011), suggesting a significant difference between the applied methods. (Fig. 3). For the remaining periods, there was no significant difference between the curves based on the back-calculated mean length or the observed lengths (Fig. 3).

Despite the apparent increase in L_{∞} for both sexes over time, the credibility intervals of all von Bertalanffy parameters, derived from the observed individual lengths-at-age, overlap across all analyzed periods (Table 2), indicating the absence of differences in growth. As the growth curve estimated with the back-calculated mean length-at-age for the period 2016–2023 did not account for the observed lengths of juveniles under one year of age, it led to a less accurate fit of the von Bertalanffy parameters, resulting in lower values for both k and t_0 (Fig. 3, Table 2).

Although a Kruskal-Wallis test indicates variability in length-at-age across the periods, it is not possible to observe a consistent pattern of increased growth by age over time (Fig. 4). However, individuals of both sexes aged five years or older showed a significant increase between the first period (1976–1979) and the last one analyzed (2016–2023).

3.2. Sexual maturation

Length at first sexual maturity (L_{50}) differs significantly between male and female *M. atricauda* (Fig. 5). L_{50} exhibits a decline in posterior distributions for both sexes from 1976–2011 (Cardoso and Haimovici,

Table 1

Observed mean total length (TL, mm) in the landings and back-calculated mean total length-at-age (TL, mm) for males and females of *Macrodon atricauda* fished along southern Brazil between 2016 and 2023.

Females								
Age (year)	n	Observed mean TL	Annulus number					
			I	II	III	IV	V	VI
1	43	258.8	252.8					
2	99	314.7	248.5	311.0				
3	142	355.5	244.8	312.3	352.7			
4	38	377.5	234.2	305.6	348.2	376.3		
5	23	400.9	236.0	299.2	343.6	374.8	398.9	
6	7	415.3	225.5	297.2	339.0	369.2	395.4	414.2
Back-calculated mean TL			244.7	309.8	350.4	375.1	397.3	414.2

Males									
Age (year)	n	Observed mean TL	Annulus number						
			I	II	III	IV	V	VI	VII
1	59	241.3	239.1						
2	46	300.4	241.6	296.4					
3	41	318.9	227.1	282.1	315.8				
4	10	330.0	222.7	275.0	305.4	327.6			
5	5	352.4	208.6	259.3	294.9	321.8	339.4		
6	4	384.7	226.4	282.8	319.9	345.6	367.9	382.6	
7	1	387.0	215.2	272.5	304.0	330.1	349.4	369.5	387.0
Back-calculated mean TL			234.6	286.6	312.8	331.1	354.7	380.0	387.0

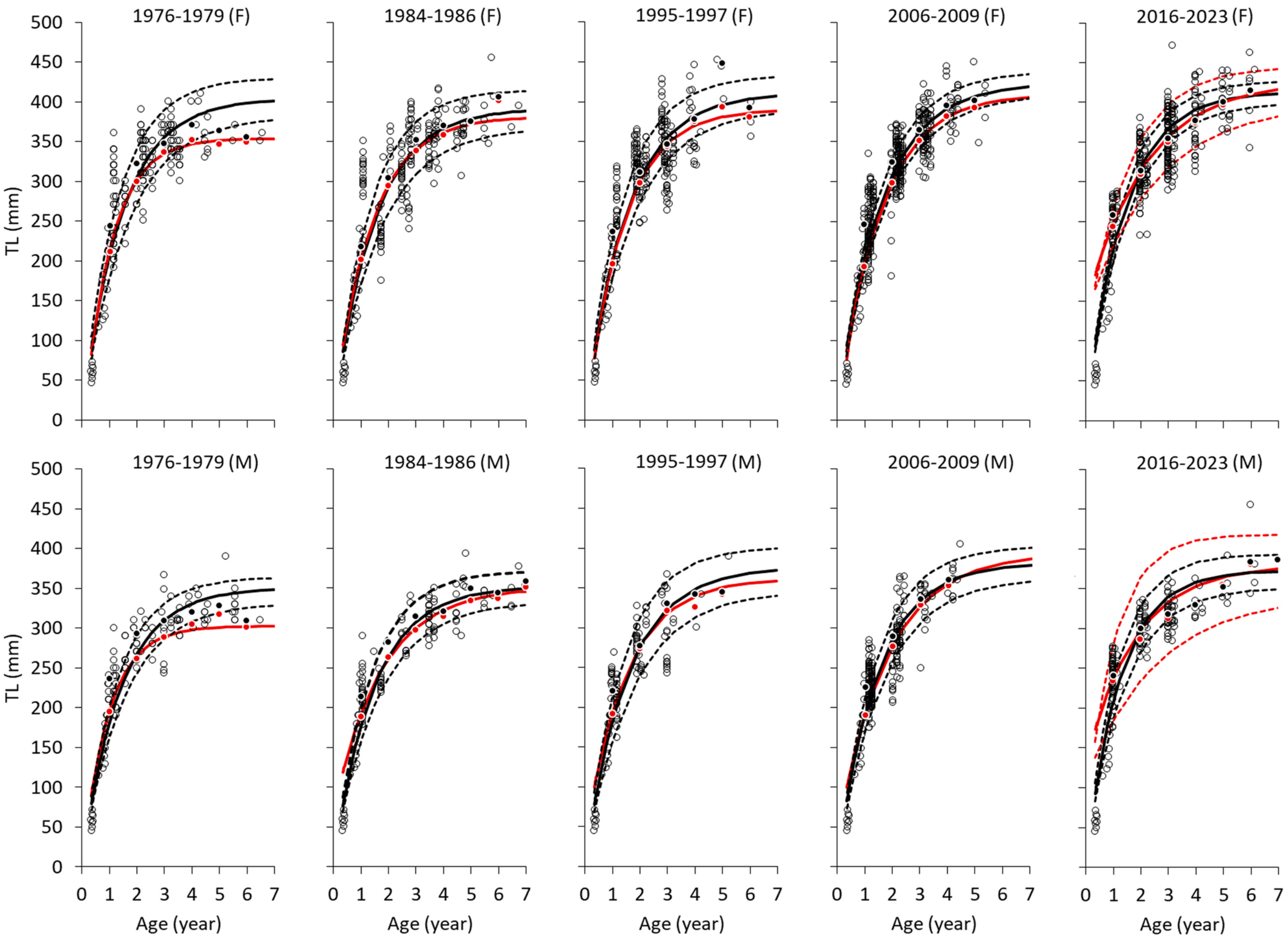

Fig. 3. Von Bertalanffy growth curves of *Macrodon atricauda* females (F) and males (M) for observed individual length-at-age (empty black circles) and back-calculated mean length-at-age (red circles) fished along southern Brazil between 1976 and 2023. The continuous line indicates the regression line. The dashed line indicates the credibility interval (α = 0.05). Black full circles indicate the observed mean lengths-at-age. Red regression lines from 1976 to 2009 were extracted from Cardoso and Haimovici (2011).

