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Age, growth, and biomass projections of red porgy *Pagrus pagrus* (Teleostei, Sparidae) after the fishery collapse in southern Brazil

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Abstract

A formerly unexploited stock of red porgy that was intensely fished along southern Brazil in the 1970s collapsed in less than a decade. Subsequently, population dynamics or stock status has not been reported, so we updated growth parameters by analysis of otolith annual-increments and micro-increments. Growth did not change after the stock collapsed, which suggested no density-dependent effect. Given the lack of growth changes and data-limitation, we used an age-structured assessment model set until 1984 to forecast relative spawning biomass and assess recovery possibilities. Projections showed that a 19 years moratorium would have been necessary for the stock to rebuild. The model suggested an annual catch of at least 170 t in the post-collapse period because the stock did not recover, and a small-scale hand-line fishery with unreported landings continued fishing. Our results reinforced the need for more curated and up-to-date data collection to properly assess and manage this formerly abundant stock.

KEYWORDS

assessment, data-limit, micro-increments, southwestern Atlantic, stock synthesis, young-of-the-year

1 | INTRODUCTION

The red porgy, *Pagrus pagrus* (Linnaeus 1758), is a protogynous hermaphroditic coastal sparid fish (Alekseev, 1983) commonly found on consolidated and sandy-shelf bottoms in temperate and subtropical regions along both margins of the Atlantic Ocean and in the Mediterranean Sea (Manooch & Hassler, 1978). The red porgy is a target of commercial and recreational fisheries throughout its range, with more than half of global catches from the southwestern Atlantic (SWA), where it is fished from northern Argentina to southeastern Brazil with bottom trawls, gillnets, hook and line, and traps (FAO, 2019). Distribution of the red porgy in the SWA is not homogeneous, with several distinct groups or stocks proposed based on parasites (Soares et al., 2018), otolith shape (Kikuchi et al., 2021), body shape (Porrini et al., 2015), and growth (García & Déspos, 2015).

In southern Brazil, the red porgy was fished lightly until experimental fishing detected large schools near the Brazil-Uruguay border in 1973 that were immediately fished by a large number of trawlers (5898 t landed in 1973, Yesaki & Barcellos, 1974). Landings rapidly decreased in the following years to less than 240 t/yr since the 1980s. Therefore, this fishery, in a typical explosive cycle, evolved from a pre-development stage to collapse in less than a decade, with no signs of recovery four decades later (Haimovici et al., 2020). Individual growth rates are highly plastic in response to intra- and inter-specific changes in density and sea temperature (Audzijonyte et al., 2016; Morrongiello & Thresher, 2015), so continued intensive fisheries exploitation may cause density-dependent long-term changes in size at age and maximum size, like other demersal species in the same region (e.g., Cardoso & Haimovici, 2011; Haimovici et al., 2021; Hamovici et al., 2022; Miranda & Haimovici, 2007).

Age of red porgy has been estimated throughout almost all of its distribution. In southern Brazil, a study of population dynamics of red porgy validated annuli formation on scales and sectioned otoliths until the 1980s, as a baseline to analyze changes in growth of the species in the region (Haimovici et al., 2020). Annual ring formation has been validated on scales (Ávila-da-Silva, 1996; Costa et al., 1997; Cotrina, 1977; Cotrina & Raimondo, 1997; Manooch & Huntsman, 1977) and opaque bands on otoliths (García et al., 2011; Harris & McGovern, 1997; Pajuelo & Lorenzo, 1996; Potts & Manooch, 2002). However, identification of the first annulus was not previously investigated. Daily growth micro-increments have the potential to elucidate growth in the first year of life and to identify the first annulus (Cavole et al., 2018; Green et al., 2009), which could substantially increase precision of individual age estimates (Campana, 2001).

In light of the heavy fishing pressure faced by red porgy in southern Brazil, our objective was to determine if growth changed after the stock collapsed and the likelihood of stock recovery under a range of harvest levels. To accurately estimate age, we examined the microstructure of otoliths of young-of-the-year red porgy to locate the first opaque annulus. We also used estimated growth parameters in a catch-length age-structured model to assess stock recovery possibilities by projecting relative stock biomass during the post-collapse period. Our findings should provide the first perspective on the red porgy stock status in the region and potentially useful information for future management.

2 | METHODS

2.1 | Microstructure of young-of-the-year otoliths

Young-of-the-year red porgy are rarely landed by commercial fishing boats, so only 12 specimens measuring 72–171 mm TL were obtained in southern Brazil between latitudes 30° S and 34° S (Figure 1) from research surveys and by observers on commercial fishing vessels during 1990–2007. For determination of the number of micro-increments, sagittal otoliths were embedded in a transparent polyester resin, and 0.2–0.3 mm cross-sections passing through the nucleus were removed with a low-speed precision saw (Isomet Buehler Ltd). Otoliths sections were progressively polished with 1500–12,000-grit silicon carbide paper (Micro-Mesh), etched with 0.5% HCl by volume for up to 1 min, immersed in water for 24 h, and mounted on histology slides with synthetic resin (Entellan Merck) (Cavole & Haimovici, 2015).

Sections were examined using transmitted light microscopy at 400× magnification, suitable for examining fast-growing otoliths with micro-increments larger than 2 μm in width (Campana & Jones, 1992). Microscope light and focus were adjusted during counting to follow the entire sequence. Micro-increments were counted twice by the same reader (a third time if counts differed by >10%) along the ventral axis from the otolith core to outer edge (Figure 2). The mean number of microstructures counted and ventral axis distance were used to identify the first annual opaque band on the macrostructure of otoliths from older specimens.

Counting the increment back to a specific event can validate its daily formation in some circumstances (Geffen, 1992). For example, the number of micro-increments between the time of capture and an event at a known date, such as hatching of seasonal spawners (Cotrina & Christiansen, 1994; Haimovici et al., 2020), can be used to infer age of young-of-the-year as an indirect validation. Thus, micro-increments in otoliths of young-of-the-year red porgy were back-calculated to verify if they corresponded to the likely date of hatching in the region.

2.2 | Otolith macrostructure analysis

Otoliths, total length (TL, mm) measured from the tip of the snout to the midpoint of the upper and lower limbs of the caudal fin, and total weight (TW, g) of red porgy from southern Brazil were collected in two periods. The first period was between 1976 and 1977, when 101 specimens measuring 240–470 TL mm were sampled from landings of bottom trawlers. The second period was between 2015 and 2019 when 562 specimens measuring 190–510 TL mm were sampled from landings of bottom trawlers ($n = 164$), hook and line ($n = 56$), purse seines ($n = 88$) and bottom gillnetting ($n = 254$).

For age estimation, sagittal otoliths were embedded in a transparent polyester resin and sectioned (0.2–0.3 mm) transversally through the nucleus with a low-speed precision saw (Isomet Buehler Ltd) and mounted on histology slides with synthetic resin (Entellan, Merk). Images of otolith sections were captured using a stereoscopic microscope at 10× magnification by a camera with a resolution of 2048 × 1536 pixels per inch. Two readers independently counted alternate opaque and translucent bands. If counts differed, otoliths were counted again by both readers and discarded from further analyses if the difference persisted. Distance between the otolith nucleus and the end of each opaque band (Figure 3) were measured with ImageJ 1.47 (www.imagej.nih.gov).

The linear relationship between total length (TL) and ventral otolith axis radius (R) was estimated for a set of 165 specimens measuring 72–510 mm TL, selected to include most specimens within each 10 mm TL class: $TL = 0.0084\,R + 0.96$; $R^2 = 0.908$ (Figure 4).

Back-calculated lengths-at-age were computed using the scale-proportional hypothesis (Francis, 1990) with the Fraser–Lee formula:

$$Li(mm) = \left[(TL - a) \left(\frac{Ri}{R} \right) \right] + a,$$

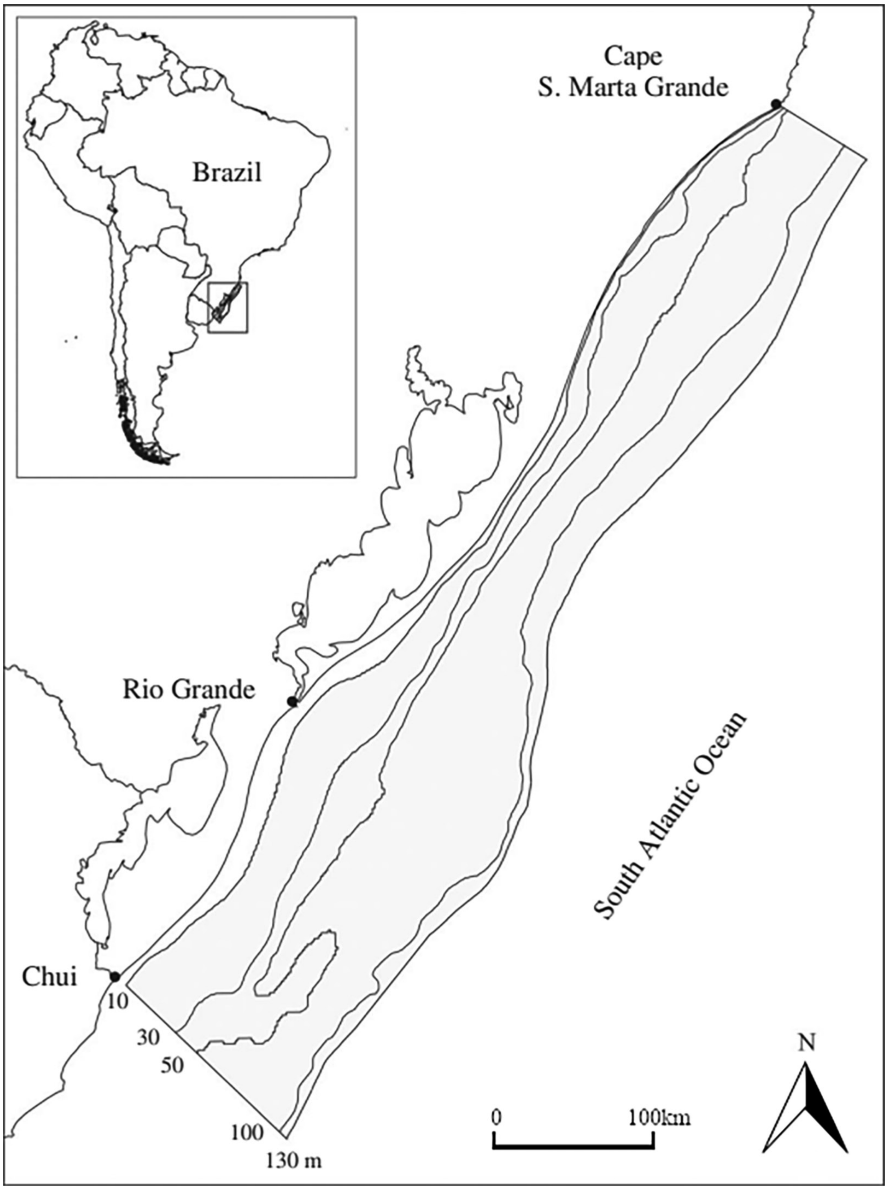

FIGURE 1 Red porgy (*Pagrus pagrus*) fishing area in southern Brazil between latitudes 30° S and 34° S. Adapted from Rovani and Cardoso (2017).

