

Long term changes in the sexual maturity and in the reproductive biomass of the southern king weakfish *Macrodon atricauda* (Günther, 1880) in southern Brazil

Luis 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

ARTICLE INFO

Article history:

Received 4 June 2013

Received in revised form 19 May 2014

Accepted 20 May 2014

Available online 16 June 2014

Keywords:

Maturation

Long term changes

Reproductive biomass

Brazil

Macrodon atricauda

ABSTRACT

The coastal demersal sciaenid fish “pescadinha” *Macrodon atricauda* has been intensely fished along southern Brazil in the last 50 years, a fact that resulted in the decrease in its abundance, maximum age and landings, and an increase in its growth. In this study, we used data from four discrete time periods between 1976 and 2011 to analyze the possible influences of fishing on the maturation parameters length (L_{50} , mm) and age (A_{50} , years) at first maturity as well as on the spawning biomass. Results indicated that the L_{50} of females and males decreased approximately 30 mm and the mean A_{50} of females was reduced from 2.2 to 1.6 years. The most plausible explanation is that these changes occurred by the harvest selective pressure of fishing implying lower fitness for individuals that mature at larger sizes. However, there is some evidence suggesting that the A_{50} may also have been driven by the decrease in the population abundance which relaxed density dependent effects responsible for delaying maturation. If constant recruitment is assumed, the increase in fishing effort and, hence, total mortalities, should have reduced female spawning biomass to 13% of the virginial biomass; however, increased growth rate and earlier maturation resulted in a reduction to only 28%. Reduced spawning biomass combined with a decrease in the reproductive potential of the population (changes in A_{50} and/or L_{50}), can make recruitment more vulnerable to environmental drivers and to any further increase in the fishing effort.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Long-term changes in the maturation dynamics of intensely exploited fish stocks have been widely reported in the literature (Trippel, 1995, 1999; Law, 2000; Saborido-Rey and Kjesbu, 2005; Marshall and McAdam, 2007). Most studies report fishes reproducing at younger age and smaller size (Jørgensen, 1990; Rijnsdorp, 1993a,b; Jørgensen et al., 2007; Sharpe and Hendry, 2009). A spawning stock comprised by smaller and younger fishes have their reproductive ability reduced (Marteinsdottir and Begg, 2002; Hutchings, 2005; Longhurst, 2010). It may have negative consequences for population growth rates (Hutchings and Fraser, 2008) and yield (Law and Grey, 1989; Stokes and Law, 2000; Conover and Munch, 2002). Moreover, it may also increase the variability in population abundance (Stergiou, 2002; Stenseth and Rouyer, 2008)

and adversely affect its ability to recover from overexploitation (Hutchings, 2005). Besides early maturation, decrease in spawning biomass also affects the population ability to recover, as the recruitment success turns more vulnerable to adverse environmental conditions (Brander, 2005; Ottersen et al., 2006, 2013). Consequently, monitoring of life history traits as well as of the spawning biomass of a fish stock is essential for the effective long-term conservation and management of the resource (Trippel, 1995; Jørgensen et al., 2007).

The sciaenid fish *Macrodon atricauda* (Günther, 1880) (some local names are *pescadinha*, *pescada-foguete*, *pescadinha-real*), inhabits shallow coastal waters in soft bottom areas from Espírito Santo state (Brazil) to northern Argentina. This species was recently discriminated from *Macrodon ancylodon* (Bloch and Schneider, 1801) from northeastern Brazil up to Venezuela (Santos et al., 2006; Carvalho-Filho et al., 2010; Cardoso et al., 2012). Genetically, *M. atricauda* comprises five populations (Rodrigues et al., 2013); the most abundant one inhabits southern Brazil, between Chui and Cape Santa Marta Grande (Lat 28°S–34°40'S) (Fig. 1) where it has been exploited by the pair bottom trawl fishery since the late 1950s

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

E-mail addresses: cardosol15@gmail.com, euvopabv@yahoo.com.br (L.G. Cardoso), docmhm@furg.br (M. Haimovici).

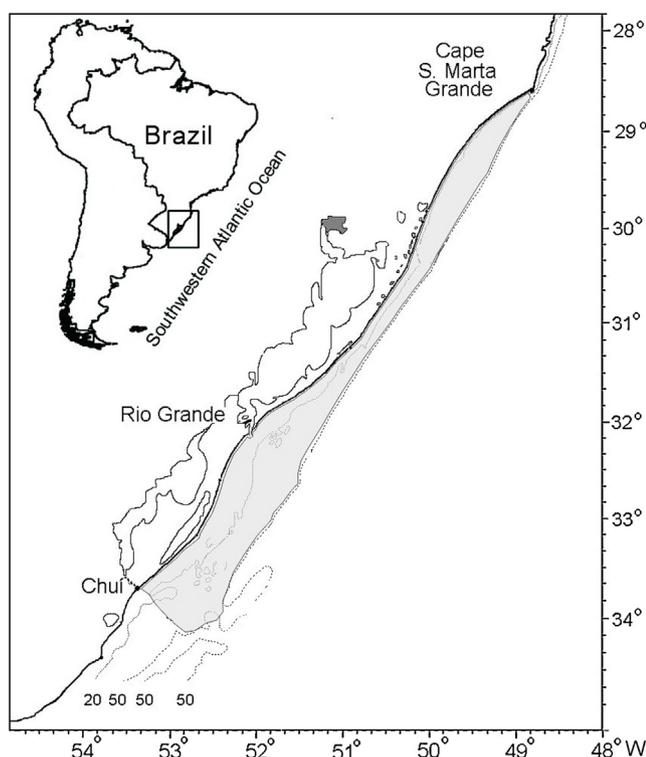


Fig. 1. Fishing area of *Macrodon atricauda* at the coastal waters of Southern Brazil (light gray).

(Yamaguti and Moraes, 1965; Yesaki and Bager, 1975; Valentini et al., 1991; Haimovici, 1998). Even though time series of catch per unit effort (CPUE) showed a population decreasing trend between 1959 and 1963 (Yamaguti and Moraes, 1965) and from 1976 to 1992 (Haimovici, 1998), intense fishing has still taken place.

The effects of intense fishing have already been identified in the *M. atricauda* life history. Cardoso and Haimovici (2011) observed the decrease of maximum age from 7 to 5 years, a fact that may be seen as an indicative of decrease in the spawning biomass. Management demands make it necessary to analyze long term trends in spawning biomass. Moreover, the growth rates, which increased in the last four decades, were possibly induced by the decrease in population density (Cardoso and Haimovici, 2011). Although no information is available, these shifts may indicate that the maturation traits have also changed. It should be investigated along with their potential causes.

The identification of the driving forces of the maturation changes is very complex (Marshall and McAdam, 2007). The most frequently cited cause is the fishing pressure (Trippel, 1995; Law,

2000), since it can influence changes in maturation in two ways: the steady removal of biomass leads to decreases in the population density, which increases food availability and relaxes density dependent effects responsible for reducing growth and delaying maturation (Barot et al., 2004). On the other hand, fisheries exert a selective pressure implying lower fitness for individuals that mature at older age and larger size. In the long term, it changes the genetic frequencies of the population and increases the proportion of individuals which reproduce earlier and smaller (Dieckmann and Heino, 2007).

