



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

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ABSTRACT

We analysed the long-term changes in the population dynamics and life history of whitemouth croaker (*Micropogonias furnieri*) off Southern Brazil, to understand how four decades of heavy fishing (1976–2017) has affected its population dynamics. In the first three decades, size and age structure were eroded with the loss of the larger (> 60 cm total length) and older (>20 yrs. old) individuals. Individual growth increased sharply until the early 2000s and stabilized thereafter. The age at first maturity decreased by one year for females, the total mortality (Z) increased three-fold, and the stock size decreased approximately 90 %. Despite changes in the population structure due to intense fishing and high exploitation rates, the landings remained high until the late 2000s and in the last decade decreased less than expected by a former stock assessment. The resilience of the stock can be explained by its life history traits: (i) high fecundity, (ii) multiple spawning events during a protracted reproductive season in coastal waters, (iii) large estuarine nursery grounds unaffected by industrial fishing and (iv) faster growth and earlier sexual maturation due to the reduction in food competition and possibly evolution via gear selectivity. However, the stabilization of individual growth rates, the high rate of exploitation and the low spawning potential warn of the risk of further population decline and fishery collapse if intense fishing pressure continues.

1. Introduction

High fishing intensity across the world has altered the dynamics and underlying biological compositions of many marine fish populations (Myers et al., 1995; Audzijonyte et al., 2016). Understanding these changes in relation to life history variability is important when specifying stock assessment models that inform decisions supporting sustainable fisheries management (Longhurst, 2010).

Changes in the population structure due to high fishing intensity reduce fish population capacity to withstand environmental variability and increases the risk of fishery economic collapse (Marteinsdottir and Thorarinsson, 1998; Rouyer et al., 2012). By introducing additional mortality, many fisheries have truncated the age structure of marine fish populations and increased the relative abundance of younger age classes (Berkeley et al., 2004; Hsieh et al., 2010). Commonly, younger and smaller fish contribute less to overall recruitment than the older and

larger ones (Palumbi, 2004; Hixon et al., 2014).

Evidence is accumulating that many marine fishes may undergo rapid changes in life-history traits, such as reproduction and growth. These changes have been attributed to fisheries-induced density-dependent factors, environmental drivers and/or evolutionary selective pressures (Audzijonyte et al., 2013; Morrongiello and Thresher, 2015). The relative importance of these drivers have been intensely debated (e.g., Olsen et al., 2004; Marshall and Browman, 2007; Kraak, 2007; Rogers et al., 2011; Therikildsen et al., 2013). However, regardless of the underlying mechanisms, the resulting trends have important implications for the assessment and management of individual species, as well as for ecosystem-based management (Audzijonyte et al., 2016). Understanding the relative importance of how genotypic (i.e., a set of genes an individual carries) and phenotypic (i.e., observable characteristics of an individual resulting from the interaction of its genotype with the environment) variability alters the population dynamics of intensely

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exploited marine fishes requires a long time series of data. Here we consider changes in expressed life history values of a sciaenid fish given its fishing history.

Marine sciaenid fishes are cosmopolitan (i.e., from tropical to temperate soft-bottom continental shelves) and widely important to fisheries worldwide. They are usually associated with large freshwater inputs, including the subtropical and warm temperate southwestern Atlantic Ocean (Longhurst and Pauly, 1987; Lowe-McConnell, 1987). Despite their importance and wide distribution, long-term studies on the population dynamics of sciaenid fishes are not frequent in the literature. For example, a comprehensive data set used by Keith and Hutchings (2012) to analyse fish population dynamics in low abundance included 204 stocks of 103 species, among which only one was a sciaenid (*Micropogonias undulatus*).

Along the extensive continental shelf of Southern Brazil (~ width 100–200 km), sciaenids are dominant in the demersal fish communities and fisheries, among which *M. furnieri* (Desmarest, 1823) is the most common (Martins and Haimovici, 2016; Haimovici and Cardoso, 2017). This species is a euryhaline demersal sciaenid fish associated with soft bottoms in coastal and estuarine regions from the Yucatán Peninsula, in southeastern Mexico down to northern Patagonia (Chao, 1981). *M. furnieri* is an important component of the coastal fish community and the main target of the demersal coastal fisheries from Rio de Janeiro State in Brazil to Bahía Blanca in Argentina (23°S - 40°S) (Chiesa et al., 2006; Carozza, 2010; Haimovici et al., 2016). Annual landings in Argentina, Uruguay and Brazil have reached over 100,000 tons in recent years (FAO, 2018). In southern Brazil, the *M. furnieri* has been fished in the Patos Lagoon Estuary and in coastal waters since the 19th century by small-scale fishers with gillnets and beach seine nets (Odebrecht, 2003). Industrial fishing using otter and pair trawls began fishing on the continental shelf in the late 1940s in this region (Yesaki and Bager, 1975) and intensified from the mid-1970s when restrictions on economic exclusive zones excluded Brazilian fishing boats from fishing off Uruguay and Argentina continental shelves (Haimovici et al., 2014).

Although *M. furnieri* has a continuous distribution in the SW Atlantic, recent studies on the genetic population structure, spawning season, and growth suggest limited connectivity among the stocks fished in southern Brazil from those in southeastern Brazil to the north and in the Common Fishery Zone of Argentina and Uruguay to the south (Vasconcellos et al., 2015; Haimovici et al., 2016). In southern Brazil, the biology and population dynamics of *M. furnieri* have been studied since the 1970s (Vazzoler, 1991) because of its high abundance and economic importance, with industrial landings regularly monitored and sampled since 1976 in the town of Rio Grande (Haimovici, 1987). In this region, this species is considered to be overfished since the 1980s (Haimovici, 1998), with a fishing mortality (F) between 2–6 times higher than the calculated fishing mortality at maximum sustainable yield (F_{MSY}) based on a surplus production model (Vasconcellos and Haimovici, 2006). However, despite low abundance compared to historical levels, this species still represents the main target of coastal demersal fishing in southern Brazil (Haimovici et al., 2016; Haimovici and Cardoso, 2017).

M. furnieri is a mid-sized (650 mm average maximum size) and long-lived (at least 38 years) fish (Schwingel and Castello, 1990; Haimovici and Unpiere, 1996). In the SW Atlantic, it is a seasonal spawner in coastal or estuarine waters (Weiss, 1981; Vazzoler, 1991; Macchi et al., 2003; Militelli et al., 2013). Pelagic eggs and larvae are carried into estuaries and coastal lagoons or retained in brackish waters where juveniles develop (Costa et al., 2013; Acha et al., 2018). Adults are opportunistic bottom-feeders that prey mainly on benthic infauna and epifauna such as polychaetas, mollusks, crustaceans and fish (Sánchez et al., 1991; Martins and Haimovici, 2020).

In this study, we aim to understand how four decades of heavy industrial fishing has affected life history values and population dynamics of *M. furnieri* and how this species has managed to stave off total collapse despite this intense removal pressure. In order to do so, we analyzed the long-term changes in growth, age and size at maturity, age and size

structure, mortality and the reproductive potential of the stock of *M. furnieri* fished along southern Brazil between 1976 and 2017. Throughout this period, we observed that the truncation of age structure has decreased the reproductive potential for this stock. As a compensatory response to the reduction in density, growth increased and the age at first maturity of females decreased. In the last two decades, the age structure and growth have stabilized. We discuss the capacity of *M. furnieri* to withstand intense fishing into the future in the light of the realized changes in life history and subsequent population dynamics. The erosion of resilience due to the drastic decrease in the spawning potential highlights the potential risk of commercial collapse of the stock due to declining population size and recent technological improvements in fishing.

2. Material and methods

The primary dataset comes from a sampling program of the industrial fishing landings in Rio Grande from 1976 to 2019, and complemented by occasional bottom trawl surveys along southern Brazil (Haimovici, 1987; Haimovici et al., 1996). The periods used for each analysis were defined by data availability (Table 1).

In the multi-species coastal industrial bottom trawl and gillnet fisheries, fish are stored on board with ice in holds without previous size classification, therefore sampling for length frequency distributions involved measuring randomly selected *M. furnieri* at the dockside landings (Haimovici, 1987). The number of specimens measured took into account the range of total lengths (TL) and the time available to sample each landing. Between 1976 and 2019, 185,919 *M. furnieri* were measured from 768 dockside landings of single bottom otter trawls, pair trawlers and gillnet boats. For these samples, the total length (TL) was measured from the tips of the snout to the end of the extended caudal fin. More detailed biological samplings included the TL, total weight (W, g), gonads weight (GW, g), sex and maturity stages, and otoliths collected for ageing. Biological sampling took place either at the dock or in the laboratory. Overall, we determined the sex of 9269 specimens, aged 5741 individuals, and recorded the total weight for 7963 individuals and the weight of 3208 gonads (Table 1).

M. furnieri has large otoliths that show alternating opaque and translucent bands, each pair corresponding to one year of life as validated by Cotrina and Lasta (1986); Schwingel and Castello (1990) and Cavole and Haimovici (2015). For age determinations, the otoliths were polished transversally up to the height of the nucleus using a grinding machine and examined with a binocular microscope with lateral transmitted light. We counted the number of opaque zones along the edge of the sulcus of the otolith surface and recorded the type of band deposited on the otolith edge (opaque or translucent). The otoliths were read independently by two readers, and if counts differed, otoliths were read again by both readers. A consensus age was determined if the difference was > 1 year among fishes with more than 5 opaque zones. The otoliths were discarded from further analyses if the difference in readings persisted. The reader agreement of the sectioned otoliths increased with size from 70 % among individuals smaller than 400 mm TL, to 95 % among the larger specimens. Higher legibility in the older specimens' otoliths is due to clearer annuli compared to smaller specimens that may present false annuli or checks due to residence in estuarine nursery grounds (Cavole and Haimovici, 2015). Cavole and Haimovici (2015) validated experimentally the daily formation of growth increments in the microstructure of the otoliths of young *M. furnieri* and observed that up to six thin opaque bands, formerly considered annuli, typically formed at 159–477 days of life.

