

Long-term changes in the age structure, mortality and biomass of the king weakfish *Macrodon atricauda* (Günther, 1880) in southern Brazil: Is it resilient enough to avoid collapse?



Luís Gustavo Cardoso*, Manuel Haimovici

Laboratório de Recursos Pesqueiros Demersais e Cefalópodes, Instituto de Oceanografia, Universidade Federal do Rio Grande (FURG), Caixa Postal 474, Avenida Itália Km 8, CEP 96201-900 Rio Grande, RS, Brazil

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ABSTRACT

Worldwide overfishing has caused the collapse of populations of excessively exploited marine fish. The coastal demersal sciaenid fish “pescadinha”, *Macrodon atricauda*, has been intensely fished since the 1960s along the southern Brazilian coast, resulting not only in decreasing abundance but also in increasing growth rates and decreasing age and length at first maturity. We analyzed the time series of several population indicators, such as catch per unit effort (CPUE), age composition of the stock, total and natural mortality and exploitation rate to investigate the long-term impact of fishing on the mortality, age structure and biomass of *M. atricauda*. Furthermore, we modeled the time-trajectory of the total biomass under an assumption of constant recruitment and discuss the limits of resilience and the risk of collapse of the fishery. The CPUE (kg/day at sea) has decreased almost 50%. Total mortality increased from 0.5 yr⁻¹ in the almost unexploited stock in the 1950s to around 1.9 yr⁻¹ in the 2000s, while the age structure changed dramatically: fishes in the landings were not older than 9 years old in the 1960s, 7 years old in the 1970s and no fish over 5 years old has been observed since the 1990s. Taking into account the growth changes, a deterministic model estimated a reduction of 67% in total biomass over five decades. In the last 30 years, the stock has withstood high exploitation rates (between 0.5 and 0.7 yr⁻¹) and has suffered a steady decline in biomass but has not collapsed, probably due to life-history traits that favor resilience: early maturation and rapid individual growth. However, the stock is at risk of collapse, taking into consideration the present non-stabilized level of high mortality, changed age structure and life history, low biomass and high exploitation rates. A precautionary approach suggests the need to reduce fishing effort.

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1. Introduction

Worldwide overfishing has caused the collapse of excessively exploited marine fish populations (Hutchings, 2000; Worm et al., 2009). By imposing an additional mortality component, fisheries have truncated the age structure by removing old age classes, a fact that, in turn, has increased the relative abundance of the youngest classes (Berkeley et al., 2004; Hsieh et al., 2010). These changes are likely to reduce the capacity fish populations have to withstand environmental variability, besides increasing the risk of commercial extinction (Longhurst, 2002; Marteinsdottir and Thorarinsson, 1998).

* Corresponding author. Tel.: +55 53 32336525.

E-mail addresses: cardosolg15@gmail.com (L.G. Cardoso), docmhm@furg.br (M. Haimovici).

The southern king weakfish *Macrodon atricauda* (Günther, 1880) (local names are pescadinha, pescada-foguete, pescadinha-real) is a sciaenid fish that inhabits shallow coastal waters in soft bottom areas near estuaries from Espírito Santo state (Brazil) to northern Argentina. This species was recently discriminated from *Macrodon ancylodon* (Bloch and Schneider, 1801), which can be found from northeastern Brazil to Venezuela (Cardoso et al., 2012; Carvalho-Filho et al., 2010; Santos et al., 2006). Five population groups of *M. atricauda* have been genetically identified (Rodrigues et al., 2014). The largest one occurs between La Plata River (Lat. 36°) estuary and Santa Marta Grande Cape in southern Brazil (Lat. 28°), where it has been one of the major targets of the pair-bottom trawl fishery since the late 1950s (Haimovici, 1998; Valentini et al., 1991; Yamaguti and Moraes, 1965; Yesaki and Bager, 1975).

Prior studies of the long-term impact of the fishery on the population dynamics showed a large increase in growth between the 1970s and 2009 that was interpreted as a density-dependent

Table 1
Numbers of sampled fishing trips, length samples, measured individuals and aged specimens per decade.

