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Age and changes in growth of the king weakfish *Macrodon atricauda* (Günther, 1880) between 1977 and 2009 in southern Brazil

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ABSTRACT

The coastal demersal sciaenid *Macrodon atricauda* (Günther, 1880), formerly *M. ancylodon* (Bloch and Schneider, 1801) was sampled for ageing during four periods (1977–1979, 1984–1986, 1997–1998 and 2006–2009) in commercial fishing and scientific surveys along southern Brazil (Lat. 30°S–34°40′S). Maximum observed age was seven years, but no fish over five years old was sampled in the last period. Marginal increment analysis of thin sections validated ageing and showed that opaque and translucent bands were laid down at all ages in spring–summer and autumn–winter, respectively. Ageing *M. atricauda* based on sectioned otoliths is highly recommended because comparisons with readings on whole otoliths showed that ages based on whole otoliths exceeded those based on sectioned otoliths for 56.5% of the aged specimens. The growth of *M. atricauda* has increased in the last four decades, most noticeably in the case of adult males over two years old and females over three years old. A threefold decrease in its density and the demersal fish community as a whole are the most likely causes of the growth increase.

1. Introduction

The king weakfish *Macrodon atricauda* (Günther, 1880) had its taxonomical status reviewed by Carvalho-Filho et al. (2010). Until recently, the accepted scientific name for king weakfish from southern Brazil was *Macrodon ancylodon* (Bloch and Schneider, 1801), with a distribution range in the western Atlantic from northern Patagonia (Lat. 43°S) in Argentina (Cousseau and Perrota, 1998) to Venezuela (Menezes et al., 2003). More recently, Santos et al. (2006) and Carvalho-Filho et al. (2010), based on genetic, meristic and morphological evidences, concluded that two distinct species occur in this geographic range: the subtropical *M. atricauda* from Espirito Santo, Brazil (Lat. 20°S) to the south and the tropical *M. ancylodon*, to the north.

In southern and southeastern Brazil, *M. atricauda* has been a major target of the bottom trawl fishery since the late 1950s (Yamaguti and Moraes, 1965; Yesaki and Bager, 1975; Valentini et al., 1991; Haimovici, 1998; Carneiro and Castro, 2005). It has also been fished in Uruguay and Argentina (Cousseau and Perrota, 1998). Because of its importance as a fishing resource, several aspects of its biology and population dynamics have been studied, including reproduction (Yamaguti, 1967; Juras and Yamaguti, 1989; Militelli and Macchi, 2004), feeding (Juras and Yamaguti, 1985), migration (Santos and Yamaguti, 1965), mortality (Yamaguti, 1968) and the age and growth of sub-adults and adults (Yamaguti and dos Santos, 1966; Haimovici, 1988).

Age determination is an important tool in fishery biology which, along with length and weight measurements, provides information on growth, age at maturity, longevity and mortality (Bagenal and Tesch, 1978). Several structures are used to age bony fishes, but otoliths are the most frequently used because they are easy to collect and preserve. Besides, information on the whole life span of the fish is recorded in this structure (Casselman, 1990; Green et al., 2009). Depending on its size and shape, the entire otolith can be read, but it can also be cut through the nucleus or in thin sections (Chilton and Beamish, 1982)

The king weakfish otolith is laterally compressed and relatively large; on its outer surface, opaque and translucent bands can be distinguished. These bands have been interpreted to be annuli in previous age and growth studies of the king weakfish in southern Brazil (Yamaguti and dos Santos, 1966; Haimovici, 1988). Although ageing has been validated through marginal increment analysis, it is difficult to identify the translucent bands on the outer edge of otoliths. Therefore, the first translucent band can easily be confused with false or juvenile rings (Haimovici, 1988). Errors in ageing influence both growth and mortality estimates. For this reason, whole otoliths, previously read from 1984 to1986, were sectioned and the readings were compared.

Changes in growth of heavily exploited fishes are common (Law, 2000) and can be attributed to density dependent causes (Bromley, 1989; Millner and Whiting, 1996; Jennings et al., 1999) or

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density independent causes, such as eutrophication (Rijnsdorp and van Leeuwen, 1996) and temperature (Thresher et al., 2007). Since the beginning of industrial fishing between Chui and Santa Marta Grande Cape (Lat. 28°S–34°40′S) in the 1950s, the king weakfish, as well as most demersal fishes, has been intensely exploited (Yesaki and Bager, 1975; Haimovici, 1998; Haimovici et al., 2006b). The availability of otoliths collected between 1976 and 2009 made it possible to evaluate changes in the growth of *M. atricauda* in southern Brazil.

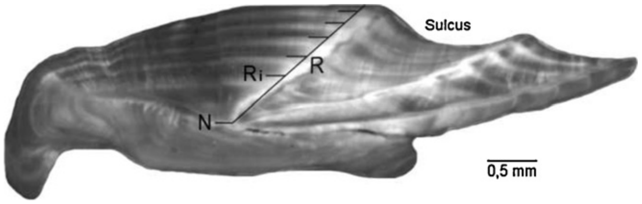

Fig. 1. Thin section examined with reflected light of a five-year-old female (*L*: 368 mm) *Macrodon atricauda* from southern Brazil. Black bars indicate the end of each opaque band. N: nucleus, R_i: the distance from the nucleus to the end of each opaque band; *R*: the distance from the nucleus to the inner edge. Opaque bands can be seen as white bands whereas translucent ones can be seen as dark bands.

2. Material and methods

Specimens sampled for ageing were landed by commercial bottom trawler in Rio Grande from 1976 to 2009 (Haimovici, 1987) and from bottom trawl surveys along southern Brazil between latitudes 30°S and 34°40′S (Haimovici et al., 1996, 2005). Samplings comprised measurements of total length (*L*, mm) and total weight (*W*, g), sex determination and extraction of *sagittae* otoliths. Otoliths of specimens that represent the whole size range and all months of the year (whenever samples were available) were selected in each one of the four periods: 1977–1979, 1984–1986, 1997–1998 and 2006–2009.

Thin transverse sections (0.20–0.25 mm) through the nucleus were made in otoliths embedded in a polyester resin with a single high concentration diamond blade of a Buehler–Isomet low-speed saw. All sections were mounted on glass slides with xylol base mounting media (ENTELAN Merck®).

Sections were examined with transmitted light under a compound microscope (35×). The opaque (clear) bands were counted, the distances from the nucleus to the end of each opaque band (R_i) and to the inner edge (*R*) were measured (in micrometric units) along the dorsal border of the sulcus and the opacity of the inner edge was recorded (Fig. 1). After several preliminary readings, the opaque bands were counted independently by two readers. A third joint reading was carried out and, in cases of disagreement, results were discarded.

