Life history, population dynamics and stock assessment of the bycatch species Brazilian flathead (*Percophis brasiliensis*) in southern Brazil

Danilo Shoiti Hirota [a,*], Manuel Haimovici [a], Rodrigo Sant'Ana [b], Bruno Leite Mourato [c], Eidi Kikuchi [a], Luís Gustavo Cardoso [a]

[a] *Laboratório de Recursos Pesqueiros Demersais e Cefalópodes, Instituto de Oceanografia, Universidade Federal do Rio Grande (FURG), Caixa Postal 474, Avenida Itália Km 8, CEP 96201-900, Rio Grande - RS, Brazil*
[b] *Universidade do Vale do Itajaí (UNIVALI), Rua Uruguai, 458, CEP 88302-901, Itajaí - SC, Brazil*
[c] *Universidade Federal de São Paulo (UNIFESP), Edifício Central, Rua Silva Jardim, nº 136, CEP: 11015-020, Santos - SP, Brazil*

ABSTRACT

The life history and population dynamics of the marine demersal bony fish *Percophis brasiliensis* were studied to assess its stock status in southern Brazil. Specimens were sampled from commercial landings, and the length, weight, sex, and maturity stage were recorded from each individual. Sagittal otoliths were removed for aging, and the gonads were weighed for maturity studies. Size compositions were also evaluated from commercial landings of different fishing fleets. The analysis of edge type validated the aging data. The oldest and largest individuals were 12 years and 718 mm in total length, respectively. Growth parameters fitted to the von Bertalanffy model were L∞ = 625.0 mm, k 0.39 year^{-1}, $t_0 = -0.26$ years for females, L∞ = 573.4 mm, k = 0.34 year^{-1}, $t_0 = -1.13$ for males and L∞ = 617.6 mm, k = 0.33 year^{-1} $t_0 = -0.82$ for both sexes. The length and age at first maturity of females were 407.7 mm and 2.2 years, respectively. The reproductive season was estimated to occur during spring from September to December, with a peak in October. The life history parameters and the reproductive season described in this study are similar to those estimated by other studies on southern stocks fished in Uruguayan and Argentinian waters. The estimated population trends presented a steady decrease between 1986 and 2005, a slight increase from 2005 and 2010, and a sharp decline until 2019. The stock status was estimated as overfished but not suffering overfishing. Despite not being a target species, the biomass decline trajectory of *Percophis brasiliensis* reflects intense targeting of other bottom trawl species in the same depth range. These results highlight the importance of life-history studies and continuous monitoring of species impacted by fisheries. Their depletion may affect the functional relationships in marine ecosystems and threaten the resilience of populations to stochastic effects such as climatic variations.

1. Introduction

Understanding the life history of commercially exploited fish stocks is essential to assess the impact of biomass removal from fisheries and establishing fishery management measures (Adams, 1980; Dowling et al., 2015; Kirkwood et al., 1994; Pope et al., 2000). The development of any harvest strategy depends on assessing the stock status and population dynamics, which depends on data availability (Dowling et al., 2015). Several models are available with varying data quantity and type requirements (Newman et al., 2015) but rely heavily on life history parameters. In general, species with faster life histories, i.e., earlier age at maturity and more rapid body growth, exhibit and support greater

mortality rates than species with slower growth and delayed maturation (Reynolds et al., 2001). However, several management measures, i.e., minimum legal sizes and closed fishing seasons, rely upon fish stocks' reproductive biology (Morgan, 2008). Overall, this demonstrates how crucial it is to understand the life history of exploited fish stocks.

The Brazilian flathead (Percophidae), *Percophis brasiliensis* (Quoy & Gaimard, 1824), is a demersal Percophidae fish species endemic in the Southwestern Atlantic Ocean between 23°S (Rio de Janeiro, Brazil) and 47°S (Santa Cruz, Argentina) (Cousseau and Perrotta, 2004; Gosztonyi and Angelescu, 1981). Morphometric, microchemistry and life history studies suggest that two different populations inhabit the Uruguayan and Argentinian waters, south and north of Necochea (Lat. 39°S) (Avigliano et al., 2015; Rico et al., 2018). However, parasitic fauna studies suggest the presence of three groups in the same region (Braicovich and Timi,

* Corresponding author.
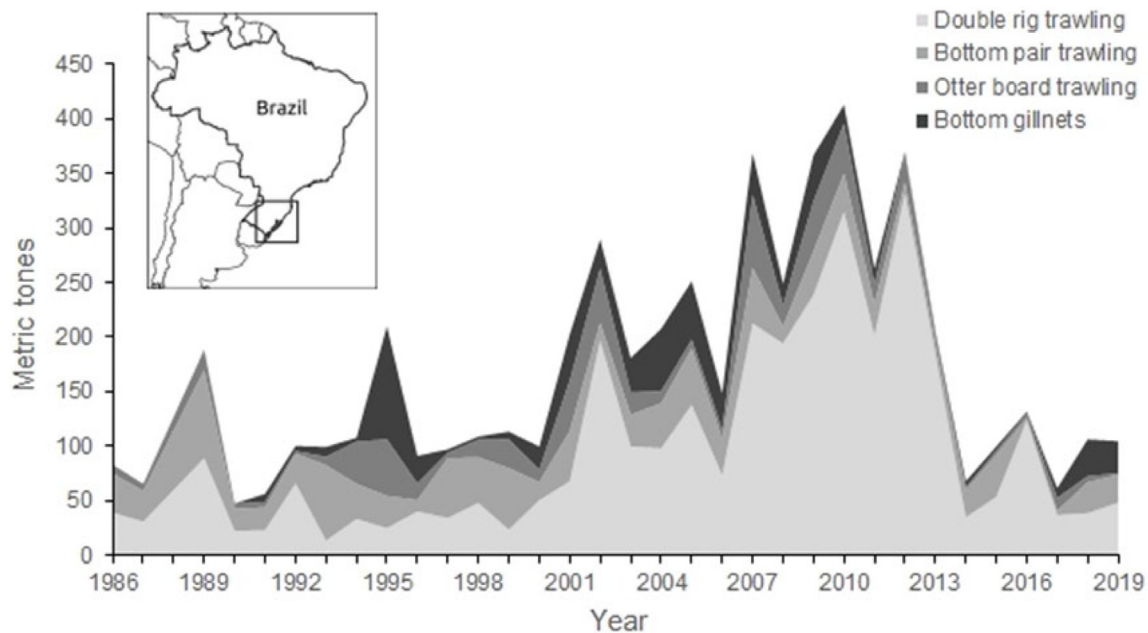*E-mail address:* danilohirota@yahoo.com.br (D.S. Hirota).

Fig. 1. Recorded *P. brasiliensis* landings from the bottom trawl and bottom gill fleet in southern Brazil between 1986 and 2019.

2008) and two other groups in southeastern and southern Brazil (SB) (Braicovich et al., 2017).

In Uruguay and Argentina, the Brazilian flathead is an important component of the multispecies coastal fishery landings (Fernández-Araoz et al., 2004; Lasta et al., 1999). Due to its commercial importance, several studies on growth, reproduction, and diet were carried out in that region (Barretto et al., 2011; Milessi and Marí, 2012; Militelli and Macchi, 2001). In SB, between Santa Marta Grande Cape (28°S) and Chui (33°S), it is not directly targeted by bottom trawling and bottom gillnet fishing fleets (FURG/SEMA, 2020; Haimovici, 1998) but comprises a significant component of commercial fishery landings. The few studies on its biology focused on prey consumption (Martins, 2000), which occurs between 20 and 200 m in depth, with a higher frequency between 20 and 60 m during the winter months (Haimovici et al., 1996, 2008).

Between 1986 and 2019, the species landings increased gradually in SB, reaching their peak in 2010, with 413 metric tons, followed by a steady decline, reaching less than 100 tons in 2019. The majority of the landings come from the bottom trawling fishing fleet, while the bottom gillnets represent a small fraction (Fig. 1). The steady landing decline in the last ten years has triggered an alert on the stock status and makes necessary an assessment of its population dynamics. Data on the size composition and catch per unit of effort of the species have been collected in two major fishing ports from the region, Itajaí in Santa Catarina State and Rio Grande in Rio Grande do Sul State (Fig. 1) (Haimovici, 1987; Haimovici and Cardoso, 2017). These data, combined with knowledge of the species' life history, make it possible to assess the stock's status.

In this context, as a first step, we described the species' life history by studying its age, growth, reproductive cycle, maturity, sex ratio, and size and age structures. Finally, we assessed the population dynamics and the stock status by applying the stock synthesis model with different configurations, including the species life history generated in this study, the available size composition data, and the times series of landings and catches per unit of effort.

2. Materials and methods

2.1. Sampling and data collection

Percophis brasiliensis were sampled from fishery landings of a commercial fishing fleet equipped with trawls and a bottom gillnet operating on the continental shelf of SB. In addition, the size composition samples were collected randomly during industrial fishing vessel landings in the Rio Grande and Itajaí ports (Table 1). The total length (TL) of specimens was measured at the lower centimeter between the snout tip and the rear part of the tail.

Biological data for life history studies were collected between August 2018 and September 2019 (n = 540). For all specimens, the total length (L, mm), weight (W, grams), sex, gonad weight (GW, grams), and maturation stage were recorded. Sexual maturation was determined macroscopically following a seven-stage scale for multiple-batch spawners based on Haimovici and Cousin (1989) as (1) virginal immature, (2) developing virginal, (3) developing, (4) advanced development, (5) running, (6) partly spent, and (7) recovering. The sagittal otoliths were removed, cleaned, and dried for storage.

2.2. Age determination

The otolith sections were examined with reflected light over a black microscope slide with a stereoscope microscope (20x). For each specimen, the number of opaque bands following the first translucent band was counted along the axis between the nucleus and the dorsal edge of the crest on the inner side (Fig. 2).

Two readers examined the otolith sections independently. When the readings differed, a third reading was performed by the two readers together. If the disagreement persisted, the readings were discarded. The mean coefficient of variation (CV) (Campana, 2001) was calculated to evaluate the precision between readings as follows:

$$CV_j = 100\% \; X \; \sqrt{\sum_{i=1}^{N} (x_{ij} - x_j)^2 / (N-1)} \Big/ x_j$$

Table 1
Number (n) of specimens measured and mean total length (mean L, mm) of *Percophis brasiliensis* sampled in the industrial fishing landings with different trawl gear and gillnets in the Rio Grande between 2007 and 2019.