2.1. Growth analysis

Two data treatments were used to fit the von Bertalanffy growth models by sex using a Bayesian approach since growth differs between sexes (Haimovici and Unpiere, 1996). The first treatment pooled

Table 1

Sample size of *M. furnieri* for sex, age, total weight, gonad weight, and number of measured fish (by sampled gear type) from 1976 to 2019 in Rio Grande, southern Brazil.

Year	Sex determinations	Aged specimens	Total weights	Gonad weights	Number of measured fish			
					Pair trawlers	Otter board trawlers	Bottom gillnet	Total
1976	775		776	334	3443	2685		6128
1977	1419		1419	739	19,216	4386		23,602
1978	962	704	962	32	17,463	1707		19,170
1979	176		489	130	6897	1982		8879
1980	55		55	53	3592	2314		5906
1981					2647	2607		5254
1982	23		23	19	4698	2721		7419
1983					997	360		1357
1984					3210	791		4001
1985					7777	792		8569
1986					10,143	814		10,957
1987	23		23	7	5587	989		6576
1988	32		32		2426	533		2959
1989	200	175		56	2673	205		2878
1990	11		11		2853	527		3380
1991	384	326	384	373	1061	1374		2435
1992	728	699	358	276	6343	1689		8121
1993					247			247
1994					80			80
1997					1850	314		2164
1998					1482		739	2221
1999	853	845	60					
2000								
2001								
2002	181	180	180					
2003	122	118	122	45				
2006					4234	320	1845	6399
2007	162	156	165		2986	65	974	4025
2008	922	917	962	180			405	405
2009	640	500	647	120	2403		2290	4693
2010	473	292	475	179	1365			1365
2011					935		1466	2401
2012					880	257	987	2124
2013	123		123	121				
2014	415	252	415	415	4210		938	5148
2015				129	1942		3792	5734
2016	228	223	229		3429	730	1814	5973
2017	362	354	53		2432	222	1841	4495
2018					1126		2919	4045
2019					2966		3843	6809
Total	9269	5741	7963	3208	133,593	28,384	23,942	185,919

age-length data across five sampling periods ("single period"). The second treatment grouped the age-length data in five sampling periods ("multiple periods"): 1976–1984, 1985–1994, 1995–2004, 2005–2013, and 2014–2019. The chosen treatment was defined by the smallest Deviance Information Criteria (DIC) value (Spiegelhalter et al., 2014).

We assumed that the age-length data followed a log-normal distribution, i.e. $y_i = \log N(\mu_i, \sigma^2)$, where y_i is the average expected length of animals in age class (or band class) i , with variance σ^2 . A logarithmic version of the von Bertalanffy equation was used:

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

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 time period 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 $p(\log$

$L_\infty, \log k, \log t_0 | D)$ (Kinas and Andrade, 2010). The posterior distribution of each estimated parameter provided an easy and clear way to compare the results among periods. All analyses were conducted using R version 3.6.1 (R Core Team, 2019). The MCMC was performed using the library JagsUI (Kellner, 2019).

2.2. Sexual maturation and reproduction

A seven stage maturation scale was used to characterize the maturity of males and females macroscopically. The seven stages are: I: Virginal immature; II: Developing virginal; III: Developing, IV: Advanced development; V: Running; VI: Partly spent; VII: Recovering (Haimovici and Cousin, 1989). Stage III was considered the onset of maturation and specimens in stages III to VI were considered sexually mature.

A gonadosomatic index (GSI) was calculated using the following formula from Wootton (1998):

$$GSI = 100 \cdot \frac{GW}{W}$$

where GW is the gonad weight and W is the total weight of the fish.

The mean GSI corresponding to virginal, immature and recovering stages (I, II and VII) differed significantly from those of maturing, mature and partly spent stages III to VI (Fig. 1). Although the same protocol describing macroscopic maturity stages was used for all years,

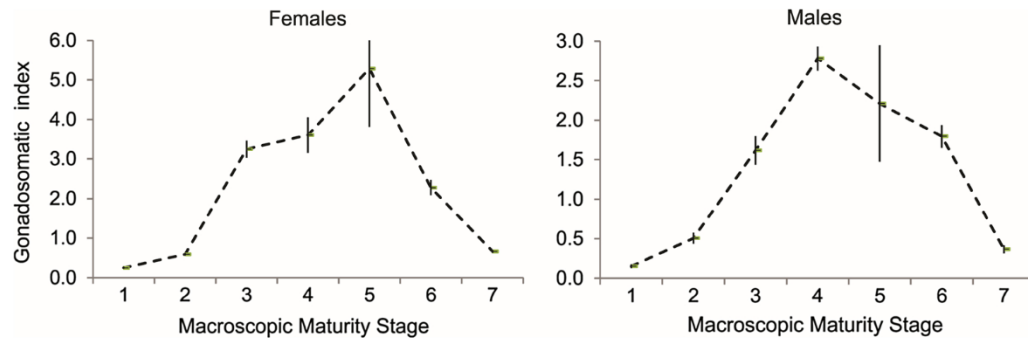


Fig. 1. Relationship between the gonadosomatic indices and macroscopic maturity stages for male ($n = 885$) and female ($n = 1384$) *M. furnieri* from southern Brazil. Vertical bars represent 95 % confidence intervals of GSI.

slight differences in interpretation by different sampling teams over time may have occurred. For this reason, we set fixed values of GSI as a criterion to identify specimens in the immature and resting stages from those in the maturation and spawning stages. Females and males with GSI greater than 2 and 1, respectively, were considered sexually mature for the estimation of the total length of first maturity. To reduce the chance of including specimens in the recovering stage (VII), only months with the majority of specimens either maturing or mature were included in the estimation of the total length at first maturity.

To analyze the annual reproductive cycle, the monthly posterior distributions of the GSI values were estimated using a Bayesian approach for females over 330 mm TL and males over 300 mm TL, most of which have already attained first maturity. The prior of GSI assumed a uniform density $[-\infty, +\infty]$ distribution. The posterior mean GSI (\bar{X}) demonstrated a normal distribution with mean μ , standard deviation $\left(\frac{s}{\sqrt{n}}\right)$, and likelihood $p(\bar{X} | \mu)$.

The sizes at maturity for each period by sex was estimated using a Bayesian approach by sex, since it is known that males mature at a smaller size (Vazzoler, 1991). A logistic model was first fit to all data spanning years 1976–1980 and 2013–2015 (Table 1). A second logistic model was fit to data for the two sampling periods individually (1976–1980 and 2013–2015). The model with the smaller DIC was chosen for further analysis.

The total number (n_i) and the number of mature specimens (y_i) were calculated for both sexes at each 30-mm total length class intervals. If θ_i denotes the probability of an individual of the i -th length class being mature, y_i was assumed to follow a binomial distribution $Bin(n_i, \theta_i)$. Data were fit to a logistic model, defined by a logit link function that transforms the parameter θ_i , restrict to the range $[0, 1]$ in the binomial distribution, with m bounded between $-\infty, +\infty$ (Kinas and Andrade, 2010). The logistic model was defined as follows:

$$m_i = g(\theta_i) = \log\left(\frac{\theta_i}{1 - \theta_i}\right)$$

$$m_i = \beta_0 + \beta_1 \cdot x_i$$

where, m_i is the probability at each x_i length class. Estimation was based on the 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:

$$L_{50} = \frac{-\beta_0}{\beta_1} \text{ and } L_{95} = \frac{2.94 - \beta_0}{\beta_1}$$

We obtained the posterior distribution $p(\beta_0, \beta_1 | D)$, where $D = \{(y_i, n_i, x_i); i = 1, \dots, k\}$, for the L_{50} and L_{95} also using Monte Carlo Markov Chain (MCMC) sampling performed using JagsUI (Kellner, 2019).

The age at first maturity (A_{50}) was computed by each sex and for both the first and the last period using the rearranged Von Bertalanffy growth model:

$$A_{50} = \frac{-\ln\left(\frac{pL_{\infty i} - pL_{50}}{pL_{\infty i}}\right)}{pk_i} + pL_{0i}$$

where $pL_{\infty i}$, pk_i and pL_{0i} were sampled from the posterior distributions of the von Bertalanffy growth parameters for each time period and pL_{50} was the posterior distribution of L_{50} .

2.3. Length compositions

Length compositions were defined in 30 mm TL bins for the trawl (years 1976–1998; 2006–2019, minus 2013) and gillnet fisheries (12 years in the range of 1998–2019; Table 1). Lengths were not sexed, as the sexed individuals were non-randomly chosen to determine the growth and the maturity ogive, thus all compositions available for the population modelling were treated as unsexed.

2.4. Mortality analysis

Length compositions from the trawl fisheries were converted to age frequencies using age-length keys to estimate the instantaneous total mortality coefficient (Z) using catch curves (Ricker, 1975). Only the data for *M. furnieri* between ages 3–9 were included to estimate Z to ensure the regression was based only on fully selected individuals (Ricker, 1975). While it is common to miss younger fish, it is also the case in the trawl fisheries that older fishes could be underrepresented because some of the larger croakers are able swim at more than 3 knots, the regular speed of the trawls, in front of the ground rope until the end of the hauls. This swimming behavior likely induces a dome-shaped (i.e., missing the smallest and largest individuals) selectivity curve, thus estimating beyond the fully selected age could overestimate the total mortality.

The catch curve of $\log(\text{catch})$ (y_i) against age (x_i) when $i = 3, \dots, 9$, was defined by the following linear model to obtain the posterior distribution for the slopes of the regressions (Z) and their credibility intervals:

$$y_i = \beta_0 + \beta_1 x_i + \omega_i$$

where β_0 is the intercept, β_1 is the slope of the linear model and ω_i is the model error. Jeffreys' priors were assumed for the parameters ($p(\beta_0, \beta_1, \sigma^2) \propto 1/\sigma^2$) and the normal distribution ($N(\beta_0 + \beta_1 x_i, \sigma)$) for $p(y_i | \beta_0, \beta_1, \sigma)$. The marginal posterior distributions of the parameters are (Kinas and Andrade, 2010):

$$p(\beta_0 | x_i, y_i) \sim St(n-2, b_0, S_{\beta_0})$$

$$p(\beta_1 | x_i, y_i) \sim St(n-2, b_1, S_{\beta_1})$$

$$p(\sigma^2 | x_i, y_i) \sim \text{GInv}\left(\frac{n-2}{2}, \left(\frac{n-2}{2}\right) S_e^2\right)$$

where b_0 and b_1 are the least-squares estimates for β_0 and β_1 , respectively, S_e^2 is the residual variance and $St(g, m, v)$ are non-central Student distributions with g degrees of freedom, mean m and scale v . The variance σ^2 follows an inverse gamma distribution. To obtain the posterior distribution of Z , we sampled 3000 values from the marginal posterior using the library MASS (Venables and Ripley, 2002).