Decade	Number of landing records	Number of length composition samples	Measured specimens	Aged specimens
1970	314	129	40,151	280
1980	674	297	86,182	308
1990	466	116	29,185	328
2000	133	35	9171	769
2010	43	17	4548	
Total	1630	594	169,237	1685

change in response to decreasing density (Cardoso and Haimovici, 2011). Moreover, age and size at maturation have also decreased. The most plausible explanation is that these changes occurred due to the selective pressure of fishing, and implies lower fitness for individuals that mature at larger sizes. However, there is some evidence that the age at maturation has also been driven by the decrease in population abundance, which mitigates density-dependent effects responsible for delaying maturation (Cardoso and Haimovici, 2014).

We analyze the time-series of several population indicators, such as catch per unit effort (CPUE), total and natural mortality, exploitation rate and the age composition of the landings to investigate the long-term impact of fishing on the mortality, age structure and biomass of *M. atricauda* and to evaluate the risks of the collapse of the fishery. We calculated the yearly mean CPUE for pair-trawler fishing trips – whose main target was pescadinha – landing in Rio Grande. We also estimated the mean yearly instantaneous coefficient of total mortality (Z) based on available information on the length frequencies and age-length keys. We also estimated natural mortalities and, then, used them to calculate yearly exploitation rates. The landing records of marine fisheries in southern Brazil have gaps and biases over time. The lack of consistent landing statistics for *M. atricauda* prevents the analysis of the long-term impact of fishing on the biomass of the stock through the application of stock assessment models. However, the consistent estimates of the age structure of the catches enabled us to build a simple deterministic model which integrates total mortality and changes in growth to show the evolution of the total biomass over the last five decades. We discuss the limits of resilience and the risk of collapse of the fishery.

2. Materials and methods

2.1. Data source and analysis

Data for the assessment of *M. atricauda* were obtained from a long-term sampling program of the coastal demersal fisheries on the Southern Brazilian shelf (28°40'–34°S). It has been carried out in Rio Grande by the Oceanography Institute of the University of Rio Grande since 1976 (Haimovici, 1987, 1998). Data on several periods representing five different decades are available (Table 1). Overall, data have included the landing records of 1630 fishing trips of pair-bottom trawlers and 594 length samples, totaling 169,000 measured individuals and 1685 aged specimens (Table 1). Haimovici (1987) described the length composition sampling strategy and Cardoso and Haimovici (2011) reported age-length keys.

2.2. Catch per unit effort (CPUE)

The quality of the commercial landing and of effort statistics in Rio Grande has not been homogeneous over the last decades. In addition, long-term changes in the CPUE based on these data are not reliable estimators of changes in abundance. Therefore, we analyzed data obtained by samplers in dockside interviews collected between 1977 and 2011. These data comprise the number of days at sea, fishing depths, total and pescadinha catch information and

the size and power of the boats from 710 pair-trawler fishing trips. CPUE is expressed as kg/day at sea, because neither the size nor the power-type of nets of the pair trawlers has changed substantially since the 1970s (Haimovici et al., 1989; Vasconcellos et al., 2006).

Pescadinha represents less than 20% of the landings of the industrial multispecific pair-trawl fishery off southern Brazil (Haimovici, 1998). To better associate catches with the effort that targets pescadinha, only trips in which it represented 30% or more of the catch ($n=413$ and), or 40% or more ($n=297$), were included in the analysis of the changes in CPUE (Chikuni, 1975). In each category, we calculated the mean CPUE values and 95% confidence intervals per year. A linear model was fitted to annual CPUEs and an analysis of variance (Zar, 1984) were used to analyze the statistical significance of the CPUE trend.

2.3. Age composition, mortality data and analysis

The smallest sizes of *M. atricauda* are poorly selected by the mesh and also discarded when caught, since specimens under 20 cm were usually landed in small numbers (Haimovici and Maceira, 1981; Cardoso and Haimovici, 2014). Thus, ages 0 and 1 are under-represented in the landings. Therefore, we calculated the percentage of individuals aged two or older for each five-year period between 1975 and 2010 to examine changes over time in the age composition of the stock.