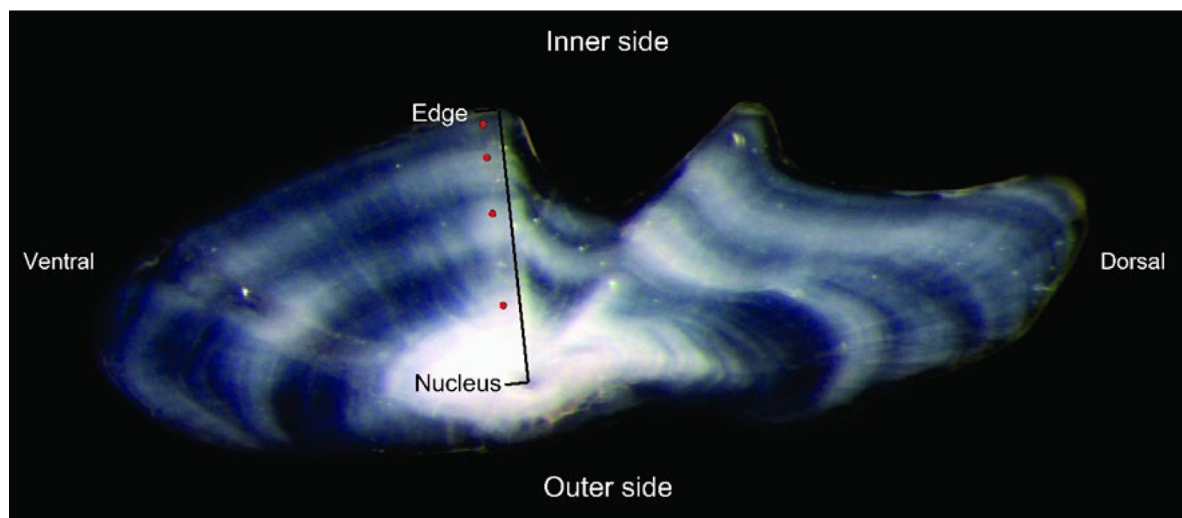| Year	Double rig bottom trawling		Pair bottom trawling		Otter board bottom trawling		Bottom gillnet fishing		Total n
	n	mean L	n	mean L	n	mean L	n	mean	
2007	183	462.2	93	496.5					276
2016			249	534.6					249
2017	496	496.6							633
2018			369	503.4	137	526.7	453	548.9	822
2019			909	506.8			434	512.9	1343

Fig. 2. Thin section examined with reflected light from a 4-year-old female *Percophis brasiliensis* from southern Brazil. Opaque bands appear as white, and translucent bands appear as dark. The red dots indicate the identified growth bands.

where CV_j is the estimated age accuracy for the *j*th fish; x_{ij} is the age determination of the *j*th fish; x_j is the mean age of the *j*th fish; and N is the number of readings.

The first annulus was considered the end of the first opaque band contiguous from the otolith nucleus. After establishing that criterion, the two readers counted the opaque bands independently and reached a 89% consensus rate and an average coefficient of variation (CV) of 7.69. This CV value was consistent with the median of the precision estimator (CV = 7.6%) calculated by Campana (2001) from several age studies, which demonstrates robustness of the age readings and all age-based estimated parameters.

2.3. Weight-length relationship

The potential model ($Wt = a \times Lt^b$) described the relationship between weight and length. Linear regression models fitted to log-transformed weight and length data were used to compare the relationships between sexes through covariance analysis ($\alpha = 0.05$) (Zar, 1984).

2.4. Reproductive cycle

The reproductive cycle was determined by analyzing the monthly changes in the gonadosomatic index (GSI), calculated as $100 \times (W/GW)$, where GW is the gonad weight in grams (Pavlov et al., 2009). Each female sampled was classified on an eight-stage maturity scale based on Militelli and Macchi (2001), which demonstrated agreement between the macroscopic and microscopic maturity scales. Females classified in stages three onward were considered to be mature. Each sampled male was classified on a seven-stage maturity scale based on Haimovici and Cousin (1989). Males classified in stages three onward were considered to be mature.

2.5. Length and age at first maturity

Data for estimating maturity ogives were selected from the reproductive season to avoid misidentification between spent and immature stages. This period was visually estimated based on the results of the seasonality of maturation. The total number (n_i) and the number of mature specimens (y_i) were calculated for each age and 30-mm total length bin. These data were fitted to a logistic model to estimate the mean length (L_{50}) and mean age (A_{50}) at which the chance of being mature was 50% and the mean length (L_{95}) at which the chance of being mature was 95%.

A Bayesian approach was used Kinas and Andrade (2010), in which θ_i denotes the probability of an individual of the *i*th *m* class being mature, and y_i was assumed to follow a binomial distribution Bin (n_i, θ_i). Data were fit to a logistic model, defined by a logit link function that transforms the parameter θ_i, restricted to the range [0, 1] in the binomial distribution, with m bounded between $-\infty$ and $+\infty$ (Kinas and Andrade, 2010). The logistic model was defined as follows:

$$m_i = g(\theta_i) = log\,(\theta_i/(1 - \theta_i))$$
$$m_i = \beta_0 + \beta_1 \cdot x_i$$

where m_i is the probability at each x_i length class. The estimation was based on the following priors:

$$\beta_0 \sim N\,(0, 0.001)\,I(-5, 5)$$
$$\beta_1 \sim N\,(0, 0.001)\,I\,(-5, 5)$$

From this model, L_{50} and L_{95} were defined as:

$$L_{50}\text{ and }A_{50} = -\beta_0/\beta_1 \text{ and } L_{95} = (2.94 - \beta_0)/\beta_1$$

The posterior distribution p ($\beta0$, $\beta1$|D), where D = {(yi, ni,xi); i = 1...,k} for the reproductive parameters, was also obtained using

Monte Carlo Markov Chain (MCMC) sampling performed using JagsUI (Kellner et al., 2019). In three chains, after 1000 burn-in runs, every tenth value of the remaining 20,000 cycles was retained, resulting in a final sample of 2000 from the posterior distribution p (log L∞, log k, log t0|D) (Kinas and Andrade, 2010). The posterior distribution of each estimated parameter provided an easy and clear method for comparing the results among periods. All analyses were conducted using R version 3.6.1 (Team, 2019).

2.6. Growth model

Two data treatments were used to fit the von Bertalanffy growth models using a Bayesian approach. The first treatment pooled age-length data for both sexes ("pooled sex"). The second treatment grouped the age-length data by sex ("separate sex"). Treatment with the smaller Deviance Information Criteria (D.I.C.) (Spiegelhalter et al., 2014) was chosen.

We assumed that the age-length data followed a log-normal distribution, i.e., $y_i = logN(u_i, \sigma^2)$, where y_i is the average expected length of animals in age class i, with variance σ^2. A logarithmic version of the VBGM was used for computational convenience as follows:

$$\mu_i = \log(L_\infty) + \log(1 - \exp(-k(i - t_0)))$$

Uninformative priors were selected

$$p(log\ L_\infty) \sim N(0, 0.001)\ I(-5, 5)$$
$$p(log\ k) \sim N(0, 0.001)\ I(-5, 5)$$
$$p(log\ t_0) \sim U(-3, 0)$$
$$p(\sigma) \sim U(0, 5)$$

We obtained posterior distributions of each parameter using Monte Carlo Markov Chain (MCMC) sampling. In three chains, after 1000 burn-in runs, every tenth value of the remaining 20,000 cycles was retained, resulting in a final sample of 2000 from the posterior distribution p (log L∞, log k, log t_0|D) (Kinas and Andrade, 2010). Thus, the posterior distribution of each estimated parameter provided an easy and straightforward way to compare the results among periods. All analyses were conducted using R version 3.6.1 (Team, 2019). The MCMC was performed using the library JagsUI (Kellner et al., 2019).

2.7. Natural mortality

The instantaneous natural mortality coefficient M was estimated as the average of four empirical estimators based on maximum age (t_{max}): $4.899\ t_{max}^{-0.916}$; $\log M = 1.717 - 1.01 \log t_{max}$; $M = 5.109/t_{max}$ (Then et al., 2015) and $M = \exp(1.44–0.982 \ln t_{max})$ (Hewitt and Hoenig, 2005). The maximum age (t_{max}) was considered to be one year older than the oldest observed in this study. This choice is based on the assumption that the number of sampled individuals may not have covered the oldest fish, whose frequency may have decreased after more than 40 years of intense fishing in the region (Haimovici and Cardoso, 2017).

2.8. CPUE standardization

Catch and effort data from more than 5969 industrial trawlers (e.g., pair trawling, otter board, and double rig trawling) fishing trips between 2000 and 2019 were used to standardize CPUE for modeling. The data were collected from different fleets landing in Santa Catarina State (Perez et al., 1998; Perez and Pezzuto, 2006; UNIVALI/EMCT/LEMA, 2020). Data from each fishing trip included year, season, boat, fishing strategy and depth range of the trip operation. The fishing strategy was defined by the application

of cluster methods to explore the factors that contributed to patterns and identify groups with similar species compositions and, presumably, similar fishing strategies and targeting (Hoyle, 2015; Sant'ana et al., 2020).

The CPUE standardization was implemented using Bayesian hierarchical models with a latent Gaussian structure to accommodate the temporal and seasonal effects. The nominal CPUE was defined as a metric kilogram of Brazilian flathead caught per trawling time. As it is a nontarget species but with commercial value, the proportion of zero catches was high in all trawling fleets; thus, the response variable was transformed by its logarithm plus one, and the likelihood of fitting the response variable was considered to follow the log-normal distribution.

The structures assumed for the models, particularly temporal and seasonal effects, define a classical observation of Gaussian Markov random fields (GMRFs) (Rue and Held, 2005). Thus, the large size of the random effects vector can cause simulation-based inference, such as MCMC, computationally inefficient or even unfeasible (Mayer et al., 2019). For this reason, a method based on numerical approximations was used for Bayesian inference in highly structured latent Gaussian models, as proposed by Rue et al. (2009). The methodology, called integrated nested Laplace approximation (INLA), uses numerical integration methods to obtain a posterior marginal distribution and bypasses the high computational time and convergence problems associated with methods such as MCMC. The functions for calculating subsequent distributions were implemented in the statistical environment R (Team, 2019) through the INLA package (Rue et al., 2013), available at www.r-inla.org.

Distinct model structures were evaluated, considering fixed and random effects for the covariates or explanatory variables, and the choice for the best fit was determined based on Deviance Information Criteria (DIC) and the Conditional Predictive Ordinate (CPO). As a measure of the diagnostic for model selection, the probability integral transform (PIT) and predictive posterior probabilities were used.

2.9. Population dynamics

A time series of spawning biomass and the current stock depletion (B_{2019}/B_0) was estimated with a model fitted to the available data using the Stock Synthesis Data-limited Tool (SS-DL tool) (Cope, 2020). The SS-DL tool uses the age-structured population dynamics model Stock Synthesis (Methot and Wetzel, 2013) to implement several data-limited assessment methods all in one modeling framework.

The SS-DL tool uses as input parameters the natural mortality (M), the von Bertalanffy growth parameters (L∞, k, and t_0), the size at 50% and 95% of maturity (L_{50} and L_{95}), the coefficients and exponents of the weight-length and weight-fecundity relationships, the stock-recruitment parameters, steepness, and initial recruitment (lnR0).