Table 2
Von Bertalanffy growth parameters (Lower and Upper credible intervals, $\alpha = 0.025$) for the observed individual length-at-age of *Macrodon atricauda* fished in south Brazil between 1976 and 2023 and for the back-calculated mean length-at-age during 2016–2023.

Sex	Period	L_∞			k			t_0		
		Mean	2.5 %	97.5 %	Mean	2.5 %	97.5 %	Mean	2.5 %	97.5 %
Females	1976–1979	404.0	381.59	429.93	0.70	0.62	0.78	-0.004	-0.01	0.00
	1984–1986	391.9	368.24	415.51	0.68	0.60	0.77	-0.008	-0.03	0.00
	1995–1997	410.2	390.56	432.54	0.66	0.59	0.73	-0.004	-0.02	0.00
	2006–2009	423.5	410.01	438.01	0.64	0.60	0.68	-0.003	-0.01	0.00
	2016–2023	413.7	400.88	427.44	0.72	0.67	0.78	-0.003	-0.01	0.00
	2016–2023 (Back-cal.)	427.7	398.94	445.67	0.47	0.40	0.66	-0.85	-1.00	-0.38
Males	1976–1979	350.5	331.97	364.06	0.714	0.65	0.796	-0.006	-0.022	0.00
	1984–1986	352.0	333.42	371.71	0.681	0.609	0.756	-0.007	-0.025	0.00
	1995–1997	375.6	346.64	401.52	0.649	0.573	0.743	-0.008	-0.029	0.00
	2006–2009	382.3	362.97	402.73	0.688	0.619	0.745	-0.003	-0.013	0.00
	2016–2023	373.5	351.96	394.01	0.802	0.725	0.893	-0.005	-0.02	0.00
	2016–2023 (Back-cal.)	380.0	342.10	418.74	0.559	0.385	0.948	-0.7	-0.993	-0.15

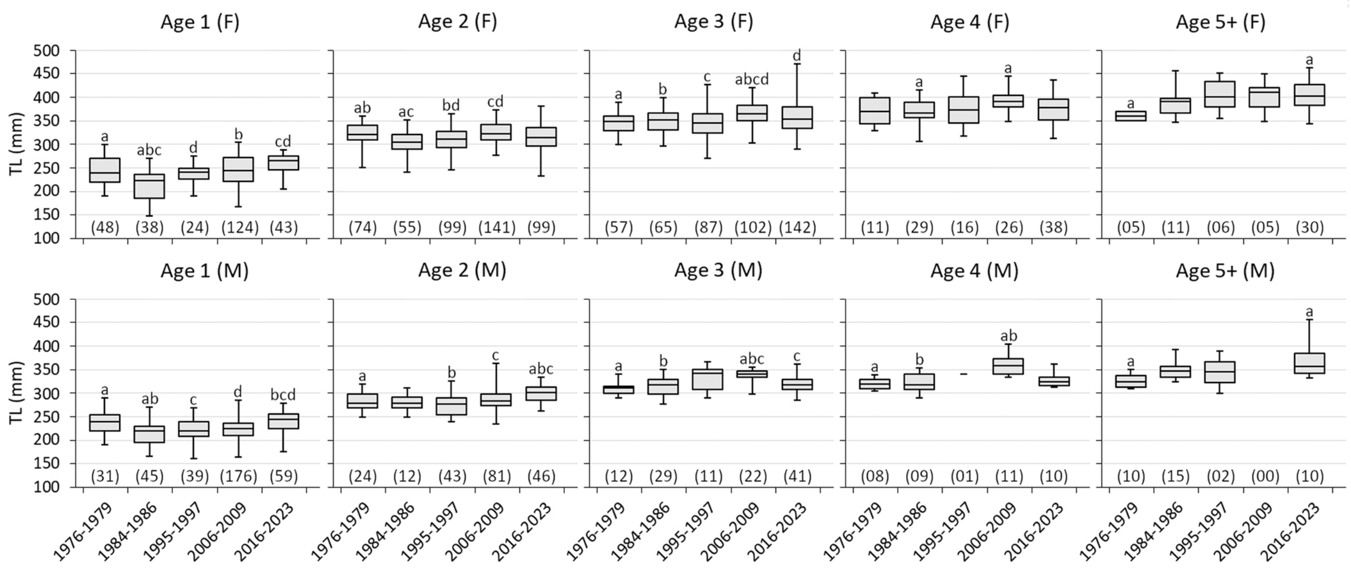

Fig. 4. Box plot representation of the length-at-age of *Macrodon atricauda* females (F) and males (M) for different periods. Similar letters above the boxes indicate significant differences between groups, as determined by the Kruskal-Wallis test ($p < 0.05$). The number of samples for each age group in each period and sex is indicated in parentheses below the corresponding box.

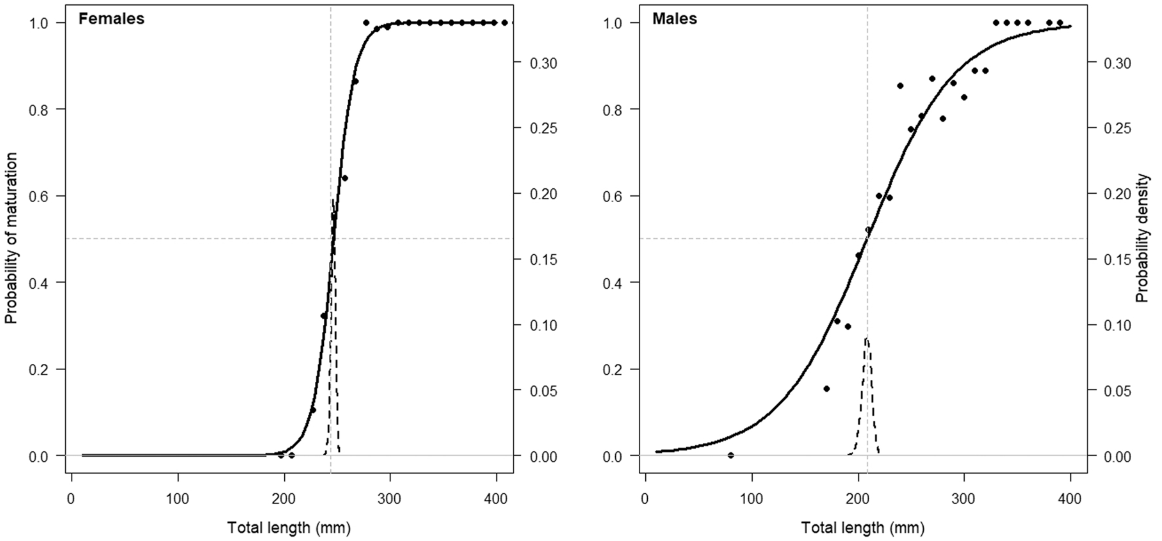

Fig. 5. Length at maturity (continuous line = fitted logistic curve; dots = observed data; dashed lines = probability density for L_{50}) for female and male *Macrodon atricauda* sampled in southern Brazil between 2016 and 2023.