In this paper, the reproductive parameters length (L_{50}) and age (A_{50}) at first maturity were estimated for four periods between 1976 and 2011 for samples of *Macrodon atricauda* from southern Brazil. Trends in these parameters were analyzed and possible drivers, such as decreasing abundance and selectivity of the fishing gear, were studied and discussed. Total mortality coefficients (Z) were estimated by decade and combined with the estimated A_{50} and the referred changes in growth rates in order to analyze the impact of fishing on the reproductive biomass (RB) of females. The role of possible life history changes on the RB were also analyzed and discussed.

2. Material and methods

2.1. Data source

Macrodon atricauda was sampled in several periods since 1976 in southern Brazil (Haimovici, 1987, 1998; Haimovici et al., 1996; Cardoso and Haimovici, 2011). Data on total fish (W, g) and gonad weight (GW, g), fish length (L, mm) and maturity stage of males and females from landings of commercial bottom trawlers that fished between latitudes 28°28' (Cape Santa Marta Grande) and 33°40' (Chui) (Fig. 1) were available from 1976 to 1980 (n : 1174), 1993 to 1988 (n : 1036), 1997 to 1998 (738) and 2008 to 2011 (n : 2035) (Table 1). Data on age were also available for four discrete periods from otolith readings validated by Cardoso and Haimovici (2011) (Table 1).

No remarkable changes in the pair trawl fishery were identified in the last four decades: boat size, engine power, trawl nets design and mesh size in the codend changed little along the years (Haimovici, 1998; Vasconcellos et al., 2006).

Data on selectivity of the fishing gear were available from two research cruises designed to study the selectivity of the trawl nets used by demersal fishery in southern Brazil. The codend of a mesh of 69 mm between opposite knots was covered with a cover net of smaller mesh (Vooren, 1983).

Two sources of data were used to estimate the instantaneous total mortality coefficients (Z). For the first two decades, from relative catch-per-effort at different ages landed by pair trawlers in

Table 1

Number of individuals of females and males of *Macrodon atricauda* selected for maturity and selectivity parameters in four periods between 1976 and 2011 from catches along southern Brazil. (L_{50}) Length at first maturation; (A_{50}) Age at first maturation; (S_{50}) Length at first capture; (Z) Instantaneous total mortality coefficient.

Estimated indices		n Females	n Males	n Females	n Males	n Females	n Males	n Females	n Males
L_{50}	Total	1976–1980		1983–1988		1997–1998		2008–2011	
	Mature	638	536	608	428	461	277	690	1345
A_{50}	Total	1976–1979		1984–1986		1997–1998		2006–2009	
	Mature	353	355	427	347	250	187	316	1082
S_{50}	Captured Selected			n Pooled sex					
				1981					
Z	Measured specimens	1976–1979		1984–1986		1997–1998		2006–2009	
		40,151		31,666		8849		9171	

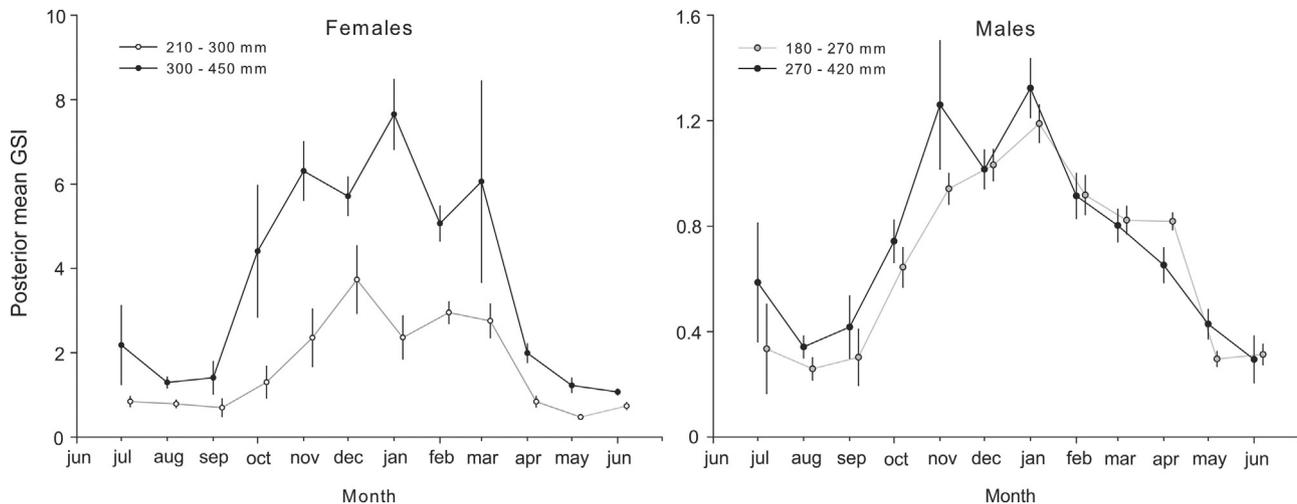


Fig. 2. Posterior mean gonadosomatic indices (GSI) and their 95% credible intervals (vertical bars) by month for *Macrondon atricauda* in Southern Brazil.

Santos (shown in Fig. 2 in Yamaguti (1968)): 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 1964, represented the 1960s. For the following decades, Z was estimated by using age-length keys introduced by Cardoso and Haimovici (2011) and length compositions in the catch of pair trawlers in Rio Grande (Table 1).

Statistical analyzes were performed using a Bayesian approach. The parameters were estimated for comparison between successive periods and different categories. The probabilistic quantification of uncertainty of estimated parameters simplified the comparisons, because it enabled to do it visually which makes unnecessary any statistical tests.

2.2. Sexual maturation analysis

A gonadosomatic index (GSI) was calculated by the formula (Wootton, 1998):

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

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

The monthly posterior distributions of the GSI were estimated by a Bayesian approach. A priori, they were assumed as distributed with a non-informative uniform density $[-\alpha, +\alpha]$. The posterior mean of GSI (\bar{X}) was assumed to have approximately normal distribution with mean μ and standard deviation S/\sqrt{n} , which indicates that the likelihood is $p(\bar{X}|\mu)$.

The seasonality of the maturation was analyzed separately for two different length ranges, 210–300 and 300–450 mm for females, and 180–270 and 270–420 mm for males. These ranges were chosen to analyze the differences on the onset in the breeding season by fishes of different sizes.

For both sexes, maturation was determined by using a seven-point scale based on macroscopic and microscopic characteristics of the gonads of sciaenid fishes: I: Virginal immature; II: Developing virginal; III: Developing, IV: Advanced development; V: Running; VI: Partly spent; VII: Recovering (Haimovici and Cousin, 1989). The stage III was considered the onset on maturation.