In addition to the life history parameters estimated in this study, the available data were landing time series by fishing fleet, annual length compositions, and one standardized abundance index for the main fishing fleet targeting *P. brasiliensis*. The data covered the main fishing fleets that operate in the study area: double rig bottom trawling (Fleet 1), pair bottom trawling (Fleet 2), otter board bottom trawling (Fleet 3), and bottom gillnet (Fleet 4) (Fig. 3). Logistic selectivity was assumed for both the bottom trawling and gillnet fisheries. It could be argued that a dome-shaped selectivity would be a better assumption for the gillnet fisheries, but the size compositions showed that large Brazilian flathead individuals were retained in the nets. The landings by fleet showed that the main fishing fleet targeting *P. brasilensis* was the double rig bottom trawling (Fleet 1) (Fig. 4).
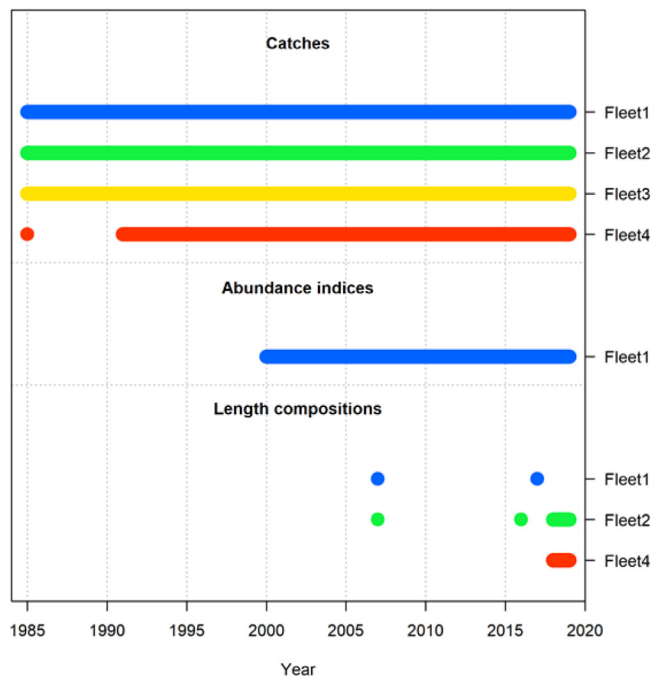
Fig. 3. Period covered by each type of data for *P. brasiliensis* sampled from industrial landings of double rig bottom trawling (Fleet 1), pair bottom trawling (Fleet 2), Otter board bottom trawling (Fleet 3), and bottom gillnet (Fleet 4) fleets in SB from 1985 to 2019.
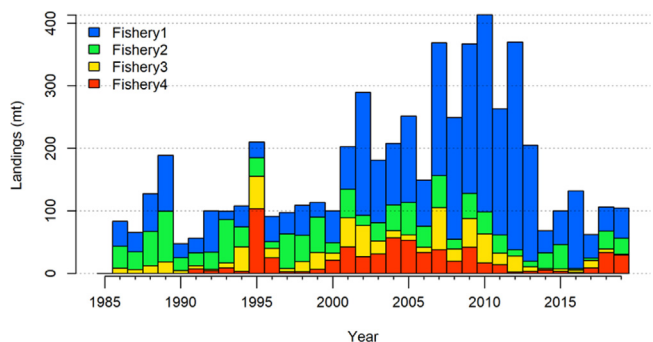

Fig. 4. Total landings by fishing fleet targeting the Brazilian flathead in southern Brazil. Double rig bottom trawling (Fleet 1), pair bottom trawling (Fleet 2), otter board bottom trawling (Fleet 3), and bottom gillnet (Fleet 4).

Model convergence was assessed using the Carvalho et al. (2021) flow chart. The first diagnostic was whether the Hessian (i.e., the matrix of second derivatives of the likelihood concerning the parameters) inverts. The second measure was an assessment of the joint residuals plot to ensure that they were randomly distributed. The third measure was the retrospective analyses conducted with five-year retrospective peels. The fourth measure was an analysis of the model prediction skills by completing a model-based hindcasting. The fifth diagnostic was a jitter analysis of parameter starting values to evaluate whether the model converged to a global solution rather than a local minimum. Starting values of all estimated parameters were randomly perturbed by 10%, and 50 trials were run.

Other diagnostics included likelihood profiling of critical parameters (steepness and natural mortality). Likelihood profiles elucidate conflicting information among various data sources, determine asymmetry around the likelihood surface surrounding point estimates and evaluate the precision of parameter estimation.
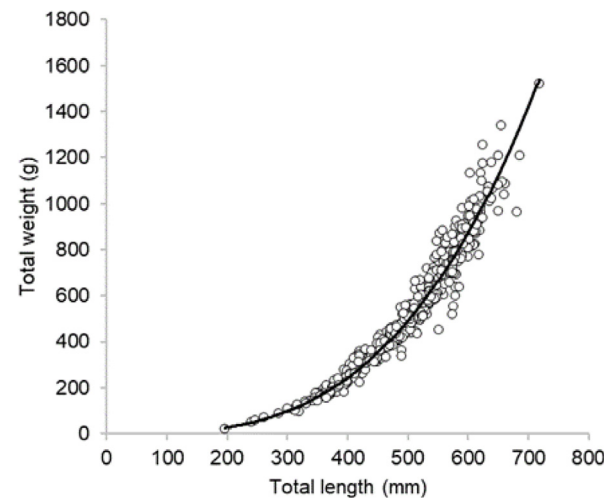

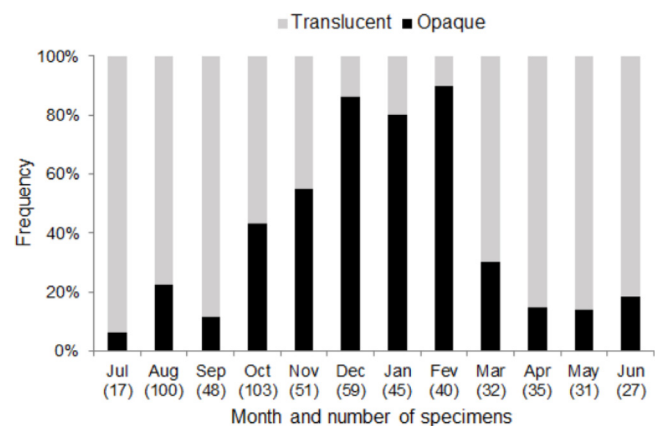**Fig. 5.** Weight-length relationship of *Percophis brasiliensis* samples in southern Brazil.

Fig. 6. Monthly frequency distribution (sample size in parentheses) of opaque (in black) and translucent (in gray) edges of thin sections of *Percophis brasiliensis* otoliths in southern Brazil.

3. Results

3.1. Weight-length relationship

The ANCOVA comparison of the log-transformed regression lines between total weights and total lengths showed no significant differences between sexes (F = 1.58; P = 0.2088 and $W_g = 2x10^{-6}L_{mm}^{3.15}$ (R^2 = 0.9582; n = 529)) (Fig. 4).

3.2. Age validation

Opaque and translucent edges of the otoliths were observed throughout the year (Fig. 5). However, a higher frequency of opaque edges was observed from November to February (76.8% on average, n = 177) (Fig. 5). This frequency was significantly higher than that from March to October (30% on average, n = 290; Chi^2 = 113.9; p ≥ 0.001). This difference supports the hypothesis of an annual periodicity formation of the opaque band in *Percophis brasiliensis* otoliths in SB (see Fig. 6).

3.3. Reproductive cycle and age and size at first maturity

P. brasiliensis, with maturing, mature and partly spawn gonads, was observed throughout the year for both sexes in SB (Fig. 7).
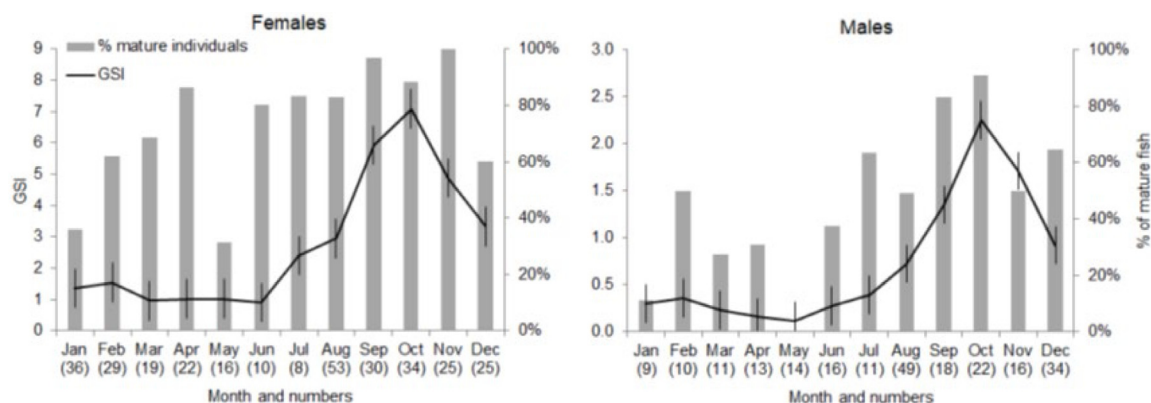
Fig. 7. Mean monthly gonadosomatic index (IGS, columns) and relative frequency of mature individuals by month (line, vertical bars represent IC95% of the mean) for both sexes of *Percophis brasiliensis* in southern Brazil.

Table 2
Logistic model parameters (β_1 and β_0) and the calculated length-at-first maturity (L_{50} (mm)), length at 95% of maturity (L_{95} (mm)) and age-at-first maturity for females *P. brasiliensis* in the Rio Grande. All parameters and indices are presented as the mean of their posterior distributions and the 2.5% ($Cr\ I_{2.5\%}$) and 97.5% ($Cr\ I_{97.5\%}$) credibility intervals.

Parameters	Females		
	Mean	$Cr\ I_{2.5\%}$	$Cr\ I_{97.5\%}$
$\beta_1 L_{50}$	0.053	0.035	0.054
$\beta_0 L_{50}$	−21.78	−29.85	−14.33
L_{50}	407.9	393	421.8
L_{95}	465.2	443.9	493.7
$\beta_1 A_{50}$	1.56	0.98	2.32
$\beta_0 A_{50}$	−3.46	−5.58	−1.73
A_{50}	2.18	1.67	2.62

However, the mean gonadosomatic indices were higher from August to December, reaching peaks in November for females and October for males. The mean GSI from September to November was significantly higher than that in the other months for both males (F = 3.302; P < 0.001) and females (F = 3.726; P < 0.001).

The lack of small male individuals in the samplings prevented us from estimating the size and age at maturity for the males. Only data from September to December were used for better separation of spent and development stages to reduce the misidentification between spent and immature stages. The credibility intervals (95%) of the logistic model parameter β_1 used to calculate the length and age at first maturity for both sexes did not include zero, which indicates a significant relationship between maturity and size and age (Table 2). The size at first maturity was estimated at 407.7 mm, and the size at 95% maturity was 469.6 mm for females. The females' age at first maturity was estimated at 2.2 years (Table 2, Fig. 8).

3.4. Age and growth

A clear annual cycle of the gonadosomatic indices and the frequency of opaque edges in the otoliths were observed (Figs. 5 and 7). Considering November as the month with the highest birth rate (Fig. 7) and that most opaque rings were formed in January, we concluded that specimens completed the first opaque band in their otoliths on average at 15 months old. Each fish was aged by summing the number of opaque bands plus three months from the first annulus formation plus the time between January first and the date of catch if the edge band was translucent. If the edge band was opaque, the time left between the landing date and January first was subtracted from the number of counted opaque bands.
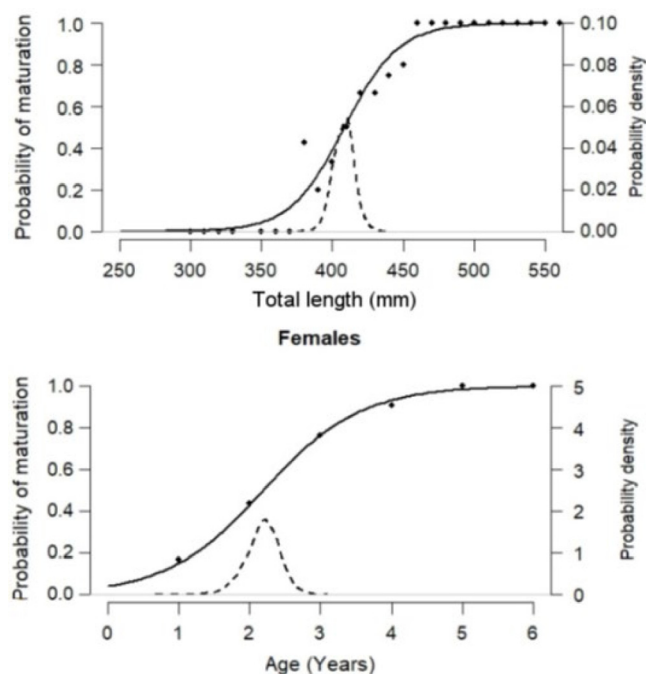

Fig. 8. First maturation lengths and their respective posterior distributions of female *Percophis brasiliensis* in southern Brazil. Dark spots: observed data; continuous line: posterior distribution of data; dashed line: probability distribution. Upper panels: size at maturity; lower panels: age at maturity.