Table 3

Model parameters (β_1 and β_0), estimated length at first sexual maturity (L_{50} mm), and age at first sexual maturity (A_{50} years) for females and males of *Macrodon atricauda* landed in Rio Grande in different periods between 1976 and 2011. L_{50} β_1 and L_{50} β_0 are the estimated logistic model parameters for calculating the length at first maturity (L_{50}). Except for A50, all parameters and indices are presented as the mean of their posterior distribution, and credible intervals of 2.5 % and 97.5 % were obtained *via* the stochastic procedure. *parameters estimated by Cardoso and Haimovici (2014).

Period	Parameters	Females			Males		
		Mean	2.5 %	97.5 %	Mean	2.5 %	97.5 %
1976–1980	*β_1	0.04	0.03	0.05	0.05	0.04	0.06
	*β_0	-10.7	-12.8	-9.1	-11.8	-13.7	-9.7
	*L_{50}	278.7	273.3	284.2	228.3	223.2	233.1
	A_{50}	1.67			1.48		
1983–1988	*β_1	0.08	0.06	0.09	0.08	0.06	0.11
	*β_0	-20.8	-25.2	-16.2	-16.4	-21.6	-13
	*L_{50}	274	269.3	278.3	203.3	198.4	207.7
	A_{50}	1.77			1.27		
1997–1998	*β_1	0.05	0.04	0.06	0.05	0.03	0.06
	*β_0	-14	-16.5	-11.7	-9	-12.3	-6.4
	*L_{50}	269.3	262.7	276.2	199.2	191.5	205.8
	A_{50}	1.62			1.16		
2008–2011	*β_1	0.12	0.1	0.14	0.07	0.06	0.08
	*β_0	-30.2	-35.6	-25.9	-14.2	-16.4	-12.4
	*L_{50}	248.8	246.5	251.2	200.8	197.6	203.7
	A_{50}	1.38			1.08		
2016–2023	β_1	0.104	0.08	0.128	0.025	0.02	0.029
	β_0	-25.6	-31.7	-19.5	-5.1	-6.3	-4.1
	L_{50}	246.5	241.9	250.4	208.4	199.1	216.5
	A_{50}	1.26			1.02		

2014) and remains stable since 2010's to the current period (Table 3). The credible intervals of the females' L_{50} estimated from 2016–2023 (L_{50} = 246.5 mm) overlap with the estimations from the 2000s (L_{50} = 248.8 mm) but without overlapping with the L_{50} estimations for the 1970s (L_{50} = 278.7 mm) and 1980s (L_{50} = 274 mm). For males, after the sharp decrease of the L_{50} from the 1970s (L_{50} = 228.2 mm) to the 1980s (L_{50} = 203.3 mm), it remains relatively stable in preceding periods: 1990s (L_{50} = 199.2 mm), 2000s (L_{50} = 200.8 mm), and 2010s (L_{50} = 208.4 mm).

For both sexes, it's possible to notice a gradual decline in the estimated age at first sexual maturity (A_{50}) between the 1970s and the 2010s (Table 3). For females, the A_{50} declined from 1.67 years in the 1970s to 1.26 years in the 2010s, while for males, the decline was from 1.48 years to 1.02 years for the same periods, respectively.

3.3. Population dynamics

Given the consistent growth pattern observed across the time series, the mean values of the von Bertalanffy parameters (Table 2) were fitted in the assessment model as time-invariant (*i.e.*, $TL_{females} = 41.2 (1 - e^{-0.645(t+0.04)})$; and $TL_{males} = 36.9(1 - e^{-0.68(t+0.06)})$). Consequently, the natural mortality parameters estimated from the Then VBF formula used in the model were 0.875 for females and 0.943 for males. Otherwise, the observed changes in the length at maturity (Table 3) were incorporated into the model through time blocks (Fig. 6). The other life-history parameters used as inputs for the assessment have already been described in the methods section.

Regarding diagnostics, the Hessian matrix for the parameter estimates in the model was positive definite. The models run relatively fast (0.45 s) and show good convergence properties. The overall fit to the length compositions and abundance index data was good. For bough data, it was observed a low value (< 30 %) of the root mean square error (RMSE; Carvalho et al., 2021), indicating a reasonably precise model fit to relative indices (Fig. 7**a**). The retrospective performance of the models is overall good, with trajectory values falling within the confidence intervals of the reference run (Fig. 7**b**). Mohn's rho statistic values showed low values, which indicates a desirable retrospective pattern according to the 'rule of thumb' proposed by Hurtado-Ferro et al. (2015).

The estimated population trends of *M. atricauda* stock in southern Brazil show a sharp decline in biomass between the beginning of the time series and the late 1990s, then a slight increase until the beginning

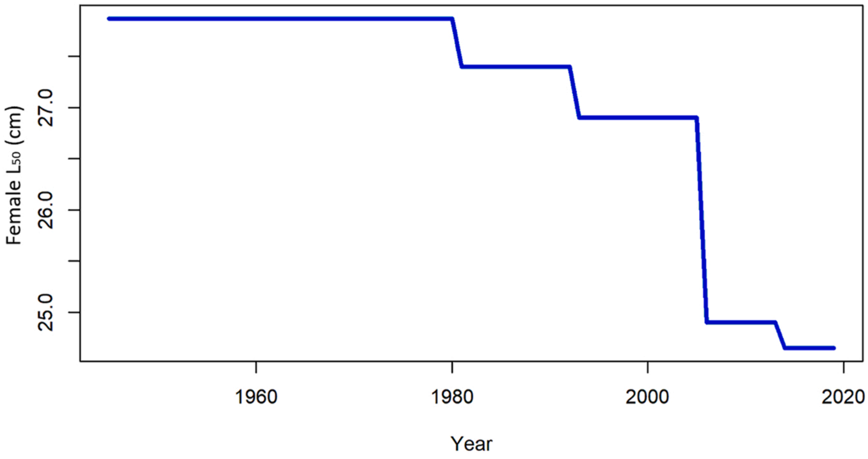

Fig. 6. Temporal variations of the length at first sexual maturity (L_{50}) used as time-blocks for the assessment model of *Macrodon atricauda* stock from southern Brazil.