The posterior distributions for the 1976–1980 and 2010–2014 periods with estimated Z s were compared using a Bayesian alternative to the t -test available in the library BEST (R version 2.12.0) (Kruschke and Meredith, 2020).

The instantaneous natural mortality coefficient M was estimated in the population dynamics model described in the Section 2.5. The exploitation rate was calculated as $E = (Z - M)/Z$ for each time period.

2.5. Population dynamics

We estimated a time series of spawning output and the current stock depletion with a model fitted to catch and length data using the Stock Synthesis modeling framework within the Stock Synthesis Data-limited Tool (SS-DL tool; Cope, 2020). The SS-DL tool uses the age-structured population dynamic model Stock Synthesis (Methot and Wetzel, 2013) to implement several common data-limited assessment methods all in one modelling framework.

The SS-DL tool uses as input parameters M , the von Bertalanffy growth parameters (L_∞ , k and t_0), the size at 50 % and 95 % maturity (L_{50} and L_{95}), the coefficients and exponents of the weight-length and the weight-fecundity relationships, the stock-recruitment parameters, steepness and initial recruitment ($\ln R_0$).

A population dynamic model was built to accommodate the

significant sex-specific growth changes among periods identified in the growth analysis (Table 2). The maturity parameters for each sex were assumed to be constant across time periods since no changes were identified in the length at maturity analysis. The weight-length coefficients and exponents were taken from Haimovici and Ignácio (2005) and the weight-fecundity relationship assumed fecundity proportional to weight. Steepness was set to 0.75, the value for the Order Perciformes using the FishLife package in R (Thorson, 2020; Thorson et al., 2017), the closest taxonomic estimate available for *M. furnieri*. Model sensitivity to the steepness value was explored using a likelihood profile. All the parameters used in the model and their treatments are provided in Table 2.

The catch time series and the annual length compositions were combined into two fleets; bottom trawling (combining pair, otter, and double rig trawling) and bottom gillnet. The length compositions of the three bottom trawling fleets were weighted by the corresponding relative catches to obtain a combined length composition. Dome-shaped selectivity was assumed for the trawl selectivity, due to the reasons mentioned in Section 2.4. In contrast, a logistic selectivity function was assumed for the gillnet fishery as large individuals are retained fully in the nets. Several model configurations were considered that either did or did not estimate recruitment deviations and/or M ; logistic selectivity for the bottom trawling fishery was also explored. The final reference model was tested for stability by initiating 100 models from different (“jittered”) starting values. This test uncovers whether the initial model converged to a local likelihood minimum and whether one could return the reference model likelihood value with different parameter starting values. Overall model convergence was considered achieved if the Hessian matrix was inverted to produce asymptotic estimates of variance on parameters and derived model output.

Table 2

Model parameter, and how they are treated in the reference Stock Synthesis model for *M. furnieri* off southern Brazil. Asymptotic standard deviation of the estimated parameters are included in parentheses next to the estimated parameter value.

		Time-blocks					Treatment
Sex	Parameter	1976–1984	1985–1994	1995–2004	2005–2013	2014–2019	
Females	L_∞ (mm)	555.8	592.6	681.5	659.9	675.5	Fixed
	k (year ⁻¹)	0.14	0.22	0.24	0.30	0.25	Fixed
	t_0	−3.65	−1.08	−0.18	−0.02	−0.28	Fixed
	L_{50} (mm)	362.9					Fixed
	L_{95} (mm)	468.5					Fixed
	Natural mortality (year ⁻¹)	0.104 (0.005)					Estimated
Males	L_∞ (mm)	490.5	563.6	668.7	620	652.2	Fixed
	k (year ⁻¹)	0.19	0.24	0.23	0.35	0.24	Fixed
	t_0	−3.15	−1.03	−0.15	−0.04	−0.58	Fixed
	L_{50} (mm)	313.6					Fixed
	L_{95} (mm)	399.2					Fixed
	Natural mortality	0.105 (0.011)					Estimated
	Weight (g)-length (cm) alpha	0.015					Fixed
	Weight (g)-length (cm) beta	2.91					Fixed
	Weight-based fecundity coefficient	1					Fixed
	Weight-based fecundity exponent	1					Fixed
Pooled sex	Steepness	0.73					Fixed
	Initial recruitment ($\ln R_0$)	3.259 (0.034)					Estimated
	Length selectivity						
	Bottom trawl						
	Peak selectivity (cm)	29.196 (0.585)					Estimated
	Width of peak selectivity (logit)	−11.448 (55.414)					Estimated
	Ascending width (ln units)	4.480 (0.233)					Estimated
	Descending width (ln units)	4.210 (0.197)					Estimated
	Selectivity in first bin (ln units)	−15					Fixed
	Selectivity of final bin (ln units)	−0.157 (0.100)					Estimated
	Gillnet						
	Peak selectivity (cm)	36.350 (0.611)					Estimated
	Width of peak selectivity (logit)	5.91					Fixed
	Ascending width (ln units)	3.505 (0.157)					Estimated
	Descending width (ln units)	−9.21					Fixed
	Selectivity in first bin (ln units)	−15					Fixed
	Selectivity of final bin (ln units)	11.5					Fixed

3. Results

3.1. Growth changes

The mean total length- and weight-at-age for both sexes of *M. furnieri* were calculated for the five periods with available data. Mean total length-at-age increased sharply between the first and the third period and stabilized during the following two periods (Fig. 2a). The changes become more evident when considering weight-at-age for ages greater than three (Fig. 2b):

The “multiple period” model (DIC = 36,982 for females and 27,117 for males) was better supported by the data than the “single period” model (DIC = 38,252 for females and 28,087), thus supporting growth curves that consider distinct time periods. The “multiple period” model diagnostics and posterior distributions of the estimated parameters are provided in the Supplementary material on the paper’s Github repository (<https://github.com/lgcaldoso/Haimovici-et-al.-Micropogonias-furnieri.-Fisheries-Research.-2021>).

The von Bertalanffy growth curves for both sexes and sexes combined illustrate a sharp increase in L_{∞} between the first three periods, followed by growth stabilization in the last two periods (Fig. 3; Table 3). Between the first and the last period, the L_{∞} increased 23.8 % for females, 34.6 % for males, and 32.2 % for pooled sexes; the growth coefficient k increased 48.8 % for females, 7.3 % for males and 33.3 % for pooled sexes.

3.2. Sex ratio, reproductive cycle and length and age changes at first maturity

Among the specimens selected for growth and maturity studies the average proportion of females was 48.9 %, for the specimens between 210–359 mm TL, 57.7 % for those between 360–599 mm and 73.5 % for those larger than 600 mm.

The annual cycle of the mean monthly GSI and the percent of mature specimens indicated that *M. furnieri* along southern Brazil has a protracted reproductive season with a peak in spring months, gradually reducing by late summer (Fig. 4). Female GSI was low between April and August, increased sharply in September, reached the highest value in

October and then decreased thereafter. A similar pattern was observed for the proportion of females in advanced maturation stages. The frequencies increased gradually from 12 % in August to 92 % in October and decreased sharply from 82 % in November to 5 % in May (Fig. 4). Male GSI increased sharply from August to September, reached the highest value in December, and then decreased gradually to low values until March. The proportion of mature males was low from May to August when it then increased from 24 % to 92 % in September, 96 % in October, 90 % in November and December and then gradually decreased until March (Fig. 4).

The proportion of mature males (GSI > 1) and mature females (GSI > 2) in 30 mm size classes sampled between November and January were used to calculate the length- and age-at-first-maturity. The comparisons were limited to the 1976–80 and the 2013–2015 time periods because of the limited sampling of young *M. furnieri* (Table 1).

The DIC of the models with pooled maturity at length data from both periods (55.86 for females and 80.10 for males) were smaller than the DIC for the model with two periods (56.91 for females and 81.07 for males; model diagnostics available in the Supplementary material). Sizes-at-maturity for females and males for use in the population model were therefore estimated using samples pooled across years. The credibility intervals (95 %) of the logistic model parameter β_1 did not include zero, which indicates a significant relationship between length and sexual maturity for both sexes (Table 4; Fig. 5). The mean total length at first maturity (L_{50}) was 313.6 mm for males and 362.9 mm for females (Table 4; Fig. 5). The mean length at which 95 % of the specimens were mature (L_{95}) were 414.3 mm for males and 468.5 mm for females (Table 4).

The estimate of A_{50} for females decreased from 3.70 yrs to 2.75 yrs while it was estimated at 2.23 yrs for the first period and at 2.19 yrs for the last period for males (Table 4, Supplementary material). Although the L_{50} did not change between the late 1970s and the early 2010s, growth curve differences led to the A_{50} reducing by one year for females.