The largest female sampled was 718 mm (TL), and the largest male was 605 mm (TL). The maximum age observed for both sexes was 12 years. Due to the difficulty in determining the sex of young specimens, all individuals smaller than 250 mm were included for adjustment of both males' and females' growth curves. The Von Bertalanffy (VB) growth model with sex as a factor had a smaller D.I.C. value (4785.9) compared with the pooled sex model (4868.5), indicating differences in growth between sexes. For females, the VB parameters were calculated as $L\infty$ = 625.0 mm, k = 0.39 year^{-1}, and t_0 = −0.26 years, and for males, they were calculated as $L\infty$ = 599.3 mm, k = 0.318 year^{-1}, and t_0 = −1.66 (Table 3). The females reached larger sizes and grew faster than males (Fig. 9), but the credibility intervals for Von Bertalanffy parameters overlapped (Table 3). For pooled sexes, the VB parameters were calculated as $L\infty$ = 617.6 mm, k = 0.33 year^{-1}, and t_0 = −0.82.

Table 3
The von Bertalanffy growth parameters by sex and pooled sexes for *Percophis brasiliensis* fished in southern Brazil and their respective credibility intervals.

Sex	Parameters								
	2.5	L∞ (cm)	97.5	2.5	k (yr $^{-1}$)	97.5	2.5	t_0	97.5
Male	545.3	573.4	612.1	0.25	0.34	0.43	−1.76	−1.13	−0.66
Female	609.2	625.0	642.6	0.34	0.39	0.44	−0.50	−0.26	−0.05
Pooled sex	599.3	617.6	639.2	0.28	0.33	0.37	−1.13	−0.82	−0.56
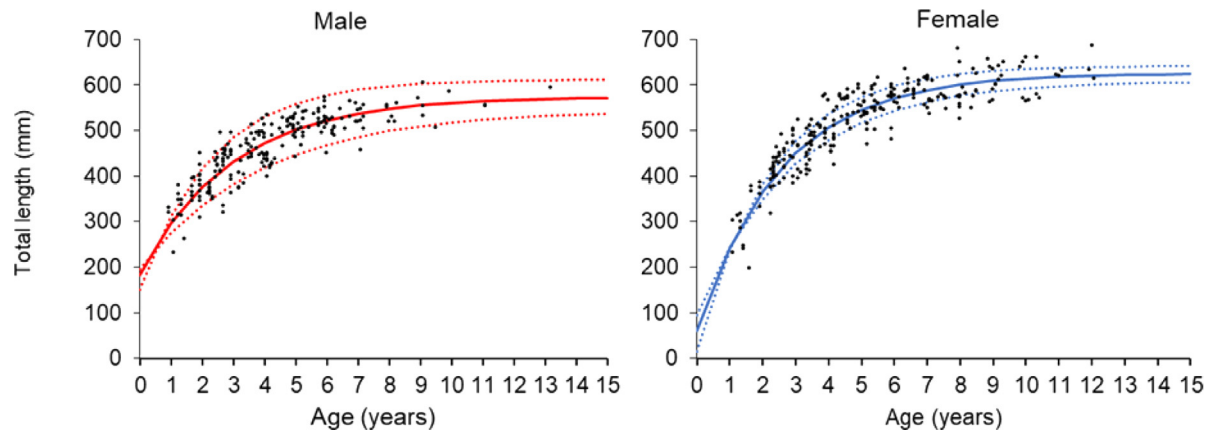
Fig. 9. Growth curves of male and female *Percophis brasiliensis* in southern Brazil. Dashed lines: 95% credibility intervals.

3.5. Population size, age, and sex structures

The mean length and age in the landings of the trawling gear were 526 mm and 4.01 years, respectively, and were 553 and 4.97 years, respectively, in the bottom gillnets. The frequency of females increased from less than 30% at the lower lengths (<330 mm) and ages (<1 yr) up to 100% among the specimens over 630 mm and the 80% of specimens older than ten years. The overall proportion of females was 56% among the entire specimen's pool.

3.6. Natural mortality

The older specimens were 12 years; therefore, the considered maximum age for the M estimate was 13 years. The mean and standard deviation of the four estimates were 0.419 and 0.105, respectively.

3.7. Population dynamics

A population dynamics model was built to accommodate the sex-specific estimated growth and maturity parameters (Table 4). The natural mortality parameter and weight-length coefficient and exponent were considered to be the same for both sexes (Table 4). Steepness was set to 0.73, which is the value for the order Perciformes using the FishLife package in R (Thorson, 2020; Thorson et al., 2017), which is the closest taxonomic estimate available for *P. brasiliensis*. All the parameters used in the model and their utilization are provided in Table 4.

The sizes at first maturity and 95% maturity for males were obtained from Militelli and Macchi (2001) since they were not estimated in this study.

The available data covered 34 years from 1985 to 2019, but not all data were available for all the years (Fig. 3). The catch time series covered the more extensive time, followed by the abundance indices (Fig. 4). The standardized catch per unit of effort (CPUE) was available from 1999 to 2019 for the double rig bottom trawling fleet. The overall CPUE presented a slight increase between 2000 and 2010, when it decreased slightly until 2019 (Fig. 10). Size compositions were available for only

a few years from 2007 and 2019 but were extremely important since they allowed the estimation of the current stock status by length-based stock assessment methods integrated into the overall model.

The overall fit to the length data was good, and residuals showed a random distribution (Fig. 11). The overall fit to the index of fleet 1 was also good, and the residuals showed a random pattern (Fig. 12).

The final gradient of the model was notably small (0.0000121), and the Hessian matrix for the parameter estimates was positive definite. The models run relatively fast (~23 s) and show good convergence properties.

The retrospective performance of the model is overall good (Fig. 13), with all values falling within the confidence intervals of the different runs. The scale of spawning stock biomass (SSB) increased as the analysis removed −4 and −5 years but without changing the overall pattern. The scale of F/FMSY did not change as the final years were removed, also without changing the overall pattern (Fig. 13).

The model shows high stability in the log-likelihood with different starting values (Fig. 14). All 50 jitter model runs converged, with 32 model runs at the total negative likelihood estimate value of the base case model run (192 likelihood units), and 18 model runs had smaller total negative likelihood values (Fig. 14). The jittered model was robust to the initial values of the parameters and provided no evidence that the base case model converged to a local minimum of the objective function instead of the global minimum.

When analyzing the model prediction ability, the fitted index and length compositions included at least one observation that fell within the hindcast evaluation period, 2015–2019 (Fig. 15). However, MASE scores >1 for the index indicated a lower predictive ability than that of the length compositions of all fleets (Fig. 15).

The estimated population trends presented a steady decrease between 1986 and 2005, a slight increase from 2005 and 2010, and a sharp decline until 2019 (Fig. 16). The current SSB was estimated at 0.68 of the SSBmsy, classifying the stock status as overfished (Fig. 16). The fishing mortality increased from 1986 until the early 2000s, remained high until the early 2010s and
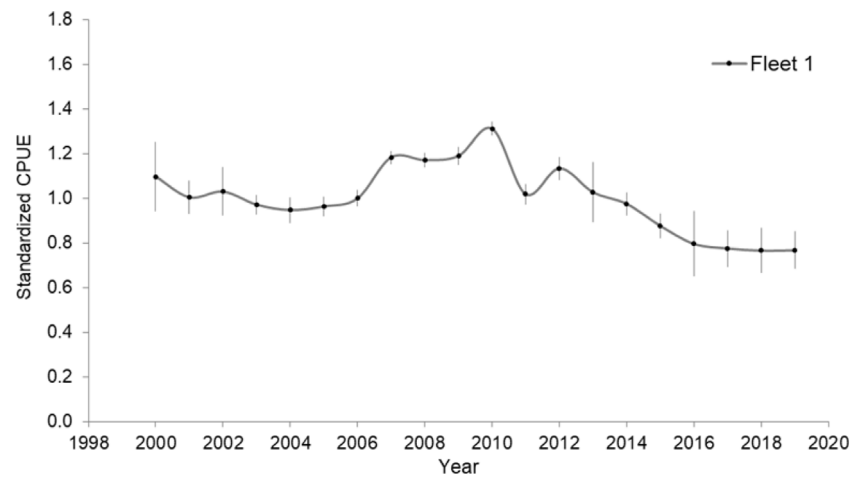
Fig. 10. The standardized catch per unit of effort for the double rig bottom trawling fleet landing *Percophis brasiliensis* fished in southern Brazil. Vertical bars indicate the coefficient of variation.
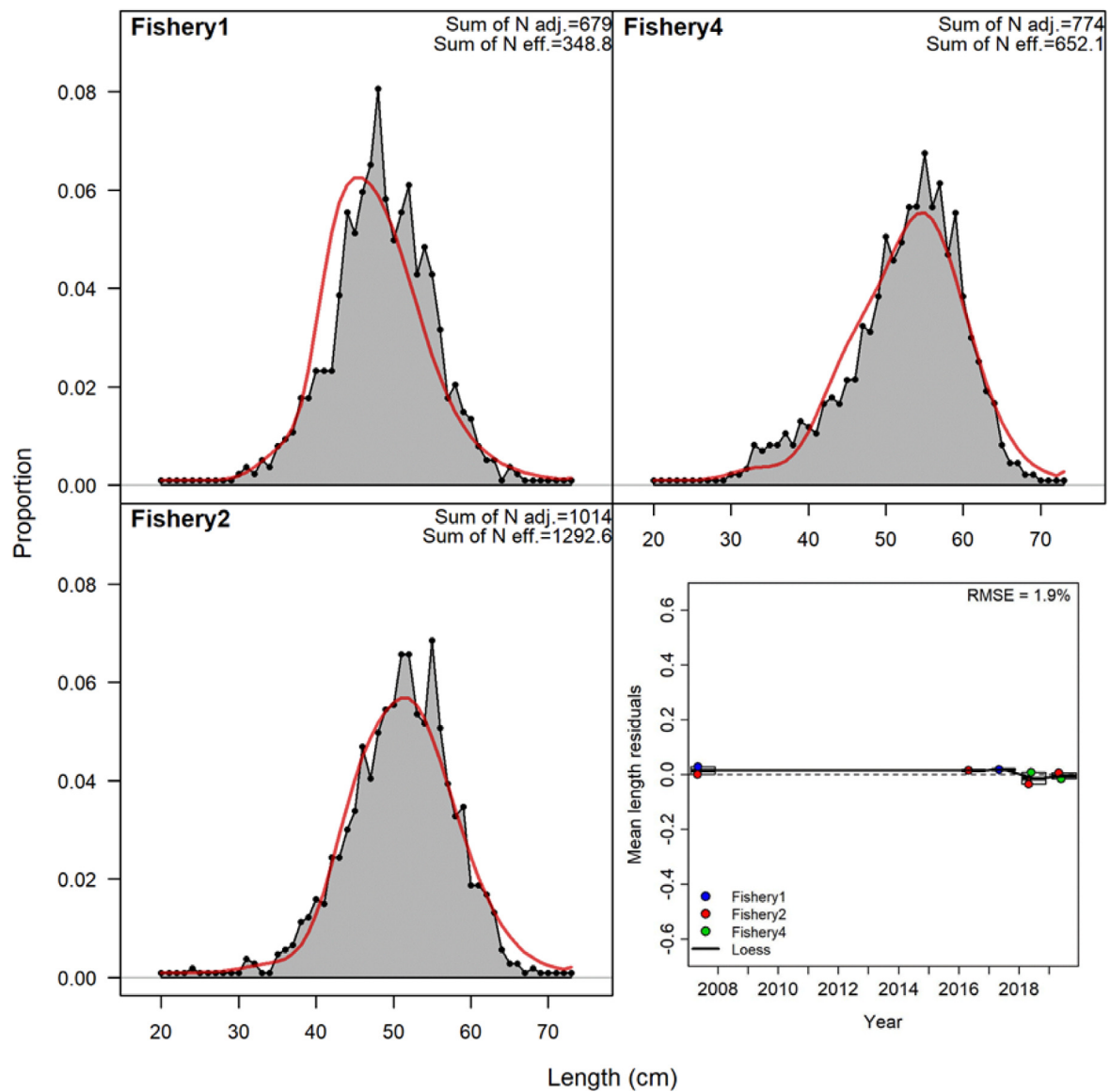