We used two sources of data to estimate the long-term changes in the instantaneous total mortality coefficients ($Z_{yr^{-1}}$). The age composition of the landings in the 1950s and 1960s was obtained by relative CPUE data at different ages: ages 6 to 8 born from 1953 to 1955, landed in 1961, represented the 1950s and ages 3 to 6 born between 1958 and 1961, landed in 1963 and 1964, represented the 1960s (Table 2). These catches were landed by pair trawlers in Santos (southeastern Brazil). These pair trawlers fished mostly along the coast of Rio Grande do Sul, as shown by Yamaguti (1968). We reduced Yamaguti's readings on whole otoliths by one year,

Table 2

Relative catch per effort by age according to Yamaguti (1968) and relative catches by age of *Macrodon atricauda* in pair trawl landings in southern Brazil.

Year	Age						
	2	3	4	5	6	7	8
1955*			0.85	0.09	0.04	4.00	
1963*	0.68	0.22	0.10	0.01	0.01		
1964*	0.49	0.46	0.05	0.01	0.01		
1976	0.74	0.19	0.04	0.03	0.01		
1977	0.72	0.19	0.05	0.03	0.00		
1978	0.64	0.24	0.07	0.04	0.00		
1979	0.72	0.20	0.05	0.03	0.01		
1984	0.56	0.31	0.09	0.03	0.01		
1985	0.60	0.29	0.09	0.02	0.01		
1986	0.54	0.32	0.09	0.03	0.01		
1987	0.54	0.32	0.10	0.03	0.01		
1989	0.63	0.27	0.08	0.02	0.01		
1997	0.69	0.27	0.03	0.01			
2006	0.73	0.22	0.05	0.00			
2007	0.82	0.15	0.03	0.00			
2009	0.83	0.15	0.02	0.00			

since it was shown that this technique tends to overestimate ages by one year (Cardoso and Haimovici, 2011).

For the following four decades, Z was estimated from catch-by-age data calculated using catch length compositions for pair trawlers landing in Rio Grande and age-length keys described by Cardoso and Haimovici (2011) (Table 2).

The instantaneous total mortality coefficient (Z) was calculated for each year for which data were available (Ricker, 1975). To obtain the posterior distribution for the slopes of the regressions (Z) and their credibility intervals, the catch curve of log (catch) (y_i) against age (x_i) when $l = 2, \dots, 5$, was defined by the following linear model:

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

where β_0 is the intercept, β_1 is the slope of the linear model and ω_i is the model error. Non-informative 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):

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

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

$$p(\sigma^2 | x_i, y_i) \sim Glnv((n-2)/2, ((n-2)/2) S_e^2)$$

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 distribution of the variance σ^2 is inverse gamma. To obtain the posterior distribution of Z , we sampled 5,000 values from the marginal posterior using the library MASS (Venables and Ripley, 2002).

The posterior distributions for the first (1955) and last (2009) years 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, 2014).

We estimated the annual natural mortality (M) in each decade considering the long-term changes in growth (Cardoso and Haimovici, 2011) and using the formula compiled by Pauly (1980):

$$\log M = -0.0066 - 0.279 \log(L_{\infty d}) + 0.6543 \log k_d + 0.4634 \log T_d$$

where $L_{\infty d}$ and k_d are, respectively, the asymptotic length and the growth rate in each decade (Cardoso and Haimovici, 2011), and T_d is the mean sea-surface temperature (SST) in each decade obtained from the Southwest Fisheries Science Center of the US National Oceanic and Atmospheric Administration (SFSC-NOAA, 2014). These means were reconstructed between 1960 and 1997 with the "Improved Extended Reconstruction of SST" method developed by Smith and Reynolds (2004) and have been obtained from satellite data from 1998 to the present. We calculated simple averages from three different locations within the fishing area of *M. atricauda* along the southern Brazilian coast to obtain the SST values for each decade (Cardoso and Haimovici, 2011).

We calculated the yearly exploitation rates ($E = (Z - M)/Z$) for two scenarios; one with a constant natural mortality equal to the Z value obtained from catch curves for the 1950s when the bottom trawl fishery started in southern Brazil (Yesaki and Bager, 1975). In the other scenario, we used the M estimates by decade. For the 1950s and 1960s, we assumed an M value equal to that for the 1970s. We calculated the correlation between the annual total mortality coefficients and CPUEs (Zar, 1984) to analyze the impact of fishing in the total mortality.