To avoid misidentification between the spent and immature stages for the estimation of maturation ogives by length, only data on specimens collected during the peak of the reproductive period were selected. This period was visually estimated based on the results of the seasonality of the maturation.

The age maturation ogives were estimated with data from December to March, as age data for the four periods in the

reproductive season were only available for those months. The ogives were estimated only for females due to lack of sufficient data on males.

The total number (n_i) and the number of mature specimens (y_i) were calculated for females at each age and for both sexes at each total length class intervals of 10 mm for all periods. If θ_i denotes the probability of an individual of the i th age or i th length class being mature, y_i was assumed to follow a binomial distribution $\text{Bin}(n_i, \theta_i)$.

Data were fitted 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, in m defined 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 probabilities at each x_i that are each age or length class.

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

$$A_{50} \text{ or } L_{50} = \frac{-\beta_0}{\beta_1}$$

To compare the estimates of A_{50} and L_{50} in different time periods the posterior distribution $p(\beta_0, \beta_1|D)$, where $D = \{(y_i, n_i, x_i); i = 1, \dots, k\}$, was obtained via the stochastic process Monte Carlo Markov Chain (MCMC). To obtain the posterior distributions of β_0 and β_1 they were considered independent and a normal distribution with mean 0 and large variance (1000) was used as priori distribution. After 50000 burn-in runs, every third value of the remaining 9000 was retained, resulting in a final sample of 3000 in the posterior distribution $p(\beta_0, \beta_1|D)$ (Kinas and Andrade, 2010). The posterior distribution of each estimated A_{50} and L_{50} provides an easy and clear way to compare the results among periods. All statistics in this study were run by R version 2.12.0. The MCMC was performed by OpenBUGS, using the libraries R2WinBUGS (Sturtz et al., 2005) and BRugs (Thomas et al., 2006).

2.3. Gear selectivity

The mean length at first capture (S_{50}) was calculated by using data from two research cruises (Vooren, 1983). In each cruise, the total number of individuals captured in the cod end and in the cover

net (n_i) and the total number of individuals selected in the cod end (y_i) for each i th length class were calculated. The y_i was assumed to follow a binomial distribution $Bin(n_i, \theta_i)$ in which θ_i denotes the probability of an individual of the i th length class to be selected. For the estimation of S_{50} , the same approach applied to the estimation of L_{50} and A_{50} was used. Hence, S_{50} was defined as:

$$S_{50} = \frac{-\beta_0}{\beta_1}$$

To obtain the posterior distribution $p(\beta_0, \beta_1 | D)$, where $D = \{(y_i, n_i, x_i); i = 1, \dots, k\}$, the S_{50} parameters β_0 and β_1 was assumed to have a normal priori distribution with mean 0 and large variance (1000). The MCMC was run as previously described for L_{50} and A_{50} .

2.4. Total mortality estimates

The instantaneous coefficient of total mortality (Z) was calculated by catch curves (Ricker, 1975). A Bayesian approach was used to obtain the mean of the posterior distribution of the negative of the slopes of the regressions ($Z = -\beta_1$). Therefore, the catch curve of $\log(\text{catch}) (y_i)$ against age (x_i) when $i = 2, \dots, 5$, was defined as the following linear model:

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

where ω_i is the error term, which represents the combined effect of the omitted variables. The non-informative Jeffreys' prior was 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 $p(y_i | \beta_0, \beta_1, \sigma)$. Thus, the marginal distributions of the parameters were defined as follows (Kinas and Andrade, 2010):

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

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

$$P(\sigma^2 | x_i y_i) \sim Glnv((n-2)/2, ((n-2)/2, S_{\sigma}^2))$$

where St denote Student distributions and $Glnv$ denote Inverse Gamma distributions; b_0 and b_1 are last squares estimates for β_0 and β_1 , respectively, and S_{σ}^2 is the residual variance. The Z estimation was obtained via the stochastic process Monte Carlo Markov Chain (MCMC). The MCMC was run as previously described in this paper.

2.5. Model of reproductive biomass

The reproductive biomass of females was modeled by decades since 1950, considering the changes in the A_{50} , in growth, total mortality and assuming a constant recruitment at age 1 ($N_1 = 1000$) per decade. They are presented as relative to the 1950s reproductive biomass, considered as the pre-fishing status of the stock. It was called relative reproductive biomass (RRB). The numbers of females by age (N_{i+1}) were obtained by applying the estimated total mortality coefficients.

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

where N_i is the number of individuals of the previous age and the Z_d is the total mortality coefficient per decade. The reproductive biomass by age (RB_i) was estimated by the following formula:

$$RB_i = N_i M_i W_i$$

where M_i is the proportion of mature females at each age and W_i is the mean individual weight per age calculated by the formula:

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

where a_f and b_f were the female weight-length relationship parameters and the L_{inf_p} , the k_p and the t_{op} were the female Von Bertalanffy

growth parameters for each time period according to Cardoso and Haimovici (2011).

We have no information on the age at first maturity of *M. atricauda* prior to exploitation. In the 1970s 75% of its L_{inf} is attained at age 2 and 80% at age 3 (Cardoso and Haimovici, 2011). It is unlikely that a small species with longevity of approximately 10 years reaches sexual maturity, neither at large sizes (Beverton and Holt, 1959) nor at old ages (Waggy et al., 2006). For this reason, the RRB in the almost unexploited stock (1950s) and approximately ten years before the beginning of the industrial fishery in the 1960s was calculated as the sum of half of the biomass of females at age 2 plus the total biomass of older ones. In addition to the scenario where growth and maturity changes, the RRB was estimated also for three different scenarios: (1) taking into account only changes in the proportion of mature females by age; (2) taking into account only changes in growth, (weights per ages) and considering the proportion of mature females by age as those of the 1950s and 1960s and (3) without considering changes in maturation nor in growth.

3. Results

3.1. Sexual maturation

GSI values were higher between October and March for females and from October to April for males (Fig. 2). It can be observed that larger adult females mature a month earlier than smaller ones (Fig. 2). The period in which the GSI values are higher for larger and smaller females and males was defined as occurring between November and March. It was considered the peak of the reproductive period.

Posterior credible intervals (95%) of β_1 do not include zero and prove a significant relationship between age and length and sexual maturity (Table 2).

The posterior distributions show decreases in L_{50} between 1976 and 2011 (Fig. 3) for both sexes. For females, the decline in the mean L_{50} was gradual between the 1970s ($L_{50} = 278.7$ mm), the 1980s ($L_{50} = 274$ mm) and the 1990s ($L_{50} = 269.3$ mm) and abrupt between the 1990s and the 2000s ($L_{50} = 248.8$ mm) without overlap in their 95% credible intervals (Table 2 and Fig. 3) between the first and the last period. For males, the decrease in L_{50} , was also statistically significant; it was abrupt between the 1970s ($L_{50} = 228.2$ mm) and the 1980s ($L_{50} = 203.3$ mm) but remains substantially the same in the former periods: the 1990s ($L_{50} = 199.2$ mm) and the 2010s ($L_{50} = 200.8$ mm) (Table 2 and Fig. 3).