3.3. Length and age composition changes

Changes in the length and age compositions for the pair trawl, otter trawl and bottom gillnet fisheries were analysed by comparing the

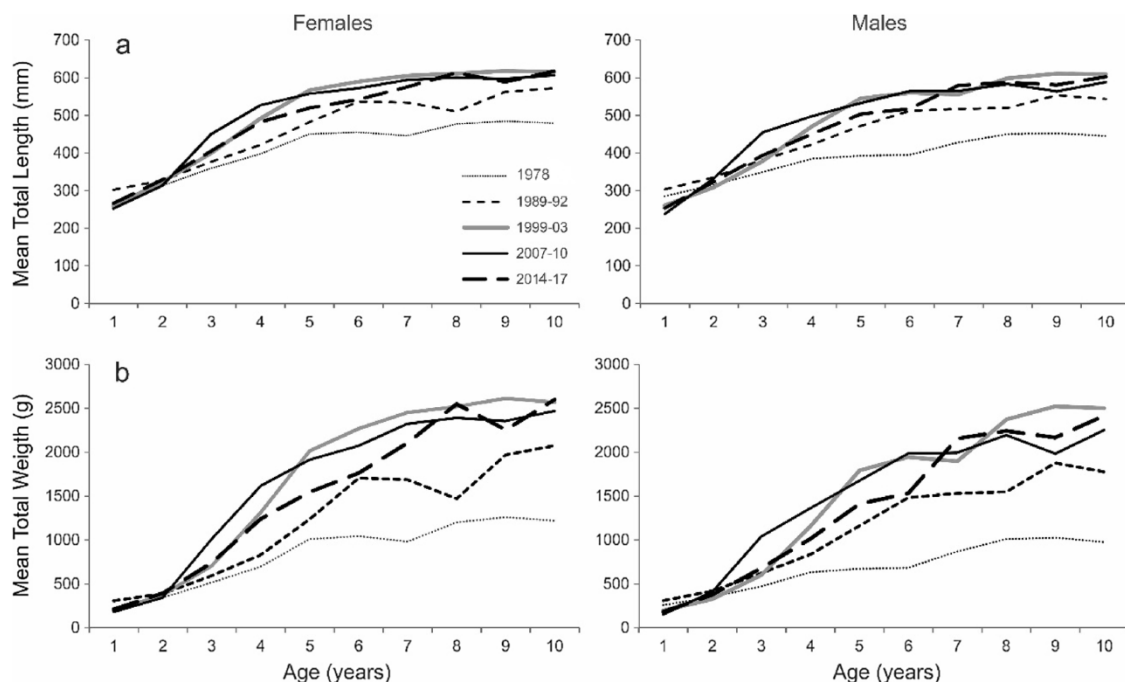


Fig. 2. Mean total length (a: upper panels) and mean total weight (b: lower panels) at ages 1 to 10 for female and male *M. furnieri* from southern Brazil in five time periods between 1978 and 2017.

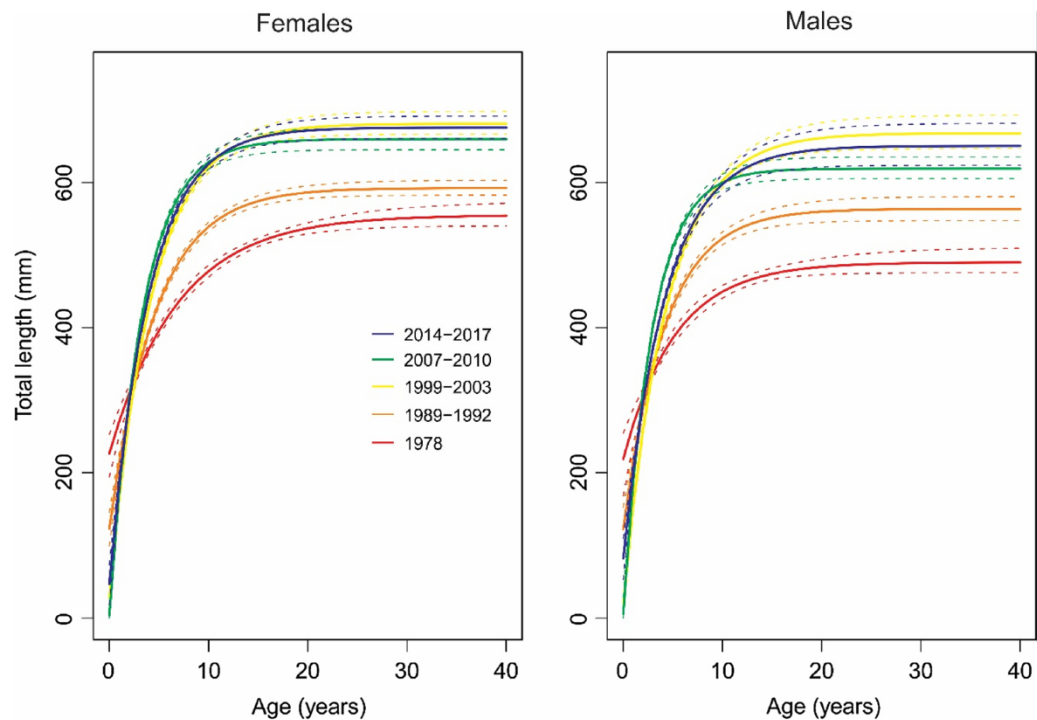


Fig. 3. Von Bertalanffy growth curves for *M. furnieri* fished along southern Brazil in five time periods between 1978 and 2017.

Table 3
The posterior means for the von Bertalanffy growth parameters (L_{∞} (mm), k (year^{-1}) and t_0) and their 95 % credible intervals for females, males and pooled sex for *Micropogonias furnieri* from southern Brazil.

Females	2.5	L_{∞}	97.5	2.5	k	97.5	2.5	t_0	97.5
1978	540.3	555.8	573.2	0.12	0.14	0.18	-4.88	-3.65	-2.52
1989–1992	582.1	592.6	603.2	0.20	0.22	0.24	-1.40	-1.08	-0.79
1999–2003	666.1	681.5	698.4	0.22	0.24	0.26	-0.36	-0.18	-0.03
2007–2010	645.6	659.9	674.7	0.29	0.30	0.32	-0.09	-0.02	0.00
2014–2017	660.7	675.5	692.4	0.23	0.25	0.28	-0.49	-0.28	-0.09
Males	2.5	L_{∞}	97.5	2.50	k	97.50	2.50	t_0	97.50
1978	475.1	490.5	510.8	0.14	0.19	0.26	-5.11	-3.15	-1.70
1989–1992	547.7	563.6	580.9	0.21	0.24	0.27	-1.46	-1.03	-0.65
1999–2003	648.2	668.7	693.6	0.20	0.23	0.25	-0.40	-0.15	-0.01
2007–2010	605.3	620.0	634.7	0.32	0.35	0.37	-0.13	-0.04	0.00
2014–2017	626.3	652.2	681.8	0.21	0.24	0.27	-0.85	-0.58	-0.34
Pooled sex	2.5	L_{∞}	97.5	2.50	k	97.50	2.50	t_0	97.50
1978	519.9	527.8	535.9	0.17	0.18	0.19	-2.99	-2.81	-2.40
1989–1992	577.1	585.8	595.0	0.20	0.22	0.24	-1.36	-1.09	-0.85
1999–2003	664.2	677.3	691.3	0.22	0.23	0.25	-0.31	-0.16	-0.03
2007–2010	632.9	643.4	654.1	0.31	0.32	0.33	-0.06	-0.02	0.00
2014–2017	660.2	673.9	687.6	0.22	0.24	0.26	-0.58	-0.42	-0.28

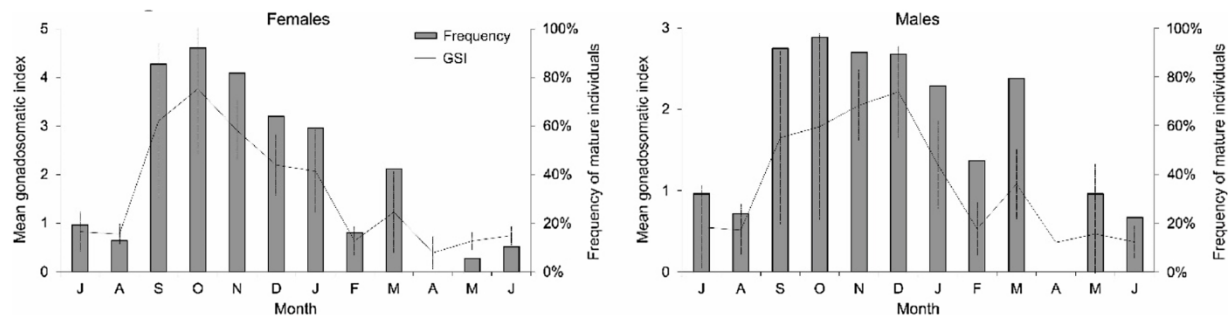


Fig. 4. Monthly mean gonadosomatic indices (dashed line) and percent of mature individuals at stages III to VI (bars) for females (left panel) and males (right panel) of *Micropogonias furnieri* in southern Brazil. Vertical bars represent 95 % confidence intervals of the monthly GSI.

Table 4

Logistic model parameters (β_1 and β_0) and the calculated length-at-first maturity (L_{50} (mm)) and the length at which 95 % of the specimens were mature (L_{95} (mm)) for *M. furnieri* landed in Rio Grande. All parameters and indices are presented as the mean of their posterior distributions and the 2.5 % ($CrI_{2.5\%}$) and 97.5 % ($CrI_{97.5\%}$) credibility intervals. The lengths at first maturity were converted to ages at first maturity (A_{50}) using VB parameters in Table 2 for each sex.

Parameters	Females			Males		
	Mean	$CrI_{2.5\%}$	$CrI_{97.5\%}$	Mean	$CrI_{2.5\%}$	$CrI_{97.5\%}$
β_1	0.028	0.024	0.033	0.029	0.024	0.035
β_0	-10.18	-12.09	-8.49	-9.25	-11.13	-7.48
L_{50}	362.9	354.9	370.6	313.6	305.8	321.1
L_{95}	468.5	453.1	485.5	414.3	399.2	430.9
A_{50} 1978	3.70	3.59	4.04	2.23	1.85	2.55
A_{50} 2014–2017	2.75	2.64	2.86	2.19	2.07	2.30

relative and accumulated frequencies (Figs. 6 and 7) for the five time periods in which both data types were available (Table 1).

The landings of pair trawlers included both small and large *M. furnieri* because they fish in all depths of the inner shelf (<100 m). For this gear, large specimens were more common until the late 1990s, although their frequency decreased sharply since 2000s. Otter board trawl fishing targeting *M. furnieri* was important in the 1970s, but decreased abruptly in the following two periods. Otter trawls are used in waters > 50 m deep, so land few small individuals; no trend was seen in the presence of larger individuals in this gear type (Haimovici et al., 1996). Gillnets use relatively large mesh sizes (Vasconcellos et al., 2014), and landed mostly larger specimens until the 1990s, and mostly mid-sized and few small specimens since the 2000s (Fig. 6).