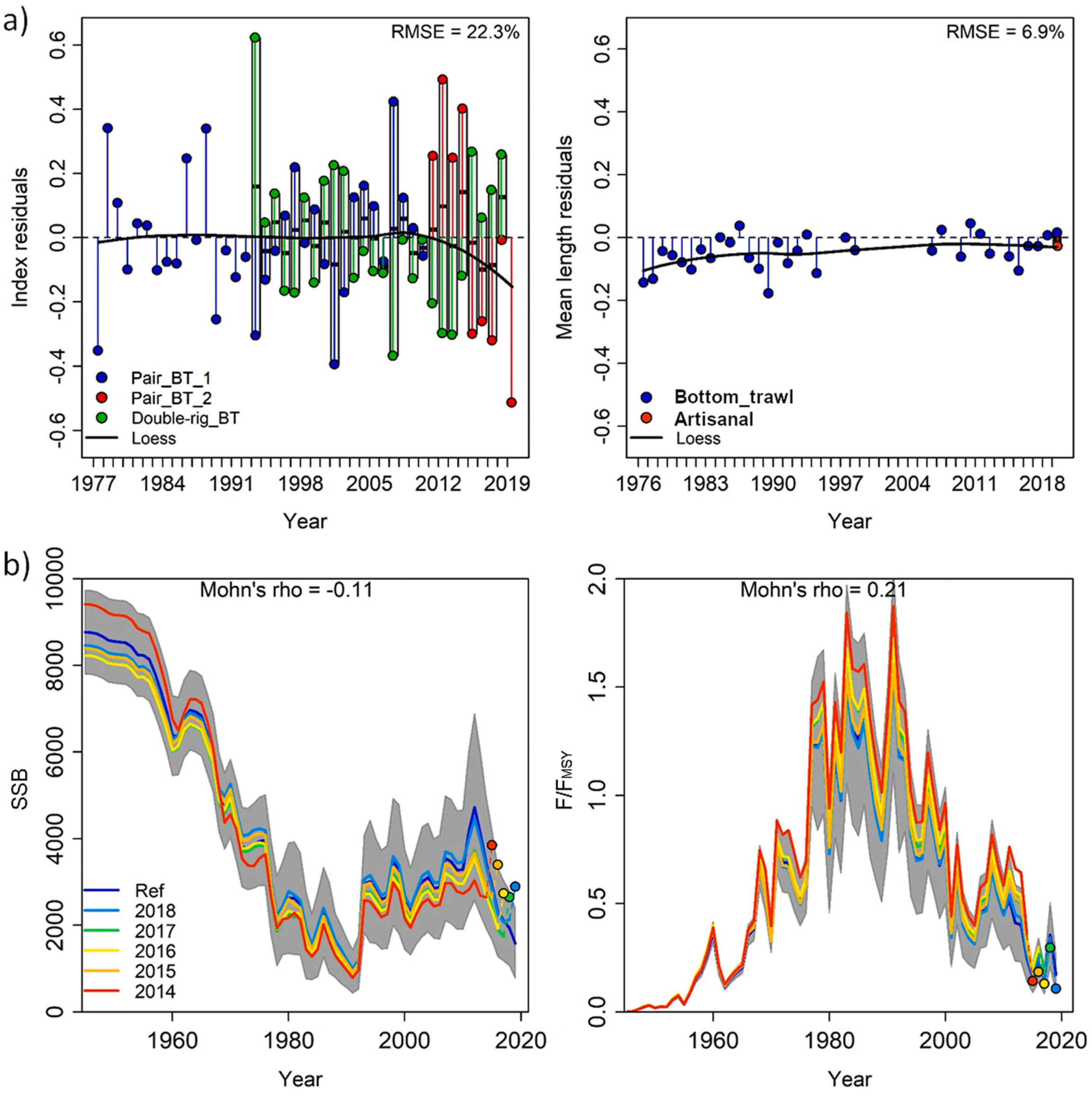

Fig. 7. a) Joint residual plot of the abundance index and annual mean length compositions estimates for the grouped fishery for the reference scenario of *Macrodon atricauda* assessment from southern Brazil. Root mean square error (RMSE) is printed at the top of the panels. b) Retrospective plots of spawning stock biomass (SSB) and the ratio of fishing mortality (F) relative to F at the maximum sustainable yield (F_{MSY}) for the reference scenario. Mohn's rho statistic values are printed at the top of the panels.

of the 2010s, when it declined again until 2019. The current stock spawning biomass (SSB_{2019}) was estimated below the SSB at the maximum sustainable yield (SSB_{MSY}), classifying the stock as overfished (Fig. 8, $SSB_{2019}/SSB_{MSY} = 0.59$). The fishing mortality dynamically increased from the beginning of the time series to the mid-1990s and then decreased gradually until 2019. The estimate of the fishing rate in the terminal year of assessment (F_{2019}) was lower than the maximum sustainable fishing rate (F_{MSY}), showing that the stocks are not under overfishing (Fig. 8, $F_{2019}/F_{MSY} = 0.17$).

4. Discussion

In a former growth study of *M. atricauda* in southern Brazil, Cardoso and Haimovici (2011) concluded a temporal growth increase for the species based on the mean back-calculated length-at-ages between 1976 and 2006. This wrong conclusion may have resulted from the limited sample size of individuals aged over five years (2 females and one male) in 1976–1979, which incidentally were smaller than many younger fishes (see Fig. 3). In the present analysis, this potential source of error was avoided by employing a methodological approach based on individuals' observed length-at-age. This approach led to the conclusion that the species' growth estimated through the von Bertalanffy model did not changed between 1976 and 2023. However, it was also possible to observe a temporal increase in the mean length of individuals aged five years or more (see Fig. 3), probably due to the smaller individuals aged 5 + sampled between 1976 and 1979, but these changes did not affect the growth parameters estimations. These older individuals likely showed a low influence on the estimates because the growth of this species is faster during the first ages, reaching greater stability after the third year of life.