Decline in the estimated mean A_{50} of females was gradual between the 1970s and the 2000s from 2.2 to 1.6 years without overlap of their 95% credible interval between the first and last periods (Table 2 and Fig. 4). It means that, in the 1970s, the first maturation occurred mostly between ages 2 and 3 while now it occurs mainly between age 1 and 2.

3.2. Gear selectivity

Posterior credible intervals (95%) of β_1 parameter of the logistic model fitted to the selectivity data do not include zero (mean $\beta_1 = 0.03$, $CrI_{2.5} = 0.028$ and $CrI_{97.5} = 0.031$) and prove a significant relationship between length and selectivity. The estimated parameters of mean S_{50} were 169.94 mm ($CrI_{2.5} = 167.08$ mm and $CrI_{97.5} = 172.97$ mm) (Fig. 5).

3.3. Total mortality

The total mortality increased threefold between the 1950 and the 2000s. The estimated instantaneous total mortality coefficients (Z) increased steadily from near 0.5 in the 1950s to near 1.2 in the

Table 2
Model parameters (β_1 and β_0), estimated maturation indices (L_{50} and A_{50}) for females and males of *Macrodon atricauda* landed in Rio Grande in different periods between 1976 and 2011. $A_{50}\beta_1$ and $A_{50}\beta_0$ are the estimated logistic model parameters for the calculation of the age at first maturity (A_{50}). $L_{50}\beta_1$ and $L_{50}\beta_0$ are the estimated logistic model parameters for the calculation of the length at first maturity (L_{50}). All parameters and indices are presented as the mean of their posterior distribution obtained via stochastic procedure. The credible intervals ($Cr I$) of 2.5 and 97.5% are presented for all parameters and indices.

Period	Parameters	Females			Males		
		Mean	$Cr I_{2.5\%}$	$Cr I_{97.5\%}$	Mean	$Cr I_{2.5\%}$	$Cr I_{97.5\%}$
1976–1979	$A_{50}\beta_1$	6.03	3.64	8.69			
	$A_{50}\beta_0$	-13.1	-19.6	-7.6			
	A_{50}	2.2	2.0	2.3			
	$L_{50}\beta_1$	0.04	0.03	0.05	0.05	0.04	0.06
1976–1980	$L_{50}\beta_0$	-10.7	-12.8	-9.1	-11.8	-13.7	-9.7
	L_{50}	278.7	273.3	284.2	228.3	223.2	233.1
1984–1986	$A_{50}\beta_1$	5.52	2.40	9.72			
	$A_{50}\beta_0$	-10.2	-18.6	-3.7			
	A_{50}	1.8	1.4	2.1			
	$L_{50}\beta_1$	0.08	0.06	0.09	0.08	0.06	0.11
1983–1988	$L_{50}\beta_0$	-20.8	-25.2	-16.2	-16.4	-21.6	-13.0
	L_{50}	274.0	269.3	278.3	203.3	198.4	207.7
1997–1998	$A_{50}\beta_1$	5.42	3.35	8.29			
	$A_{50}\beta_0$	-9.11	-13.71	-5.50			
	A_{50}	1.7	1.5	1.8			
	$L_{50}\beta_1$	0.05	0.04	0.06	0.05	0.03	0.06
1997–1998	$L_{50}\beta_0$	-14.0	-16.5	-11.7	-9.0	-12.3	-6.4
	L_{50}	269.3	262.7	276.2	199.2	191.5	205.8
2006–2009	$A_{50}\beta_1$	5.35	3.29	8.53			
	$A_{50}\beta_0$	-8.9	-13.8	-5.7			
	A_{50}	1.6	1.5	1.8			
	$L_{50}\beta_1$	0.12	0.10	0.14	0.07	0.06	0.08
2008–2011	$L_{50}\beta_0$	-30.2	-35.6	-25.9	-14.2	-16.4	-12.4
	L_{50}	248.8	246.5	251.2	200.8	197.6	203.7

1970s (Fig. 6). In the 1980s, Z has a small decrease and, thereafter, it increased up to near 1.8 in the 2000s (Fig. 6).

3.4. Female's reproductive biomass model

Four scenarios for the changes in the reproductive biomass of the females (RRB) along five decades are shown in Fig. 7. When changes in growth and maturation were taken into account, the RRB in the 1960s was reduced to 85% of the pristine biomass and decreased to 35% in the 1970s. After a little recovery in the 1980s, when it reaches 46%, the RRB decreased again reaching 41% in the 1990s and 28% in the 2000s. When just the maturation changes were considered, the RRB was reduced to 83% in the 1960s and 34% in the 1970s, recovered a little in the 1980s to 43% and decreased again to 39% in the 1990s and 28% in the 2000s. When just growth changes were considered, the RRB was reduced to 76% in the 1960s and 26% in the 1970s. Again, after a little recovery in the 1980s to 33%, it decreased to 22% in the 1990s and 10% in the 2000s. In a scenario in which growth and age at maturation remain the same along time, in the 2000s the RRB should have decreased to 9% of the pristine biomass.

4. Discussion

The observed decreasing trend in the length and age at first maturity of *Macrodon atricauda* must be analyzed with some caveat. These reproductive parameters can vary in the short and long term (Saborido-Rey and Kjesbu, 2005). The use of pooled data collected in some long time periods, such as 6 years between 1983 and 1988, can hide short term changes. Although our results cannot support strong conclusions about the maturation changes, various plausible hypotheses can explain the causes of the changes observed in the maturation trends.

The decrease in size at maturation was gradual between the 1970s and the 2000s for females while, for males, it was abrupt between the 1970s and the 1980s and remained stable for the

following 25 years. This fact remains difficult to be explained. The phenotypic plasticity (Roff, 1992) of life history traits, such as growth and reproduction, is a response to environmental variability, but there are genetically determined constrains (Houston and McNamara, 1992; Dieckmann and Heino, 2007). The L_{50} of males in the last decades was around 200 mm, which corresponds to age one (Cardoso and Haimovici, 2011) and the A_{50} of females was near 1.5 years. Since *M. atricauda* is a seasonal breeder in southern Brazil in spring and summer (Fig. 2), A_{50} cannot keep decreasing. Thus, it is reasonable to conclude that the species is near its lowest limits of size and age at maturation.