2.4. Total relative biomass

We modeled changes in the total relative biomass of *M. atricauda* over six decades, starting in 1950, considering the changes in growth and total mortality and assuming constant recruitment. The assumption of constant recruitment is the most optimistic scenario, but it is necessary due to the lack of adequate landings data which prevents the construction of an index of recruitment. Furthermore, this assumption is based on the characteristics of a species that has a broad spawning season, i.e., 6 months, from October to March (Cardoso and Haimovici, 2014), and inhabits shallow coastal waters (Menezes et al., 2003). Myers (2001) showed, in a meta-analysis, that the variability of recruitment is inversely proportional to the spawning duration and that it is less variable for species that occupy the continental shelves due to their higher environmental stability by comparison with offshore habitats.

We considered the first decade (1950) to represent the pre-fishing status of the stock and applied the posterior mean total mortality coefficients per year to obtain the numbers of individuals by age using the following formula:

$$N_i = N_{i-1} e^{-Z_d}$$

where N_{i-1} is the number of individuals of the previous age and the Z_d are the yearly posterior mean total mortality coefficients. We assumed that the N of age one (the recruits) was normally distributed with a standard deviation equal to 30%. The biomass by age (B_i) was calculated for each posterior N_i using the following formula:

$$B_i = N_i W_i$$

where W_i is the mean individual weight by age calculated as

$$W_i = a_f (L_{inf_p} (1 - e^{-k_p(i-t_{op})}))^{b_f}$$

where a_f and b_f are the weight-length relationship parameters and L_{inf_p} , k_p and t_{op} are the von Bertalanffy growth parameters for each time period (Cardoso and Haimovici, 2011). Total biomass was expressed relative to that in the 1950s.

3. Results

3.1. Catch per unit effort

Fig. 1 shows the mean annual CPUE (kg/day) and the 95% confidence intervals by year between 1977 and 2011. The decrease in the annual CPUEs was less significant in those trips with 30% or more, from nearly 2600 kg/day to nearly 1800 kg/day, representing a decrease of 28%. The CPUE decrease was more significant for those trips with catches of 40% or more pescadinha, from almost 3600 kg/day to about 1600 kg/day; a decrease of 54%. Linear models show a significant decrease only in the slope for the trips with 40% or more of pescadinha in the total catch ($F = 9.97$, $p = 0.003$).

3.2. Age composition, mortality and exploitation rate estimates

The age composition of the adult stock has also changed. Fishes that were 7 years old disappeared in the mid-1980s, whereas there were no fish older than 5 years in 2005. There was an increase in the percentage of the younger age class (2 years) due to the loss of the older fish (Fig. 2).

The mean instantaneous total mortality coefficient (Z) increased over time from 0.55 yr^{-1} in the pristine state, in the 1950s, to 1.91 yr^{-1} in recent decades (Fig. 3a). Over the last five decades, there have been three distinct periods: 1950–1960, when the mean Z was low and remained between 0.55 and 0.65 yr^{-1} ; 1976 and 1986, when the mean Z was between 1.12 and 1.33 yr^{-1} and, then,