In which *TL* was total length at the time of capture, *Li* was length at the age of formation of the ith ring, *Ri* was the distance between the focus and each age ring, and *a* was the intercept of the regression of otolith radius on fish length.

The von Bertalanffy length-age model, adjusted by a Bayesian approach, was used to quantify growth of red porgy following the approach described by Rovani and Cardoso (2017). Because the red porgy is a protogynous species and sexes do not differ in growth (Haimovici et al., 2020), von Bertalanffy parameters were estimated for pooled sexes.

For each period, two growth curves were calculated, one for mean back-calculated length-at-age and another for individual back-calculated lengths-at-age, to quantify variability associated with individual fish. Different fishing gears used in the two periods can differ in selectivity, which could affect growth analysis, so growth curves were also estimated using only samples from trawl catches in the most recent period to compare with trawl samples from the earlier period.

Age-length data (mean or individual back-calculated) were assumed to follow log-normal distributions: $y_i = \log N\left(\mu_i, \sigma^2\right)$, where y_i was the length distribution with an average expected length at age (or length class) *i* with variance σ^2. A log-transformed version of the von Bertalanffy equation was used for computational convenience:

$$\mu_i = \log\left(L_\infty\left(1 - e^{-k(i-t_0)}\right)\right).$$

Uninformative *priors* were used:

$$p\left(logL_\infty\right) \sim dN(0{,}0.001)\, I\,(-5, 5),$$

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

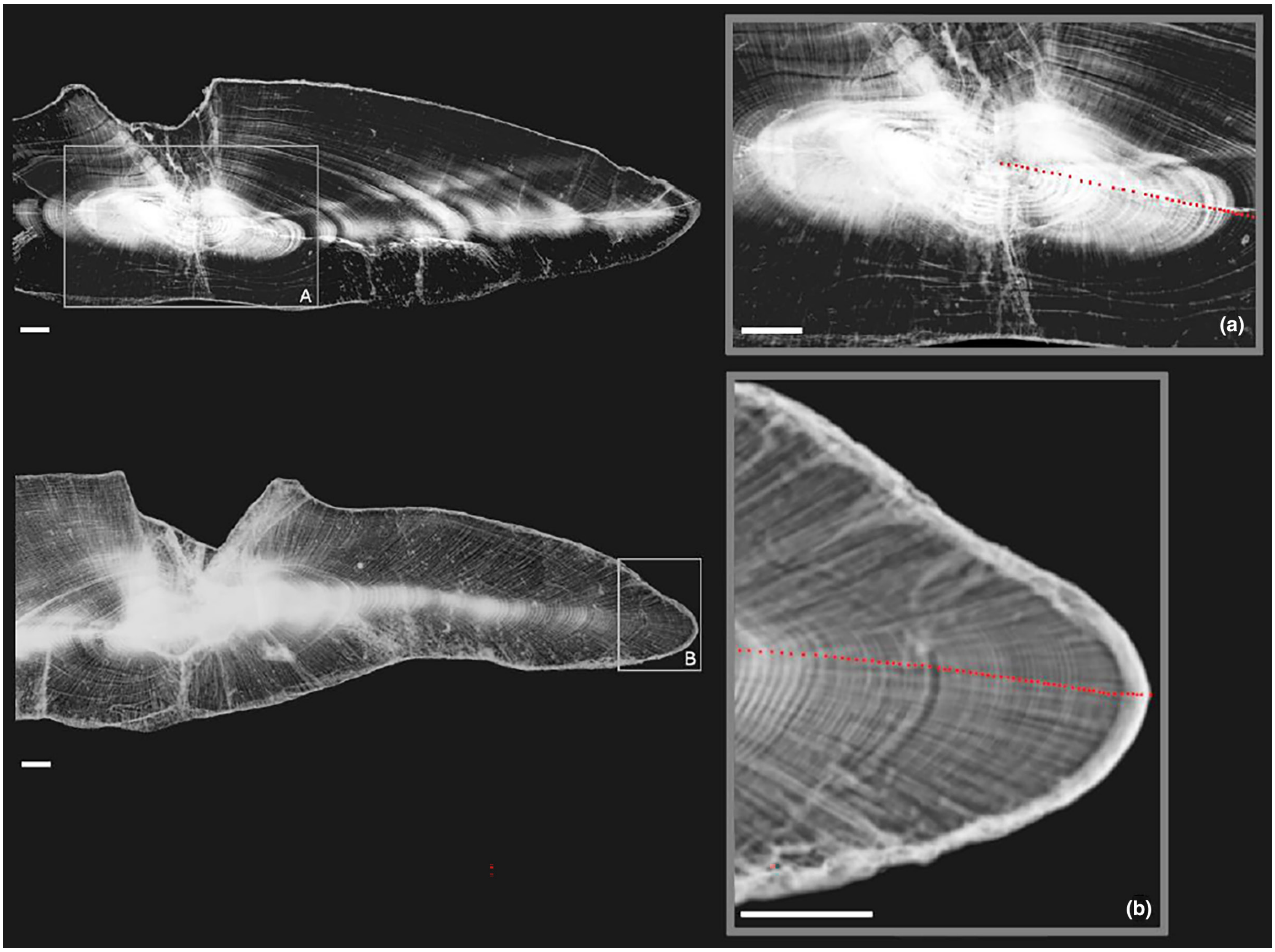

FIGURE 2 Micro-increments (red pointed line) in thin otolith sections of young-of-the-year red porgy (*Pagrus pagrus*) from southern Brazil (a) with 113 mm total length showing 155 daily growth increments, evidencing the nucleus micro-increments; and (b) with 129 mm total length showing 161 daily growth increments, evidencing the border micro-increments. Scale bars 0.1 mm.

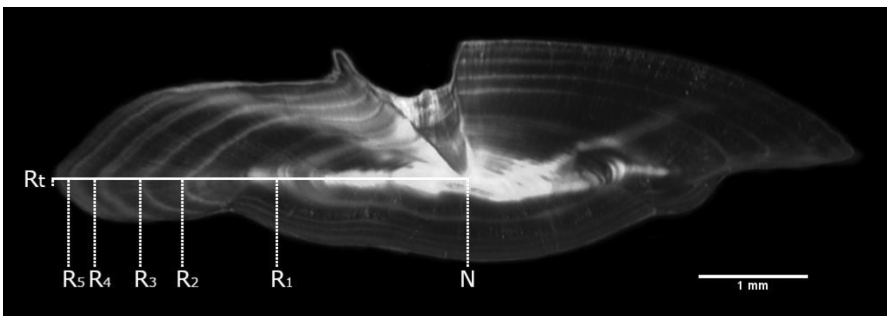

FIGURE 3 Thin section examined of a five-year-old (TL: 360 mm) red porgy (*Pagrus pagrus*) from southern Brazil examined with incident light over a dark background. Dashed white lines indicate the nucleus (*N*), the end of each opaque band (Ri), and the border (Rt). The solid white line at the ventral axis indicates the measured distance from the nucleus to opaque bands and the border.

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

Posterior distributions for each period were developed from Markov Chain Monte Carlo analysis, to compare growth parameter estimates among periods and fleets. After 10,000 burn-in runs, every second value of remaining 20,000 runs was retained, for a final sample of 10,000 in the posterior distribution (log L_∞, log k, log t_0) (Kinas & Andrade, 2010). The posterior distribution of each estimated parameter was used to compare parameter estimates between periods. Analyses used R version 2.12.0. The MCMC used *OpenBUGS*, from *R2WinBUGS* (Sturtz et al., 2005) and *BRugs* (Thomas et al., 2006).

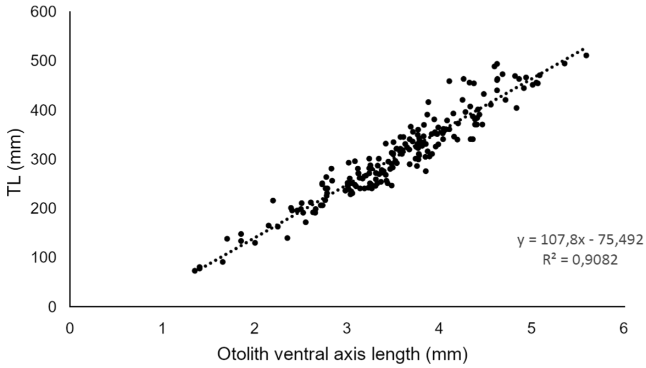

FIGURE 4 Linear relationship between total length and the otolith ventral axis length of 165 red porgies (*Pagrus pagrus*) sampled between 1976–2019 in southern Brazil.

2.3 | Population dynamics and biomass projections

Status of the red porgy stock from Brazil was assessed using the Stock Synthesis Data-limited Tool framework (SS-DL tool; Cope, 2020), based on the Stock Synthesis (SS3) (Methot & Wetzel, 2013), likelihood-based statistical catch-at-age modeling package from multiple data sources to characterize population dynamics through time. SS3 is a flexible tool for fisheries management applications, from which we used the catch-length version for data-limited fisheries (Cope, 2020). Life history parameters affect the absolute scale of biomass, so the catch-length version for data-limited fisheries was appropriate for studies of relative stock biomass projections under current conditions of data available for the red porgy in southern Brazil.