Fig. 11. Aggregated length composition fitted for each fleet for the assessment model for *P. brasiliensis* from southern Brazil. The red line indicates the aggregated modeled length composition showing the fit to the observed length data. Joint residual plot of the length composition fits (bottom right panel). Double rig bottom trawling (Fishery 1), pair bottom trawling (Fishery 2), and bottom gillnet (Fishery 4). . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4

Model parameter inputs into the Stock Synthesis Data Limited Tool (SS-DL tool) and how they are utilized in the reference Stock Synthesis model for *P. brasiliensis* off southern Brazil.

| Parameter	Male	Female	Treatment
L_∞ (cm)	57.3	62.5	Fixed
$k_{year}{}^{-1}$	0.34	0.39	Fixed
t_0	−1.13	−0.25	Fixed
L_{50} (cm)	28.9	40.7	Fixed
L_{95} (cm)	33	46.2	Fixed
Natural mortality	0.41 (0.05)		Fixed
Weight (g)-length (cm) alpha	0.0026		Fixed
Weight (g)-length (cm) beta	3.105		Fixed
Weight-based fecundity coefficient	1		Fixed
Weight-based fecundity exponent	1		Fixed
Steepness	0.71		Fixed
Initial recruitment (lnR_0)	0.72		Estimated
Bottom trawling (Fleet 1) length at 50% selectivity	45		Estimated
Bottom trawling (Fleet 1) length at peak selectivity	50		Estimated
Bottom gillnet (Fleet 2) length at 50% selectivity	55		Estimated
Bottom gillnet (Fleet 2) length at peak selectivity	65		Estimated
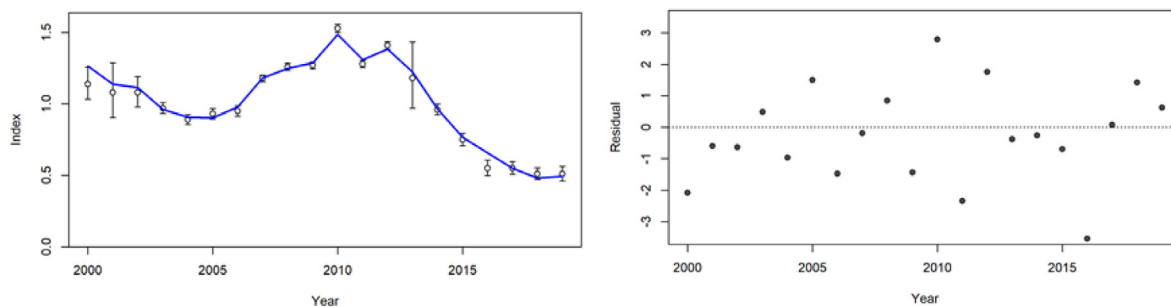
Fig. 12. Fit of the modeled index series to the observed index data (left panel) and the fit residuals from the modeled index series for *P. brasiliensis* from southern Brazil.
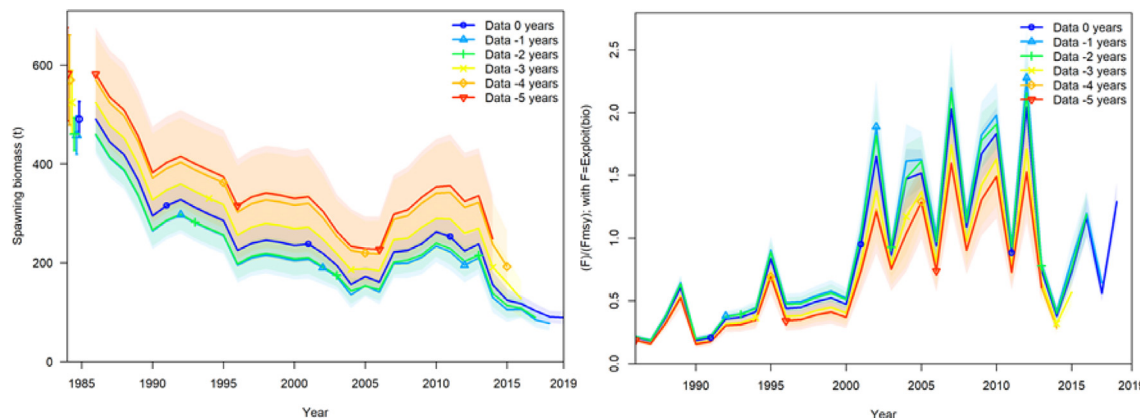

Fig. 13. Retrospective plots of spawning biomass and F/Fmsy for *P. brasilensis* from southern Brazil.

presented a steep decline until 2014, when it began increasing again. It reached high values (F>F*msy*) in 2019, causing us to conclude that the stock is suffering from overfishing (Fig. 12). The recruitment estimations did not show deviations until the 2000s since they presented a dynamic pattern with positive deviations between 2000 and 2010 and negative deviations between 2010 and 2016 (Fig. 16).

The sensitivity to recruitment compensation (i.e., steepness) and natural mortality (*M*) were explored using likelihood profiles (Fig. 17). These parameters are often difficult to directly measure but can have a large effect on population scale and relative size. The base model value of $h = 0.71$ was determined by the life history meta-analysis (Thorson et al. 2017), as the model lacked strong information to estimate steepness. Most of the information used to estimate the steepness was obtained from the

length compositions, as seen in the likelihood profiles (Fig. 17). The estimated population indices (initial spawning biomass, final spawning biomass, and depletion) did not show strong sensitivity to steepness (Fig. 17). Regarding the natural mortality, most information was obtained from the recruitment and index, as seen in the likelihood profiles. Some population indices showed slight sensitivity to M, with the initial spawning biomass slightly decreasing and the fraction of unfished increasing as M increased (Fig. 17). However, the final spawning biomass did not change according to M value (Fig. 17).

4. Discussion

The present study generated essential data on the life history and population dynamics of *Percophis brasiliensis* fished in
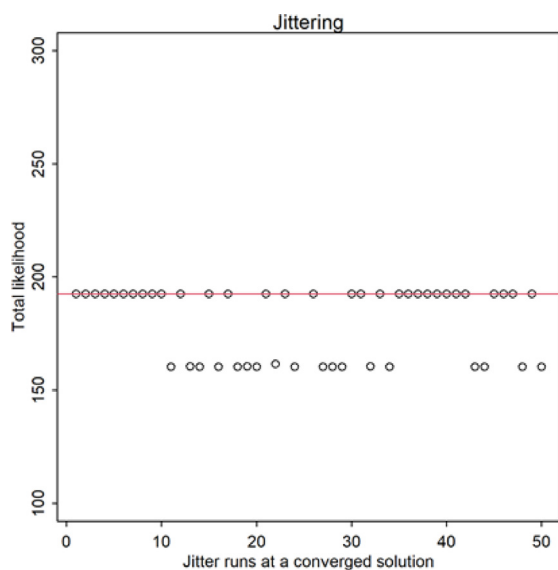
Fig. 14. Total likelihood for the jittered models for *P. brasiliensis* from southern Brazil.

SB. Furthermore, the life history parameters combined with the available information on landing time series, size composition, and catch per unit of effort allowed us to assess the current stock status in SB. However, the assessment is "data-limited"; length compositions are lacking for the early years, and an index from the gillnet fleet is missing. Thus, the results should be cautiously interpreted.

4.1. Reproduction

The reproduction of *P. brasiliensis* was studied in detail in its southern range by Militelli and Macchi (2001), who showed that the species is a multiple-batch spawner. Furthermore, Rodrigues (2012) showed that although females in different maturity stages were observed year-round, high gonadosomatic indices were found only in spring and summer when active spawning females were observed histologically. In SB, although different maturity stages were observed year-round, monthly mean gonadosomatic indices were higher from July to December, with peaks from September to November (Fig. 7); therefore, spawning is limited to spring. Rodrigues (2012, and references therein) recorded spawning activities in El Rincon and the Argentine-Uruguayan Common Fishing Zone (CFZAU) at temperatures between 12 °C and 19 °C and salinities lower than 33 ups in several spring surveys. The authors also recorded waterfronts and recirculation cells favoring larval and juvenile retention in enriched shallow warm waters in El Rincon. The species shares the spawning grounds with several other abundant bony fishes, such as *Micropogonias furnieri, Umbrina canosai,* and *Cynoscion guatucupa.* Although we have limited data on the circulation and bottom seawater temperatures in SB, the range of temperatures of the spawning grounds observed in Argentina was observed in SB only in September and November in bottom trawl surveys (Martins and Haimovici, 2017). It was lower than 14 °C in August and higher than 20 °C in February and April in the 1980s, while primary production is higher in spring and lower in summer (Ciotti et al., 1995; Odebrecht and Castello, 2001). Therefore, the high bottom temperatures and low primary productivity may not be adequate for *P. brasiliensis* reproduction during summer in SB.

4.2. Age and growth

The observed opaque edge deposition during spring and summer agrees with previous observations in Argentina-Uruguay (AU) coastal waters (Barretto et al., 2011; López et al., 2019). The same pattern was observed in bony species such as *Macrodon atricauda* (Gunther 1880) (Cardoso and Haimovici, 2011), *Cynoscion guatucupa* (Cuvier 1830) (Vieira and Haimovici, 1993), *Umbrina canosai* Berg 1895 (Haimovici and Reis, 1984), *Dules auriga* (Rovani and Cardoso, 2017), and *Cynoscion jamaicensis* (Alves et al., 2020).