Otherwise, in the same region, growth changes have been observed for the same period for other abundant demersal sciaenid fishes: *Micropogonias furnieri* (Haimovici et al., 2021); *Umbrina canosai* (Haimovici et al., 2022); *Cynoscion guatucupa* (Miranda and Haimovici, 2007) and *Cynoscion jamaicensis* (Alves et al., 2020). Except for *C. jamaicensis*, these studies used individual length-at-age data to estimate the von Bertalanffy parameters, thereby avoiding potential biases similar to those identified in Cardoso and Haimovici (2011). Moreover,

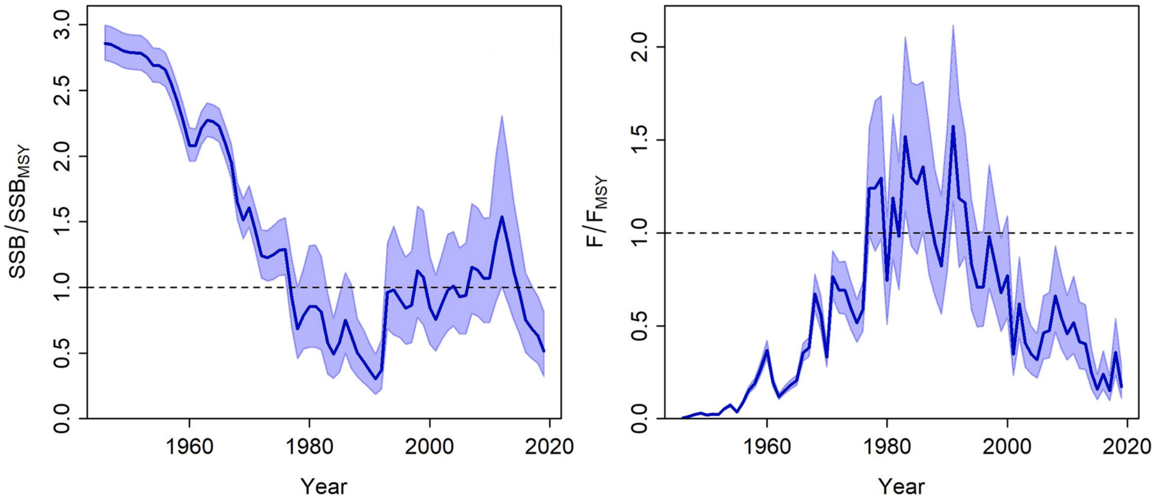

Fig. 8. Estimated time series for the reference scenario of *Macrodon atricauda* assessment from southern Brazil. Panels represent Spawning stock biomass (SSB) relative to SSB at the maximum sustainable yield (SSB/SSB_{MSY}) and the ratio of fishing mortality (F) relative to F at the maximum sustainable yield (F_{MSY}).

for all these species, the changes were more pronounced among the older fish and were attributed to reductions in abundance resulting from fishing pressure.

In short-lived species such as *M. atricauda*, reaching a maximum age of 9 years (Yamaguti and Santos, 1966), it is likely that insufficient time exists to observe the same growth phenomenon that occurred for the other long-lived sciaenid in the region, which reach maximum ages of 18 years for *C. guatucupa* (Miranda and Haimovici, 2007); 26 years for *U. canosai* (Haimovici et al., 2006); and 38years for *M. furnieri* (Haimovici et al., 2021). In those studies, the most prominent length change was observed among the older ages. On the other hand, in the case of *C. jamaicensis*, also a short-lived coastal species that reaches a maximum age of 9 years, increase in growth have been observed by comparing the mean back-calculated lengths at ages between the 1970s and 2010s (Alves et al., 2020). It's important to highlight that during the first analyzed period, the study was constrained by a limited sample size, with only five individuals aged six years and no individuals for older age groups. Consequently, the observed increase in growth seems to be influenced by a methodological bias similar to that observed in the 1976–1979 period for *M. atricauda*. However, further studies would be necessary to confirm this speculation. Nevertheless, changes in the length at first maturity remain consistent for both *C. jamaicensis* (Alves et al., 2020) and *M. atricauda* (Cardoso and Haimovici, 2014).

If fluctuations in population density had no impact on *M. atricauda*'s growth pattern, other factors like fishing-induced evolution might have counteracted density-dependent effects (Dunlop et al., 2009). Drastic declines in population density could also trigger evolutionary shifts in life history, leading to slower growth, increased reproductive investment, and earlier maturation (Audzijonyte et al., 2016). Therefore, if the *M. atricauda* population adapted to slower growth due to heightened fishing pressure, any density-dependent alterations in growth might have been obscured. To investigate these hypotheses, more direct assessments of evolution, such as genetic markers, would be essential for untangling the influences of fisheries-induced evolution and density-dependent changes in individual growth of *M. atricauda* in southern Brazil.

Cardoso and Haimovici (2014) observed a reduction trend in the total length at first sexual maturity (L_{50}) from the 1970s to the 2000s, with a significant decrease from the 1990s to 2000s for females and from 1970s to the 1980s for males with a stabilization until the 2000s (Cardoso and Haimovici, 2014). In this study, the estimated L_{50} did not change from the estimated by Cardoso and Haimovici (2014) for the 2000s, revealing a stabilization since the 2000s for males and since the 1980s for males. However, when converting L_{50} into age at first sexual maturity (A_{50}) using estimated growth curves, a consistent gradual reduction of A_{50} is observed across all analyzed periods. Cardoso and Haimovici (2014) attributed these changes to selective pressure that removes the fastest-growing fishes and delays maturation from the population (Law, 2000; Heino and Godø, 2002). As *M. atricauda* is a seasonal breeder in southern Brazil in spring and summer in southern Brazil, Cardoso and Haimovici (2014) suggested that the maturity changes were near their lowest limits since A_{50} cannot keep decreasing to ages below one year. Thus, we corroborate Cardoso and Haimovici (2014) conclusion that the species probably reached its smallest size and age limits at maturation since these parameters showed stability in the last decades. Furthermore, for other sciaenid fishes (*i.e.*, *M. furnieri* and *U. canosai*), changes in the maturation pattern have also stabilized, even with continuous and intense exploitation of these resources over decades in southern Brazil (Haimovici et al., 2021, 2022).

The apparent stability of the life-history parameters observed for *M. atricauda* in recent years may be attributed to a combination of traits that promote resilience and recovery (Reynolds, 2003; Reynolds et al., 2001), which includes high fecundity (Militelli and Macchi, 2004); low age at maturity (Cardoso and Haimovici, 2014; Yamaguti, 1967); fast individual growth; and a relatively short lifespan (Cardoso and Haimovici, 2011; Haimovici, 1998; Yamaguti and Santos, 1966). In fact, after 50 years of intense fishing, *M. atricauda* remains an important coastal demersal species in the landings of southern Brazil (Haimovici and Cardoso, 2017), demonstrating resilience despite persistent targeting at low stock size in the past decades.