Fishery creates a selective pressure toward low age and small size at maturation by removing the genotypes of the fastest growing fishes and delayed maturation from the population (Law, 2000; Heino and Godø, 2002). Ernande et al. (2004) demonstrated that, when the minimum harvest size is below the maturation reaction norm, modeled populations presented evolutionary effects of decreasing age and size at maturation. The length at first catch (S_{50}) of *M. atricauda* in the pair trawl fishery was smaller than the L_{50} in all periods under study and the correspondent age was lower than one year (Cardoso and Haimovici, 2011). It means that the minimum harvest size of *M. atricauda* was always below the maturation reaction norm and the selection pressure applied by fishing could be creating an evolutionary response toward decreasing age and size of maturation. Thus, it is plausible to propose that the observed decrease in the A_{50} and L_{50} , if it really represents a decreasing trend in the maturation parameter can be interpreted as a result of selective pressure of the fishery toward individuals maturing at younger ages and smaller sizes. However, fishery may also influence age and size at maturation by decreasing the population density. It may increase the individual energy availability resulting in faster growth and earlier maturation due to the phenotypic plasticity of the population (Heino et al., 2002; Dieckmann and Heino, 2007). This hypothesis requires reduced abundance. In fact, increasing total mortality (Z) and decreasing catches and CPUEs (Yamaguti and Moraes, 1965; Haimovici, 1998) indicate gradual reduction

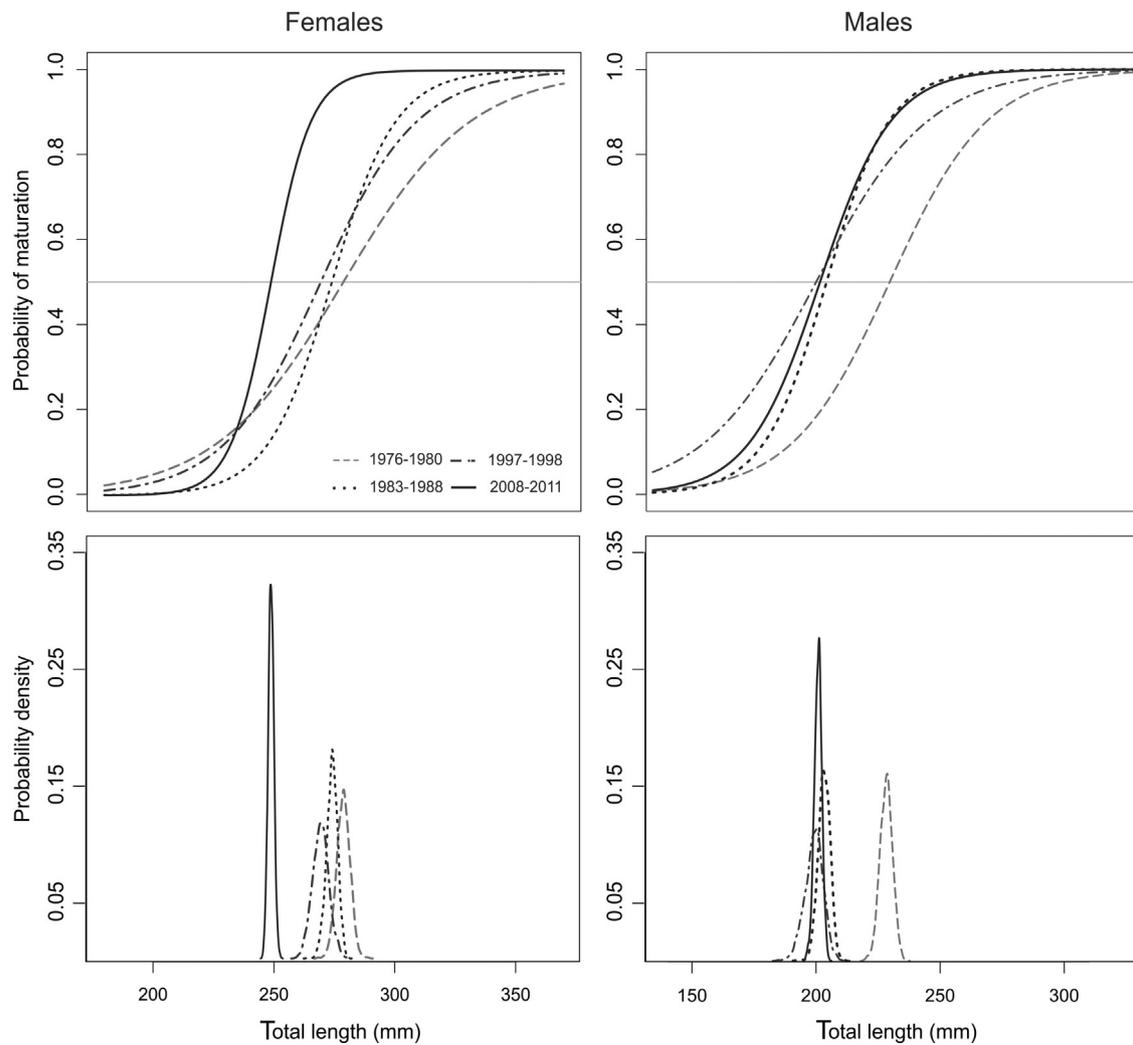


Fig. 3. Length maturity ogives (upper panels) and the posterior distribution of the estimated L_{50} (lower panels) for females and males of *Macrodon atricauda* fished along southern Brazil between 1977 and 2011.

in abundance. Furthermore, competition for prey may also have decreased, not only due to the decrease in the abundance of *M. atricauda*, but also because intense bottom trawl fishery affected the abundance of other predator species (Haimovici, 1998), such as *Cynoscion guatucupa* (Miranda and Haimovici, 2007), the main competitor for shrimps, squids and small fishes along the southern Brazil inner shelf (Martins, 2000). This evidence of declining density combined with the increasing size per age (Cardoso and Haimovici, 2011) enable us to think that density dependent processes are part of the life history changes of *M. atricauda*. Shifts in the reproductive parameters induced by density dependent processes would usually lead to lower A_{50} and higher L_{50} (Grift et al., 2003; Pérez-Rodríguez et al., 2010; Engelhard and Heino, 2004); however, in our case, both A_{50} and L_{50} are lower. If the observed data reflect the real A_{50} in the last decades, it can be interpreted as a density dependent change; in other words, fishes are growing faster and reaching maturity at earlier age due to higher energy availability.

Furthermore, other environmental changes, such as water temperature, cannot be discarded as possible explanations. Independent evidence provided by other studies carried out in the region (Schroeder and Castello, 2010; Hirata et al., 2010) suggests that coastal waters have got warmer. Evidence of increasing air temperature anomalies and river flows of the Patos Lagoon basin were attributed to global warming by Schroeder and Castello (2010). On the other hand, another study reported a significant

rising trend of the water level of the Mirim lagoon and attributed it to the high frequency of El Niño-Southern Oscillation (ENSO) events in the second half of the 20th century (Hirata et al., 2010). The influence of the temperature on the maturation processes was demonstrated for wild populations by Morgan and Colbourne (1999) and, in experimental conditions, by Tobin and Wright (2011), who reported that an increase in 4 °C in the water temperature can decrease the L_{50} of the *Melanogrammus aeglefinus*, a temperate marine fish, in about 4 cm.