The mean coefficient of variation (CV) was used to evaluate the precision of the annual increment counted between readings (Campana and Jones, 1992):

$$CV_j = 100\% \times \frac{\sqrt{\sum_{i=1}^{R}(X_{ij} - X_j)^2/(R-1)}}{X_j}$$

where CV_j is the age precision estimate for the *j*th fish; X_{ij} is the age determination of the *j*th fish by the *i*th reader; X_j is the mean age of the *j*th fish and *R* is the number of readings.

Ages read in the sectioned otoliths of 238 specimens sampled from 1984 to 1986 were compared with those read in the same whole otoliths by Haimovici (1988), who examined the outer surface of the otoliths with reflected light over a black background.

The periodicity of the formation of opaque and translucent bands on the edge of the otoliths was evaluated. It was based on the analysis of the type of edge and marginal increment (MI). The translucent and opaque bands on the edge of the otolith section were counted monthly and displayed as relative frequencies (%). The monthly mean width of the translucent bands formed on the edge of the sections was calculated for each specimen and grouped monthly for each age class. The MI was calculated as the quotient between the distance from the nucleus to the end of the last opaque

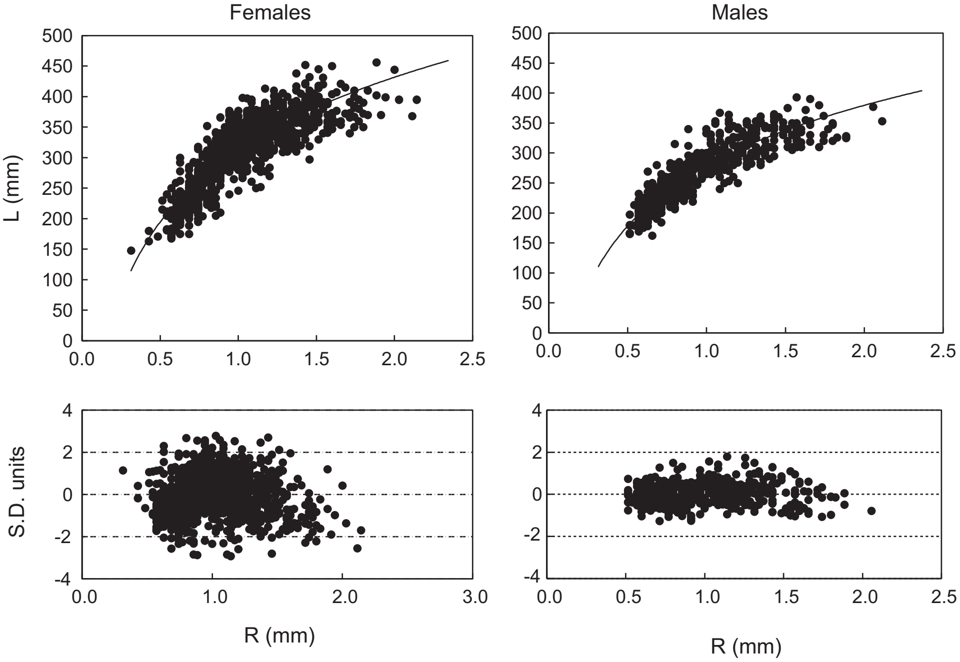

Fig. 2. Relationship between total length *L* (mm) and the distance from the nucleus to the inner surface of the otoliths *R* (mm) of Macrodon *atricauda*. Lower panels: error distributions in standard deviation units.

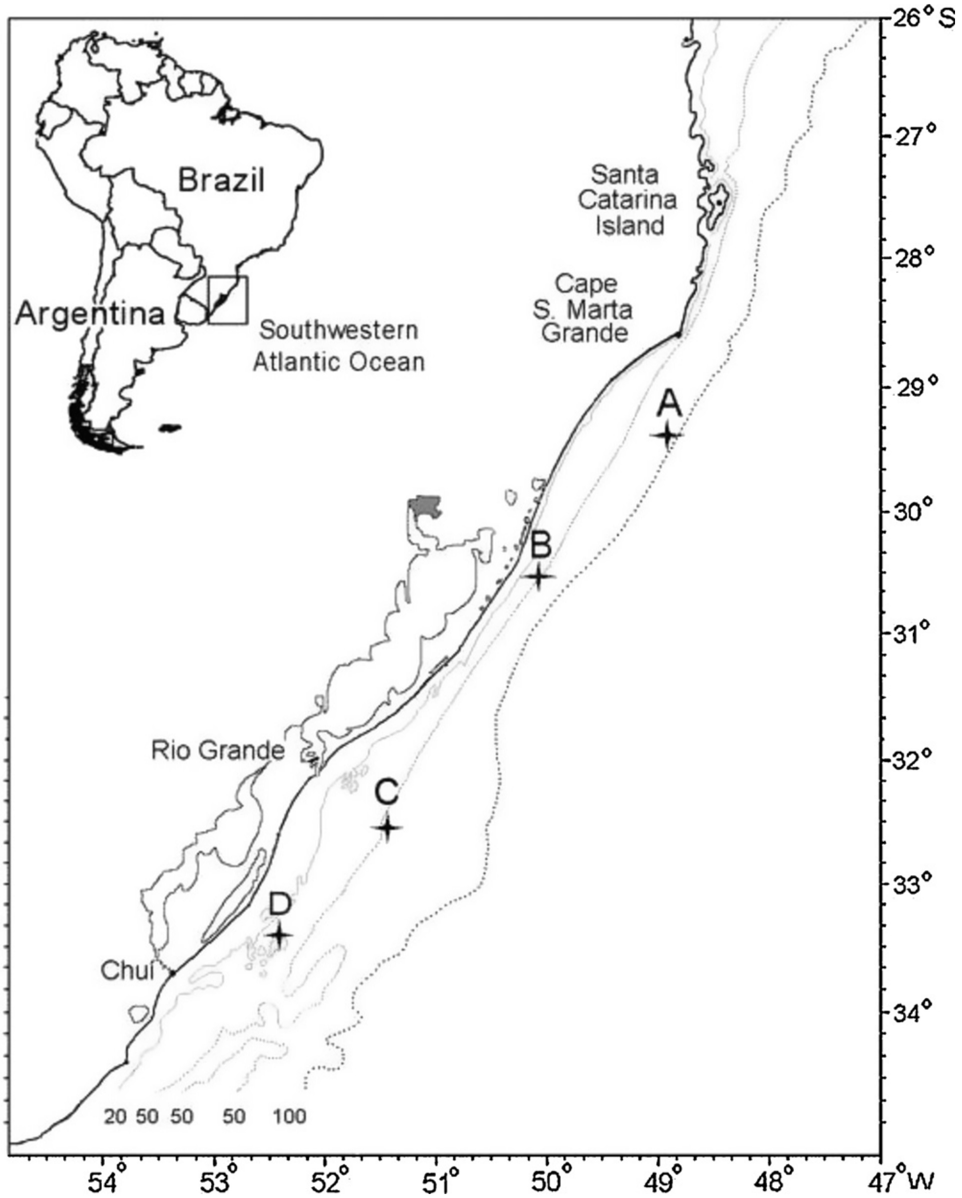

Fig. 3. Study area in the southwestern Atlantic Ocean indicating the locations where monthly average SST values (°C) between 1982 and 2009 were obtained (A: 48°50′W, 29°25′S; B: 50°05′W, 30°30′S; C: 51°27′W, 32°31′S; D: 52°30′W, 33°30′S).