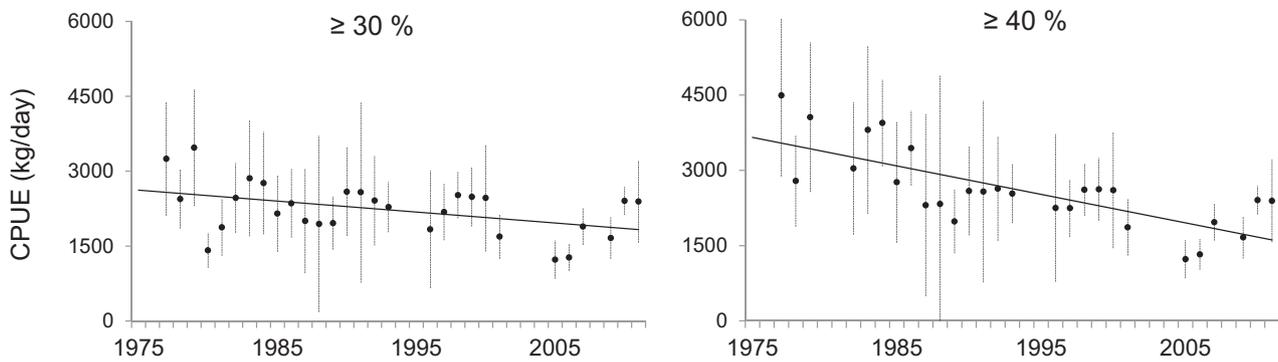


Fig. 1. Mean catch per unit effort (kg/day) of *Macrodon atricauda* per year in southern Brazil. Left: fishing trips in which the species was over 30% of the total catches. Right: over 40% of the total catches. Black lines are the fitted linear models. Vertical lines are 95% credibility intervals.

reached 1.4 yr^{-1} in 1997; and between 1.75 and 1.91 yr^{-1} in the 2000s (Fig. 3a). The posterior distribution of estimated Z did not overlap between the first and the last decade and the 95% credible interval of the difference between the first (1955) and last (2009) did not include zero (mean = -1.3822 yr^{-1} ; 2.5% = -1.3865 ; 97.5% = -1.3779) (Fig. 4), which indicates that the increase in Z over time is statistically significant.

The natural mortality values obtained by Pauly's formula decreased between 1970s and 2000 (Fig. 3b). In the 1970s, the mean M was 0.51 yr^{-1} ; it decreased gradually to 0.41 , 0.35 and 0.33 yr^{-1} in the subsequent three decades, respectively. The increasing pattern of the exploitation rate (E) was the same as the Z pattern (Fig. 3c), because the former is derived from the latter. The exploitation rate reached values between 0.5 and 0.6 in the 1970s, the 1980s and in 1997, then increased steadily until it reached about 0.7 in the last decade if a constant ($M=0.5 \text{ yr}^{-1}$) equal to Z in the 1950s is assumed. Considering the M values obtained by Pauly's formula for each decade, the exploitation rate was about 0.08 in the 1950s and then gradually increased to between 0.19 and 0.22 in the 1960s and 0.56 in the late 1970s. In the 1980s, E was about 0.6 ; it reached 0.75 in 1997, and between 0.81 and 0.83 in the 2000s (Fig. 3c).

3.3. Biomass changes

The modeled total biomass has decreased since the start of the fishery in the 1950s (Fig. 5). In the 1960s, the biomass decreased to between 85 and 83% of the pristine biomass. In the 1970s, it kept decreasing, to between 50% and 43% of the 1950 biomass, and

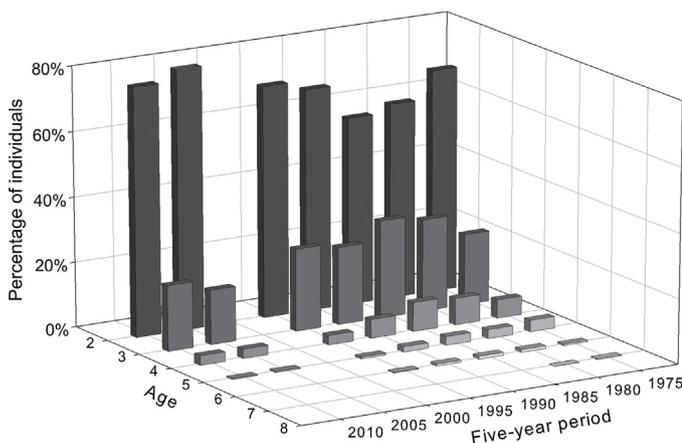


Fig. 2. Relative age composition in five-year periods at two years old or older for *Macrodon atricauda* from southern Brazil in the landings of the pair trawlers in Rio Grande from 1975 to 2012.

remained stable until the 1980s. In the 1990s, it dropped to 41% and in the 2000s, to 35% to 33% of initial biomass. The overlap of the linear trend of the CPUE shows a similar reduction of approximately 65% between the 1950s and the 2000s, assuming that the CPUE of the 1950s was 100% . This agreement among the trends of the biomass and of the CPUE may show the predictive power of the model.