Opaque and translucent band deposition may be driven by endogenous factors, such as diet and reproduction, and exogenous processes, such as seasonal changes in the water temperature or photoperiod, which can result in seasonal changes in food availability (Green et al., 2009; Morales-Nin, 2000). In this region, the seasonal shift of the subtropical convergence western boundary changes the bottom seawater temperature seasonally, reaching up to 10 °C (Martins et al., 2017), inducing considerable differences in the primary productivity between seasons (Odebrecht and Castello, 2001).

The maximum observed age and the VB growth parameters estimated in this study differed from those of previous studies (Table 5). In Argentina, San Roman (1974) only counted up to seven growth bands, probably missing several annuli, resulting in low *k* and high *L∞* estimates. The maximum number of observed annuli was 19 by Barretto et al. (2011), 17 by Rico et al. (2018), and 14 by López et al. (2019). These maximum numbers of annuli were substantially higher than the 12 opaque bands in our study, suggesting higher longevity in the colder southern range of the species distribution, as it cannot result from the highest exploitation in SB since bottom trawl fishing was equally intense for many decades in both regions (Haimovici and Cardoso, 2017; Rico et al., 2018).

Although we did not find significant differences in the VB growth parameters between males and females (Table 3), differences between sexes were observed in all studies, with females growing larger than males. When comparing the growth curve from this study with the most recent growth curve in the ZCPAU (2013, in Rico et al., 2018), it can be observed that *P. brasiliensis* from SB attains a smaller *L∞* and at an earlier time in life than the species in its southern range (Fig. 18). It was also observed that the estimated sizes at ages 1 to 4 were smaller in the ZCPAU than in SB in this study. This difference in early-life growth may be an artifact resulting from the differences in the interpretation of the nuclei of the otoliths. Previous studies in the southern range of this species may discriminate more opaque bands near the nucleus, resulting in older Ager interpretations for small-sized fish than those in this study. It is possible that in SB at lower latitudes, yearlings are born earlier and grow longer before forming the first opaque band than those born at higher latitudes in Argentina, where comparable seawater temperatures are reached later. The lower maximum age in SB can reflect either the depletion of the older fish caused by intense fishing or, most likely, lower longevity due to higher water temperatures, as observed for stocks of other species (Beverton, 1987).

4.3. First maturation

In SB, the first maturity of females was estimated at 407.9 mm and 2.18 years, and in Argentina and Uruguay, it was estimated at 383.4 mm (Militeli & Macchi, 2001), 367 mm (Rodrigues, 2012), and 2.56 years (Rico et al., 2018). Thus, differences are slight and all within the confidence intervals of the values in SB. However, the maturity at a larger size and lower age in SB cannot be discarded, as the differences are congruent with those observed in growth (Item 4.2).
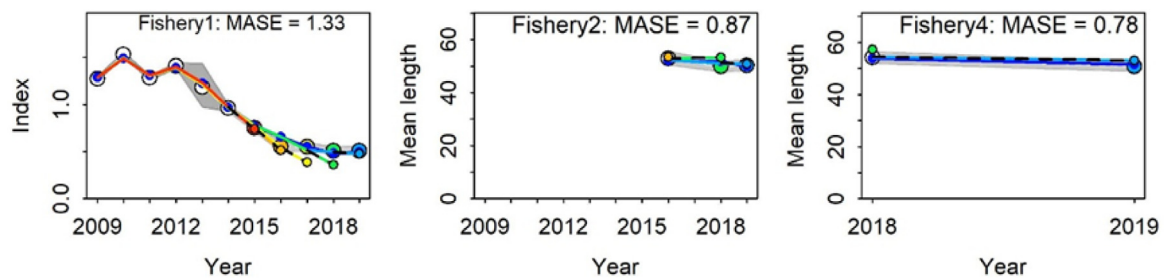
Fig. 15. Hindcasting plots for the index and length composition fits for *P. brasiliensis* from southern Brazil.

Table 5

Maximum recorded ages and growth parameters of von Bertalanffy of *P. brasiliensis* in different studies throughout its distribution in Argentina, Uruguay, and southern Brazil.

Reference	Sampling area	Sampling period	N (age)	Sex	Older age	L∞ (mm)	k (yr^{-1})	t_0
San Roman (1974)	Argentina	1971	392	M+F	7	862.0	0.17	0.25
Perrotta and Fernández-Giménez (1996)	AUCFZ El Rincon. Argentina	1993 1993	250 351	M+F M+F	12 12	683.9 707.8	0.19 0.14	−1.96 −2.86
Barretto et al. (2011)	AUCFZ	1998–2004	439 414	M F	19 15	581.0 652.0	0.26 0.29	−2.02 −1.15
Rico et al. 2012 *in* Rico et al. (2018)	AUCFZ	2005	463 534 1004	M F M+F	16	623.5 704.8 676.7	0.28 0.26 0.25	−0.50 −0.16 −0.37
Sanz et al.. MS. in Rico et al. (2018)	AUCFZ	2013	298 446 744	M F M+F	17	640.3 686.5 673.8	0.30 0.33 0.31	0.04 0.52 0.28
López et al. (2019)	San Martin Gulf. Argentina	2009–2014	97 196 294	M F M+F	12 14	545.8 783.1 860.6	0.36 0.11 0.08	−0.46 −3.61 −5.51
This study	Southern Brazil	2018–2019	297 215 514	M F M+F	12 12	573.4 625.3 617.6	0.34 0.39 0.37	−1.13 −0.26 −0.82

4.4. Is there a single stock in the region?

Whether the stock along SB is a continuity of the stock in the AUCFZ is relevant for stock assessment. In Uruguay and Argentina, the species is considered to migrate toward deeper waters in winter and return to coastal waters to reproduce in spring, mainly in the El Rincon region (Barretto et al., 2011; Rodrigues, 2012). *P. brasilinesis* is also considered to migrate in the cold season toward the north of the Rio de la Plata front (Jaureguizar et al., 2004) and further north to SB waters, according to Rico et al. (2018). However, this hypothesis is not sustained by the monthly distribution of the landings in the three locations along with the species distribution: the ZEE of Argentina, south of 39°S, the Argentinian–Uruguayan Common Fishery Zone and in the SB landings in Rio Grande and Itajai. In all three regional series, the lower landings occurred during the winter, which indicates no exchanges of individuals between the regions during these months (Fig. 19).

The differences observed in growth, age, and spawning period length, although not conclusive, also contribute to the hypothesis of limited connectivity between the two regions. This view is supported by the differences in the assemblages of long-lived larval parasites between the two regions (Braicovich et al., 2017), distinct from those observed in the species' southern range. The stock structuration is attributed to latitudinal gradients in oceanographic conditions, mainly temperature and salinity (Cantatore et al., 2015). Therefore, for management purposes, we recommend a separate stock assessment.

To obtain a better conclusion, DNA studies may be necessary to validate these conclusions.

4.5. Stock assessment

The availability of landing series, size composition, and abundance index combined with the life history parameters estimated in this study made it possible to assess the current stock status and reconstruct the spawning output trajectory of the *Percophis brasiliensis* SB stock.

The declining biomass trajectory until the early 2000s is in agreement with the stock assessment of the species in the Common Fishery Zone between Uruguay and Argentina. However, according to Model 1, the current stock depletion in SB is 0.25, which is higher than that estimated by Rico et al. (2018) (0.43) for the ZCPAU. This result initially appears counterintuitive, as *P. brasiliensis* is not directly targeted in SB; however, in this last region, intense bottom trawl fishing targeted other species in the same depth range that *P. brasiliensis* inhabits (Haimovici and Cardoso, 2017). According to our modeling, the current stock status is overfished, an expected result after 50 years of poorly managed intense fishing on demersal species in the region (Haimovici and Cardoso, 2017).
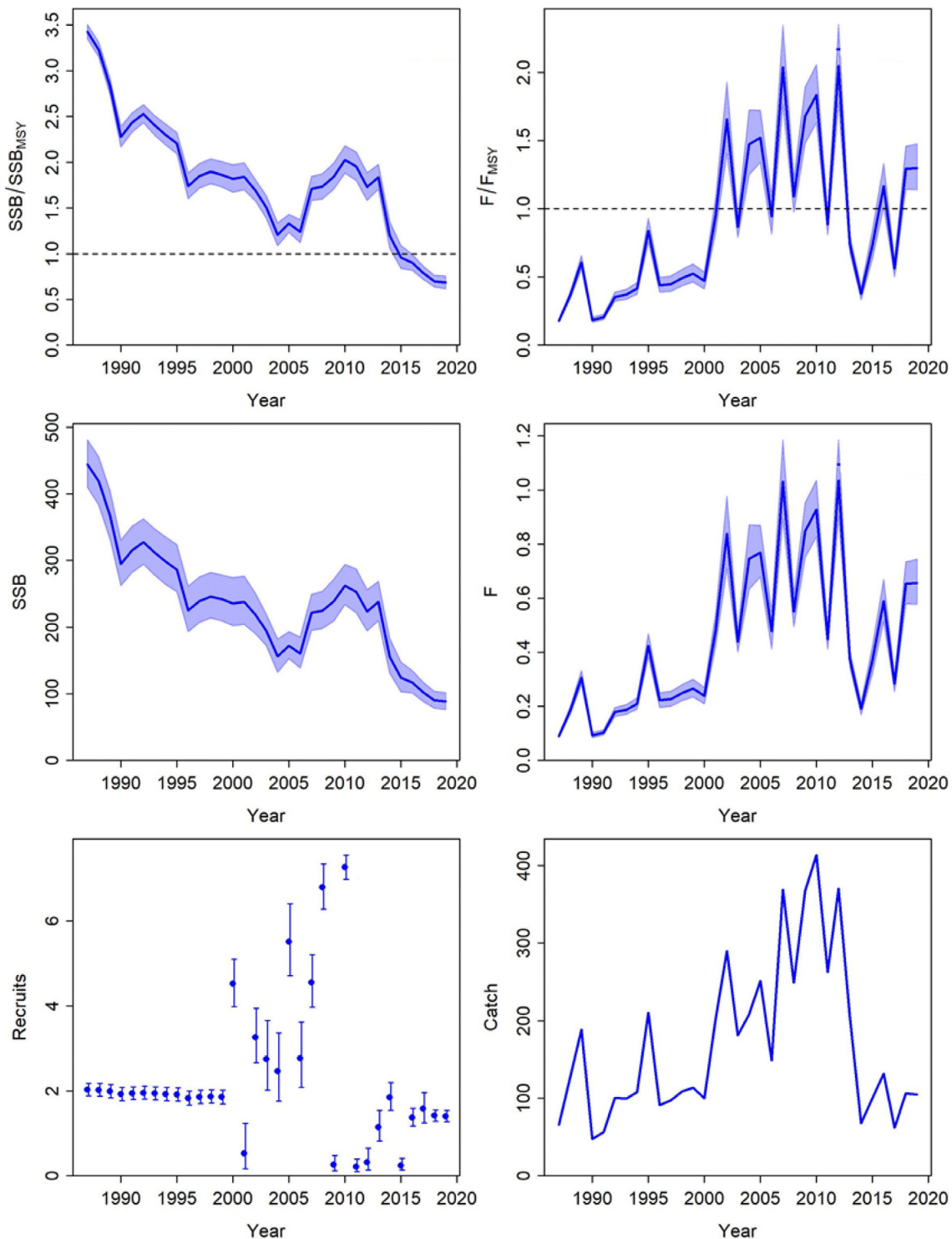
Fig. 16. Estimated time series from 1985 to 2019 for *P. brasiliensis* from southern Brazil. Spawning biomass (SSB)/SSBmsy (top left panel), fishing mortality (F)/Fmsy (top right panel), spawning biomass (middle left panel), fishing mortality (middle right panel), recruits (bottom left panel), and catch time series (bottom right panel).