band (R_n) and the distance from the nucleus to the edge (R), where

$$\mathrm{MI} = \frac{R - R_n}{R}$$

This formula is adequate for fast-growing fish (Campana, 2001). The terminology used for the otolith description follows Chilton and Beamish (1982).

To evaluate the seasonality of the otolith growth, the margin width was defined as the distance from the tip of the last translucent band to the edge of the sections ($\mathrm{MW} = R - R_n$). Analysis of covariance ($\alpha = 0.05$) (Zar, 1984) was used to compare seasonality in the growth of the otoliths.

For growth studies, back-calculated length-at-age data was preferred over observed length-at-age data because the former are less sensitive to gear selectivity and on board discard of small fish.

The body proportional hypothesis: $f(L) = a + bS$ was assumed to compare regressions models of measurements of length (L) from the focus to the edge (R) of the otolith sections at the time of capture (Francis, 1990). Best fit regressions for females and males were:

$$\text{females}: \; L = 171.23 \times \ln R + 131.23 \quad (R^2 = 0.723;\; n = 1006)$$

$$\text{males}: \quad L = 145.27 \times \ln R + 278.8 \quad (R^2 = 0.807;\; n = 560)$$

Covariance analysis showed significant differences ($p < 0.001$) between the two regressions with higher adjusted mean R for females (Fig. 2). Therefore, females were found to be larger than males considering the same otoliths radius.

Individual total length at the time of the formation of the ith opaque band was back-calculated as:

$$\text{females}: \; L_i = \frac{(L \times (\ln(R_i) + 1.829))}{\ln(R) + 1.829}$$

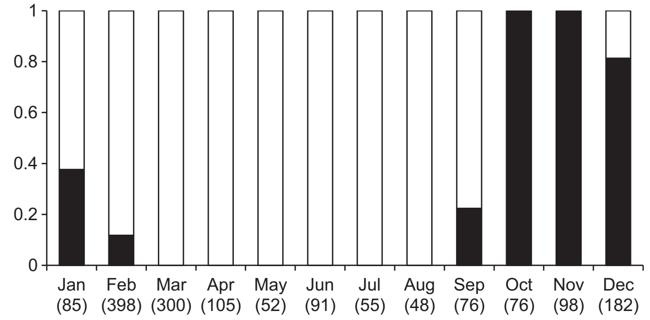

Fig. 4. Seasonal pattern of translucent (white) and opaque (black) edges of the otolith thin sections of *Macrodon atricauda* in southern Brazil (the number of otoliths examined monthly are in brackets).

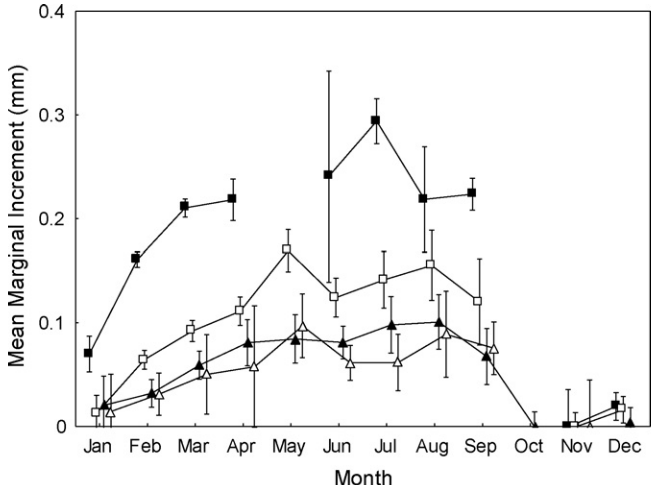

Fig. 5. Monthly mean marginal translucent increment on sectioned otoliths of *Macrodon atricauda* at ages: 1 (-■ -); 2 (-□-); 3 (–▲-) and 4–7 (-△-). Vertical bars indicate the confidence interval ($\alpha = 0.05$).

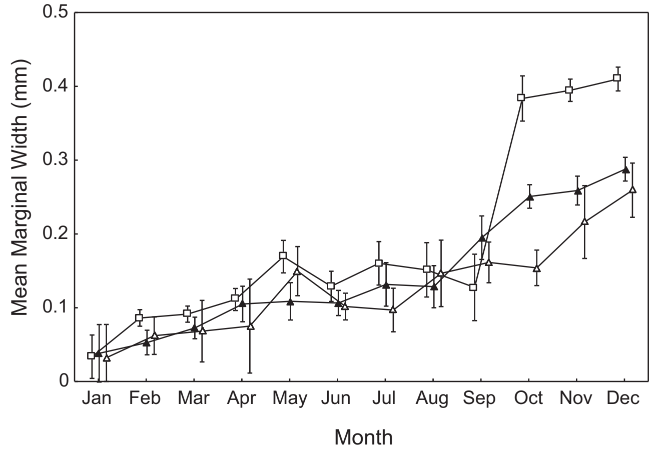

Fig. 6. Monthly mean marginal width on sectioned otoliths of *Macrodon atricauda* at ages 2 (-□-); 3 (–▲-) and 4–7 (-△-). Vertical bars indicate the confidence interval ($\alpha = 0.05$).

$$\text{males}: L_i = \frac{(L \times (\ln(R_i) + 1.919))}{\ln(R) + 1.919}$$

where R_i is the distance from the nucleus to the end of the ith opaque band on the sections of the otoliths.

Statistical differences of mean back-calculated length-at-age among periods were tested using analysis of variance.

Table 1
Comparison between readings of thin sections and whole otoliths of 238 individuals of *M. atricauda* from Southern Brazil sampled in 1984 – 1986. Mean CV is the mean coefficient of variation between the readings.