The proportion of *M. furnieri* above L_{50} landed by pair trawlers decreased from 70 % to 28 % from the start to the end of the sampling period. Virtually all specimens caught were larger than the length of first maturation at the start of the industrial gillnet fishery in 1989–1992, but in the last two periods, 75 % and 87 % individuals were over L_{50} (Fig. 7). The proportion of older fishes in the landings of pair trawlers and gillnets decreased gradually until the 2000s and stabilized during the last two periods (Fig. 6). Only 5 % and 12 % of the *M. furnieri* in the landings of pair trawlers and gillnets during 2013–17, were over 4 years, respectively (Fig. 6).

3.4. Mortality and exploitation rate

Estimated Z gradually increased over time (Fig. 8a). The mean of the

difference between Z from the first and the last periods was -0.358 yr^{-1} and did not include zero (-0.362 to -0.353 , 2.5 % and 97.5 % CrI , respectively) which indicates a statistically significant difference (see Supplementary material for more details).

The M values estimated using the population dynamics model were 0.104 yr^{-1} (s.d. = 0.005 yr^{-1}) for females and 0.105 yr^{-1} (s.d. = 0.011 yr^{-1}) for males (Table 2). We used the average value for both sexes of (0.1045 yr^{-1}) to estimate exploitation rates and assumed M was constant over time. Across time, the exploitation rates increased from 0.53 in the first period to 0.85 and 0.82 in the last two periods, respectively (Fig. 8b). The natural logarithm of the frequencies by age for all ranges of ages for each period illustrates the gradual decrease of survival over time (Fig. 8c).

3.5. Population dynamics

Stock Synthesis provides a way to combine the above data into an integrated model to see how changes in biological compositions and life history parameters determine the population dynamics. The time-series of size compositions from 1976 to 2019 for the bottom trawling showed a decrease in the frequency of larger individuals through time despite the growth curve indicating larger average asymptotic sizes; the time series for the bottom gillnet was more variable (Fig. 7; see Supplementary material model output plots for additional plots), although this fleet was missing samples from the earlier time period.

Landings were dominated by bottom trawlers up until 1986, but from 1989 onwards, many former trawlers switched gear to gillnets and became responsible for the bulk of landings (Fig. 9). Total landings in 1976 were of ~ 14,000 t in 1976, peaked at ~16,000 t the 2000s and decreased to minimum of ~ 6,000 t in the mid-2010s, increasing slightly in recent years.

The best fit (“reference”) assessment model estimates sex-specific M but not annual recruitment deviations, while assuming selectivity for the bottom trawling fishery is dome-shaped. The overall fit to the length data was acceptable (Fig. 10; see the Supplementary material for more detailed fits). Estimates of M (female = 0.104 yr^{-1} ; male = 0.105 yr^{-1} ; Table 2) reveal little difference between the sexes. The population trend indicates a distinct decrease from 2000, supporting the expected downward trajectory of stock size and recruitment potential (Fig. 11). Most of the additional models explored also show low stock sizes in current years (Fig. 12). The one exception is when M is fixed to external estimates and recruitment deviations are estimated. In this model specification, recent recruitment is enormous, driving a massive rebound in the stock size. Estimates of recent recruitments are notoriously uncertain (shown by the uncertainty intervals in Fig. 12), but even

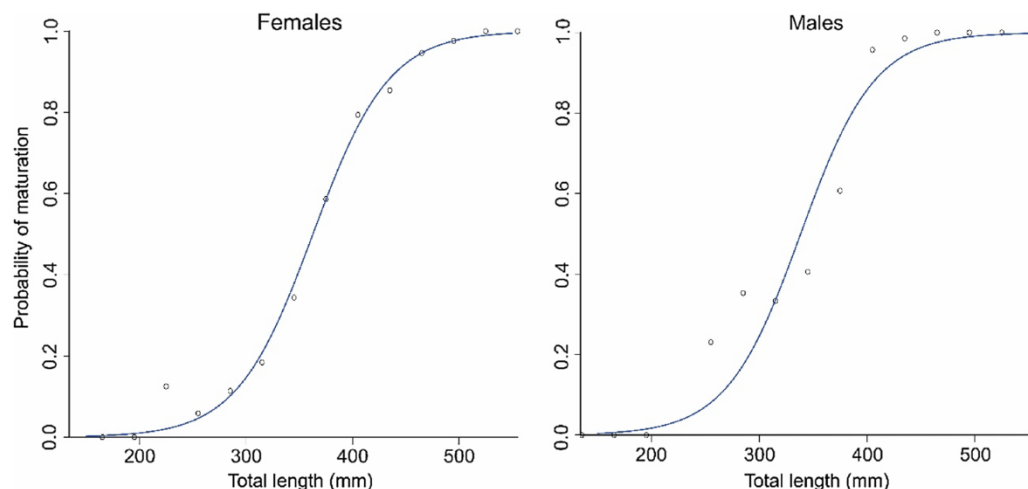


Fig. 5. Maturity-at-length ogives fitted to maturity at length data pooled for two time periods for female and male *M. furnieri* sampled in southern Brazil.

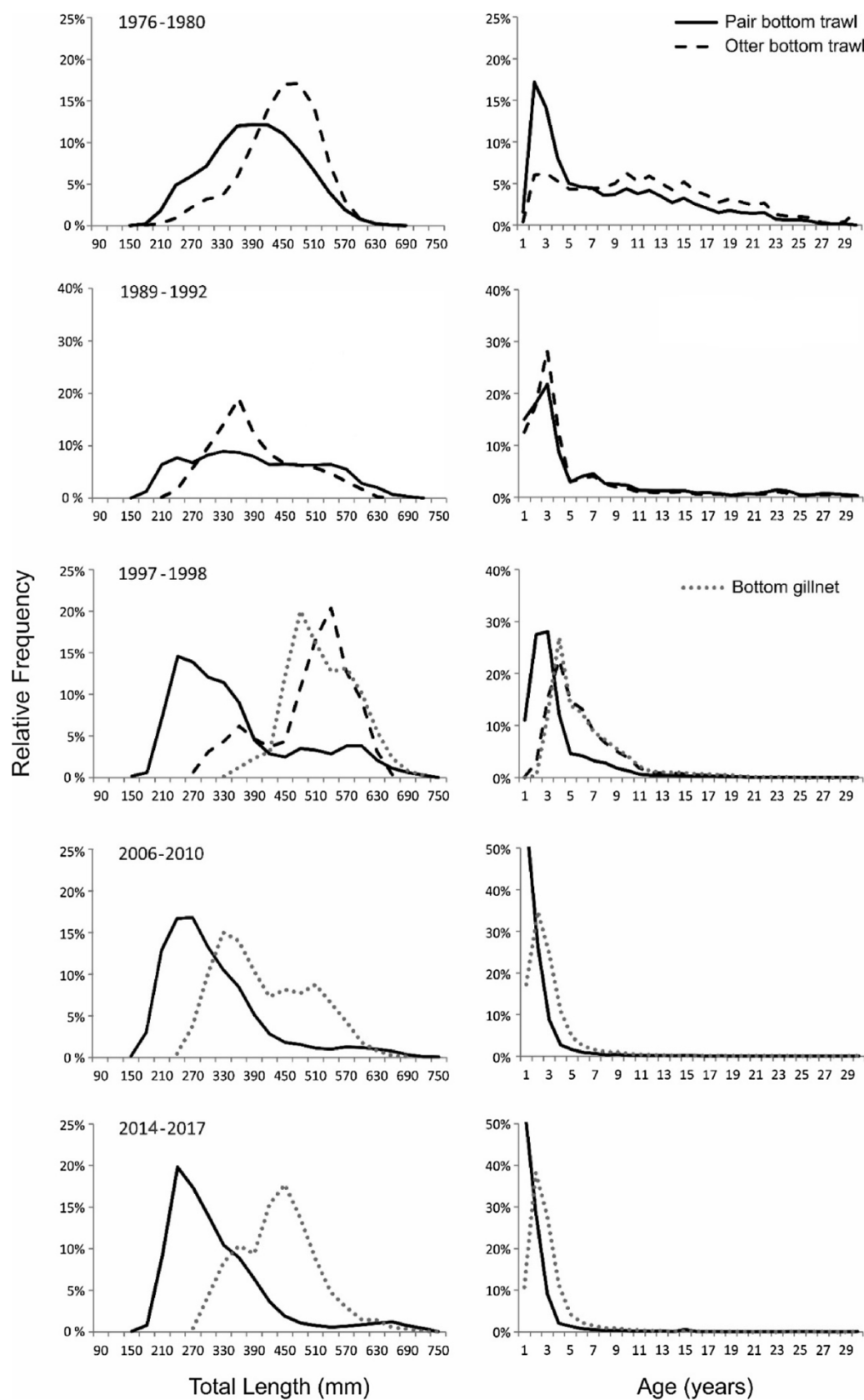


Fig. 6. Relative frequency percentage of length and age for *M. furnieri* along southern Brazil in the landings of pair trawl, otter trawl and gillnet industrial fisheries along Southern Brazil in five sampling periods between 1976 and 2017.