Following several fishery management agencies worldwide that consider 40% and even 30% of the unfished biomass as a limit for a maximum sustainable yield (Punt et al., 2014), any increase in the fishing effort would lead to overfishing of the *P. brasiliensis* stock. However, Pauly and Froese (2020) argue that fishery management should maintain the fish population's biomass above the MSY level for increasing stock yields and that

this would allow them to better fulfill their ecological roles as prey or predator. The intense fishing in the region (Haimovici and Cardoso, 2017) may have pushed the *P. brasiliensis* stock from SB to its limit, and whether it can be considered overfished or not depends upon the objectives of Brazilian fishery management.

These results highlight the importance of life-history studies and continuous monitoring of all species, including those that
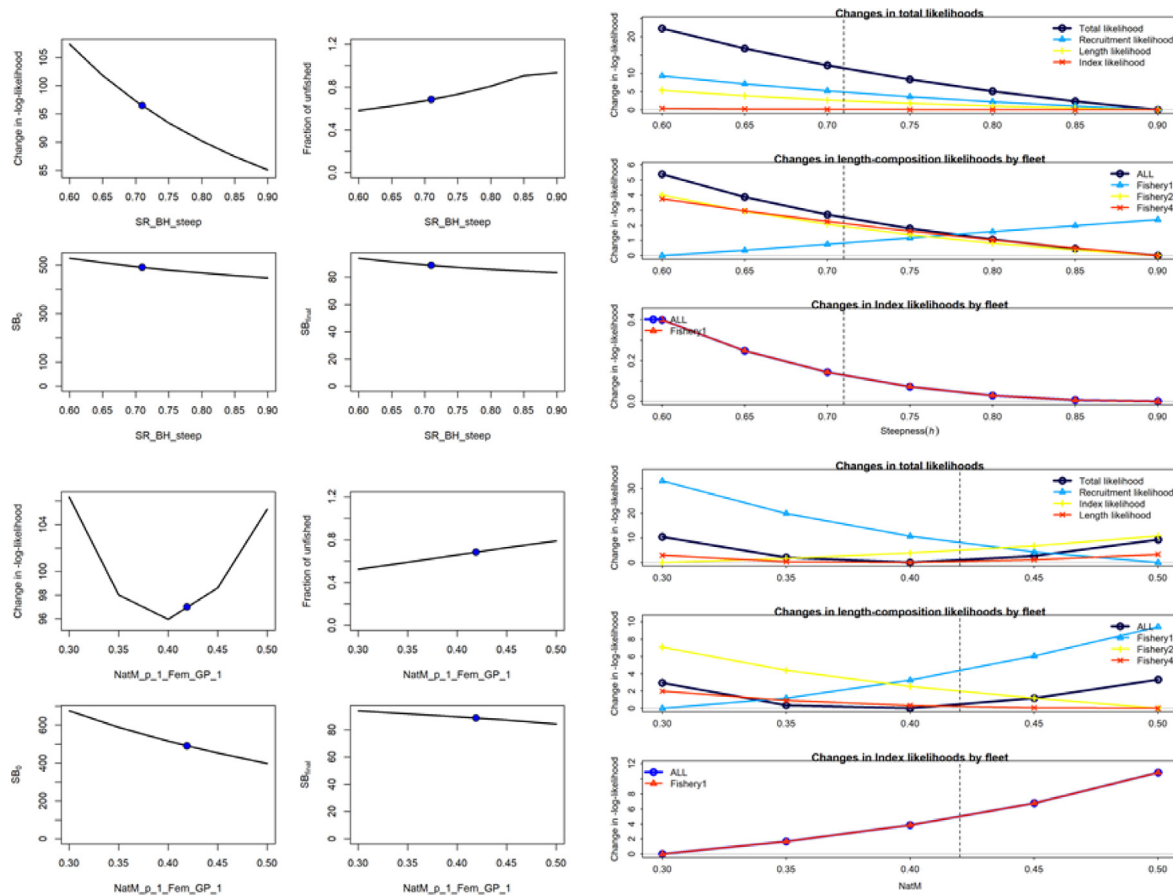
Fig. 17. Likelihood profiles for the reference model. Left top and bottom panels (clockwise): Likelihood profile, fraction of unfished biomass, initial spawning biomass and current spawning biomass. The blue dot indicates the reference model value. Right top and bottom panels (top to bottom): Likelihood component profiles by likelihood element, length compositions and index.
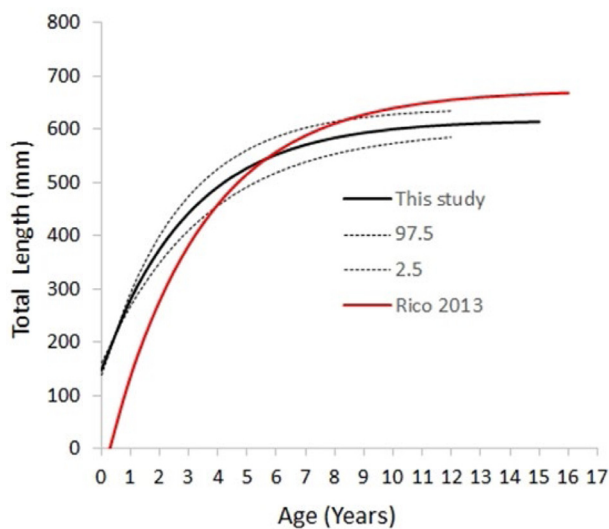

Fig. 18. The von Bertalanffy growth curve and 95% credibility intervals estimated for *Percophis brasiliensis* in southern Brazil in 2018–19 (black solid and dashed lines) and in the CFZAU in 2013 (Rico et al., 2018) (in red). . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
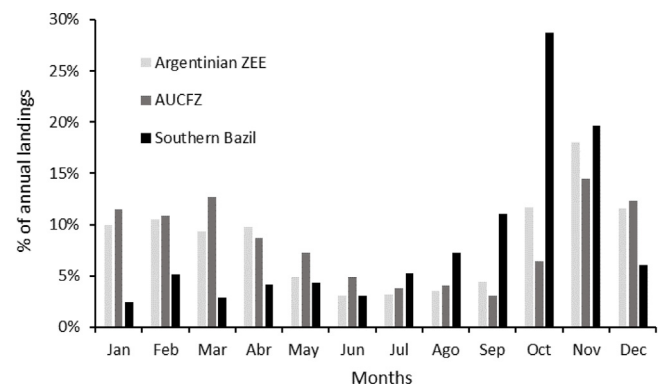

Fig. 19. Monthly landings as percentages of the Argentinian ZEE annual landings, south of 39°S, the Common Fishery Zone of Argentina and Uruguay (AUCFZ) and southern Brazil (sources in the text).

are not the main target of fisheries, as intense fishing may make their populations less resilient to stochastic effects such as climatic variations and threaten their functional roles in marine ecosystems.

CRediT authorship contribution statement

Danilo Shoiti Hirota: Formal analysis, Writing – original draft. **Manuel Haimovici:** Investigation, Methodology, Writing – original draft, Writing – review & editing. **Rodrigo Sant'Ana:** Writing

– review & editing. **Bruno Leite Mourato:** Writing – review & editing. **Eidi Kikuchi:** Writing – review & editing. **Luís Gustavo Cardoso:** Supervision, Writing – original draft, Writing – review & editing, Resources, Project administration.

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.

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References

Adams, P.B., 1980. Life history patterns in marine fishes and their consequences for fisheries management. Fish. Bull. 78 (1), 1–12.

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. Regional Stud. Mar. Sci. 34, 101063.

Avigliano, E., Saez, M.B., Rico, R., Volpedo, A.V., 2015. Use of otolith strontium: calcium and zinc: calcium ratios as an indicator of the habitat of *Percophis brasiliensis* Quoy & Gaimard, 1825 in the southwestern Atlantic Ocean. Neotrop. Ichthyol. 13 (1), 187–194.

Barretto, A.C., Sáez, M.B., Rico, M.R., Jaureguizar, A.J., 2011. Age determination, validation, and growth of Brazilian flathead (*Percophis brasiliensis*) from the southwest Atlantic coastal waters (34-41 s). Latin Amer. J. Aquatic Res. 39 (2), 297–305.

Beverton, R.J., 1987. Longevity in fish: some ecological and evolutionary considerations. In: Evolution of Longevity in Animals. Springer, Boston, MA, pp. 161–185.

Braicovich, P.E., Pantoja, C., Pereira, A.N., Luque, J.L., T. Timi, J.U.A.N., 2017. Parasites of the Brazilian flathead *Percophis brasiliensis* reflect west Atlantic biogeographic regions. Parasitology 144 (2), 169.

Braicovich, P.E., Timi, J.T., 2008. Parasites as biological tags for stock discrimination of the Brazilian flathead *Percophis brasiliensis* in the south-west Atlantic. J. Fish Biol. 73 (3), 557–571.

Campana, S.E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. 59 (2), 197–242.

Cantatore, D.M.P., Timi, J.T., Timi, J., 2015. Marine parasites as biological tags in South American atlantic waters, current status and perspectives. Parasitology 142 (1), 5.

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.

Carvalho, F., Winker, H., Courtney, D., Kapur, M., Kell, L., Cardinale, M., ..., R.D., 2021. A cookbook for using model diagnostics in integrated stock assessments. Fish. Res. 240, 105959.

Ciotti, Á.M., Odebrecht, C., Fillmann, G., Moller, Jr., O.O., 1995. Freshwater outflow and subtropical convergence influence on phytoplankton biomass on the southern Brazilian continental shelf. Cont. Shelf Res. 15 (14), 1737–1756.

Cope, J., 2020. The stock synthesis data-limited tool (SS-DL tool). https://github.com/shcaba/SS-DL-tool#the-stock-synthesis-data-limited-tool-ss-dl-tool Acessed on April, 24, 2021.

Cousseau, M.B., Perrotta, R.G., 2004. Peces marinos de Argentina. Biología, distribución, pesca. INIDEP Publicaciones Especiales, Mar del Plata, p. 163.

Dowling, N.A., Dichmont, C.M., Haddon, M., Smith, D.C., Smith, A.D.M., Sainsbury, K., 2015. Guidelines for developing formal harvest strategies for data-poor species and fisheries. Fisheries Research 171, 130–140.

Fernández-Araoz, N.C., Lagos, N., Carozza, C.R., 2004. Asociación íctica costera bonaerense variado costero. In: Evolución de Las Capturas Desembarcadas Por la Flota Comercial Argentina (1998-2003). Inf. Téc, Vol. 4. INIDEP, p. 21.

FURG/SEMA, 2020. Boletim da Pesca Industrial Marinha no Rio Grande do Sul – 2019. Laboratório de Recursos Pesqueiros Demersais e Cefalópodes - Instituto de Oceanografia FURG., p. 28, Atualizado em 23/04/2020.