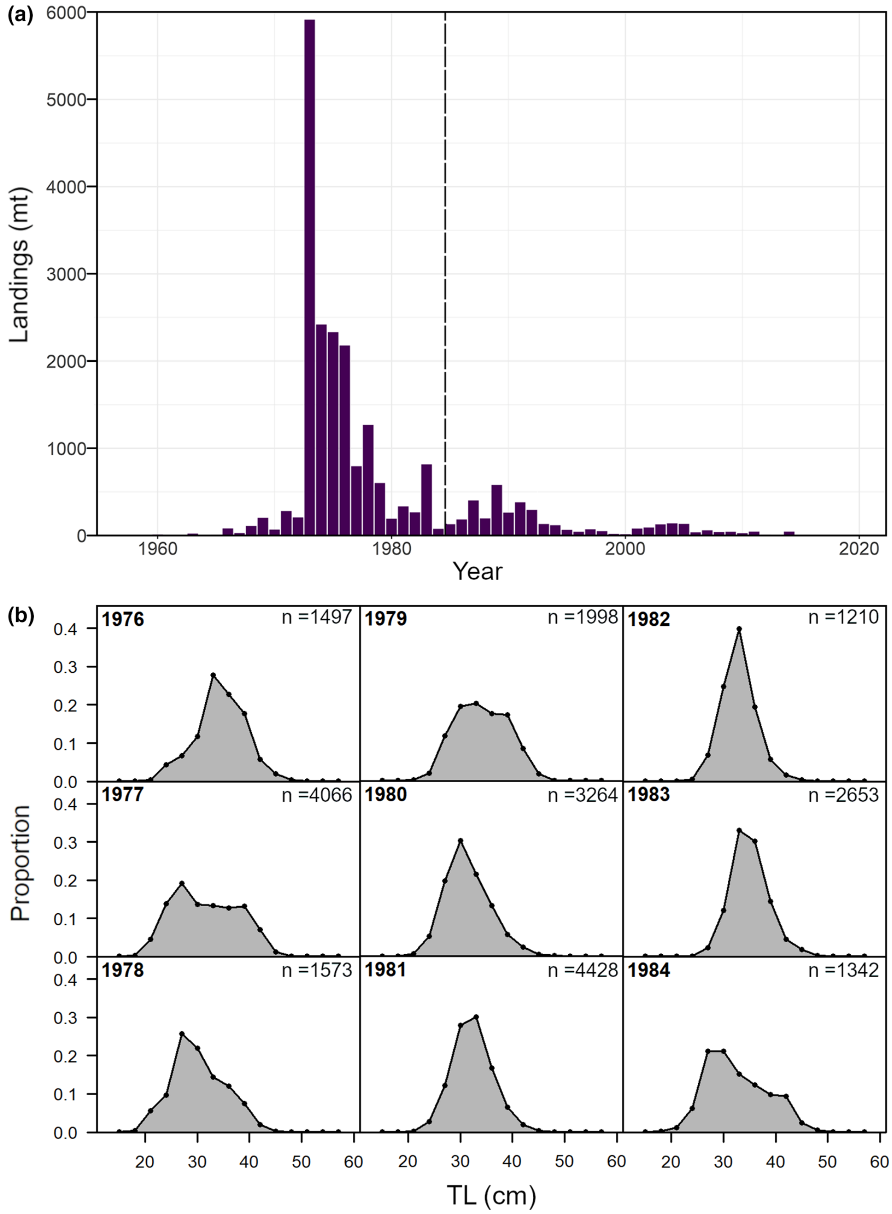

FIGURE 5 Annual catch (a) and length composition (b) time series reported for red porgy (*Pagrus pagrus*) in southern Brazil. The dashed line indicates the last year (1984) in which catches were incorporated into the assessment model.

Catch date	Back-calculated birth date	TL (mm)	Daily growth increments	Ventral axis distance (mm)
7-06-1991	27-01-1991	137	131	1.7
7-06-1991	21-01-1991	139	137	1.9
7-06-1991	12-12-1990	133	176	1.9
7-06-1991	28-12-1990	129	161	1.9
7-06-1991	24-12-1990	171	165	1.8
6-07-2001	25-04-2001	164	134	2.0
18-04-2002	16-12-2001	115	123	1.7
18-04-2002	14-11-2001	113	155	1.5
15-04-2008	26-10-2007	90	171	1.7
15-04-2008	28-11-2007	72	139	1.4
15-04-2008	23-12-2007	80	114	1.4
15-04-2008	15-11-2007	77	151	1.4
Mean		**116.6 ± 34.3**	**146 ± 41**	**1.69 ± 0.22**

Note: Mean and standard deviation of measurements are in bold.

TABLE 1 Back-calculated birth date of 12 young-of-the-year red porgy (*Pagrus pagrus*) based on the number of daily micro-increments counted along the ventral axis of thin otolith sections sampled by research surveys and observers on commercial fishing vessels from southern Brazil between latitudes 30° S and 34° S during 1990–2007.

The model was set for catches during 1958–1984 (Ibama/Ceperg, 2011) and length-compositions during 1976–1984 (Haimovici et al., 2020) (Figure 5). After that period, size data were not available and reported catches were doubtful because a small number of handline fishing boats continued targeting the species with low and frequent unreported landings (Haimovici et al., 2020). Stock recovery was assessed using future projections during 1985–2023 to explore scenarios for managing constant catches during the post-collapse period.

Models were set up to reconstruct red porgy historical spawning stock biomass (SSB) until 1984 for a single fleet, one area, one sex, yearly structured, and assuming a standard Beverton-Holt stock-recruitment with log of initial recruitment (*ln R0*) estimated using maximum likelihood (MLE). Deviations from the stock-recruit relationship were assumed only for the period when length composition data were available (i.e., from 1976 to the end of the period). Selectivity was parameterized as length-based, with model estimating parameters with a logistic pattern.

The model was based on pre-specified life history parameters for growth (L_∞; k; and t_0), natural mortality (M), length at maturity (L_{50} and L_{95}), length-weight relationship, and steepness (h: the proportion of initial recruitment, when spawning stock biomass is reduced to 20% of virginal biomass; Francis, 1992). Growth parameters were estimated from this study for the historical period. Instantaneous natural mortality was estimated from, $M = 5.109/t_{max}$ (Then et al., 2015). Maturity parameters were from Militelli et al. (2017). Length-weight parameters were from Haimovici et al. (2020), and the weight-fecundity relationship assumed fecundity was proportional to weight. Steepness has not been estimated for the southwest Atlantic red porgy, so 0.39 was for the species in the southeastern United States (Davis, 2003). Stock productivity was highly uncertain, so a grid of alternative steepness values ($h = 0.33$–0.45 in 0.02 steps) that incorporated the value estimated in the last assessment (Sedar., 2020) was used to explore model sensitivity to the steepness value.

Before projections of relative stock status (SSB/SSB_{MSY}), the reference model was evaluated through hindcast analysis in the R package *ss3diags* (Carvalho et al., 2021). Subsequently, the reference model and alternative scenarios of steepness were aggregated into a model corresponding to the mean SSB/SSB_{MSY} trajectory, forecast with 20 constant catches from 0 t, and ranging from 10 to 370 t in 20 t steps. Projections were carried out by setting the "*forecast. file*" in the SS3 framework (Methot et al., 2020) from the last year of the time series for 39 years (1985–2023). The projection output was obtained with the package *r4ss* implemented in SS3 (Taylor et al., 2021). Estimated probabilities of the stock above SSB_{MSY} (not overfished) in a year for a given constant catch for the joint distribution of projections used a Monte-Carlo multivariate lognormal (MVLN) approximation with 100,000 iterations (Walter & Winker, 2019).

3 | RESULTS

3.1 | Young-of-the-year age

Thin otolith sections of 12 young-of-the-year red porgy 72–171 mm TL had a concentric pattern of micro-increments that we assumed were daily. The number of micro-increments ranged 114–176, and except for one specimen, back-calculated birth dates were from 26 October to 27 January (Table 1), which were within the reproductive season of red porgy in southern Brazil (Haimovici, 1998). For a mean total length of 116.6 ± 34.3 mm, the number of micro-increments was 146 ± 41, and the distance between the otolith nucleus and the ventral border was 1.69 ± 0.22 mm (Table 1).

Mean total length (117 mm) and the mean ventral axis of otoliths (1.69 mm) of young-of-the-year red porgy corresponded to an average of 150 days after birth (Table 1). The end of the first opaque band in otoliths of red porgy older than 1 year, in the recent period analyzed, averaged 1.84 mm along the ventral axis and 126 mm

TABLE 2 Mean and back-calculated lengths at age of red porgy (*Pagrus pagrus*) fished in southern Brazil by trawl fleets during 1976–1977 and trawl or all fleets during 2015–2019.

1976–1977 (trawl fleets)												
			Age (years)									
Annuli number	***n***	**Observed mean TL (mm)**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
2	1	240	97	182								
3	11	261	111	200	260							
4	21	314	116	203	266	302						
5	20	341	116	206	261	305	334					
6	18	353	106	202	256	295	325	352				
7	8	360	119	217	275	302	325	344	358			
8	7	370	139	236	280	309	330	346	359	365		
9	4	398	118	203	277	309	332	354	374	386	398	
10	1	410	125	186	245	292	319	337	356	374	390	410
Mean back-calculated TL (mm)			116	204	265	302	327	347	362	375	394	410
Mean otolith axis distance (mm)			1.80	2.65	3.20	3.56	3.79	3.98	4.08	4.14	4.25	4.27
2015–2019 (trawl fleets)												
			Age (years)									
Annuli number	***n***	**Observed mean TL (mm)**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
2	26	225	120	200								
3	42	273	118	201	262							
4	57	305	115	192	258	304						
5	19	324	119	196	253	297	323					
6	10	349	119	204	259	295	327	346				
7	5	376	123	204	269	302	333	355	369			
9	3	399	126	216	258	308	331	351	369	385	397	
10	2	427	150	223	270	300	328	357	379	395	409	421
Mean back-calculated TL (mm)			124	205	261	301	328	352	372	390	403	421
Mean otolith axis distance (mm)			1.80	2.55	3.13	3.52	3.76	3.93	4.10	4.19	4.31	4.33
2015–2019 (all fleets)												
			Age (years)									
Annuli number	***n***	**Observed mean TL (mm)**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
2	41	239	124	209								
3	116	278	122	205	267							
4	181	312	121	200	263	309						
5	87	339	123	204	259	302	335					
6	41	368	126	212	270	309	341	367				
7	35	368	121	206	263	297	323	346	363			
8	18	383	124	211	264	295	324	345	366	382		
9	12	408	127	213	260	299	329	353	373	389	404	
10	15	426	146	237	285	321	348	370	382	397	411	423
Mean back-calculated TL (mm)			126	211	266	305	333	356	371	390	408	423
Mean otolith axis distance (mm)			1.84	2.60	3.15	3.52	3.78	3.96	4.09	4.26	4.37	4.47

Note: Mean back-calculated lengths and mean otolith axis distance of annual bands formation by age are also shown (*n* = Number of sampled individuals).

back-calculated total length (Table 2). Thus, microstructure analysis confirmed the first annual increment that was identified using minimum and maximum counts and assigned birth dates.