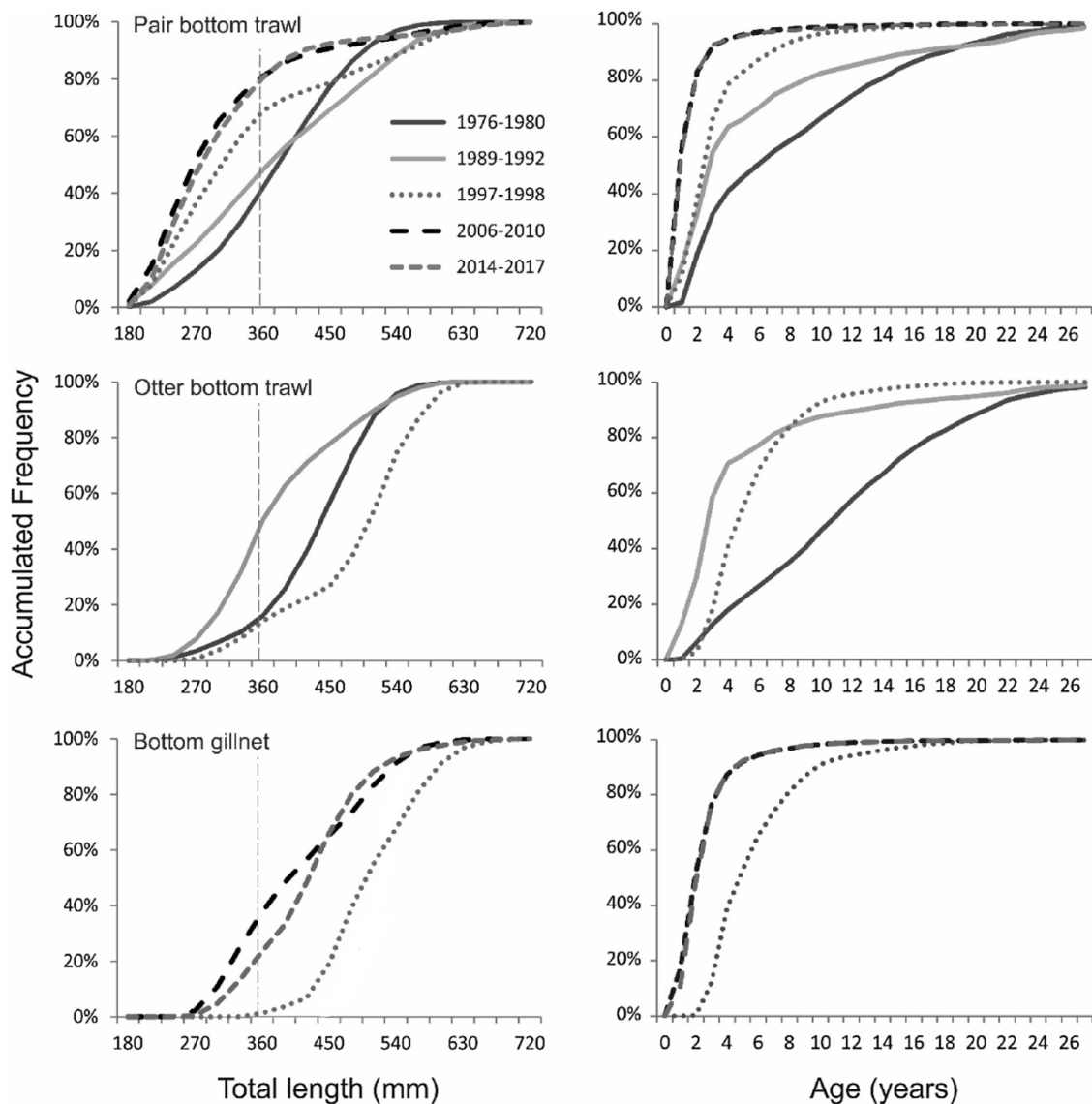


Fig. 7. Accumulated frequency percentage of the length and age composition for *M. furnieri* fished along southern Brazil. Landings come from pair trawl, otter trawl and gillnet industrial fisheries in five sampling periods between 1976 and 2017. Dashed vertical line in the left panels represents the mean length at first maturity for females.

with uncertainty considered, the population grows exponentially due to large recruitment. Fits to the length data are largely similar in each model and current length compositions have low contrast, so there are no details in the current data to strongly differentiate these hypotheses, although following historical trends it seems highly unlikely such persistent and large recruitments exist.

The sensitivity to recruitment compensation (i.e., steepness) was explored using a likelihood profile (Fig. 13). This parameter is often difficult to directly measure, but can have a large effect on population scale and relative size. While the base model value of $h = 0.75$ was determined by life history meta-analysis, the model lacked strong information to estimate steepness (Fig. 13). Most of the information came from the trawl fishery length composition. The absolute abundance of the population showed sensitivity to steepness, while the low relative abundance maintained across the span of steepness values (Fig. 13), but with different trajectories (Fig. 14). There was a particularly interesting dichotomy in absolute and relative stock size when steepness was greater than 0.5 (Fig. 14). The lower steepness values ($h \leq 0.5$) lead to a consistent decline in population trajectory, whereas $h > 0.5$ lead to a population increase.

4. Discussion

Changes in the population structure and dynamics have been recorded for many fish stocks around the world as a response to heavy fishery exploitation (e.g., Bianchi et al., 2000; Sharpe and Hendry, 2009; Audzijonyte et al., 2013, 2016). The erosion of the size and age structure, the gradual increase in the total mortality and exploitation rates, and the low stock size in current years, as observed for *M. furnieri* in southern Brazil, are all indicators of population decline. These trends are similar to those observed for the stock targeted by the Uruguayan and Argentinian fleets in their Common Fisheries Zone (Haimovici et al., 2016), with stock depletion at 30 % of unfished levels in 2017 (CTMFM, 2017).

Vasconcellos and Haimovici (2006) analyzed the catch and effort time series from 1976 to 2002 and predicted that, if intense fishing continued, the *M. furnieri* stock would likely collapse in the future. However, after an additional 15 years of intense fishing, *M. furnieri* continues to be the most important coastal demersal species in the landings of southern Brazil, demonstrating a resilience despite persistent targeting at low stock size. The question becomes how much longer can

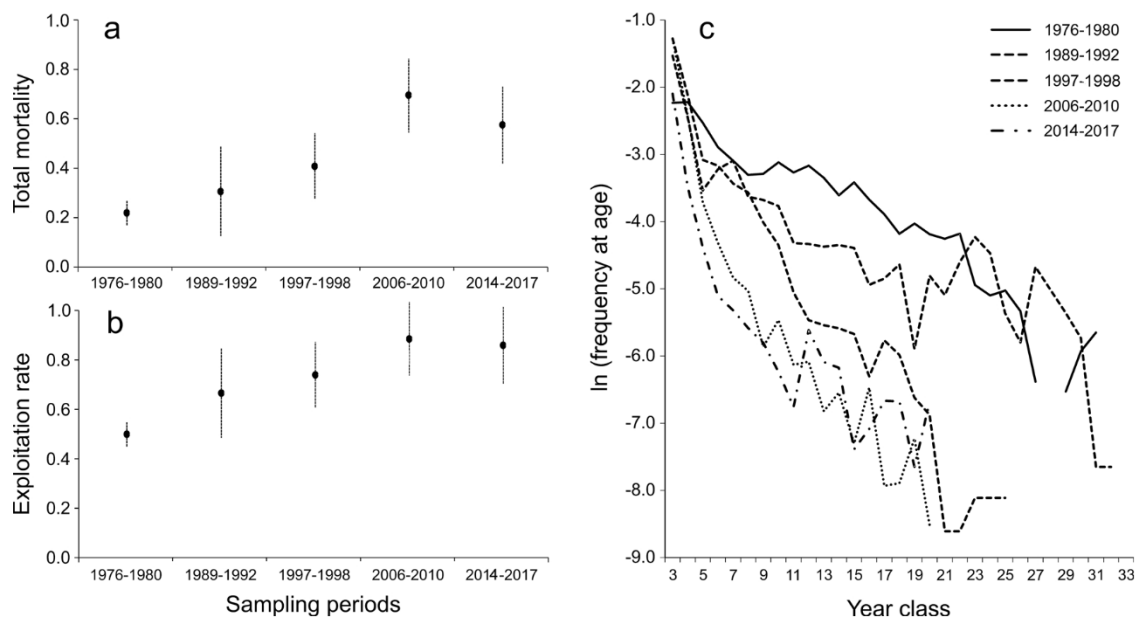


Fig. 8. (a) Instantaneous total mortality coefficients (Z) of *M. furnieri* aged 3 to 9, fished along southern Brazil and their 95 % credibility intervals, calculated as the slope of curves combining age-length keys and yearly length compositions, (b) Exploitation rates considering a natural mortality of $M = 0.104$ and (c) Natural logarithms of relative frequencies at age per year classes in five sampling periods between 1976 and 2017.

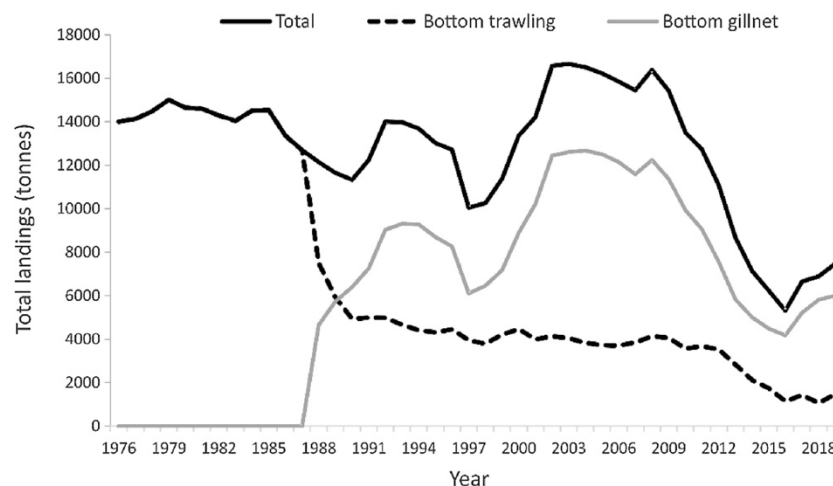


Fig. 9. Time series of the recorded landings of *M. furnieri* from bottom trawling and bottom gillnets in southern Brazil from 1976 to 2019 (moving average of 5 years).

this resilience keep the stock from collapse?

Stock resilience is likely due to a combination of flexible life history traits and fishery characteristics, specifically: (i) the flexibility in growth and first maturation associated with decreasing population density, (ii) high reproductive potential, (iii) coastal spawning grounds that do not overlap with fishing grounds, and (iv) large estuarine nurseries with abundant food in which fishing pressure on the juveniles is relatively low.