L classes mm	Mean CV (%)	Differences: sections – whole otoliths				
		−2	−1	0	1	2
100–149				1		
150–199	11.7		6	18		
200–249	29.8	4	25	20		
250–299	20.8	1	24	14	2	
300–349	17.3	2	35	18	1	
350–399	13.0	2	33	22	3	1
400–449	7.9		2	2		
450–459				1		
Total	18.7	9	125	96	6	1
%		3.8	52.7	40.5	2.5	0.4

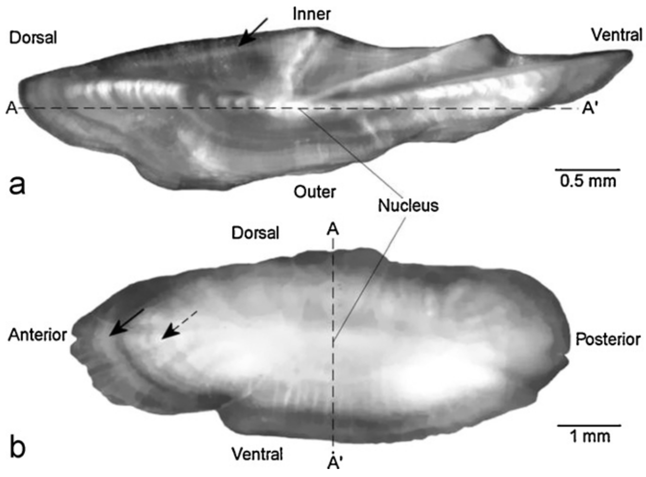

Fig. 7. Posterior surface of a thin section (a) and outer surface (b) of the otolith of a one-year-old male (*L*: 208 mm) of *Macrodon atricauda* from southern Brazil examined with reflected light over a black background. Black arrows indicate an annual opaque band and a dotted arrow shows a false opaque band following a translucent check. A–A′ indicates the line of the section on otoliths.

Mean back-calculated length-at-age data was fitted by a non-linear iterative quasi-Newton algorithm to the von Bertalanffy growth model (VBGM) $L_t = L_\infty(1 - e^{-k(t-t_0)})$, where L_t is the length (mm) at age t (years), L_∞ is the asymptotic length (mm), k is the instantaneous growth coefficient and t_0 is the theoretical age at zero length (years). A likelihood ratio test ($\alpha = 0.05$) was used to compare growth curves between sexes and among periods (Cerrato, 1990; Aubone and Wöhler, 2000).

The parameters of the potential weight-length equations ($W_t = aL_t^b$) were calculated using linear regression based on log transformed weights and lengths, and the slopes were compared between sexes, among periods and seasons using analysis of covariance ($\alpha = 0.05$) (Zar, 1984). Theoretical growth in weight was estimated by transforming length-at-age data into weight-at-age data based on the potential weight–length equations. Calculations of absolute weight gain were based on the differences among mean theoretical weights at consecutive ages (Araújo and Haimovici, 2000).

Monthly average sea surface temperatures (SST, °C), between 1982 and 2009 in four locations along southern Brazil (Fig. 3), were consulted from the Physical Oceanography Distributed Active Archive Center (PODAAC, 2011). These means were calculated using the “optimum interpolation method” of satellite data and *in situ* measurements (ship and buoy) to generate high resolution sea surface climatology (Reynolds and Smith, 1995).

Table 2
Observed mean total length (*L*, mm) in the landings. Back-calculated mean total length-at-age (*L*, mm) for male and female of *M. atricauda* fished along southern Brazil in four periods between 1976 and 2009.

Females

1977–1979

Age (years)	*n*	Observed mean *L* (mm)	Annulus number					
			I	II	III	IV	V	VI
1	48	243.5	221.6					
2	74	322.0	212.6	312.8				
3	57	347.3	202,0	286.9	340.3			
4	11	370.5	207.6	290.6	332.2	363.8		
5	3	363.3	187.7	268.3	307.3	336.5	355.2	
6	2	355.0	158.9	249.4	285.9	308.9	333.0	348.9
Total	195		195	147	73	16	5	2
Back-calculated mean *L* (mm)	210.5	299.3	336.2	351.8	346.3	348.9		
Growth increment (mm)		88.8	36.9	15.6	–5.5	2.6		

Males

1977–1979

Age (years)	*n*	Observed mean *L* (mm)	Annulus number					
			I	II	III	IV	V	VI
1	31	236.5	208.8					
2	24	283.8	193.8	278.0				
3	12	309.7	182.4	252.3	298.6			
4	8	320.6	187.0	253.0	287.0	311.3		
5	9	328.9	177.1	246.1	281,0	304.4	321.3	
6	1	310.0	153.0	223.1	248.5	269.5	283.1	301.1
Total	85		85	54	30	18	10	1
Back-calculated mean *L* (mm)			194.8	262.2	288.5	305.5	317.5	301.1
Growth increment (mm)				67.5	26.3	17.0	12.0	–16.4

Females

1984–1986

Age (years)	*n*	Observed mean *L* (mm)	Annulus number					
			I	II	III	IV	V	VI
1	38	217.9	182.2					
2	55	304.3	203.3	291.1				
3	65	351.8	208.8	300.0	343.3			
4	29	370.0	203.3	294.5	334.8	360.4		
5	7	375.7	199.3	271.8	318.6	347.4	368.4	
6	4	406.5	209.7	296.2	335.4	364.6	386.4	401.6
Total	160		198	160	105	40	11	4
Back-calculated mean *L* (mm)	201	294.6	339	358.6	375.0	401.6		
Growth increment (mm)		93.6	44.4	19.6	16.4	26.6		

Males

1984–1986

Age (years)	*n*	Observed mean *L* (mm)	Annulus number						
			I	II	III	IV	V	VI	VII
1	45	213.8	191.7						
2	12	282.3	191.4	262.6					
3	29	314.5	190.9	268.5	303.1				
4	9	321.1	168.8	254.3	289.7	311.3			
5	8	349.4	190.2	267.2	301.6	328.4	345.1		
6	5	344.2	181.1	247.7	280.9	303.5	323.0	337.4	
7	2	359.0	167.3	245.7	277.4	300.9	319.5	336.6	351.8
Total	110		110	65	53	24	15	7	2
Back-calculated mean *L* (mm)			188.5	263.0	297.5	314.5	334.3	337.2	351.8
Growth increment (mm)				74.5	34.5	17.0	19.8	2.8	14.6

Females

1997–1998

Age (years)	*n*	Observed mean *L* (mm)	Annulus number					
			I	II	III	IV	V	VI
1	24	235.9	214.7					
2	99	310.9	197.9	306.7				
3	87	346.1	185.3	287.2	343.4			
4	16	377.8	193.9	293.4	345.2	376.9		
5	2	448.0	201.3	304.7	383.1	423.8	448.0	
6	4	382.3	186.9	277.3	315.8	343.7	365.3	380.3
Total	232		232	208	109	22	6	4
Back-calculated mean *L* (mm)			194.5	297.0	343.4	375.1	392.8	380.3
Growth increment (mm)				102.5	46.4	31.7	17.7	–12.6