3.2 | Growth

Otoliths from 1976–1977 had well-marked opaque bands. During 2015–2019, only four otoliths had no discernible growth band and were discarded. The oldest fish had 26 annuli during 1976–1977 and 18 annuli during 2015–2019. Mean back-calculated length-at-age did not differ significantly between periods (Wilcoxon-Mann–Whitney, $p > 0.05$).

Red porgy older than 10 years were rare, with only 10 individuals during 1976–1977 and 11 during 2015–2019. None of these individuals were from the trawl fleet for the current period, which would bias back-calculated lengths-at-age and growth. Therefore, growth analysis included only individuals younger than 11 years (Figure 6). Parameters of length-age growth models did not differ between 1976–1977 and 2015–2019 or fleet structures (Table 3), because credible intervals of growth parameters overlapped (Figure 6).

3.3 | Stock assessment

The input parameters used in the SS3 reference model, their respective treatments, and the data source are represented in Table 4. Trajectories of estimated spawning biomass (*SSB*) and relative spawning biomass (SSB/B_{MSY}) sharply decreased after the mid-1970s and stabilized until the mid-1980s (Figure 7). For the reference model and six alternative scenarios (i.e., $h = 0.33$ to 0.45 in 0.02 steps), models showed periods of an overfished state of the stock after the mid-1970s until the end of the series ($SSB_{1984}/B_{MSY} < 1.0$). The ratio of estimated SSB_{1984}/SSB_{MSY} was positively related to steepness, and ranged from a low of 0.089 ($h = 0.33$) to a high of 0.261 ($h = 0.45$), with a median of 0.152 for the reference case ($h = 0.39$).

The positive relation between steepness and SSB/SSB_{MSY} was supported by significant changes in the total likelihood gradient (Figure 8). Despite that, the length-composition and recruitment did not apparently conflicts and low influence regarding the steepness. This result, added to the lack of a calculated steepness value for the southern stock of red porgy in Brazil, reinforced the implementation of an uncertainty grid around this parameter.

Trends and scale in *SSB* were similar in retrospective years, with a consistently positive, but slight, retrospective bias that fell within 95% confidence intervals of the reference trajectory (Figure 9). The small Mohn's *rho* statistic (0.35) and corresponding 'hindcast *rho*' were stable (0.37) for *SSB*, so the model was consistent as sequential years of data were removed. Also, the hindcast diagnostic plot for expected values of observed length data based on forward projections fell within the evaluation period as sequential years of data were removed (Figure 9). Mean absolute scaled error (MASE) scores <1 indicated adequate prediction skill for corresponding mean length estimates (Carvalho et al., 2021). Based on these diagnostics, we assumed the model had sufficient prediction skill for future projections.

3.4 | Biomass projections

For the lowest steepness ($h = 0.33$), the stock would recover in 2023 only with constant catches below 50 t, whereas for the highest steepness ($h = 0.43$), constant catches below 330 t would be sufficient ($SSB_{2023}/SSB_{MSY} > 1$). As a result of the seven aggregated scenarios, the stock would have at least a 60% probability of recovery in 2023 with a constant catch of 150 t or less (Figure 10; Table 5). For a closure scenario (constant catch = 0 t), the stock would rebuild in at least 19 years with 60% probability of $SSB_{2003}/SSB_{MSY} > 1$. Although constant catches between 170 and 290 t would enable SSB/SSB_{MSY} to increase, the stock would remain overfished in 2023.

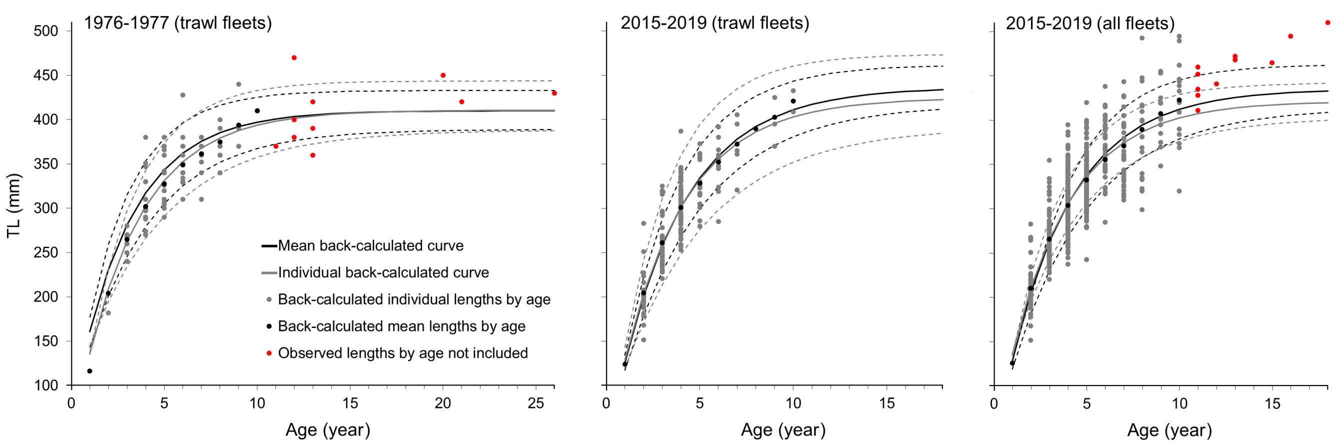

FIGURE 6 Von Bertalanffy growth curves for red porgy (*Pagrus pagrus*) individual (gray circles) and mean back-calculated length-at-age (black circles) in southern Brazil by trawl fleets during 1976–2019 and trawl or all fleets during 2015–2019. The continuous line indicates the regression line. The dashed line indicates the credibility interval ($\alpha = 0.05$). Red circles indicate the observed lengths by age not included in the analysis.

TABLE 3 Von Bertalanffy growth parameters (Lower and Upper credible intervals, $\alpha = 0.025$) for mean and individual back-calculated length-at-age of red porgy (*Pagrus pagrus*) fished in south Brazil by trawl fleets during 1976–1977 and trawl or all fleets during 2015–2019.

Period	Fleet	Back-calculation	L_∞ (Cr.I.)	*k* (Cr.I.)	t_0 (Cr.I.)
1976–1977	Trawl	Mean	410 (389–433)	0.33 (0.27–0.39)	−0.51 (−0.7 – −0.35)
		Individual	411 (388–444)	0.31 (0.23–0.37)	−0.30 (−1.04 – −0.01)
2015–2019	Trawl	Mean	437 (418–462)	0.28 (0.23–0.32)	−0.23 (−0.42 – −0.08)
		Individual	425 (392–474)	0.29 (0.21–0.36)	−0.25 (−0.71 – −0.01)
	All	Mean	435 (414–463)	0.29 (0.24–0.34)	−0.22 (−0.43–0.34)
		Individual	421 (404–442)	0.30 (0.25–0.35)	−0.29 (−0.64 – −0.03)

TABLE 4 Input parameters, treatments, values, and sources for a Stock Synthesis reference model of red porgy (*Pagrus pagrus*) from southern Brazil.

Parameters	Treatment	Values	Source
t_{max} (year)	Fixed	26	This study
L_∞ (cm)	Fixed	41	
k (year^{-1})	Fixed	0.33	
t_0 (cm)	Fixed	−0.51	
Natural mortality (*M*)	Fixed	0.2	
L_{50} (cm)	Fixed	24.5	Militelli et al., 2017
L_{95} (cm)	Fixed	30	
Length (cm)-Weight (kg) alpha	Fixed	1.735e-03	Haimovici et al., 2020
Length (cm)-Weight (kg) beta	Fixed	2.979	
Steepness (*h*)	Fixed	0.39	Davis, 2003
Initial recruitment (*ln R0*)	Estimated	8.59	MLE
Selectivity peak (cm)	Estimated	35.27	MLE
Selectivity ascending width (cm)	Estimated	48.23	MLE

4 | DISCUSSION

In species with a clearly interpretable otolith microstructure, like red porgy in this study, micro-increment counts can be used to confirm the location of the first annulus (Campana, 2001). Daily formation of micro-increments on otoliths of young-of-the-year red porgy was not experimentally proved, but was inferred by equivalence of the number of micro-increments, otolith size, total length, and back-calculated birthday in relation to the spawning season of red porgy in the region. In southern Brazil, red porgy reproduce in spring (Haimovici et al., 2020), so coincidence of the correct birthday back-calculated from otolith micro-increment counts supports an assumption of daily formation of micro-increments on red porgy otoliths.

Individual growth did not change substantially between 1976–1977 and 2015–2019, like long-term changes in red porgy growth associated with changes in density of stocks in Argentina, Uruguay, and the southeastern United States (Figure 11). A lack of growth change in southern Brazil may be caused by the red porgýs diet in the region depending on fish and squids that are part of the plankton-based food webs (Capitoli & Haimovici, 1993). Similarly, growth did not change in response to changing density for early ages of stripped seakfish *Cynoscion guatucupa* (Miranda & Haimovici, 2007) that fed primarily on zooplankton and small fish that were also part of plankton-based food webs (Vieira, 1990). In contrast, growth increased in recent decades for the most important species in the demersal industrial trawl fishery along southern Brazil (*Micropogonias furnieri*, Haimovici et al., 2021; *Umbrina canosai*, Haimovici et al., 2006; Hamovici et al., 2022; *Macrodon atricauda*, Cardoso & Haimovici, 2011; older *C. guatucupa*, Miranda & Haimovici, 2007), all of which feed primarily on epibenthic and benthic invertebrates that are part of detritus food webs (Cardoso & Haimovici, 2016; Martins, 2000; Vieira, 1990). Higher abundances and densities of sciaenid fishes imply a high intra-specific competition for food that declined in response to intense biomass removal by fishing, thereby resulting in lower predation pressure and increased availability of food per individual that increased growth as a density-dependent response (Cardoso & Haimovici, 2016). Red Porgy were much lower in abundance and density than other sciaenids: only 3.2% of total landings from the region and ~25 kg-per-day-at-sea by bottom trawlers at the peak of the fishery (Haimovici et al., 2006). Therefore, the lack of growth response we found for red porgy in southern Brazil, which contrasted with other species in the same region, may have been related to their relatively small impact on the food supply of far more energetic planktonic-based food webs than detritus (Christensen & Pauly, 1993).