4.1. Growth and maturation flexibility

Growth and maturation are highly plastic traits with rapid responses to changes in food availability, water temperature, and intra- and interspecific competition (Enberg et al., 2012; Morrongiello and Thresher, 2015). Changes in life history traits, such as the size and age at first maturity of heavily fished populations, can also be driven by genetic factors (Law, 2007; Dieckmann and Heino, 2007). However, because the

size at first maturity of *M. furnieri* did not decrease after 40 years of intense fishing in southern Brazil, there is no evidence of genetically-driven changes in maturity size. On the other hand, individual growth, particularly of pre-adults (late juveniles) and adults of *M. furnieri* increased sharply between the 1970s and the early 2000s. Since 1976, the weight at intermediate ages increased 100 % and the L_{∞} and k parameters of von Bertalanffy increased by more than 30%. This kind of change is expected under reduced intraspecific competition and/or increased food availability. Intense industrial fishing decreased the abundance of epibenthic feeders such as elasmobranchs (Vooren and Klippel, 2005) and teleost (Haimovici and Cardoso, 2017) species, which in turn increased prey biomass (e.g., polychaetes, bivalves, shrimps and crabs). First maturation usually depends on obtaining a critical size and/or age (Roff, 1991). More food availability can allow individuals to reach this size earlier in life. Additionally, fishery selectivity may provide advantage to fish with earlier maturation because they reproduce before they are caught. Thus, increased food availability

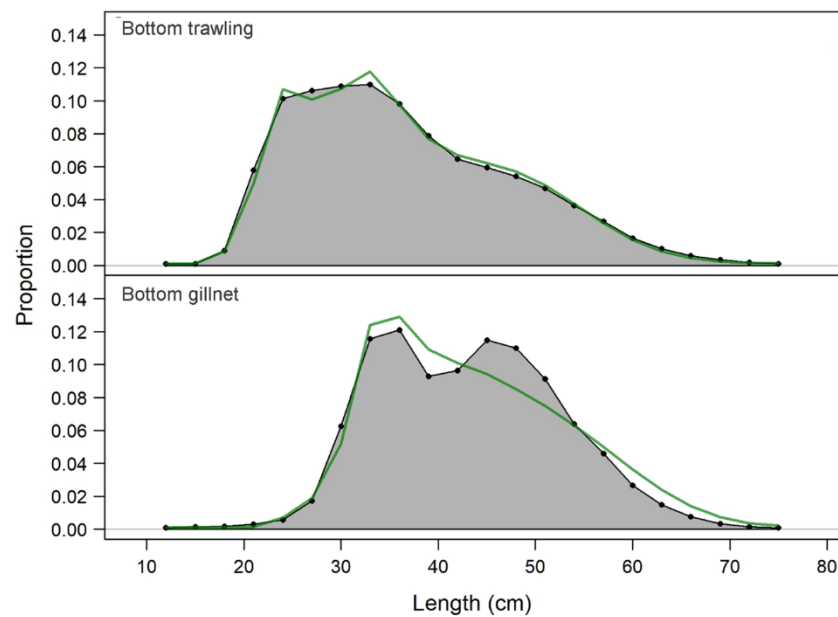


Fig. 10. Aggregate length composition fit by fleet for the reference assessment model for *M. furnieri* from southern Brazil. Green line (web version) indicates the aggregate modelled length composition showing the fit to the observed length data.

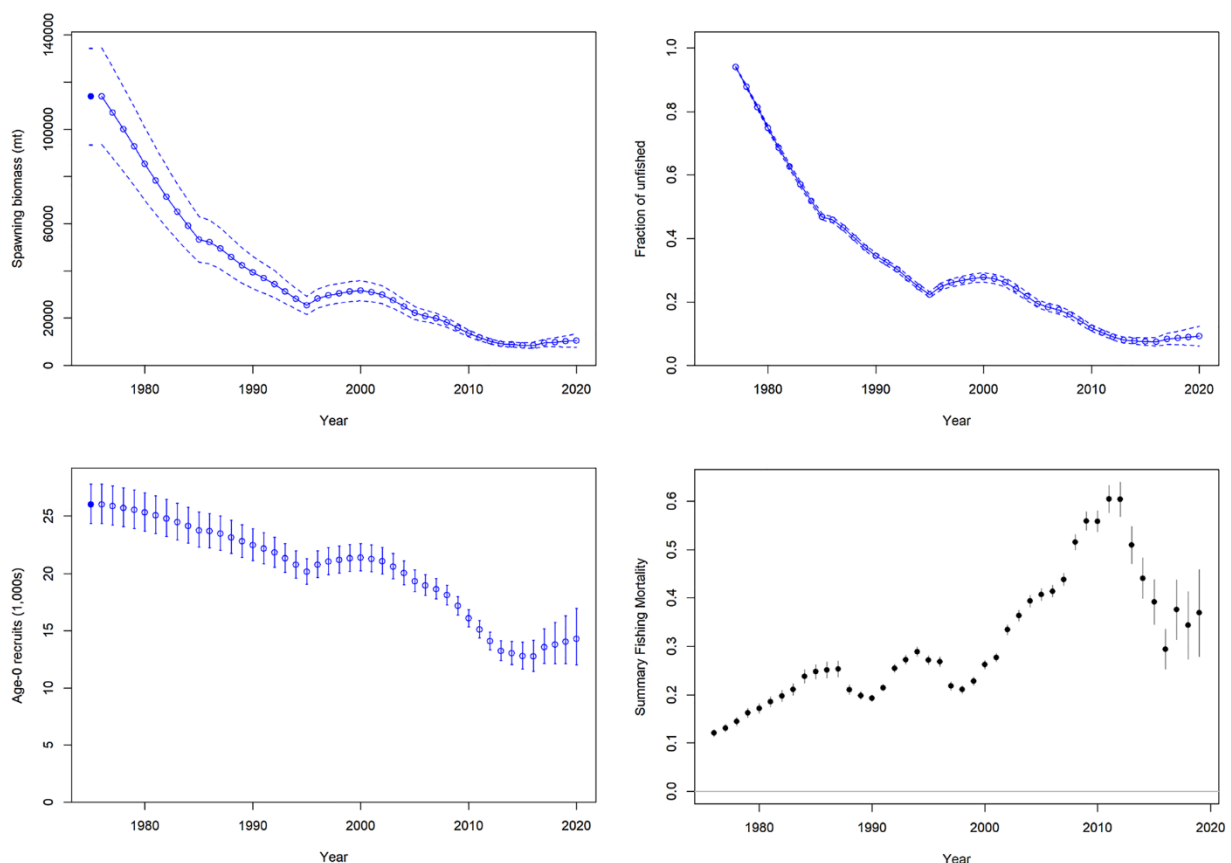


Fig. 11. Spawning biomass (top left panel), relative spawning biomass (top right panel), recruitment (bottom left panel), and fishing mortality (bottom right panel) from 1976 to 2019 for *M. furnieri* from southern Brazil. 95 % confidence intervals indicated by dashed (top panels) and vertical (bottom panels) lines.

likely contributes to the acceleration of growth rates and sizes, but the lack of change in size at maturity with reduction in female age at maturity, could result from both density-dependent processes and selective pressure from fisheries (Trippel, 1995).

4.2. High reproductive potential

M. furnieri has a protracted spawning season of over six months with high overall reproductive potential. It is a long-lived species that matures early in life (3 years old) at around 10 % of its maximum observed

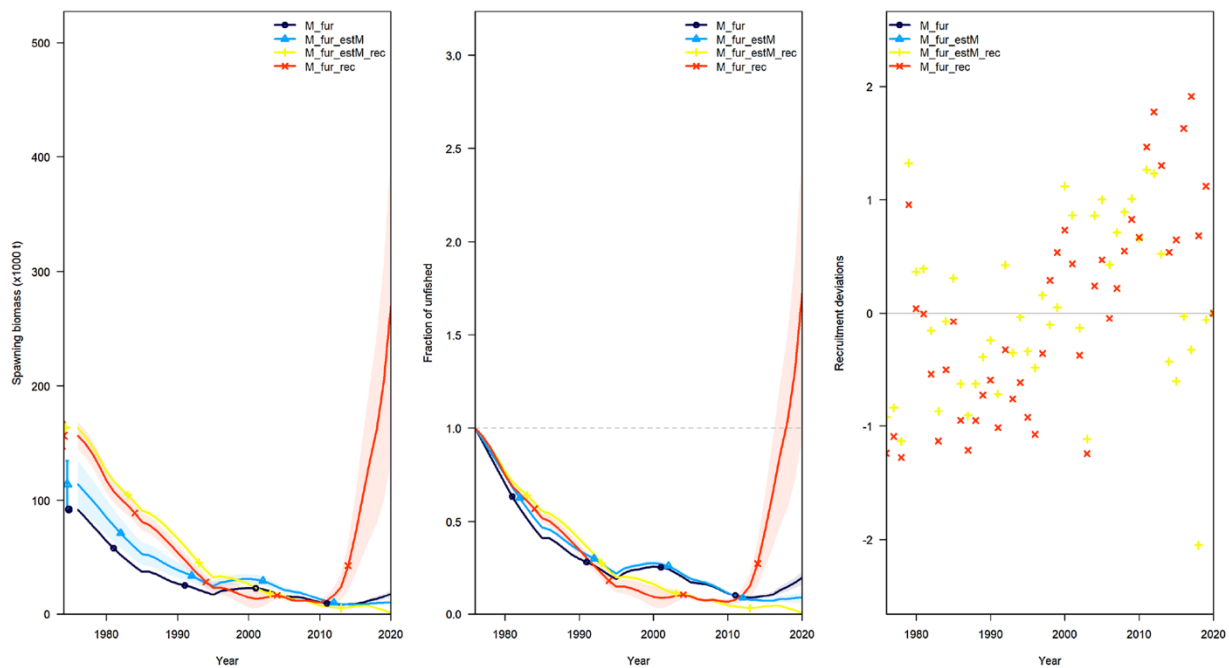


Fig. 12. Comparison plot of spawning output (left panel), relative spawning output (middle panel) and recruitment deviations (right panel) for four models that either do or do not estimate natural mortality (“estM”) and recruitment (“rec”). The reference model is labeled “M_fur_estM” as it does estimate natural mortality, but not recruitments.

age (or longevity). Therefore, each female can contribute to the reproductive output of the population for many years. Moreover, the species has a high annual batch fecundity estimated in several million eggs (Macchi et al., 2003).