The simplified relative reproductive biomass modeling of females with no recruitment fluctuations showed that changes, mainly in maturation but also in growth, have partly compensated the effects of increasing mortality rates (Fig. 7). By comparison with growth changes, decrease in the A_{50} was the main factor which is responsible for avoiding a further decrease in the RRB of females. The recruitment of a higher percentage of fishes at lower ages in the spawning biomass prevented the decline of the spawning population up to 13% of the virginial biomass; it occurred when no maturation changes were considered. Nevertheless, a decrease in 72% of the virginial biomass, even when maturation is considered (compensatory effect), is worrisome for future yields since little or no recovery was shown to be associated with declines of more than 60% of the population (Hutchings and Reynolds, 2004).

However, the reproductive potential of a fish population is not only affected by the spawning biomass but also by variables such

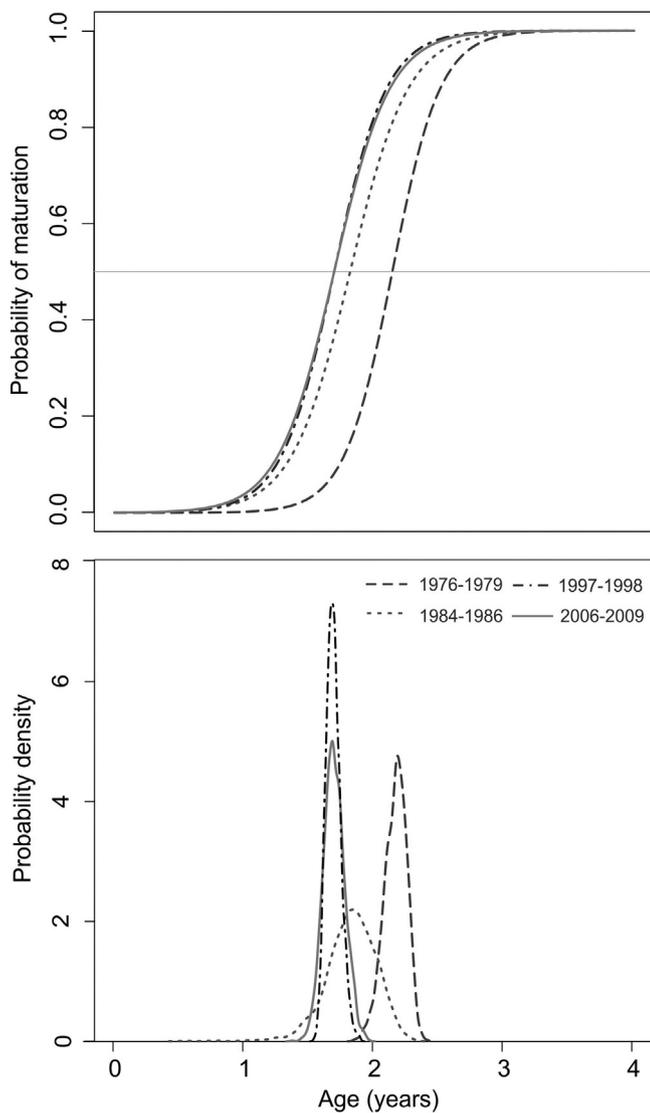


Fig. 4. Age maturity ogives (upper panels) and the posterior distribution of the estimated A_{50} (lower panels) for females of *Macrodon atricauda* fished along southern Brazil between 1976 and 2009.

as mean population fecundity and offspring viability, which varies with age, size, condition of spawning fish and spawning experience (Trippel, 1999; Marteinsdottir and Begg, 2002; Palumbi, 2004). Larger females of *M. atricauda* have a higher contribution to the reproductive output, since the fecundity is positively related with length (Juras and Yamaguti, 1989; Militelli and Macchi, 2004) and they have longer breeding seasons than smaller ones (Fig. 2). Thus, although the decrease in the L_{50} associated with higher mortality can compensate the decrease in spawning biomass, it may lead to lower overall fecundity of the population. The spawning mean age and “experience” also seem to decrease as the maximum age of females in the catches decreased from 8 years in the 1960s (Yamaguti and Santos, 1966), to 6, in the 1980s and to 5, in the 2000s (Cardoso and Haimovici, 2011). Besides, no further decrease in the age at maturation is possible and growth seems to be stabilized (Cardoso and Haimovici, 2011). For this reason, the stability of the reproductive biomass may be near its limit, leaving recruitment more vulnerable to environmental changes and, thus, suggesting that any further increase in the fishery effort may be followed by the collapse of the stock.

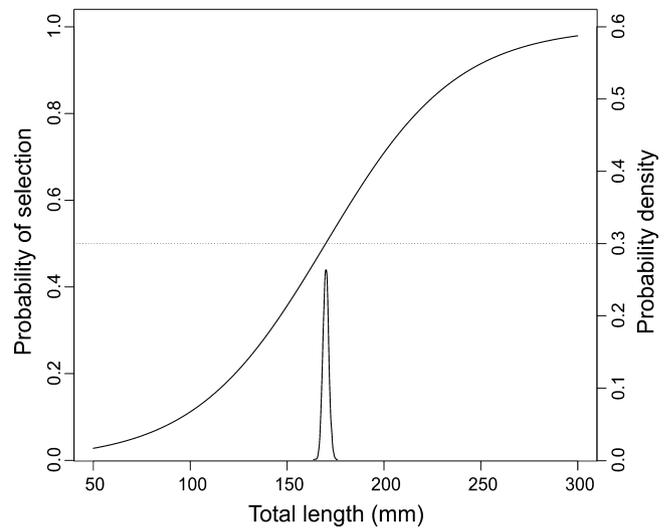


Fig. 5. Selectivity ogive (left axis) and the posterior distribution of the total length at first capture S_{50} (right axis) of a 69 mm cod end mesh size in the pair trawl bottom fishery for *Macrodon atricauda* in southern Brazil.

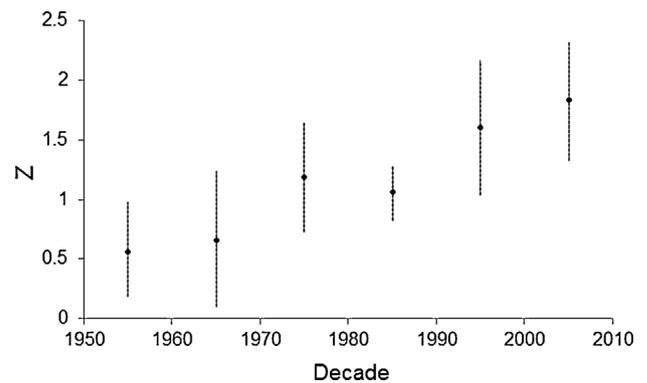


Fig. 6. Instantaneous total mortality coefficients (Z) by decade for the *Macrodon atricauda* population of southern Brazil calculated from catch curves with a Bayesian approach. Vertical lines indicate 95% credible intervals.