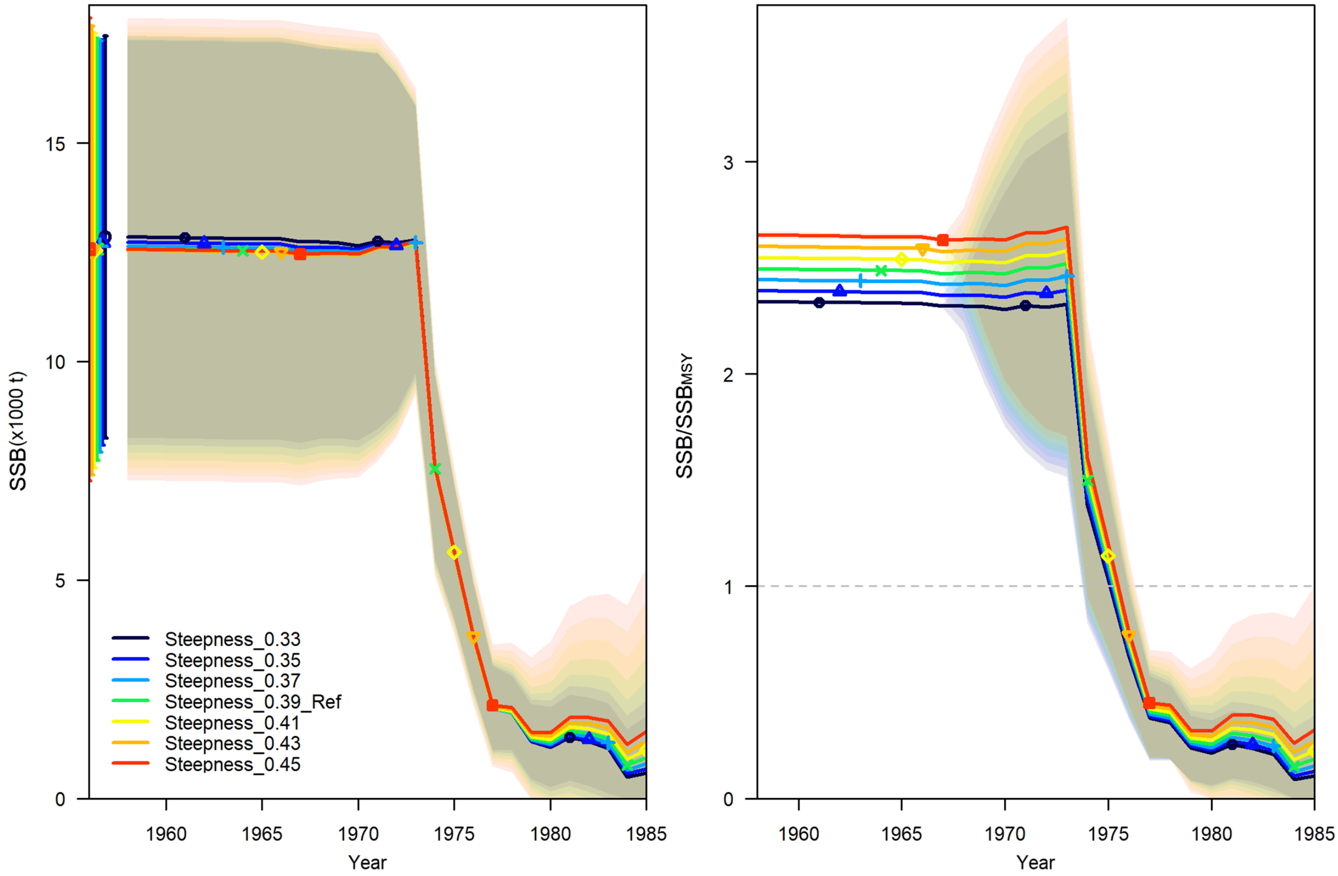

FIGURE 7 Spawning stock biomass (*SSB*) and relative spawning biomass (SSB/SSB_{MSY}) trajectories estimated for red porgy (*Pagrus pagrus*) stock from southern Brazil from 1958–1984. The colored trajectories correspond to the scenarios evaluated for the steepness uncertainty grid (i.e., $h = 0.33–0.45$ in 0.02 steps). Shaded areas are the 95% confidence intervals for each scenario.

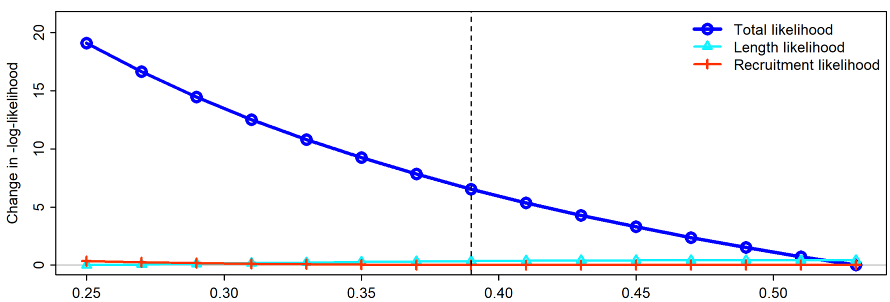

FIGURE 8 Log-likelihood profile for steepness for the red porgy (*Pagrus pagrus*) stock assessment from southern Brazil, showing the contribution of total data, length composition and recruitment likelihood components. The dotted vertical line indicates the fixed input value for the reference model ($h = 0.39$).

If changes in population density did not affect red porgy growth, other factors, such as fishing-induced evolution, could have counteracted density-dependent effects (Dunlop et al., 2009). Drastic declines in population density can also cause life history evolution toward slower growth, higher reproductive investment, and maturation at younger ages (Audzijonyte et al., 2016). Thus, if the red porgy stock evolved toward slower growth, in response to intense fishing mortality, a density-dependent change in growth could have been masked. To test such hypotheses, more direct measures of evolution, such as genetic markers, would be necessary to disentangle effects of fisheries-induced evolution and density-dependent change in individual growth of red porgy in south Brazil.

Life history parameters based on growth and reproduction are available for the red porgy in southern Brazil (Haimovici et al., 2020). However, fishery-dependent data, such as length composition and catches, are only available for relatively short periods, and several problems are currently associated with collecting this information in the region. This deficient amount of data can affect results of assessments, including estimation of stock status indicators and benchmarks used in management (Davis & Berkson, 2006). In this situation, projection models can represent a population's evolution from an initial state (where data are still available) to the future under different management regimes or states of nature (Patterson et al., 2001). For example, in a baseline study before the start of overexploitation of red porgy in southern Brazil, total mortality and

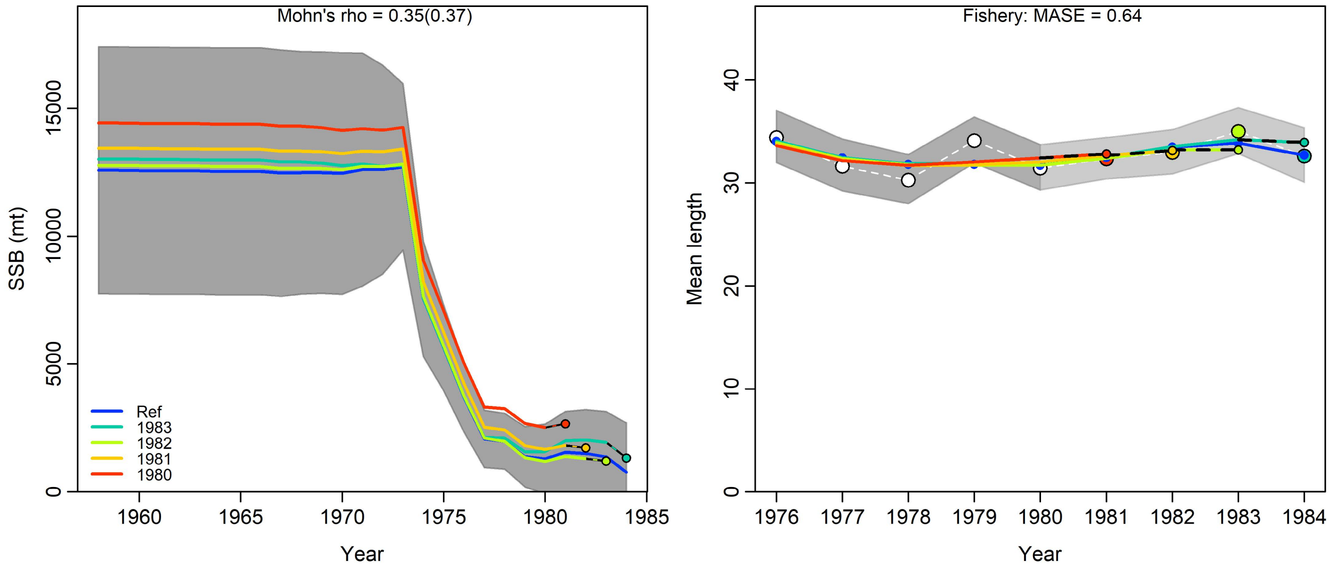

FIGURE 9 Retrospective analysis of estimates of spawning stock biomass (left panel). Mohn's *rho* statistic and the corresponding 'hindcast *rho*' values (in brackets) are printed at the top of the panel. One-year-ahead projections denoted by color-coded dashed lines with terminal points are shown for each model. Hindcasting plots for the length composition data (right panel) showing observed (large points connected with dashed line), fitted (solid lines), and one-year-ahead forecast values (small terminal points). Gray shaded areas are the 95% confidence intervals from the reference model of the red porgy (*Pagrus pagrus*) stock assessment from southern Brazil.

exploitation rate increase rapidly from 1973 through the beginning of the 1980s, after which the fishery collapsed in less than a decade (Haimovici et al., 2020). Similarly, until 1984, when length composition, catch reports, and life history parameters were still being monitored in the region, our catch-length model showed that the stock was overfished ($B_{1984}/B_{MSY}<1$). after this period, if catches remained constant at the mean value during 1985–2019 (i.e., 110 t), spawning stock biomass would have a 69% probability of recovery in 2023. Considering the mean catches reported in the last 30 years of 78.3 t (1990–2019) remained constant after the collapse, the stock would have an 87%–96% probability of recovering in 2023, which is unlikely. The stock has not recovered (Haimovici et al., 2020), so catch would need to remain at or below 150 t for 39 years to rebuild the stock, which is unlikely because the fishery is not managed in the region.