4.3. Coastal spawning grounds

Along southern Brazil, *M. furnieri* spawns mostly in marine coastal waters during a protracted reproductive season that last up to ~ 6 months (Weiss, 1981). Pelagic eggs and larvae are carried into the Patos Lagoon Estuary (PLE) and to a lesser degree to other coastal lagoons where juveniles develop (Costa et al., 2013). This behaviour makes *M. furnieri* less vulnerable to gillnets that have led to the collapse of other large and long-lived species in the narrow entrance of the Patos Lagoon (e.g., the sciaenid *Pogonias courbina* (formerly *P. cromis*) and the marine catfishes *Genidens barbatus* and *G. planifrons*) (Haimovici and Cardoso, 2017).

4.4. Large nursery grounds with abundant food and limited fishing pressure on juveniles

In this region, the main nursery grounds for juveniles of *M. furnieri* are the highly productive brackish waters in the PLE, which extends 100 km landward from its mouth. Larvae, which start pelagic, recruit to the bottom at 20–30 mm TL, where they feed actively on infauna and epifauna organisms (Gonçalves et al., 1999). Early juveniles grow fast in the estuarine conditions (Costa et al., 2013) before leaving the estuary towards coastal waters in their second year of life (Cavole and Haimovici, 2015). In the PLE, fishing pressure is limited to small-scale fishing and generally low since no industrial fishing is allowed and the minimum legal size for *M. furnieri* is 250 mm TL (Haimovici and Cardoso, 2017).

4.5. Resilience and sustainability

M. furnieri in southern Brazil has high reproductive potential, spawns in marine waters, and occupies large nurseries with abundant food and limited fishing pressure when juveniles. These combined factors

contribute to the overall stock resilience. However, due to more than 20 years of high exploitation rates (> 0.5), there is evidence that *M. furnieri* could be reaching its adaptive capacity for resilience. For example, *M. furnieri* has not increased its growth rates over the past two decades, lost up to 90 % of its reproductive output, and size and age structure of females is drastically reduced. Big old fat fecund female fish (BOFFFFs) are described as producing more and larger eggs with higher amounts of yolk, resulting in faster growing larvae and higher survivability (Palumbi, 2004; Hixon et al., 2014). While this phenomenon has not been looked at for *M. furnieri*, if relevant, a truncated population structure may destabilize populations and hinder recovery. This was ubiquitously documented in the cod populations from Canada, where landings from all cod stocks decreased from almost half a million metric tons in 1987 to 22,000 metric tons in 1994 (Trippel, 1995).

Other factors in addition to high fishing effort may have been responsible for the observed changes in the size composition of *M. furnieri* in southern Brazil. For example, it was not possible to identify what caused the higher frequencies of larger *M. furnieri* (> 550 mm TL) in the 1989–92 landings compared with the 1976–1980 landings (Fig. 3). This increase in size is not consistent with the steady decrease in the proportion of older for all gears over time (Fig. 6). We hypothesize that a market demand for large *M. furnieri* may have influenced the choice of skippers for fishing grounds in which the proportion of larger fishes was higher. Regardless of these inconsistencies, the general pattern of increasing growth and mortality rates and decreasing spawning potential is consistent and clear.

4.6. Future of the *M. furnieri* stock and fishery

Even with a life history that favours resilience and adaptation, persisting high rates of exploitation pose a risk of collapse to the *M. furnieri* resource. Novel and less expensive technologies can greatly increase the fishing power of industrial fishing fleets and efficiently locate and remove a dwindling population, thus overrunning the capacity of stocks to naturally rebuild (Csirke, 1984; Pauly et al., 2002). In addition, government subsidies can mask the true economic viability of a fishery. These factors are observed in southern Brazil, where in recent years even

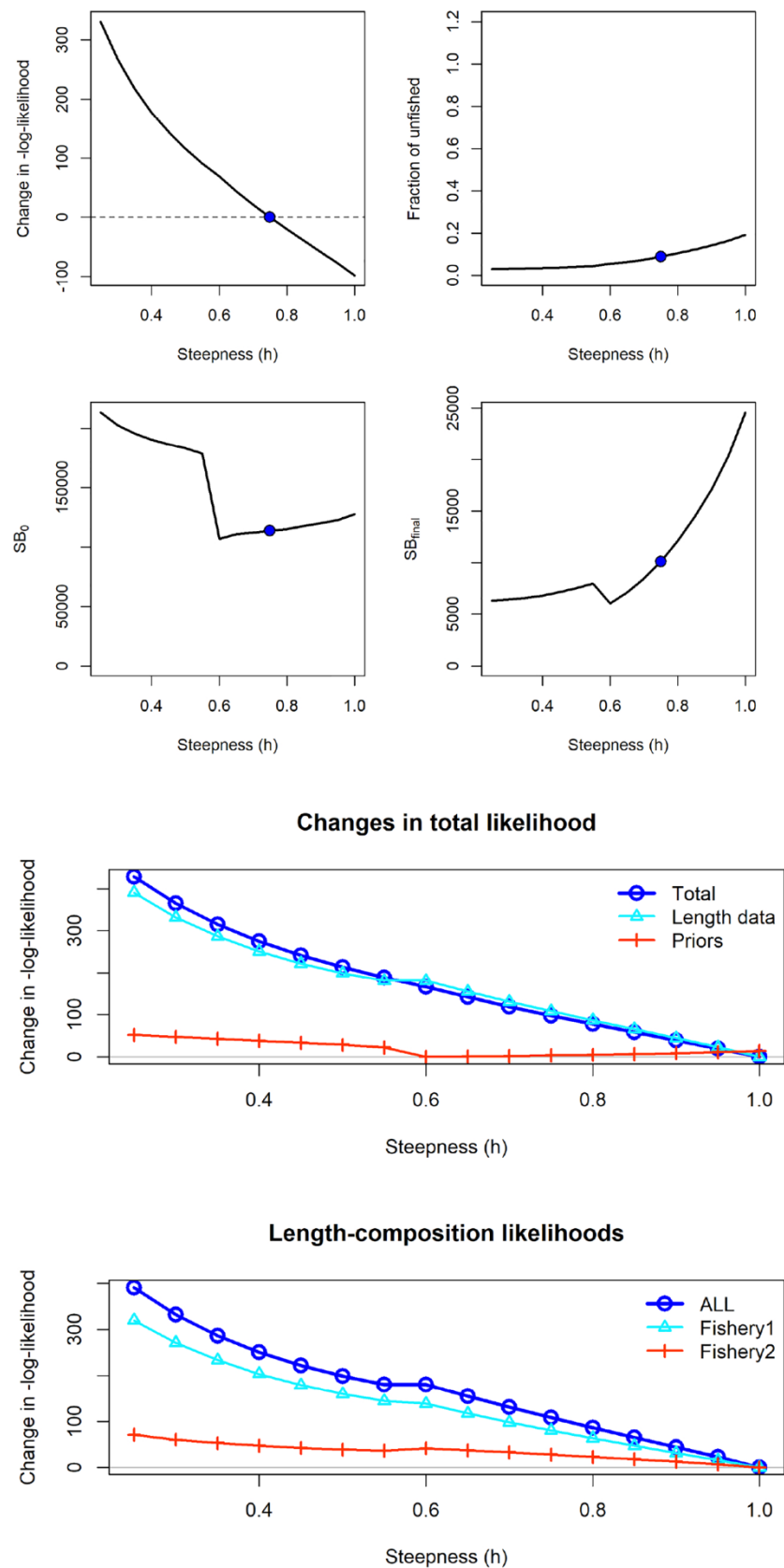


Fig. 13. Likelihood profiles for the reference model. Top four panels (clockwise): Likelihood profile, relative spawning biomass, initial biomass and current biomass. Blue dot (web version) indicates the reference model value. Bottom two panels: Likelihood component profiles by likelihood element (top figure) and length data fleet (bottom figure).

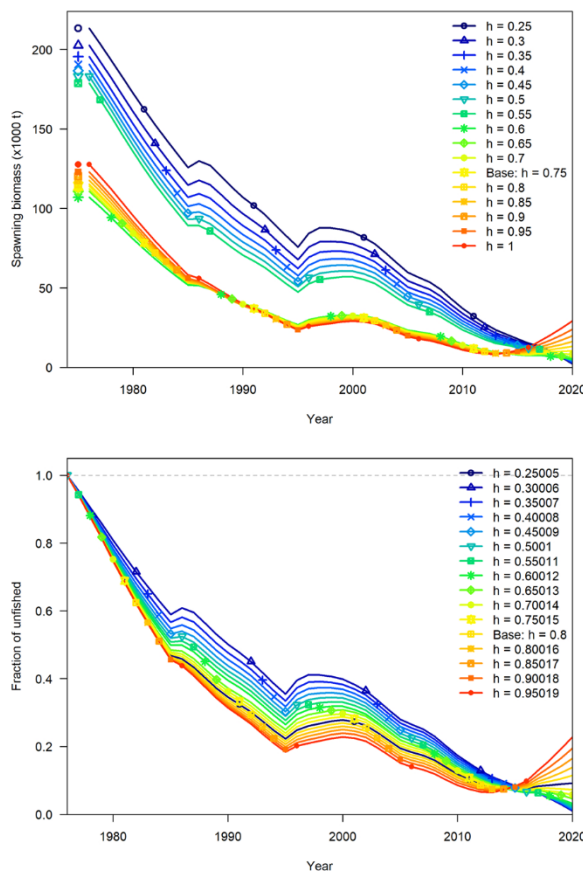


Fig. 14. Time series of spawning biomass (upper panel) and relative spawning biomass (lower panel) for each value in the steepness likelihood profile.

small-scale boats fishing with gillnets have been equipped with sonars that greatly increase the ability to locate and encircle entire spawning aggregations of *M. furnieri* in coastal waters. We recommend that fisheries management recognize these signals in the population and take a precautionary approach by reducing the fishing effort for this species to ensure a sustainable, healthier population and better yields in the future.

CRediT authorship contribution statement

Manuel Haimovici: Conceptualization, Methodology, Writing - original draft. **Leticia Maria Cavole:** Investigation, Formal analysis, Writing - original draft. **Jason M. Cope:** Formal analysis, Writing - original draft. **Luís Gustavo Cardoso:** Formal analysis, Writing - original draft, Software.

Declaration of Competing Interest

The authors report no declarations of interest.

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