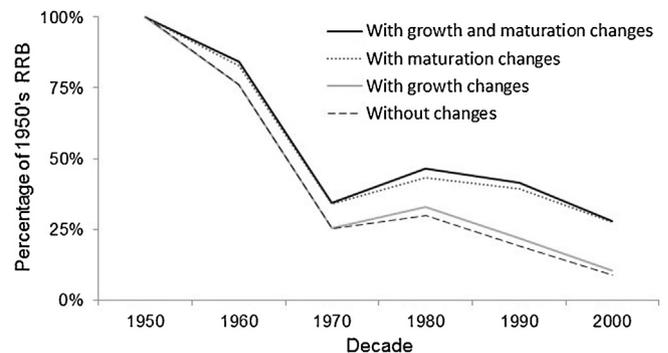


Fig. 7. Modeled female's relative reproductive biomass (RRB) by decade of *Macrodon atricauda* population from southern Brazil. Full black line: Considering long term changes in growth and decreased age at maturation. Dotted black line: Considering only decreased age at maturation. Full gray line: Considering only changes in growth. Dashed black line: Without considering neither changes in growth nor maturation.

Acknowledgements

The authors thank all students and technicians that participated in the data collection and processing and the *Universidade Federal do*

Rio Grande for continuous logistic support for more than 35 years. The Brazilian National Scientific and Technological Research Council (CNPq) is acknowledged for the scholarship granted to L.G.C (Process 141777/2011-7) and the fellowship granted to M.H.