Intensive fishing activities since the 1950s have led to a decline in the region's catches of estuarine and coastal species (Haimovici and Cardoso, 2017). Cardoso et al. (2022) analyzed the catches of the main sciaenids stocks in southern Brazil, which are shared connection with those along the Argentine-Uruguayan Common Fishing Zone (Timi et al., 2005; Haimovici et al., 2016; Canel et al., 2019; Kikuchi et al., 2021) and observed a decline in landings in the last decade for these species (*i.e.*, *M. furnieri*, *U. canosai*, *M. atricauda,* and *C. guatucupa*) in both regions. Thus, Cardoso et al. (2022) concluded that the reduction in catches in southern Brazil appears to represent a consistent regional pattern. Indeed, as observed for those species, the abundance and catches of *M. atricauda* are expected to decrease after decades of high exploitation rates. Although fishing effort has decreased in recent decades, reaching a $F/F_{MSY} < 1$ in 2019, the current spawning biomass (SSB_{2019}) was estimated at 59 % of the spawning biomass required to generate the maximum sustainable yield (SSB_{MSY}), which classifies the stock as overfished. Based on the classifications of demersal stocks' exploration state in the southeast and south of Brazil proposed by Perez and San'Ana (2022a, 2022b), the reference point estimated for *M. atricauda* in southern Brazil classify this stock as "biological safety, but it requires action by the fisheries management authorities." In essence, it would be advisable to implement preventive measures to restore this stock's biomass levels.

Available data on landings, length composition, and abundance, combined with life-history parameters estimated in this study, allowed us to assess the exploitation status of *M. atricauda* stocks in southern Brazil just until 2019. After this period, the Sustainable Fisheries State Policy Act (Rio Grande do Sul State Law 15,223/2018) banned all motor-powered bottom trawling up to 12 miles from the state's 570 km of marine Brazilian southernmost coast which decreased the fishing effort upon the stock. Decades of scientific evidence supported that the ban would generate sustainable ecosystem benefits while safeguarding continuous revenues for small-scale and industrial fisheries (Cardoso et al., 2021). Since *M. atricauda* is a fast-living coastal species, the effects of this measure have likely affected the estimates of the status of this stock. In fact, individuals older than five years were not observed in the 2000s sampling but were present in the samplings after the trawling ban (Fig. 3), indicating a survival increase due to the decrease in fishing mortality. Therefore, updating the data from this fishery is essential to understanding the factors that influence recovery dynamics and the associated timescales. However, unfortunately, there is still no agency responsible for systematically monitoring and updating fishing data in Brazil, posing challenges to stock assessment updates. Maintaining up-to-date fishing data is crucial for implementing suitable management strategies, ensuring sustainable practices, and optimizing future yields.

CRediT authorship contribution statement

Luis Gustavo Cardoso: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Eidi kikuchi:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Bruno L. Mourato:** Writing – review & editing, Software, Methodology, Investigation, Formal analysis, Data curation. **Rodrigo Sant'Ana:** Writing – review & editing, Software, Methodology, Formal analysis, Data curation. **Manuel Haimovici:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Maíra de Sousa Almeida:** Methodology, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES)— Finance code 001; and also by the National Council for Scientific and Technological Development—CNPq and the Ministry of Fisheries and Aquaculture—MPA within the scope of the Call MCTI/MPA/CNPq No. 22/2015—Ordenamento da Pesca Marinha Brasileira.

Author Agreement Statement

We the undersigned declare that this manuscript is original, has not been published before and is not currently being considered for publication elsewhere.

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

We understand that the Corresponding Author is the sole contact for the Editorial process. He is responsible for communicating with the other authors about progress, submissions of revisions and final approval of proofs

References

Almeida, M.S., 2010. Crescimento no primeiro ano de vida da pescadinha *Macrodon ancylodon* (Bloch & Scneider 1801) do extremo sul do Brasil (Undergraduate thesis). Federal University of Rio Grande (FURG), Brazil.

Alves, A.V., Haimovici, M., Cardoso, L.G., 2020. Long-term changes in the life history of the Jamaican weakfish, *Cynoscion jamaicensis* (Vaillant and Bocourt, 1883), in southern Brazil. Reg. Stud. Mar. Sci. 34, 101063 https://doi.org/10.1016/j.rsma.2020.101063.

Audzijonyte, A., Fulton, E., Haddon, M., Helidoniotis, F., Hobday, A.J., Kuparinen, A., Morrongiello, J., Smith, A.D.M., Upston, J., Waples, R.S., 2016. Trends and management implications of human-influenced life-history changes in marine ectotherms. Fish Fish. 17 (4), 1005–1028. https://doi.org/10.1111/faf.12156.

Canel, D., Levy, E., Soares, I.A., Braicovich, P.E., Haimovici, M., Luque, J.L., Timi, J.T., 2019. Stocks and migrations of the demersal fish *Umbrina canosai* (Sciaenidae) endemic from the subtropical and temperate Southwestern Atlantic revealed by its parasites. Fish. Res. 214, 10–18. https://doi.org/10.1016/j.fishres.2019.02.001.

Cardoso, L.G., Haimovici, M., 2011. Age and changes in growth of the king weakfish Macrodon atricauda (Günther, 1880) between 1977 and 2009 in southern Brazil. Fish. Res. 111, 177–187. https://doi.org/10.1016/j.fishres.2011.06.017.

Cardoso, L.G., Haimovici, M., 2014. Long term changes in the sexual maturity and in the reproductive biomass of the king weakfish *Macrodon atricauda* (Günther, 1880) in southern Brazil. Fish. Res. 160, 120–128. https://doi.org/10.1016/j.fishres.2014.05.012.

Cardoso, L.G., Haimovici, M., 2015. Long-term changes in the age structure, mortality and biomass of the king weakfish *Macrodon atricauda* (Günther, 1880) in southern Brazil: is it resilient enough to avoid collapse? Fish. Res. 167, 174–179. https://doi.org/10.1016/j.fishres.2015.02.012.

Cardoso, L.G., Haimovici, M., 2016. Density-dependent changes in the feeding behaviour of *Macrodon atricauda* of southern Brazil. J. Fish Biol. 7 (1) https://doi.org/10.1111/jfb.12974.

Cardoso, L.G., Sant'Ana, R., Mourato, B.L., Kikuchi, E., Haimovici, M., Perez, J.A.A., 2022. Capítulo 5.4. Os impactos da pesca demersal sobre o ambiente marinho. In: Perez, J.A.A., Sant'Ana, R. (eds.), A pesca Demersal nas Regiões Sudeste e Sul do Brasil: Síntese Espacial e Modelo de Gestão baseada no Ecossistema. Relatório Final do Projeto MEEE PDSES - Subsídios Científicos para o Manejo Espacial e com Enfoque Ecossistêmico da Pesca Demersal nas Regiões Sul e Sudeste do Brasil. Chamada MCTI/MPA/CNPq no. 22/2015, Ordenamento da Pesca Marinha Brasileira. Processo 445782/2015, 2022 (Relatório técnico), pp. 211–32.