Similar to the red porgy stock we studied, extensive commercial and recreational fisheries harvest of red porgy from North Carolina to Florida in the southeastern United States caused stocks to decline in the early 1980s (Vaughan et al., 1992). As the stock decline became more evident, an emergency moratorium prohibited harvest by all fisheries between 1999 and 2000 (Davis & Berkson, 2006). After this period, the fishery was reopened, under a series of management measures: established management reference points and defined rebuilding strategy; marine protected areas; commercial quota; size limit; and seasonal closure (Sedar., 2020). However, even after applying these management measures, the most recent stock assessment indicated that the stock had not yet rebuilt and remained overfished ($B_{2017}/B_{MSY}=0.27$; Sedar., 2020). In the absence of stock recovery, other factors besides fishing pressure could have been at play. Evidence suggests that recruitment failure was partially or mostly responsible for red porgy abundance declines in the North Atlantic, and harvest regulations were unlikely to achieve sustainable management goals until recruitment increased (Bacheler et al., 2023). Previously, stock projections from 2000 to 2025 indicated that a 12 years moratorium would be needed to rebuild the stock (Davis & Berkson, 2006). In contrast, for the stock in southern Brazil, we projected the stock would take 19 years to recover under a harvest moratorium. Therefore, with no management of the fishery and a small number of hand-line fishing boats still targeting red porgy (Haimovici et al., 2020), the southern Brazilian stock should not be expected to recover by 2023, similar to other demersal fish stocks in south Brazil that also suffered intense fishing pressure in the previous century, are currently in a state of overexploitation, and have no likelihood of recovery (e.g., *M. furnieri*, Haimovici et al., 2021; *U. canosai*, Hamovici et al., 2022; *Percophis brasiliensis*, Hirota et al., 2022; *Prionotus punctatus*, Rodriguez et al., 2023). In contrast, red porgy from the Argentine-Uruguayan Common Fishing Zone recovered since the late 1990s after a period of overexploitation (CTMFM, 2021). Recovery of this stock was attributed to multiple factors that generated favorable conditions, including protective measures for the trawl fleet, a Total Allowable Catch (TAC), seasonal closed area, and increased harvest of Argentine red shrimp (*Pleoticus muelleri*) that caused fishing effort to move to higher latitudes (García, 2020, 2022; García & Lagos, 2021).

The extent to which changes in environmental characteristics and overfishing affect stock biomass and population structure have important implications for stock recovery. In addition to the lack of management measures that could enable recovery of the southern Brazilian stock, many other environmental factors could influence population structure and hinder recovery, such as recruitment failure

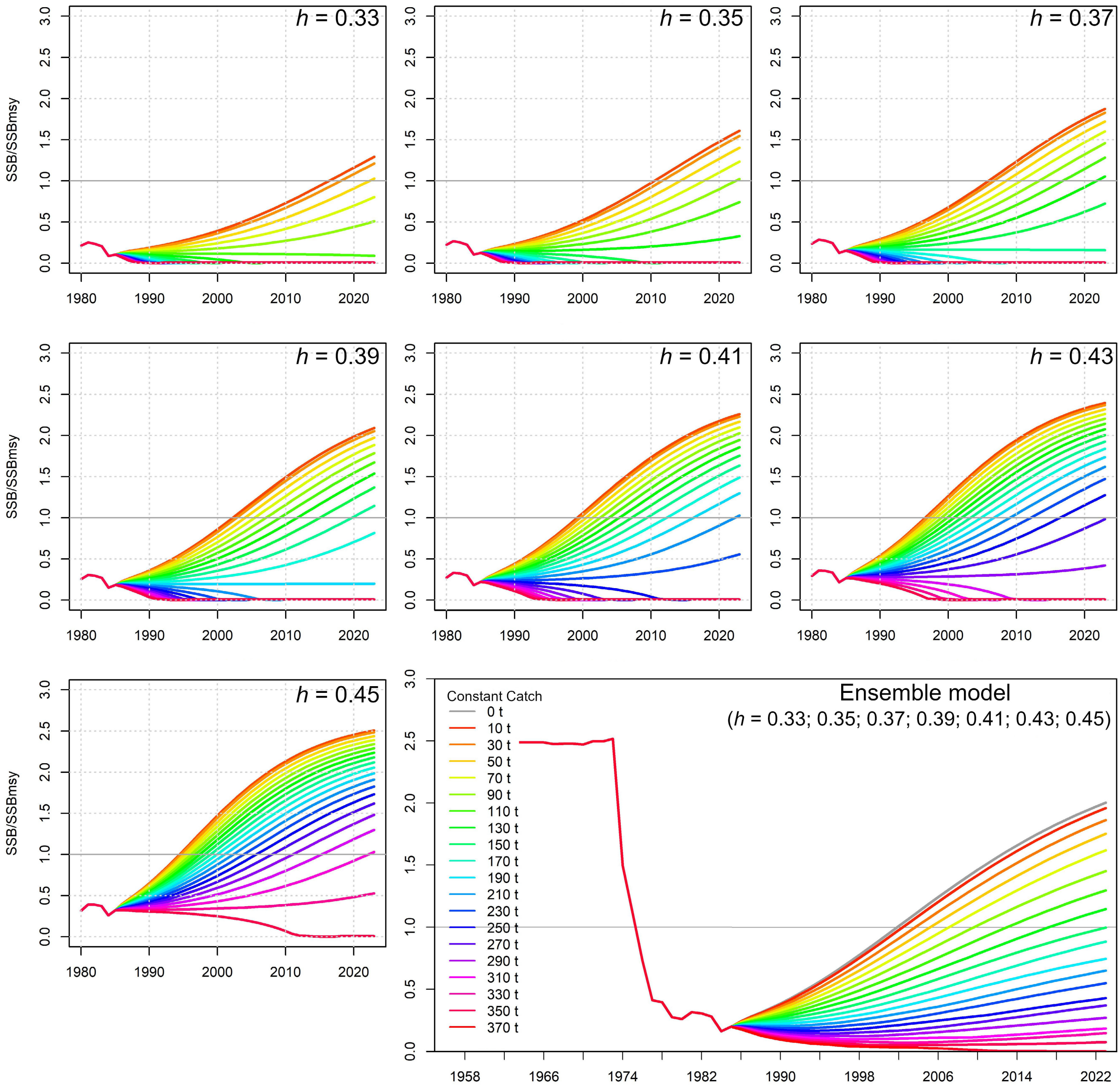

FIGURE 10 Sensitivity analysis performed for the deterministic projections of the seven scenarios (i.e., $h=0.33$–0.45 in 0.02 steps) and the ensemble model showing the trends in the relative spawning stock biomass (SSB/SSB_{MSY}) at 20 constant catch grid runs ranging from 0 t and 10 to 370 t (in 20 t steps), for the red porgy (*Pagrus pagrus*) stock from southern Brazil between 1985–2023.

due to changes in water temperature, current speed or direction, and mismatch of plankton blooms with spawning. Slow recovery of the red porgy stock may also be caused by depensation, which refers to a decline in the population growth rate per capita when abundance falls below a critical threshold level (Hutchings & Reynolds, 2004). After the collapse of the red porgy stock in southern Brazil, relative spawning stock biomass during 1977–1984 fell below 15% of the spawning biomass that would provide maximum sustainable yield in our simulations, likely reaching the threshold level for depensation. Reducing population size to this low threshold may also reduce the per capita birth rate by reduced mate availability, lower fertilization success, changes to operational sex ratios, and reduced intensity of social interactions during spawning (Rowe & Hutchings, 2003). Depensation has been suggested as an explanation for slow recovery of many other marine fish stocks (Frank & Brickman, 2000; Hutchings, 2001a, 2001b; Shelton & Healey, 1999).

Recovery of a stock depends on how societies and governments respond to population collapse (Hutchings & Reynolds, 2004), for this is crucial to understand the factors that influence recovery dynamics and the associated timescales (Enberg et al., 2009). Although many of our results are speculative, we provided new information about the population recovery dynamics after the

TABLE 5 Estimated probabilities of the red porgy (*Pagrus pagrus*) stock from southern Brazil being above SSB_{MSY} (not overfished) in a given year for a given constant catch (C.c.) level, based on 100,000 iterations of the MVLN approximation.

C.c.	1985	1987	1989	1991	1993	1995	1997	1999	2001	2003	2005	2007	2009	2011	2013	2015	2017	2019	2021	2023
0t	0	0	1	4	9	17	27	38	49	60	69	78	85	91	95	97	99	100	100	100
10t	0	0	1	4	9	17	27	38	49	59	69	78	85	91	95	97	99	100	100	100
30t	0	0	1	4	9	16	25	35	46	56	66	74	82	88	92	96	98	99	100	100
50t	0	0	1	4	8	15	23	31	41	50	59	67	74	80	86	91	94	96	98	99
70t	0	0	1	4	8	14	21	29	37	45	52	59	66	72	78	83	87	91	94	96
90t	0	0	1	4	8	13	20	27	33	40	47	53	58	63	69	73	77	81	84	87
110t	0	0	1	4	8	13	19	26	32	38	43	48	52	55	58	61	63	65	67	69
130t	0	0	1	4	8	12	17	23	28	34	39	43	47	51	54	57	59	62	63	65
150t	0	0	1	3	6	10	15	20	25	29	34	38	42	46	49	51	54	56	58	60
170t	0	0	1	3	5	8	11	15	19	23	27	31	35	39	42	45	48	51	53	55
190t	0	0	1	2	3	5	8	11	13	16	19	22	25	28	31	34	38	41	43	46
210t	0	0	0	1	2	3	4	5	6	7	8	8	9	10	11	11	12	12	13	13
230t	0	0	0	1	1	1	1	1	1	2	2	3	3	4	4	4	5	5	6	6
250t	0	0	0	0	0	0	0	1	1	1	2	2	2	3	3	3	4	4	5	5
270t	0	0	0	0	0	0	0	0	1	1	1	2	2	2	3	3	3	4	4	4
290t	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2	2	3	3	3	3
310t	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	2	2
330t	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
350t	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
370t	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