References

- Barot, S., Heino, M., O'Brien, L., Dieckmann, U., 2004. Long-term trend in the maturation reaction norm of two cod stocks. *Ecological Applications* 14 (4), 1257–1271.
- Beverton, R.J.H., Holt, S.J., 1959. A review of the lifespans and mortality rates of fish in nature and their relation to growth and other physiological characteristics. In: Wolstenholme, G.E.W., O'Connor, M. (Eds.), *CIBA Foundation Colloquia on Ageing: The Lifespan of Animals 5*. Churchill Ltd, London, UK, pp. 142–180.
- Brander, K., 2005. Cod recruitment is strongly affected by climate when stock biomass is low. *ICES J. Mar. Sci.* 62, 339–343.
- Cardoso, L.G., Haimovici, M., 2011. Age and changes in growth of the king weakfish *Macrondon atricauda* (Günther, 1880) between 1977 and 2009 in the southern Brazil. *Fisheries Research* 111 (3), 177–187.
- Cardoso, L.G., Santos, S., Haimovici, M., 2012. Differences in the otoliths support the distinction of the genus *Macrondon* into two species in the south-western Atlantic Ocean. *Marine Biodiversity Records* 5, e93.
- Carvalho-Filho, A., Santos, S., Sampaio, I., 2010. *Macrondon atricauda* (Günther, 1880) (Perciformes: Sciaenidae), a valid species from the southwestern Atlantic, with comments on its conservation. *Zootaxa* 2519, 45–58.
- Conover, D.O., Munch, S.B., 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297 (5578), 94–96.
- Dieckmann, U., Heino, M., 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. *Mar. Ecol. Prog. Ser.* 335, 253–269.
- Engelhard, G.H., Heino, M., 2004. Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? *Mar. Ecol. Prog. Ser.* 272, 245–256.
- Ernande, B., Dieckmann, U., Heino, M., 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. *Proc. R. Soc. Lond. B* 271, 415–423.
- Grift, R.E., Rijnsdorp, A.D., Barot, S., Heino, M., Dieckmann, U., 2003. Trends in reaction norms for maturation in the North Sea plaice. *Mar. Ecol. Prog. Ser.* 257, 247–257.
- Haimovici, M., 1987. Estratégia de amostragens de comprimentos de teleósteos demersais nos desembarques da pesca de arrasto no litoral sul do Brasil. *Atlântica* 9, 65–82.
- Haimovici, M., 1998. Present state and perspectives for the Southern Brazil shelf demersal fisheries. *Fisheries Management and Ecology* 5, 277–289.
- Haimovici, M., Cousin, J.C.B., 1989. Reproductive biology of the castanha *Umbrina canosai* (Pisces, Scianidae) in southern Brazil. *Rev. Brasil. Biol.* 49, 523–537.
- Haimovici, M., Martins, A.S., Vieira, P.C., 1996. Distribuição e abundância de teleósteos demersais sobre a plataforma continental do sul do Brasil. *Rev. Brasil. Biol.* 56 (1), 27–50.
- Heino, M., Godø, O.R., 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. *Bull. Mar. Sci.* 70, 639–656.
- Heino, M., Dieckmann, U., Godø, O.R., 2002. Measuring probabilistic maturation reaction norms for age and size at maturation. *Evolution* 56, 669–678.
- Hirata, F.E., Möller Jr., O.O., Mata, M.M., 2010. Regime shifts, trends and interannual variations of water level in Mirim Lagoon, southern Brazil. *Pan-Am. J. A. S.* 5 (2), 254–266.
- Houston, A., McNamara, J., 1992. Phenotypic plasticity as a state-dependent life-history decision. *Evolutionary Ecology* 6 (3), 243–253.
- Hutchings, J., 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 62 (4), 824–832.
- Hutchings, J.A., Fraser, D.J., 2008. The nature of fisheries- and farming-induced evolution. *Mol. Ecol.* 17 (1), 294–313.
- Hutchings, J.A., Reynolds, J.D., 2004. Marine fish population collapses: consequences for recovery and extinction risk. *BioScience* 54, 297–309.
- Jørgensen, T., 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *Jour. du Cons. Int. pour l'Expl. de la Mer* 46, 235–248.
- Jørgensen, C., Enberg, K., Dunlop, E.D., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Erdmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M., Rijnsdorp, A.R., 2007. Managing evolving fish stocks. *Science* 318, 1247–1248.
- Juras, A.A., Yamaguti, N., 1989. Sexual maturity, spawning and fecundity of king weakfish *Macrondon ancylodon*, caught off Rio Grande do Sul State (southern coast of Brazil). *Bolm. Inst. Oceanogr. S. Paulo* 37 (1), 51–58.
- Kinas, P.G., Andrade, H.A., 2010. Introdução à Análise Bayesiana (com R). *Mais Que Nada, Porto Alegre*, 240 pp.
- Law, R., 2000. Fishing selection and phenotypic evolution. *ICES Journal of Marine Sciences* 57, 659–668.
- Law, R., Grey, D.R., 1989. Evolution of yields from populations with age-specific cropping. *Evol. Ecol.* 3 (4), 343–359.
- Longhurst, A.R., 2010. *Mismanagement of Marine Fisheries*. Cambridge University Press, New York, 320 pp.
- Marshall, C.T., McAdam, B.J., 2007. Integrated perspectives on genetic and environmental effects on maturation can reduce potential for errors of inference. *Mar. Ecol. Prog. Ser.* 335, 301–310.
- Marteinsdottir, G., Begg, G.A., 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* 235, 235–256.
- Martins, A.S., 2000. *As assembleias e as guildas tróficas de peixes e cefalópodes demersais na plataforma continental e talude superior do extremo sul do Brasil*. PhD Thesis. Federal University of Rio Grande, Rio Grande, Brazil.
- Militelli, M.L., Macchi, G.J., 2004. Spawning and fecundity of king weakfish, *Macrondon ancylodon*, in the Río de la Plata estuary, Argentina – Uruguay. *J. Mar. Biol. Ass. U.K.* 84 (2), 443–447.
- Miranda, L.V., Haimovici, M., 2007. Changes in the population structure, growth and mortality of stripped weakfish *Cynoscion guatucupa* (Sciaenidae, Teleostei) of Southern Brazil between 1976 and 2002. *Hydrobiologia* 589, 69–78.
- Morgan, M.J., Colbourne, E.B., 1999. Variation in maturity-at-age and size in three populations of American plaice. *ICES Journal of Marine Science* 56, 673–688.
- Ottersen, G., Hjermann, D., Stenseth, N.C., 2006. Changes in spawning stock structure strengthens the link between climate and recruitment in a heavily fished cod stock. *Fish. Oceanogr.* 15, 230–243.
- Ottersen, G., Stige, L.C., Durant, J.M., Chan, K.S., Rouyer, T.A., Drinkwater, K.F., Stenseth, N.C., 2013. Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. *Mar. Ecol. Prog. Ser.* 480, 205–225.
- Palumbi, S.R., 2004. Why mothers matter. *Nature* 430 (7000), 621–622.
- Pérez-Rodríguez, A., Morgan, J., Koen-Alonso, M., Saborido-Rey, F., 2010. Disentangling genetic change from phenotypic response in reproductive parameters of Flemish Cap cod *Gadus morhua*. *Fisheries Research*, <http://dx.doi.org/10.1016/j.fishres.2012.09.004>.
- Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191, 382.
- Rijnsdorp, A.D., 1993a. Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea Plaice, *Pleuronectes platessa* L. *Oecologia* 96, 391–401.
- Rijnsdorp, A.D., 1993b. Relationship between juvenile growth and the onset of sexual maturity of female North Sea plaice, *Pleuronectes platessa*. *Can. J. Fish. Aquat. Sci.* 50, 1617–1631.
- Rodrigues, R., Santos, S., Haimovici, M., Saint-Paul, U., Sampaio, I., Schneider, H., 2013. Mitochondrial DNA reveals population structuring in *Macrondon atricauda* (Perciformes: Sciaenidae): a study covering the whole geographic distribution of the species in the southwestern Atlantic. *Mitochondrial DNA*, <http://dx.doi.org/10.3109/19401736.2013.792053>.
- Roff, D.A., 1992. *The Evolution of Life Histories: Theory and Analysis*. Chapman and Hall, New York, USA.
- Saborido-Rey, F., Kjesbu, O.S., 2005. Growth and Maturation Dynamics, 26 pp. <http://hdl.handle.net/10261/47150>
- Santos, S., Hrbek, T., Farias, I.P., Schneider, H., Sampaio, I., 2006. Population genetic structuring of the king weakfish, *Macrondon ancylodon* (Sciaenidae), in Atlantic coastal waters of South America: deep genetic divergence without morphological change. *Molecular Ecology* 15, 4361–4373.
- Schroeder, F.A., Castello, J.P., 2010. An essay on the potential effects of climate change on fisheries in Patos Lagoon, Brazil. *Pan-Am. J. A. S.* 5 (2), 320–330.
- Sharpe, D.M.T., Hendry, A.P., 2009. Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evolutionary Applications* 2, 260–275.
- Stenseth, N.C., Rouyer, T., 2008. Ecology: destabilized fish stocks. *Nature* 452 (7189), 825–826.
- Stergiou, K.I., 2002. Overfishing, tropicalization of fish stocks, uncertainty and ecosystem management: resharping Ockham's razor. *Fish. Res.* 55, 1–9.
- Stokes, K., Law, R., 2000. Fishing as an evolutionary force. *Mar. Ecol. Prog. Ser.* 208, 307–309.
- Sturtz, S., Ligges, U., Gelman, A., 2005. R2WinBUGS: A Package for Running WinBUGS from R. *Journal of Statistical Software* 12 (3), 1–16.
- Thomas, A., O'Hara, B., Ligges, U., Sturtz, S., 2006. Making BUGS Open. *R News* 6 (1), 12–17.
- Tobin, D., Wright, P.J., 2011. Temperature effects on female maturation in a temperate marine fish. *J. Exp. Mar. Fish. Biol. Ecol.* 403, 9–13.
- Trippel, E.A., 1995. Age at maturity as a stress indicator in fisheries. *Bioscience* 45, 759–771.
- Trippel, E.A., 1999. Estimation of stock reproductive potential: history and challenges for Canadian Atlantic gadoid stock assessments. *J. Northwest Atl. Fish. Sci.* 25, 61–81.
- Valentini, H., de Castro, P.M.G., Servo, G.J.M., de Castro, L.A.B., 1991. Evolução da pesca das principais espécies demersais da costa sudeste do Brasil, pela frota de arrasteiros de parelha baseada em São Paulo de 1968 a 1987. *Atlântica* 13, 87–96.
- Vasconcellos, M.C., Kalikoski, D.C., Haimovici, M., Abdallah, P.R., 2006. Capacidad excesiva del esfuerzo pesquero en el sistema estuario costero del Sur de Brazil. *Capacidad de pesca y manejo pesquero en América Latina y el Caribe*, vol. 461. FAO, Roma, pp. 275–311.
- Vooren, C.M., 1983. Seleção pela malha na pesca de arrasto da Castanha Umbrina canosai, Pescação Cynoscion striatus e Pescadinha Macrondon ancylodon no Rio grande do Sul. *Documentos Técnicos de Oceanografia, Rio Grande*, 32 pp.
- Waggy, G.L., Brown-Peterson, N.J., Peterson, M.S., 2006. Evaluation of the Reproductive Life History of the Sciaenidae in the Gulf of Mexico and Caribbean

- Sea: "Greater" versus "Lesser" Strategies? In: Proceedings of the 57th Gulf and Caribbean Fisheries Institute, vol. 57, St. Petersburg, FL, pp. 263–281.
- Wootton, R.J., 1998. Ecology of Teleost Fishes. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Yamaguti, N., 1968. Mortalidade da pescada-foguete, *Macrodon ancylodon*. Bolm. Inst. Oceanogr. S. Paulo 17 (1), 67–70.
- Yamaguti, N., Moraes, A.E.D., 1965. Análise da pesca da pescada foguete na costa centro sul do Brasil. Bolm. Inst. Oceanogr. S. Paulo 14, 115–124.
- Yamaguti, N., Santos, E.P., 1966. Crescimento da pescada-foguete (*Macrodon ancylodon*): aspecto quantitativo. Bol. Inst. Oceanogr. S. Paulo 15 (1), 75–78.
- Yesaki, M., Bager, K.J., 1975. Histórico da evolução da pesca industrial em Rio Grande. Série Documentos Técnicos SUDEPE/PDP (11).