Cardoso, L.G., Haimovici, M., Abdallah, P.R., Secchi, E.R., Kinas, P.G., 2021. Prevent bottom trawling in southern Brazil. Science 372. https://doi.org/10.1126/science.abh0279 (138-138.

Carvalho, F., Winker, H., Courtney, D., Kapur, M., Kell, L., Cardinale, M., et al., 2021. A cookbook for using model diagnostics in integrated stock assessments. Fish. Res. 240, 105959 https://doi.org/10.1016/j.fishres.2021.105959.

CEPERG, 1945–2011. Desembarque de pescados no Rio Grande do Sul. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. Centro de Pesquisa e Gestão dos Recursos Pesqueiros Lagunares e Estuarinos. Rio Grande, RS, Projeto Estatística Pesqueira.

CEPSUL, 1978–1999. Centro de pesquisa e extensão pesqueira das regiões sudeste e sul. Superintendência do Ibama no Estado de Santa Catarina. Itajaí, SC, Desembarques controlados de pescados no Estado de Santa Catarina.

Chrysafi, A., Kuparinen, A., 2016. Assessing abundance of populations with limited data: lessons learned from data-poor fisheries stock assessment. Environ. Rev. 24 (1), 25–38. https://doi.org/10.1139/er-2015-0044.

Cope, J.M., 2020. The Stock Synthesis Data-limited Tool (SS-DL tool). ⟨https://github.com/shcaba/SS-DL-tool#the-stock-synthesis-datalimited-tool-ss-dl-tool⟩ (Accessed 25 July 2023).

Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E., Wilmers, C. C., 2009. Human predators outpace other agents of trait change in the wild. Proc. Natl. Acad. Sci. USA 106, 952–954. https://doi.org/10.1073/pnas.0809235106.

Dieckmann, U., Heino, M., 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. Mar. Ecol. Prog. Ser. 335, 253–269. https://doi.org/10.3354/meps335253.

Dunlop, E.S., Enberg, K., Jørgensen, C., Heino, M., 2009. Toward Darwinian fisheries management. Evolut. Appl. 2 (3), 245–259. https://doi.org/10.1111/j.1752-4571.2009.00087.x.

Francis, R., 1990. Back-calculation of fish length: a critical review. J. Fish Biol. 36, 883–902. https://doi.org/10.1111/j.1095-8649.1990.tb05636.x.

FURG-MPA, 2012–2018. Boletim Estatístico da Pesca Marinha do Sul do Rio Grande do Sul. Laboratório de Estatística Ambiental, Universidade Federal do Rio Grande, RS.

FURG-SEMA, 2020. Boletim da pesca industrial marinha no Rio Grande do Sul - 2019. Laboratório de Recursos Pesqueiros Demersais e Cefalópodes. Universidade Federal do Rio Grande, RS.

Haimovici, M., 1998. Present state and perspectives for the Southern Brazil shelf demersal fisheries. Fish. Manag. Ecol. 5, 277–289. https://doi.org/10.1046/j.1365-2400.1998.540277.x.

Haimovici, M., Cardoso, L.G., 2017. Long-term changes in the fisheries in the Patos Lagoon estuary and adjacent coastal waters in Southern Brazil. Mar. Biol. Res. 13, 135–150. https://doi.org/10.1080/17451000.2016.1228978.

Haimovici, M., Cousin, J.C.B., 1989. Reproductive biology of the castanha *Umbrina canosai* (Pisces, Scianidae) in southern Brazil. Rev. Bras. Biol. 49, 523–537.

Haimovici, M., Absalonsen, L., Velasco, G., Miranda, L.V., 2006. Diagnóstico do estoque e orientações para o ordenamento da pesca de Umbrina canosai (Berg, 1895). In: Rossi-Wongtschowski, C.L.D.B.;, Ávila-da-Silva, A.O.;, Cergole, M.C. (Eds.), Análise das Principais Pescarias Comerciais da Região Sudeste-Sul do Brasil: Dinâmica Populacional das Espécies em Explotação – II. USP, São Paulo, pp. 77–85.

Haimovici, M., Cardoso, L.G., Unpierre, G.R., 2016. Stocks and management units of *Micropogonias furnieri* (Desmarest, 1823) in southwestern Atlantic. Lat. Am. J. Aquat. Res. 44, 1080-–11095. https://doi.org/10.3856/vol44-issue5-fulltext-18.

Haimovici, M., Cavole, L.M., Cope, J.M., Cardoso, L.G., 2021. Long-term changes in population dynamics and life history contribute to explain the resilience of a stock of *Micropogonias furnieri* (Sciaenidae, Teleostei) in the SW Atlantic. Fish. Res. 237, 105878 https://doi.org/10.1016/j.fishres.2021.105878.

Haimovici, M., Kikuchi, E., Cardoso, L.G., 2022. Changes in the population structure and life history associated with long-term intense fishing of the Argentinian croaker Umbrina canosai in southern Brazil. Aquat. Living Resour. 35, 12. https://doi.org/10.1051/alr/2022012.

Heino, M., Godø, O.R., 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bull. Mar. Sci. 70, 639–656.

Hurtado-Ferro, F., Szuwalski, C.S., Valero, J.L., Anderson, S.C., Cunningham, C.J., Johnson, K.F., Licandeo, R., McGilliard, C.R., Monnahan, C.C., Muradian, M.L., Ono, K., Vert-Pre, K.A., Whitten, A.R., Punt, A.E., 2015. Looking in the rear-view mirror: bias and retrospective patterns in integrated, age-structured stock assessment models. ICES J. Mar. Sci. 72, 99–110. https://doi.org/10.1093/icesjms/fsu198.

Hutchings, J.A., 2000. Collapse and recovery of marine fishes. Nature 406, 882–885. https://doi.org/10.1038/35022565.

Kikuchi, E., Cardoso, L.G., Canel, D., Timi, J.T., Haimovici, M., 2021. Using growth rates and otolith shape to identify the population structure of *Umbrina canosai* (Sciaenidae) from the Southwestern Atlantic. Mar. Biol. Res. 17 (3), 272–285. https://doi.org/10.1080/17451000.2021.1938131.

Kinas, P.G., Andrade, H.A., 2010. Introdução à Análise Bayesiana (com R). Mais Que Nada, Porto Alegre.

Kuparinen, A., Boit, A., Valdovinos, F.S., Lassaux, H., Martinez, N.D., 2016. Fishing-induced life history changes degrade and destabilize harvested ecosystems. Sci. Rep. 6 (1), 1–9. https://doi.org/10.1038/srep22245.