Males

1997–1998

Age (years)	*n*	Observed mean *L* (mm)	Annulus number				
			I	II	III	IV	V
1	39	220.4	206.5				
2	43	277.1	180.9	273.3			
3	11	330.7	192.6	282.4	329.1		
4	1	342.0	104.0	223.6	285.1	332.2	
5	2	345.0	182.2	269.3	300.9	323.7	342.1
Total	96		96	57	14	3	2
Back-calculated mean *L* (mm)			191.8	274.0	321.8	326.5	342.1
Growth increment (mm)				82.2	47.8	4.7	15.7

Table 2
(Continued)

Females							
2006–2009							
Age (years)	*n*	Observed mean *L* (mm)	Annulus number				
			I	II	III	IV	V
1	124	245.9	209.5				
2	141	324.6	185.7	301.1			
3	102	364.5	193.8	298.3	353.4		
4	26	395.1	160.8	289.4	348.7	384.0	
5	5	401.6	150.9	270.4	330.6	370.5	392.9
Total	398		398	274	133	31	5
Back-calculated mean *L* (mm)			193.1	298.4	351.6	381.8	392.9
Growth increment (mm)				105.3	53.2	30.2	11.1

Males						
Age (years)	*n*	Observed mean *L* (mm)	Annulus number			
			I	II	III	IV
1	176	225.3	195.3			
2	81	289.4	180.7	274.5		
3	22	336.9	190.9	287.3	331.0	
4	11	361.1	187.2	279.6	326.9	353.7
Total	290		290	114	33	11
Back-calculated mean *L* (mm)			190.6	277.5	329.7	353.7
Growth increment (mm)				86.9	52.2	24.1

Table 3
Results of a one-way ANOVA of mean back-calculated lengths by periods at each age for females and males of *M. atricauda*.

Age	Females		Males	
	F-value	*p*	*F*-value	*p*
1	7.15	0.0001	0.67	0.5712
2	0.77	0.5120	6.75	0.0002
3	6.36	0.0003	26.46	<0.0001
4	5.02	0.0027	12.52	<0.0001
5	2077	0.1311		

Table 4
Von Bertalanffy's growth parameters and their confidence intervals ($\alpha = 0.05$) for males, females and pooled sex of *M. atricauda* caught in southern Brazil.

	L_∞	k	t_o	W_∞
Females				
1976–1979	353.3 ± 11.2	0.99 ± 0.20	0.09 ± 0.16	429.8
1984–1986	381.5 ± 17.4	0.73 ± 0.15	−0.03 ± 0.17	557.7
1995–1997	389.9 ± 20.2	0.74 ± 0.15	0.06 ± 0.16	600.5
2006–2009	409.8 ± 12.6	0.66 ± 0.75	0.04 ± 0.86	711.0
Males				
1976–1979	302.4 ± 6.9	1.04 ± 0.54	0.01 ± 0.55	250.3
1984–1986	350.9 ± 15.9	0.57 ± 0.14	−0.37 ± 0.32	404.1
1995–1997	361.8 ± 69.9	0.67 ± 0.44	−0.13 ± 0.48	446.0
2006–2009	394.0 ± 143.5	0.56 ± 0.70	−0.17 ± 0.95	568.9
Pooled sex				
1976–1979	333.7 ± 11.32	1.10 ± 0.26	0.10 ± 0.18	352.7
1984–1986	355.3 ± 4.34	0.82 ± 0.06	0.01 ± 0.06	434.8
1995–1997	390.9 ± 9.58	0.68 ± 0.06	−0.03 ± 0.07	597.8
2006–2009	410.5 ± 12.04	0.61 ± 0.06	−0.05 ± 0.07	703.66

Density changes of *M. atricauda* and of the whole demersal community, between 1979 and 2008, were assessed by examining catch-per-unit-effort (CPUE) series of kg per day at sea of standard industrial pair trawlers (the main fleet responsible for weakfish landings). Data were obtained by sampling landings (Haimovici, 1987; Haimovici et al., 2006b) and from official landing statistics reported annually by IBAMA/CEPERG (1978–2008). The king weakfish CPUE series was corrected by its percentage in the landings to account for changes in the focus of the multispecific pair trawl fishery along over time (Chikuni, 1976).

3. Results

3.1. Ageing in thin otolith sections

Overall, 1656 specimens measuring from 148 mm to 456 mm and collected in four decadal periods between 1977 and 2009 had otolith sections examined for ageing. The coincidence between two independent readings was 70.9% and the mean coefficient of variation between readers was 7.34%. After the joint reading, the coincidence increased to 94.6%. Most of the 90 otolith sections discarded for ageing belonged to females (83%) and 71% belonged to fishes that measured over 300 mm.

A total of 1566 fishes were aged and used in the analysis distributed in the four time periods (1977–1979 *n*: 280; 1984–1986 *n*: 270; 1997–1998 *n*: 328; 2006–2009 *n*: 688). The oldest sampled fishes were two seven-year-old males from the 1986 samplings. The oldest females were six years old and were found in the first three periods. In the last period under investigation, the oldest male and female were 4 and five years old, respectively.

In the otolith sections, translucent bands appear larger than the opaque bands. The analysis of the type of band on the edge of the sectioned otoliths showed that opaque edges increased from 25% in September to 100% in October and December, and decreased to 10% in February. From March to August, the edges of all sections were translucent (Fig. 4).

Table 5
Comparisons of von Bertalanffy growth parameters applying a likelihood ratio test between periods for females (F) and males (M) of *M. atricauda* caught in southern Brazil. (SSRG: sum of squares of the residues of the general model; SSRR sum of squares of the residues of the restricted model.)