4. Discussion

The analysis of a long series of landing records and data on length and age composition has enabled us to describe the long-term trends in the exploitation status of the stock of *M. atricauda*, despite the lack of reliable landings data. The increase in total mortality was

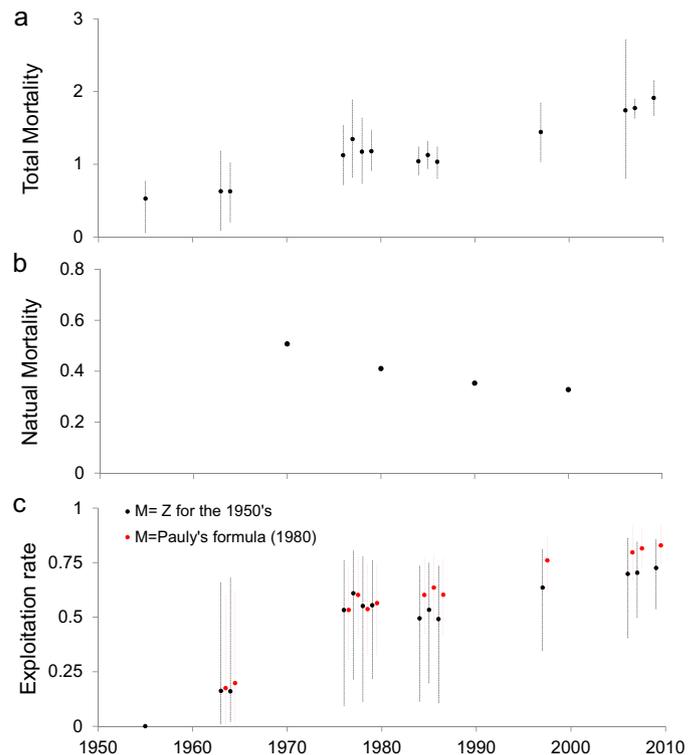


Fig. 3. (a) Instantaneous coefficient of the total mortality by year for *Macrodon atricauda* off southern Brazil (1955–2011). Vertical lines: 95% credible intervals. (b) Natural mortality rates per decade. (c) Exploitation rates (E) per year calculated with M s equal to Z estimated for the 1950s (black circles) and M by each decade from Pauly's formula (red circles). Vertical lines: 95% credible intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

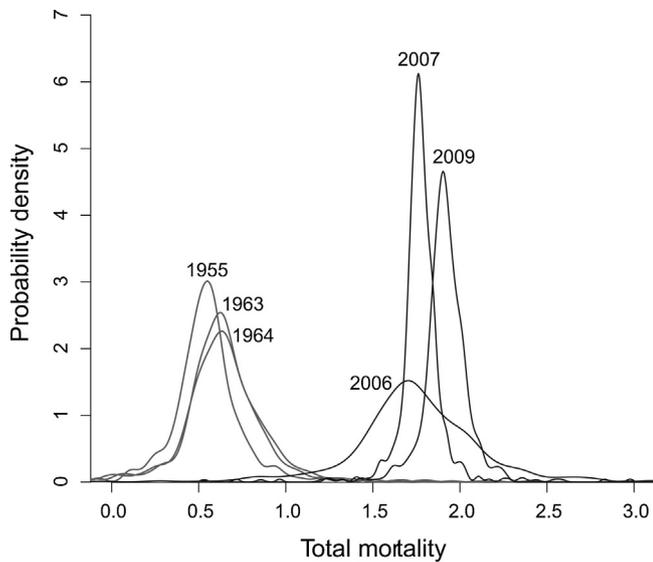


Fig. 4. Posterior distributions of the instantaneous coefficient of the total mortality in 1955, 1963 and 1964 and in 2006, 2007 and 2009.

driven by an increase in fishing mortality, since the increase in Z is negatively correlated with the decrease in the CPUE when *M. atricauda* represented 40% or more of the catch (Pearson's $r = -0.51$; $p = 0.019$) and considering that natural mortality has decreased. Besides the estimates of M obtained from Pauly's formula, a more comprehensive analysis of the data suggests a scenario of increased food availability. Changes in total mortality occurred during a period in which the yields of the overall continental shelf demersal fish abundance decreased sharply in southern Brazil (Haimovici, 1998; Vasconcellos et al., 2006). The decrease in the abundance of *M. atricauda* and its potential competitor *Cynoscion guatucupa* (Miranda and Haimovici, 2007) on shrimps, squids and small fishes along the southern Brazil inner shelf (Martins, 2000), may have increased the food availability for pescadinhas, which is consistent with the observed increase in weight by age (Cardoso and Haimovici, 2011).