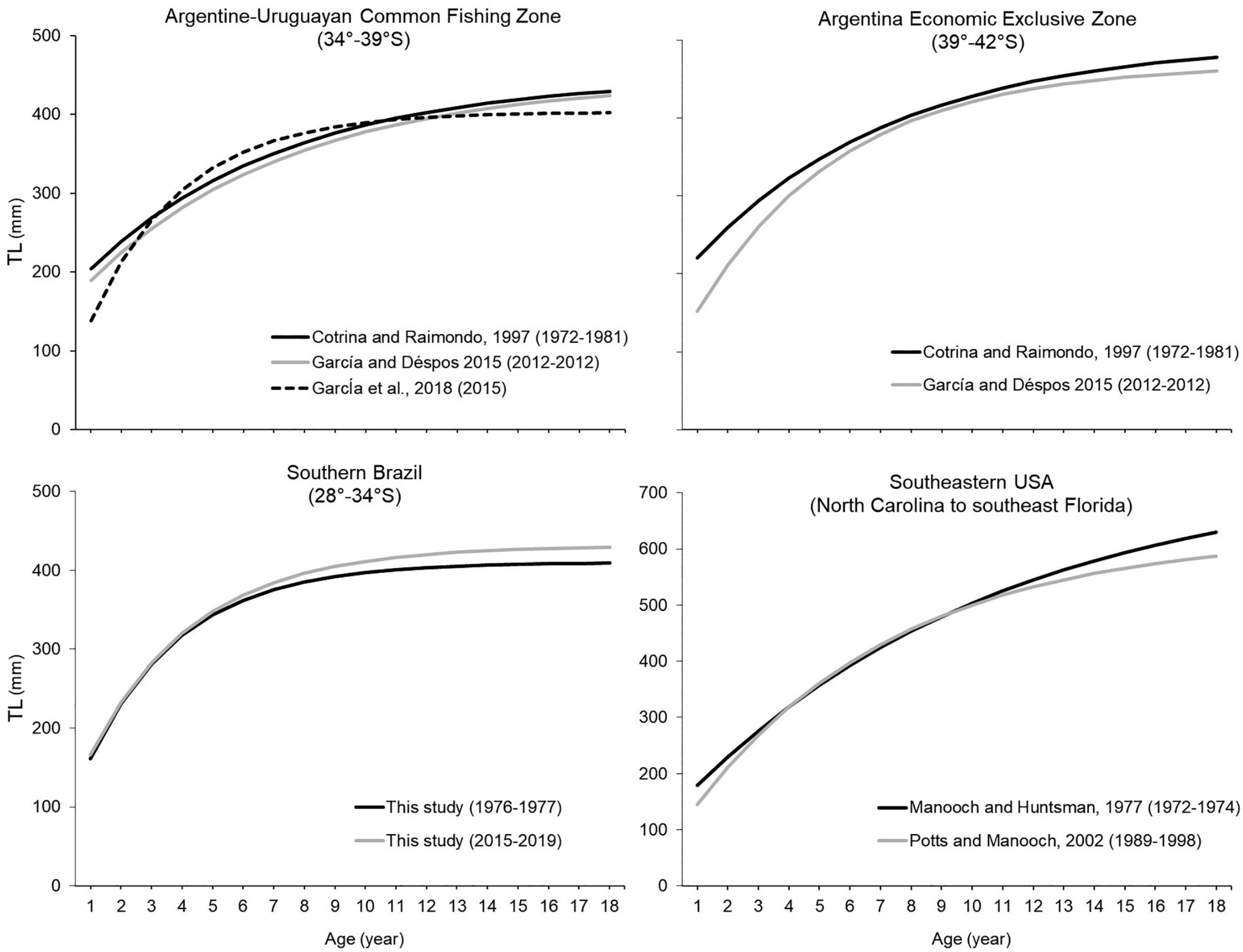

FIGURE 11 Comparison of the length-at-age back-calculated for different stocks of red porgy (*Pagrus pagrus*) of Argentine-Uruguayan Common Fishing Zone, Argentina Economic Exclusive Zone, southern Brazil, and southeastern USA. For each reference, the years sampled to perform the growth curves are in parentheses.

fishery collapsed. This information is crucial for future management and highlights challenges and knowledge gaps that must be elucidated to support decision-making. Finally, unless more accurate and up-to-date fishery data are collected, stock status and recovery of the red porgy stock in south Brazil will not be easy to accurately assess. However, based on our finding that the stock is still overfished, like other important commercial species in the region, fishery managers must recognize the urgent need to implement management strategies to recover this highly depleted stock.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

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. The research did not involve experiments or harm to animals and did not require any permission under Brazilian animal welfare laws.

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REFERENCES

Alekseev, F. (1983) Hermaphroditism in porgies (Perciformes, Sparidae). Sexual structure of the populations, mechanism of its formation and evolution in scups, *Pagrus pagrus*, *P. Orphus*, *P. Ehrenbergi* and *P. Auriga*. *Journal of Ichthyology*, 23, 61–73.

Audzijonyte, A., Fulton, E., Haddon, M., Helidoniotis, F., Hobday, A.J., Kuparinen, A. et al. (2016) Trends and management implications of human-induced life-history changes in marine ectotherms. *Fish and Fisheries*, 17, 1005–1028. Available from: https://doi.org/10.1111/faf.12156

Ávila-da-Silva, A.O. (1996) *Idade, crescimento, mortalidade e aspectos reprodutivos do pargo, Pagrus pagrus (Teleostei: Sparidae), na costa do Estado de São Paulo e adjacências*. Tese de Mestrado: Instituto Oceanográfico da Universidade de São Paulo, São Paulo, p. 116.

Bacheler, N.M., Klibansky, N., Bubley, W.J. & Smart, T.I. (2023) Low recruitment drives the decline of red porgy (*Pagrus pagrus*) along the Southeast USA Atlantic coast: inferences from fishery-independent trap and video monitoring. *PLoS One*, 18(7), e0286078. Available from: https://doi.org/10.1371/journal.pone.0286078

Campana, S.E. (2001) Accuracy, precision, and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*, 59(2), 197–242. Available from: https://doi.org/10.1111/j.1095-8649.2001.tb00127.x

Campana, S.E. & Jones, C.M. (1992) Analysis of otolith microstructure data. In: Stevenson, D.K. & Campana, S.E. (Eds.) *Otolith microstructure examination and analysis. Canadian special publication of fisheries aquatic sciences 117*. Ottawa: Department of Supply and Services, pp. 73–100.

Capitoli, R. & Haimovici, M. (1993) Alimentacion del besugo (*Pagrus pagrus*) en el extremo sur del Brasil. *Frente Maritimo*, 14, 81–86.

Cardoso, L. & Haimovici, M. (2011) Age and changes in growth of the king weakfish *Macrodon atricauda* (Günther 1880) between 1977 and 2009 in southern Brazil. *Fisheries Research*, 111(3), 177–187. Available from: https://doi.org/10.1016/j.fishres.2011.06.017

Cardoso, L. & Haimovici, M. (2016) Density-dependent changes in the feeding behavior of *Macrodon atricauda* of the southern Brazil. *Journal of Fish Biology*, 89, 1002–1008. Available from: https://doi.org/10.1111/jfb.12974

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

Cavole, L.M., Cardoso, L.G., Almeida, M.S. & Haimovici, M. (2018) Unravelling growth trajectories from complicated otoliths - the case of Brazilian codling *Urophycis brasiliensis*. *Journal of Fish Biology*, 92(5), 1290–1311. Available from: https://doi.org/10.1111/jfb.13586

Cavole, L.M. & Haimovici, M. (2015) The use of otolith microstructure in resolving issues of ageing and growth of young *Micropogonias furnieri* from southern Brazil. *Marine Biology Research*, 11(9), 933–943. Available from: https://doi.org/10.1080/17451000.2015.1031799

Christensen, V. & Pauly, D. (1993) *Trophic models of aquatic ecosystems*. Makati, Philippines: International Center for Living Aquatic Resources Management. ICLARM Conference Proceedings No. 26, p. 390.

Cope, J.M. (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 Accessed 25 July 2023.

Costa, P.A.S., Fagundes-Netto, E.B., Gaelzer, L.R., Lacerda, P.S. & Monteiro-Ribas, W.M. (1997) Crescimento e ciclo reprodutivo do Pargo-rosa (*Pagrus pagrus* Linnaeus, 1758) na Região do Cabo Frio, Rio de Janeiro. *Nerítica*, 11, 139–154.

Cotrina, C.P. (1977) Interpretación de las escamas del besugo del Mar Argentino. *Pagrus pagrus* (L). en la determinación de edades. *Physis*, 36(Sec A), 31–40.

Cotrina, C.P. & Christiansen, H.E. (1994) El comportamiento reproductivo del besugo (*Pagrus pagrus*) en el ecosistema costero bonaerense. *Revista de Investigación y Desarrollo Pesquero*, 9, 25–58.

Cotrina, C.P. & Raimondo, M.C. (1997) Estudio de edad y crecimiento del besugo *Pagrus pagrus* del sector costero bonaerense. *Revista de Investigación y Desarrollo Pesquero*, 11, 95–118.

CTMFM. (2021) Estado de los recursos pesqueros administrados por la comisión técnica mixta del frente marítimo en la zona común de ppesca argentino-uruguaya. *Informe SOFIA*, 2021, 68–73. Available from: https://ctmfm.org/upload/biblioteca/202203/sofia-2021_ctmfm-164745933158.pdf Accessed 2st March 2023.

Davis, M.L. (2003) *Assessment of the South Atlantic red porgy (Pagrus pagrus) population under a moratorium. Master thesis in fisheries and wildlife sciences*. Virginia: Faculty of the Virginia Polytechnic Institute and State University, p. 153.

Davis, M.L. & Berkson, J. (2006) Effects of a simulated fishing moratorium on the stock assessment of red porgy (*Pagrus pagrus*). *Fishery Bulletin*, 104, 585–592.

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

Enberg, K., Jørgensen, C., Dunlop, E.S., Heino, M. & Dieckmann, U. (2009) Implications of fisheries-induced evolution for stock rebuilding and recovery. *Evolutionary Applications*, 2(3), 394–414. Available from: https://doi.org/10.1111/j.1752-4571.2009.00077.x

FAO. (2019) FishstatJ. http://www.fao.org/fishery/statistics/software/fishstatj/en Reviewed: 15 December 2019.

Francis, R.I.C.C. (1990) Back-calculation of fish length: a critical review. *Journal of Fish Biology*, 36(6), 883–902. Available from: https://doi.org/10.1111/j.1095-8649.1990.tb05636.x

Francis, R.I.C.C. (1992) Use of risk analysis to assess fishery management strategies: a case study using orange roughy (Hoplostethus atlanticus) on the Chatham rise, New Zealand. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(5), 922–930. Available from: https://doi.org/10.1139/f92-102

Frank, K.T. & Brickman, D. (2000) Allee effects and compensatory population dynamics within a stock complex. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 513–517. Available from: https://doi.org/10.1139/cjfas-57-3-513

García, S. (2020) Pesquería Argentina de besugo (*Pagrus pagrus*). Capturas y esfuerzo del año 2019. *Informe de Investigación INIDEP.*, 65, 1–14.