	Comparisons between periods					
	1976–1979 and 1984–1986		1984–1986 and 1995–1997		1995–1997 and 2006–2009	
	F	M	F	M	F	M
SSRG	1.78	3.85	1.86	2.72	1.65	1.19
SSRR	21.01	15.70	10.15	20.75	5.90	4.02
X^2 obs	24.67	14.07	16.97	20.32	12.76	10.98
Probability	<0.001	0.003	0.001	<0.001	0.005	0.012
Ho	Rejected	Rejected	Rejected	Rejected	Rejected	Rejected

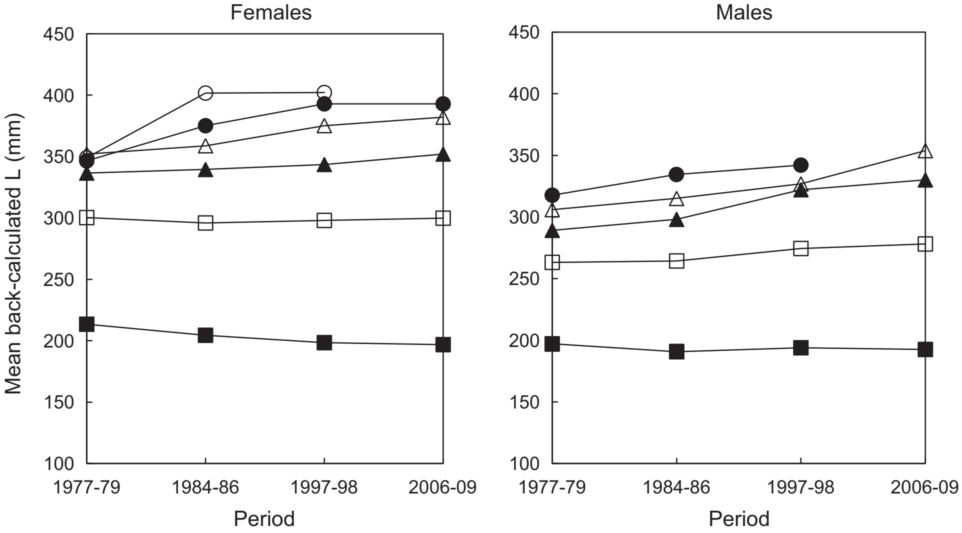

Fig. 8. Mean back-calculated length by periods at ages: 1 (-■–); 2 (-□-); 3 (–▲-); 4 (-△-); 5 (-●-) and 6 (-○-) for females and 1–5 for males of *Macrodon atricauda* caught in southern Brazil.

Monthly mean marginal increments calculated separately for specimens with one to four or more opaque bands (ages 1–4+) were low from October to January and increased gradually to maximum values between June and September (Fig. 5). The same pattern was observed for all ages.

Both edge type and marginal increment analyses consistently show an annual periodicity in the formation of an opaque band from spring to summer and a translucent band in autumn and winter for fishes at different ages. This alternation validates the ageing of the king weakfish from southern Brazil. Spawning of *M. atricauda* in southern Brazil and opaque band formation on its otoliths takes place in spring and summer and the number of opaque zones represents approximately the number of years of life. Due to this coincidence, it was possible to assume January 1st as the birth date of all specimens.

The analysis of covariance which compared three four-month periods (January to April, May to August, September to December) of the annual increase of the otolith margin showed significant differences for ages 2 ($p = 0.003$), 3 ($p < 0.001$) and from 4 to 7 ($p < 0.001$). It can be concluded that the fastest growth was between September and December, it slowed down from January and April and was practically nonexistent between May and August (Fig. 6).

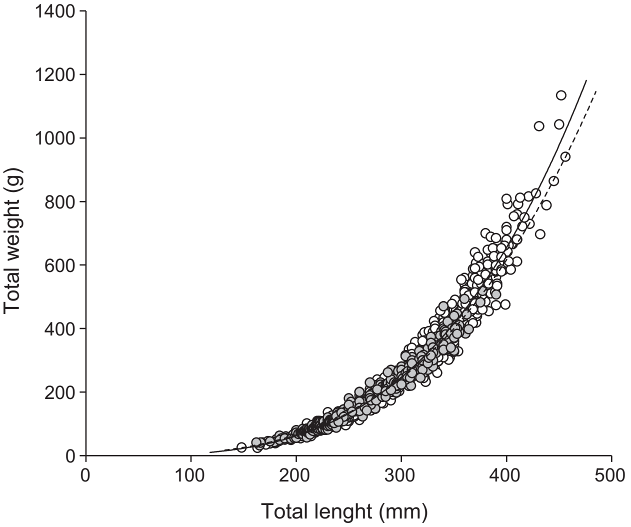

Fig. 9. Weight-length relationship of *M. atricauda* caught in southern Brazil. White circles: females; grey circles: males. Continuous line: regression line for females. Dashed line: regression line for males.

3.2. Comparison between readings of whole otoliths and thin sections

Readings were coincident in 40.5% of the specimens; they were one year lower in the thin sectioned otoliths in 52.7%, and two years lower in 3.8%. In the case of 2.9% of the specimens, thin sections yielded ages one year or more over the ages of the whole otoliths (Table 1). The mean coefficient of variation between reading techniques were, on average, 18.7% and attained up to 29.8% for fishes between 200 and 249 mm *L* (Table 1).

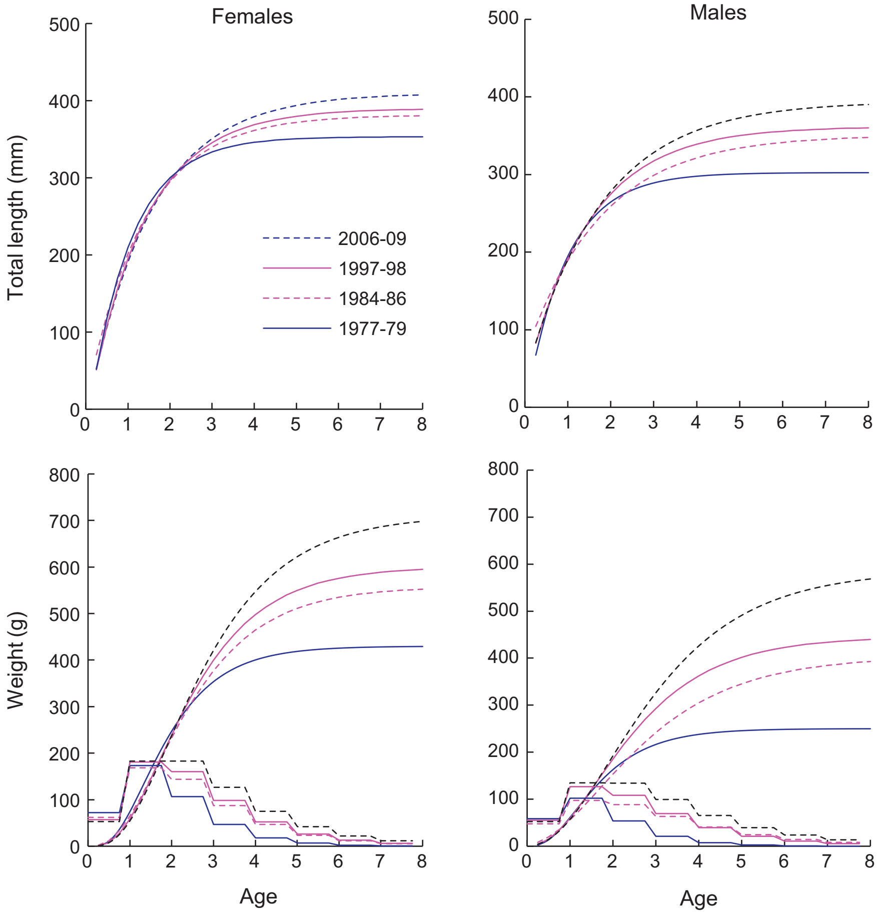

Fig. 10. Growth curves in length and weight and absolute yearly growth in weight of *M. atricauda* fished along southern Brazil between 1977 and 2009.