An increase in mortality since the start of the industrial fishery, and the changes in the age composition of the stock have consisted of three stages (Fig. 4). In the first stage, mortality increased steadily up to 1976 and fish above seven years old disappeared from the landings (Yamaguti, 1968). In the second stage, from 1976 to the late 1980s, the mortality remained stable with little variation but the fishes above 5 years old were fewer (Fig. 2). In the third stage,

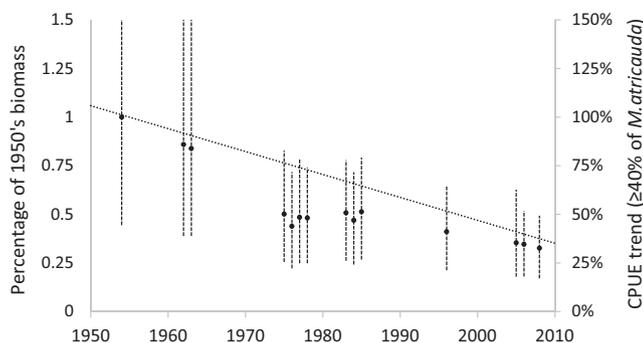


Fig. 5. Left vertical axis: The modeled total relative biomass per year for the population of *Macrondon atricauda* in southern Brazil (circles). The biomasses are presented as a proportion of the biomass in the 1950s. Dashed lines indicate 90% confidence intervals. Right vertical axis: Linear trend of CPUE for the fishing trips with catches of 40% or more of *M. atricauda*, considering the CPUE of the 1950s as 100% (dotted line).

from 1997 to the late 2000s, mortality increased sharply, and the age composition stabilized with just five-year classes. The present increasing mortality and changed age composition of the *M. atricauda* stock has been an indicator of potential collapse.

Modeled biomass decreased sharply between the 1950s and the 1970s, stabilized in the two subsequent decades and kept decreasing in the 2000s to about 35% of the pristine biomass (Fig. 5). These changes need to be considered in the context of the life-history theory (Hutchings, 2002; Roff, 2002). The apparent stability from the 1970s to the 1990s might be the result of a combination of life-history traits that favor resilience and recovery (Reynolds, 2003; Reynolds et al., 2001), such as high fecundity (Militelli and Macchi, 2004), low age at maturity (Cardoso and Haimovici, 2014; Yamaguti, 1967), rapid individual growth and a relatively short lifespan (Cardoso and Haimovici, 2011; Haimovici, 1998; Yamaguti and Santos, 1966). However, resilience has a limit, since there are genetically determined boundaries to the plasticity of life-history traits (Dieckmann and Heino, 2007; Houston and McNamara, 1992). For *M. atricauda*, some of them have reached their limits by fishery exploitation: increasing growth rates (Cardoso and Haimovici, 2011) and decreasing size and age at maturation (Cardoso and Haimovici, 2014). Moreover, the depletion of older fishes can also reduce resilience, as it has been associated with periods of stock decline (Marteinsdottir and Thorarinsson, 1998; Trippel et al., 1997). Therefore, the decrease in biomass between the 1990s and the 2000s seems to indicate a decreased resilience.

In a global analysis of well-studied fish stocks, Worm et al. (2009) associated increasing exploitation rates with decreases in biomass and increases in the risk of collapse. They predicted that the risk of collapse was 90%, with uncertainty intervals between 70 and 100% for stocks with the same exploitation rate, as *M. atricauda* in southern Brazil is subject to (E between 0.7 and 0.8). The stock has withstood high exploitation rates for about 20 years and has experienced further decrease in abundance without collapsing in the last decade. However, even with a life history that favors resilience, the persistence of high exploitation might endanger the long-term productivity of the population. It would not be an overstatement to say that, at the present level of high mortality and changed age structure life history, the *M. atricauda* stock in southern Brazil is at risk of collapse and that a precautionary approach suggests the need to reduce fishing effort.

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