Law, R., 2000. Fishing, selection and phenotypic evolution. ICES J. Mar. Sci. 57, 659–668. https://doi.org/10.1006/jmsc.2000.0731.

Longhurst, A.R., 2010. Mismanagement of Marine Fisheries. Cambridge University Press.

Marteinsdottir, G., Thorarinsson, K., 1998. Improving the stock recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. Can. J. Fish. Aquat. Sci. 55, 1372–1377. https://doi.org/10.1139/f98-035.

Methot, R.D., Wetzel, C.R., 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. Fish. Res. 142, 86–99. https://doi.org/10.1016/j.fishres.2012.10.012.

Militelli, M.I., Macchi, G.J., 2004. Spawning and fecundity of king weakfish, *Macrodon ancylodon*, in the Río de la Plata estuary, Argentina-Uruguay. J. Mar. Biol. Assoc. UK 84 (2), 443–447. https://doi.org/10.1017/S0025315404009427h.

Miranda, L.V., Haimovici, M., 2007. Changes in the population structure, growth and mortality of striped weakfish *Cynoscion guatucupa* (Sciaenidae, Teleostei) of southern Brazil between 1976 and 2002. Hydrobiologia 589, 69–78. https://doi.org/10.1007/s10750-007-0721-7.

Perez, J.A.A., Sant'Ana, R., 2022a. A pesca Demersal nas Regiões Sudeste e Sul do Brasil: Síntese Espacial e Modelo de Gestão baseada no Ecossistema. Relatório Final do Projeto MEEE PDSES - Subsídios Científicos para o Manejo Espacial e com Enfoque Ecossistêmico da Pesca Demersal nas Regiões Sul e Sudeste do Brasil. Chamada MCTI/MPA/CNPq no. 22/2015, Ordenamento da Pesca Marinha Brasileira. Processo 445782/2015, 2022 (Relatório técnico).

Perez, J.A.A., Sant'Ana, R., 2022b. Tropicalization of demersal megafauna in the western South Atlantic since 2013. Commun. Earth Environ. 3, 227. https://doi.org/10.1038/s43247-022-00553-z.

Pérez-Rodríguez, A., Morgan, J., Koen-Alonso, M., Saborido-Rey, F., 2013. Disentangling genetic change from phenotypic response in reproductive parameters of Flemish Cap cod *Gadus morhua*. Fish. Res. 138, 62–70. https://doi.org/10.1016/j.fishres.2012.09.004.

PMAP/UNIVALI, 2019. Estatística Pesqueira de Santa Catarina. Consulta Online. Projeto de Monitoramento da Atividade Pesqueira do Estado de Santa Catarina. Laboratório de Estudos Marinhos Aplicados (LEMA), da Escola do Mar, Ciência e Tecnologia (EMCT) da Universidade do Vale do Itajaí (UNIVALI).

Reynolds, J.D., 2003. Life histories and extinction risk. In: Blackburn, T.M., Gaston, J.K. (Eds.), Macroecology. Blackwell, Oxford, UK, pp. 195–217.

Reynolds, J.D., Mace, G.M., Redford, K.H., Robinson, J.G., 2001. Conservation of Exploited Species. Cambridge University Press, Cambridge, U.K.

Rodrigues, R., Santos, S., Haimovici, M., Saint-Paul, U., Sampaio, I., Schneider, H., 2014. Mitochondrial DNA reveals population structuring in Macrodon atricauda (Perciformes: Sciaenidae): a study covering the whole geographic distribution of the species in the southwestern Atlantic. Mitochondrial DNA 25 (2), 150–156. https://doi.org/10.3109/19401736.2013.792053.

Saborido-Rey, F., Kjesbu, O.S., 2005. Growth and Maturation Dynamics. DOI: ⟨http://hdl.handle.net/10261/47150⟩.

Sagarese, S.R., Walter, J.F., Isely, J.J., Bryan, M.D., Cummings, N., 2015. A Comparison of Data-rich Versus Data-limited Methods in Estimating Overfishing Limits (SEDAR46-DW-01). SEDAR, North Charleston.

Sturtz, S., Ligges, U., Gelman, A., 2005. R2WinBUGS: a package for runningWinBUGS from R. J. Stat. Softw. 12 (3), 1–16. https://doi.org/10.18637/jss.v012.i03.

Thomas, A., O'Hara, B., Ligges, U., Sturtz, S., 2006. Making BUGS open. R N. 6 (1), 12–17.

Thorson, J.T., Maureaud, A.A., Frelat, R., Mérigot, B., Bigman, J.S., Friedman, S.T., Palomares, M.L.D., Pinsky, M.L., Price, S.A., Wainwright, P., 2023. Identifying direct and indirect associations among traits by merging phylogenetic comparative methods and structural equation models. Methods Ecol. Evol. https://doi.org/10.1111/2041-210X.14076.

Timi, J.T., Luque, J.L., Sardella, N.H., 2005. Parasites of *Cynoscion guatucupa* along South American Atlantic coasts: evidence for stock discrimination. J. Fish Biol. 67 (6), 1603–1618. https://doi.org/10.1111/j.1095-8649.2005.00867.x.

Taylor, I.G., Doering, K.L., Johnson, K., F., Wetzel, C.R., Stewart, I.J., 2021. Beyond visualizing catch-at-age models: lessons learned from the r4ss package about software to support stock assessments. Fish. Res. 239, 105924 https://doi.org/10.1016/j.fishres.2021.105924.

Then, A.Y., Honeig, J.M., Hall, N.G., Hewitt, D.A., 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. ICES J. Mar. Sci. 72 (1), 82–92. https://doi.org/10.1093/icesjms/fsx199.

Valentini, H., de Castro, P.M.G., Servo, G.J.M., Castro, L.A.B., 1991. Evolução da pesca das principais espécies demersais da costa sudeste do Brasil, pela frota de arrasteiros de parelha baseada em São Paulo de 1968 a 1987. Atlântica 13, 87–96.

Yamaguti, N., 1967. Desova da pescada-foguete *Macrodon ancylodon*. Bol. do Inst. Oceanogr. 16 (1), 101–106.

Yamaguti, N., Moraes, A.E.D., 1965. Análise da pesca da pescada foguete na costa centro sul do Brasil. Bol. do Inst. Oceanogr. 14, 115–124.

Yamaguti, N., Santos, E.P., 1966. Crescimento da pescada-foguete (*Macrodon ancylodon*): aspecto quantitativo. Bol. do Inst. Oceanogr. 15 (1), 75–78.

Yesaki, M., Bager, K.J., 1975. Histórico da evolução da pesca industrial em Rio Grande. In: Série Documentos Técnicos SUDEPE/PDP, 11.