In the whole otoliths of young *M. atricauda*, opaque checks were more common before the first opaque annual band. A single opaque band is evident between the opaque nucleus and a translucent edge of the section of the left otolith of a one-year-old specimen (Fig. 7a). On the outer surface of the right otolith of the same fish, a thin juvenile translucent check was considered to be the end of the first opaque band and the fish was wrongly aged 2 (Fig. 7b).

3.3. *Back-calculation*

The values of back-calculated mean length at each age were consistent between the mean observed length at the earlier age and the following age, except for some older ages with small sample sizes. Back-calculated total length at age decreased with increasing ages (Rosa Lee phenomenon (Chugunova, 1963)) and the difference was most evident at age 1 (Table 2).

The mean back-calculated length-at-age differed significantly among periods for males at ages over 2 and females at ages 1 and over 3 (Table 3). The mean back-calculated lengths in the different sampling periods showed an increasing trend over time for males aged over 2 and females aged over 3 (Fig. 8). The mean observed lengths-at-ages 1 and 2 were higher in the period 1977–1979, when compared to the two following periods (Table 2) and the mean back-calculated length-at-age 1 was significantly higher in the first period.

3.4. *Weight–length relationships*

The relationships between total weight (*W*) and total length (*L*) of both sexes adjusted based on a potential model (Fig. 9) were:

$$W_{\text{females}} = 9.68 \times 10^{-7} \times L^{3.39} \quad (R^2 = 0.9758,\ n = 739)$$

$$W_{\text{males}} = 2.56 \times 10^{-6} \times L^{3.22} \quad (R^2 = 0.9752,\ n = 439)$$

$$W_{\text{pooled\_sexes}} = 1.36 \times 10^{-6} \times L^{3.33} \quad (R^2 = 0.9789,\ n = 1178)$$

Significant differences were observed due to sex ($p = 0.02$) and three-month-long seasons ($p < 0.001$) but no significant differences were observed among the periods ($p = 0.20$). Up to 280 mm *L*, males were heavier than females; differences in weight decreased with increasing sizes: 6.0% at 200 mm, 2.7% at 240 mm and 0.1% at 280 mm. Females larger than 280 mm were heavier than males of the same length classes. Weight variability increased with increasing sizes: 0.01% at 281 mm, 2.2% at 320 mm and 4.2% at 360 mm. Females and males were heavier in spring when compared with the other seasons.

3.5. *Growth*

As the weight–length relationships did not differ among periods ($p = 0.20$), W_∞ was calculated based on L_∞ and the corresponding weight–length relationship parameters. For both sexes, L_∞

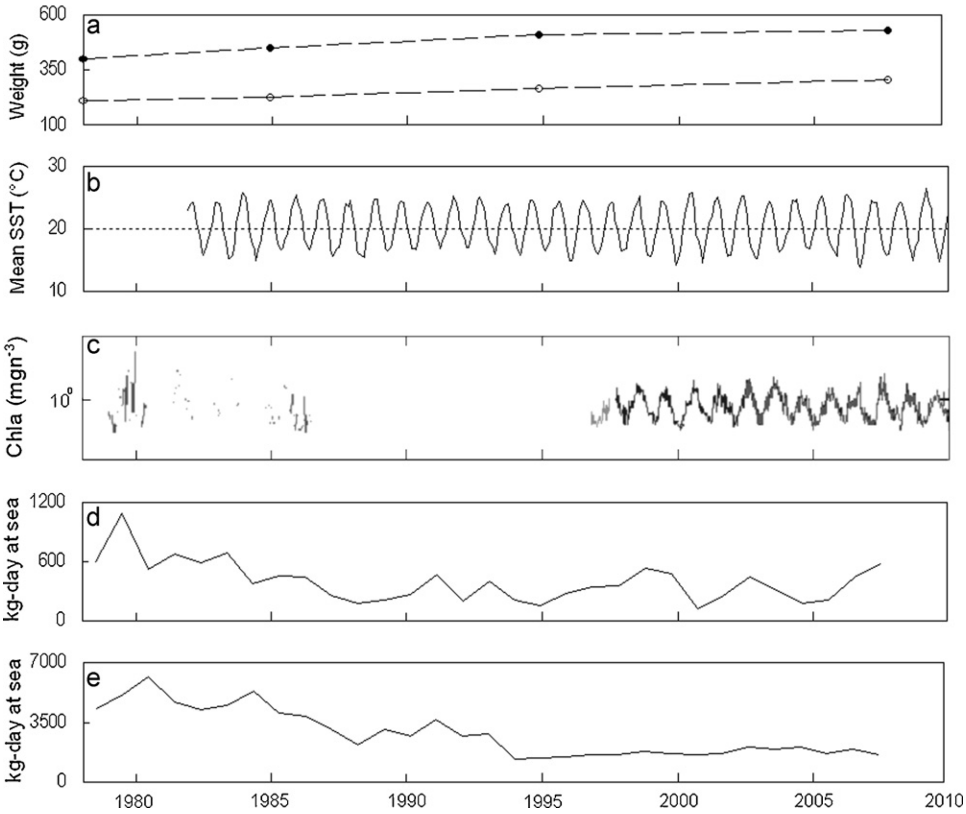

Fig. 11. Changes in growth of *Macrodon atricauda* and potentially related factors from 1978 to 2010. (a) mean weight of females aged 3–5 (●) and males aged 2–4 (○); (b) mean sea surface temperature; (c) chlorophyll-*a* (Ciotti et al., 2010); (d) CPUE of *Macrodon atricauda* in the trawl fishery. (e) CPUE of all species in the trawl fishery.

increased and *k* decreased with time (Table 4). The growth parameters were significantly different among the four sampled periods (Table 5).

Percent increases between the first and last periods increased with age at ages 2–5 for males: 5.2%, 13.5%, 19.8%, 23.9% in length and 17.6%%, 50.4%, 78.7%, 99.5% in weight. Percent increases for females between ages 3 and 5 were 5.2%, 9.6%, 12.4% in length and 18.9%, 36.6%, 48.6% in weight. Gain in weight between ages was higher between ages 1 and 2 and decreased subsequently. This pattern was observed in all four periods (Fig. 10).