Gosztonyi, A.E., Angelescu, V.A., 1981. Resultados de las investigaciones ictiológicas de la campaña I del B/I Shinkai Maru en el Mar Argentino (10.04-09.05. 1978). In: Campañas de Investigación Pesquera Realizadas en el Mar Argentino por los B/I Shinkai Maru y Walter Herwig y el B/P Marburg, años 1978 y 1979. Resultados de la parte Argentina, p. 383.

Green, B.S., Mapstone, B.D., Carlos, G., Begg, G.A. (Eds.), 2009. Tropical Fish Otoliths: Information for Assessment, Management and Ecology (Vol. 11). Springer Science & Business Media..

Haimovici, M., 1987. Estratégia de amostragem de comprimentos de teleósteos demersais nos desembarques da pesca de arrasto no litoral sul do Brasil. Atlântica 9 (1), 65–82.

Haimovici, M., 1998. Present state and perspectives for the southern Brazil shelf demersal fisheries. Fish. Manage. Ecol. 5 (4), 277–289.

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 (1), 135–150.

Haimovici, M., Cousin, J.C.B., 1989. Reproductive biology of the castanha Umbrina canosai (Pisces, Sciaenidae) in Southern Brazil. Rev. Brasil. Biol. 49 (2), 523–537.

Haimovici, M., Martins, A.S., Vieira, P.C., 1996. Distribuição e abundância de peixes teleósteos demersais sobre a plataforma continental do sul do brasil. Rev. Brasil. Biol. 56 (1), 27–50.

Haimovici, M., Reis, E.G.L., 1984. Determinação de Idade e Crescimento da Castanha Umbrina Canosai, (Pisces, Sciaenidae) Do Sul Do Brasil, Vol. 7. Rio Grande, Atlântica, pp. 25–46.

Haimovici, M., Rossi-Wongstchowski, C.L.D.B., Bernardes, R.Á., Fischer, L.G., Vooren, C.M., dos Santos, R.A., Rodrigues, A.R. (Eds.), 2008. Prospecção Pesqueira de Espécies Demersais Com Rede de Arrasto-de-Fundo Na Região Sudeste-Sul do Brasil. IOUSP.

Hewitt, D.A., Hoenig, J.M., 2005. Comparison of two approaches for estimating natural mortality based on longevity. Fish. Bull. 103 (2), 433.

Hoyle, J.A., 2015. Fish species composition, distribution and abundance trends in the open-coastal waters of northeastern Lake Ontario, 1992–2012. Aquatic Ecosyst. Health Manage. 18 (1), 89–100.

Jaureguizar, A.J., Menni, R., Guerrero, R., Lasta, C., 2004. Environmental factors structuring fish communities of the Río de la Plata estuary. Fish. Res. 66 (2–3), 195–211.

Kellner, K., Kellner, M.K., SystemRequirements, J.A.G.S., 2019. Package 'jagsUI'.

Kinas, P.G., Andrade, H.A., 2010. Introdução à análise Bayesiana (Com R). Porto Alegre, Mais Que Nada Administração Cultural.

Kirkwood, G.P., Beddington, J.R., Rossouw, J.A., 1994. In: Edwards, P.J., May, R.M., Webb, N.R. (Eds.), Harvesting Species of Di¡Erent Lifespans. Large-Scale Ecology and Conservation Biology. pp. 199–227.

Lasta, C.A., Carozza, C.R., Ruarte, C.O., Jaureguizar, A.J., 1999. Ordenamiento Pesquero en el Ecosistema Costero Bonaerense. INIDEP Inf. Téc. Int., p. 25.

López, M.E., Ocampo Reinaldo, M., Rodrigues, K.A., Rico, M.R., Sáez, M.E., González, R.A., 2019. Primeros datos sobre edad y crecimiento del pez palo brasileño *Percophis brasiliensis* (Piscis: Perciformes) en el Golfo San Matías, norte de la Patagonia (Argentina). MAFIS-Mar. Fish. Sci. 32 (2), 103–114.

Martins, A.S., 2000. As Assembléias e as Guildas Tróficas de Peixes ósseos e Cefalópodes Demersais da Plataforma Continental e Talude Superior do Extremo sul do Brasil. Federal University of Rio Grande, Brazil.

Martins, A.S., Costa, P.A.S., Haimovici, M., Braga, A.C., Mincarone, M.M., 2017. Ecologia trófica do néctor demersal da plataforma e talude continental da Bacia de Campos. Comunidades Demersais e Bioconstrutores: caracterização ambiental regional da Bacia de Campos. Atlântico Sudoeste 4, 167–185.

Martins, A.S., Haimovici, M., 2017. Seasonal mesoscale shifts of demersal nekton assemblages in the subtropical South-western Atlantic. Mar. Biol. Res. 13 (1), 88–97.

Mayer, F.P., Sant'ana, R., Ribeiro Junior, P.J., 2019. Modelagem da estrutura temporal das capturas incidentais em pescarias comerciais através de modelos hierárquicos Bayesianos. Rev. Bras. Biom. Lavras 37 (4), 1–10. http://dx.doi.org/10.28951/rbb.v37i4.417.

Methot, Jr., 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.

Milessi, A.C., Marí, N.R., 2012. Ecología trófica del pez palo, *percophis brasiliensis* (Quoy y Gaimard, 1825) en el ecosistema costero argentino-uruguayo (34°'S-41°'S).

Militelli, M.I., Macchi, G.J., 2001. Preliminary estimate of spawning frequency and batch fecundity of Brazilian flathead, Percophis brasiliensis, in coastal waters off Buenos Aires Province. Sci. Mar. 65 (2), 169–172.

Morales-Nin, B., 2000. Review of the growth regulation processes of otolith daily increment formation. Fish. Res. 46 (1–3), 53–67.

Morgan, M.J., 2008. Integrating reproductive biology into scientific advice for fisheries management. J. Northwest Atlantic Fish. Sci. 41.

Newman, D., Berkson, J., Suatoni, L., 2015. Current methods for setting catch limits for data-limited fish stocks in the United States. Fish. Res. 164, 86–93.

Odebrecht, C., Castello, J.P., 2001. The convergence ecosystem in the southwest atlantic. In: Coastal Marine Ecosystems of Latin America. Springer Berlin Heidelberg, pp. 147–165.

Pauly, D., Froese, R., 2020. MSY needs no epitaph—but it was abused. ICES J. Mar. Sci..

Pavlov, D.A., Emel'yanova, N.G., Novikov, G.G., 2009. In: Jakobsen, T., Fogarty, M.J., Megrey, B.A., Moksness, E. (Eds.), Fish Reproductive Biology: Implications for Assessment and Management. Wiley-Blackwell, Oxford, UK, Chap. 3.

Perez, J., Lucato, S., Andrade, A.H., Pezzuto, P.R., Ribeiro, M.R., 1998. Programa de amostragem da pesca industrial desenvolvido para o porto de Itajaí, SC. Brazilian J. Aquatic Sci. Technol. 2 (1), 93–108.

Perez, J.A.A., Pezzuto, P.R., 2006. A Pesca de Arrasto de Talude do Sudeste e Sul do Brasil: Tendências da Frota Nacional Entre 2001 e 2003, V. 32, N.2,. Boletim do Instituto de Pesca, São Paulo, pp. 127–150.

Perrotta, R.G., Fernández-Giménez, A., 1996. Estudio preliminar sobre la edad y el crecimiento del pez palo Percophis brasiliensis (Quoy & Gaimard, 1824). INIDEP Inf. Téc., p. 10.

Pope, J.G., Macdonald, D.S., Daan, N., Reynolds, J.D., Jennings, S., 2000. Gauging the impact of fishing mortality on non-target species. ICES J. Mar. Sci. 57 (3), 689–696.

Punt, A.E., A'mar, T., Bond, N.A., Butterworth, D.S., de Moor, C.L., De Oliveira ., J.A., Szuwalski, C., 2014. Fisheries management under climate and environmental uncertainty: control rules and performance simulation. ICES J. Mar. Sci. 71 (8), 2208–2220.

Reynolds, J.D., Jennings, S., Dulvy, N.K., 2001. Life histories of fishes and population responses. In: Conservation of Exploited Species. Cambridge University Press, Cambridge, UK, pp. 147–168.

Rico, M.R., Lagos, A.N., Rodríguez, J.S., Lorenzo, M.I., 2018. Estado de la PesquerÍa de Pez Palo (*Percophis Brasiliensis*) en el áRea Del Río de la Plata, Zona Común de Pesca Argentino-Uruguaya y Aguas Jurisdiccionales Adyacentes al Norte de Los 39 S. Mar, 25. Publ. Com. Téc. Mix. Fr., pp. 117–146.

Rodrigues, K.A., 2012. Estrategia Reproductiva Del Pez Palo, *Percophis Brasiliensis* (Quoy et Gaimard, 1824) en Aguas Costeras de la Provincia de Buenos Aires. Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Mar del Plata.

Rovani, A.T., Cardoso, L.G., 2017. Life history and initial assessment of fishing impacts on the by-catch species *dules auriga* (Teleostei: Serranidae) in southern Brazil. J. Fish Biol. 91 (3), 896–911.

Rue, H., Held, L., 2005. Gaussian Markov Random Fields: Theory and Applications. CRC Press.

Rue, H., Martino, S., Chopin, N., 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. J. R. Stat. Soc. B 71, 319–392.

Rue, H., Martino, S., Lindgren, F., Simpson, D., Riebler, A., 2013. INLA: Functions which allow to perform full Bayesian analysis of latent Gaussian models using integrated nested Laplace approximaxion. R package version 0.0-1386250221.

San Roman, N.A., 1974. Crecimiento del pez palo, *Percophis brasiliensis* Quoy y Gaimard, 1824, del Atlántico Sur (Perciformes, Trachinoidei). Physis, Sección A 33.

Sant'ana, R., Mourato, B., Hazin, F., Travassos, P., 2020. Albacore (*Thunnus alalunga*) catch-per-unit-effort standardization: an update based on Brazilian longline fishery fleet data (1998–2018). Collect. Sci. Pap. ICCAT 77 (7), 179–189.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P., Van der Linde, A., 2014. The deviance information criterion: 12 years on. J. R. Stat. Soc. Ser. B Stat. Methodol. 48, 5–493.

Team, R.C., 2019. R foundation for statistical computing. R: A language and environment for statistical computing.

Then, A.Y., Hoenig, J.M., Hall, N.G., Hewitt, D.A., Handling editor: Ernesto Jardim, 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.

Thorson, J.T., 2020. Predicting recruitment density dependence and intrinsic growth rate for all fishes worldwide using a data-integrated life-history model. Fish and Fisheries 21 (2), 237–251.

Thorson, J.T., Munch, S.B., Cope, J.M., Gao, J., 2017. Predicting life history parameters for all fishes worldwide. Ecol. Appl. 27 (8), 2262–2276.

UNIVALI/EMCT/LEMA, 2020. Estatística Pesqueira de Santa Catarina. Consulta on-Line. 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, Disponível em:. Acesso em, 28/04/2021.

Vieira, P.C., Haimovici, M., 1993. Idade e crescimento da pescada-olhuda *Cynoscion striatus* (Pisces, Sciaenidae) no sul do Brasil. Atlântica 15, 73–91.

Zar, J.H., 1984. Biostatistical Analysis, second ed. Prentice-Hall, Englewood-Cliffs, New Jersey.