García, S. (2022) Pesquería Argentina de besugo (*Pagrus pagrus*). Año 2020. *Informe de Investigación INIDEP.*, 2022, 9–22.

García, S. & Déspos, J. (2015) Crescimento y mortalidade natural del besugo (*Pagrus pagrus*) em aguas del Atlántico sudoccidental (34° a 42° S). *Informe de Investigación INIDEP.*, 96, 1–20.

García, S. & Lagos, A.N. (2021) Estandarización de la CPUE de besugo (*Pagrus pagrus*) com información de la flota comercial argenina que operó al norte de los 39°S. Período 2000-2019. *Informe de Investigación INIDEP.*, 31, 1–13.

García, S., Zavatteri, A. & Sáez, M.B. (2011) Estudio de edad y crecimiento del besugo (*Pagrus pagrus*) en aguas del Atlántico sudoccidental (34° a 42°S). *Informe de Investigación INIDEP.*, 24, 1–26.

Geffen, A.J. (1992) Validation of otolith increment deposition rate. In: Stevenson, D.K. & Campana, S.E. (Eds.) *Otolith microstructure examination and analysis*, Vol. 117. Ottawa, Canada: Canadian Special Publications in Fisheries and Aquatic Sciences, pp. 101–113.

Green, B.S., Mapstone, B.D., Carlos, G. & Begg, G.A. (2009) *Tropical fish otoliths: information for assessment, management and ecology.*

Reviews: methods and Technologies in Fish Biology and Fisheries. New York, USA: Springer, p. 328.

Haimovici, M. (1998) Present state and perspectives for the southern Brazil shelf demersal fisheries. *Fisheries Management and Ecology*, 5, 227–289. Available from: https://doi.org/10.1046/j.1365-2400.1998.540277.x

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

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

Haimovici, M., Kikuchi, E., Cardoso, L.G. & Moralles, R. (2020) The population dynamics of the red porgy *Pagrus pagrus* along southern Brazil, before its fishery collapse in the 1980s: a baseline study. *Aquatic Living Resources*, 33, 10. Available from: https://doi.org/10.1051/alr/2020010

Hamovici, M., Kikuchi, E. & Cardoso, L.G. (2022) Changes in the population structure and life history associated with long-term intense fishing of the Argentinian croaker *Umbrina canosai* in southern Brazil. *Aquatic Living Resources*, 35, 12. Available from: https://doi.org/10.1051/alr/2022012

Harris, P. & McGovern, J. (1997) Changes in the life history of red porgy, *Pagrus pagrus*, from the southeastern United States, 1972-1994. *Fishery Bulletin*, 95, 732–747.

Hirota, D.S., Haimovici, M., Sant'Ana, R., Mourato, B.L., Kikuchi, E. & Cardoso, L.G. (2022) Life history, population dynamics and stock assessment of the bycatch species Brazilian flathead (*Percophis brasiliensis*) in southern Brazil. *Regional Studies in Marine Science*, 55, 102597. Available from: https://doi.org/10.1016/j.rsma.2022.102597

Hutchings, J.A. (2001a) Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 108–121. Available from: https://doi.org/10.1139/f00-228

Hutchings, J.A. (2001b) Influence of population decline, fishing, and spawner variability on the recovery of marine fishes. *Journal of Fish Biology*, 59, 306–322. Available from: https://doi.org/10.1111/j.1095-8649.2001.tb01392.x

Hutchings, J.A. & Reynolds, J.D. (2004) Marine fish population collapses: consequences for recovery and extinction risk. *Bioscience*, 54(4), 297–309. Available from: https://doi.org/10.1641/0006-3568(2004)054[0297:MFPCCF]2.0.CO;2

Ibama/Ceperg. (2011) Desembarque de pescados no Rio Grande do Sul. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. *Centro de Pesquisa e Gestão dos Recursos Pesqueiros Lagunares e Estuarinos*. Rio Grande, RS: Projeto Estatística Pesqueira, p. 40. Available from: https://demersais.furg.br/images/producao/Estatistica_rs_2011.P

Kikuchi, E., García, S., da Costa, P.A.S., Cardoso, L.G. & Haimovici, M. (2021) Discrimination of red porgy *Pagrus pagrus* (Sparidae) potential stocks in the South-Western Atlantic by otolith shape analysis. *Journal of Fish Biology*, 98(2), 548–556. Available from: https://doi.org/10.1111/jfb.14598 Accessed 21 October 2023.

Kinas, P.G. & Andrade, H.A. (2010) *Introdução à análise bayesiana (com R)*. Porto Alegre, Brasil: Editora Mais Que Nada, p. 240.

Manooch, C.S. & Hassler, W.W. (1978) Synopisis of biological data on the red porgy, *Pagrus pagrus* (Linnaeus). *FAO Fisheries Synopsis*, 116, 1–19.

Manooch, C.S. & Huntsman, G.R. (1977) Age, growth, and mortality of the red porgy, *Pagrus Pagrus*. *Transactions of the American Fisheries Society*, 106(1), 26–33. Available from: https://doi.org/10.1577/1548-8659(1977)106%3C26:AGAMOT%3E2.0.CO;2

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*. Tese de Doutorado: Instituto de Oceanografia da Universidade de Federal do Rio Grande, p. 169.

Methot, R.D. & Wetzel, C.R. (2013) Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. *Fisheries Research*, 142, 86–99. Available from: https://doi.org/10.1016/j.fishres.2012.10.012

Methot, R.D., Wetzel, C.R., Taylor, I.G. & Doering, K. (2020) *Stock synthesis user manual: version 3.30.15*. Seattle: NOAA Fisheries.

Militelli, M.I., López, S., Rodrigues, K.A., García, S. & Macchi, G.A. (2017) Reproductive potential of *Pagrus pagrus* (Perciformes: Sparidae) in coastal waters of Buenos Aires Province (Argentina) and Uruguay (34°–39°S). *Neotropical Ichthyology*, 15, e160127. Available from: https://doi.org/10.1590/1982-0224-20160127

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

Morrongiello, J.R. & Thresher, R.E. (2015) A statistical framework to explore ontogenetic growth variation among individuals and populations: a marine fish example. *Ecological Monographs*, 85(1), 93–115. Available from: https://doi.org/10.1890/13-2355.1

Pajuelo, J.G. & Lorenzo, J.M. (1996) Life history of the red porgy *Pagrus pagrus* (Teleostei: Sparidae) off the Canary Islands, central East Atlantic. *Fisheries Research*, 28, 163–177. Available from: https://doi.org/10.1016/0165-7836(96)00496-1

Patterson, K., Cook, R., Darby, C., Gavaris, S., Kell, L., Lewy, P. et al. (2001) Estimating uncertainty in fish stock assessment and forecasting. *Fish and Fisheries*, 2(2), 125–157. Available from: https://doi.org/10.1046/j.1467-2960.2001.00042.x

Porrini, L.P., Iriarte, P.J.F., Iudica, C.M. & Abud, E.A. (2015) Population genetic structure and body shape assessment of *Pagrus pagrus* (Linnaeus, 1758) (Perciformes: Sparidae) from the Buenos Aires coast of the Argentine sea. *Neotropical Ichthyology*, 13(2), 431–438. Available from: https://doi.org/10.1590/1982-0224-20140149

Potts, J.C. & Manooch, C.S.I.I.I. (2002) Estimated ages of red porgy from fishery-dependent and fishery-independent data and comparison of growth parameters. *Fishery Bulletin*, 100(1), 81–89.

Rodriguez, A.R., Haimovici, M., Kikuchi, E., Sant'Ana, R., Mourato, B.L., Alvarez Perez, J.A. et al. (2023) Life history and stock synthesis assessment of *Prionotus punctatus* (Teleostei, Triglidae) in southern Brazil. *Fisheries Management and Ecology*, 30(4), 392–405. Available from: https://doi.org/10.1111/fme.12631

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. *Journal of Fish Biology*, 91(3), 896–911. Available from: https://doi.org/10.1111/jfb.13390

Rowe, S. & Hutchings, J.A. (2003) Mating systems and the conservation of commercially exploited marine fish. *Trends in Ecology & Evolution*, 18(11), 567–572. Available from: https://doi.org/10.1016/j.tree.2003.09.004

Sedar. (2020) *SEDAR 60 South Atlantic red porgy stock assessment report*. North Charleston, SC: SEDAR, North Charleston SC, p. 181 pp. Available from: http://sedarweb.org/sedar-60

Shelton, P.A. & Healey, B.P. (1999) Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 1521–1524. Available from: https://doi.org/10.1139/f99-124

Soares, I.A., Lanfranchi, A.L., Luque, J.L., Haimovici, M. & Timi, J.T. (2018) Are different parasite guilds of *Pagrus pagrus* equally suitable sources of information on host zoogeography? *Parasitology*

Research, 117(6), 1865–1875. Available from: https://doi.org/10.1007/s00436-018-5878-7

Sturtz, S., Ligges, U. & Gelman, A. (2005) R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical Software*, 12(3), 1–16. Available from: https://doi.org/10.18637/jss.v012.i03

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

Then, A.Y., Honeig, J.M., Hall, N.G. & Hewitt, D.A. (2015) Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES Journal of Marine Science*, 72(1), 82–92. Available from: https://doi.org/10.1093/icesjms/fsu136

Thomas, A., O'Hara, B., Ligges, U. & Sturtz, S. (2006) Making BUGS Open. *R News*, 6(1), 12–17.

Vaughan, D.S., Huntsman, G.R., Manooch, C., Rohde, F.C. & Ulrich, G.F. (1992) Population characteristics of the red porgy, *Pagrus pagrus*, stock off the Carolinas. *Bulletin of Marine Science*, 50(1), 1–20.

Vieira, P.J.C. (1990) *Biologia populacional de Cynoscion striatus (Pisces: Scianidae) no litoral sul do Brasil*. Rio Grande do Sul, Brasil: Master's thesis. Instituto de Oceanografia da Universidade de Federal do Rio Grande, p. 81.

Walter, J. & Winker, H. (2019) Projections to create Kobe 2 strategy matrix using the multivariate log-normal approximation for Atlantic yellowfin tuna. *Collective Volume of Scientific Papers*, 76(6), 725–739.

Yesaki, M. & Barcellos, B. (1974) *Desenvolvimento da pesca do pargo-roseo ao largo da costa sul do Brasil*. Rio de Janeiro, Brasil: Programa de Pesquisa e Desenvolvimento Pesqueiro do Brasil, p. 18.

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