4. Discussion

In comparison with the previous ageing methods based on whole otoliths of *M. atricauda*, thin sections improved the reading and decreased the bias. It also allowed consistent validation of the formation of an opaque band and a translucent one in the otoliths every year, at all ages, separately. The otolith growth is a combination of endogenous and exogenous factors throughout the lifetime of a fish. Alternate dense mineral rich and less dense mineral bands form under an annual periodicity in most species (Green et al., 2009). The relative optical density of bands on the king weakfish otoliths differ when observed in the whole otoliths and in the sections: on the outer surface of the whole otoliths, narrow translucent bands are seen between wider opaque bands. On the sections, opaque bands appear to be narrower than the translucent ones (Fig. 1). Additionally, the thin translucent checks were easier to detect because they lack the gradual change of the transparency of the annual bands confirmed by the marginal increment analysis.

Underestimations of ages read on the whole otoliths are frequent in the case of long-living and slow-growing species from temperate regions; the last annulus becomes thin and difficult to discriminate (Campana, 2001). A different pattern was observed for the king weakfish in which ages are overestimated in the readings of whole otoliths. In these readings, false annuli or checks can be seen mostly before the first translucent band.

Checks are caused by exogenous factors such as environmental stress (Panfili et al., 2009). The king weakfish is a coastal sciaenid associated with soft bottoms and fresh water outputs, such as those from the La Plata River and Patos-Mirim Lagoon system (Piola et al., 2000). Irregular salinity changes in this environment may affect metabolism and be reflected as checks on the otoliths, particularly in the first year of life, before the onset of the adult reproductive displacements (Santos and Yamaguti, 1965)

Growth cycles are related to physiological changes that result from the influence of factors such as temperature, reproduction and feeding regime (Morales-Nin, 2000). Marginal width analysis of the sliced otoliths (Fig. 6) and the seasonality in the band formation (Figs. 4 and 5) showed that both the formation of the opaque bands and the fastest growth occur between September and December (from early spring to early summer). In this period, water temperature is increasing and the primary production on the shelf is the highest (Ciotti et al., 2010). It is also coincident with gonadal maturation prior to the beginning of the spawning that extends until autumn (Juras and Yamaguti, 1989; Militelli and Macchi, 2004). The formation of the opaque bands on the otoliths and the fastest corporal growth are associated in most species under study (Fowler, 2009).

The larger sizes of the mean observed length-at-ages 1 and 2 in the first period, compared with the two following periods and with the mean back-calculated length- at-early-ages in the first period, were attributed to the onboard selection pattern prior to the 1980s. In this period, Haimovici and Maceira (1981) observed that only king weakfish over 200 mm, in summer and autumn, and 223 mm, in winter and spring, were landed by trawlers. With decreasing catches in the following periods, smaller fishes began to be landed.

The gradual increase in length and weight by age for both sexes (Fig. 11a) promoted the increase of L_∞ and the decrease of k for *M. atricauda* during the period under study. The decrease in the value of k does not mean a decrease in the growth rate, but rather reflects a constraint of the Bertalanffy model for growth description when there is a strong increase in L_∞. Pauly (1979) associates a decrease in L_∞ and an increase in k with increasing stress factors such as temperature, fish density and food availability. In this perspective, increases in L_∞ and decreases in k may suggest a decrease in some stress factors.

Apart from density, factors that can lead to changes in fish growth were examined first, such as changes in temperature and primary production (Millner and Whiting, 1996; Jennings et al., 1999; Law, 2000; Thresher et al., 2007). The monthly mean sea surface temperature in selected locations along the southern Brazil continental shelf do not show any evident trend of change from 1982 to 2008 (Fig. 11b), however records of SST anomalies, mainly caused by the ENSO phenomenon were observed (Lentini et al., 2000). It could be argued that SST may not represent the temperatures in the water column but *M. atricauda* inhabits shallow coastal waters, mostly under 30 m deep (Haimovici et al., 1996) in which stratification is frequently disrupted by alternating southwesterly and northeasterly winds in the region (Möller et al., 2008). A short series (1998–2010) of primary productivity (chlorophyll-*a*) in the same region did not show any trend of change, either (Fig. 11c). Just the interannual variations associated with the plume of the La Plata River were observed (Ciotti et al., 2010).

The relationship between growth and density of *M. atricauda* and demersal fishes in the region was examined. Time series of CPUE of king weakfish and all demersal fishes caught by pair trawlers were examined. CPUE of king weakfish peaked at 1100 kg-day in 1980, decreased sharply until 1994 and has stabilized at around 400 kg-day in recent years (Fig. 11d). Total pair trawl CPUE peaked at 6000 kg-day in 1980, decreased sharply until 1994 and has stabilized at around 2000 kg-day in recent years (Fig. 11e). Thus, a threefold decrease in the overall density of *M. atricauda* and of its potential predators and competitors on the inner shelf along southern Brazil can be assumed and associated with the increasing growth of adult *M atricauda*.

In addition, the increasing individual growth could be related to increasing availability of food. Juvenile and small adults of *M. atricauda* feed predominantly on the shrimp *Artemesia longinaris*, while larger females depend progressively more on fish, including cannibalism (Juras and Yamaguti, 1985). *A. longinaris* has been the target of double rig bottom trawlers in the region since 1985 but no CPUE data on its fishery are available because the fishing boats shift from targeting shrimp with small mesh nets to fishing flatfishes with larger mesh in the same fishing trips (Haimovici and Mendonça, 1996). Recorded landings increased until 2004 (Valentini and Pezzuto, 2006). However, this information is not accurate as for some years landings were pooled with those of another shrimp. In a scenario of decreasing abundance of the king weakfish and of potential competitors and of apparent stability or increase in the abundance of its main prey, it is reasonable to think that individual food availability for the king weakfish has increased.

In the same region, growth changes have been observed for the other abundant demersal sciaenid fishes (Haimovici, 1998): *Micropogonias furnieri*, between 1976 and 2002 (Haimovici and Ignácio, 2005); *Umbrina canosai*, between 1976 and 2001 (Haimovici et al., 2006a) and *Cynoscion guatucupa*, between 1976 and 2002 (Miranda and Haimovici, 2007). In all these cases as for *M. atricauda*, the changes were larger for the older fishes and were attributed to decreases in abundance due to fishing pressure. In the first two long-lived species, L_∞ and k increased while in the last two short-lived species L_∞ increased and k decreased, despite the fact that in all four species, the average length-at-age has increased.

5. Conclusions

A consistent validation of the yearly formation of alternate translucent and opaque bands at all ages was possible on thin sections of *M. atricauda* otoliths. Ageing *M. atricauda* on sectioned otoliths is highly recommended because using length-at-age keys based on overestimated ages read on whole otoliths can lead to the underestimation of growth and total mortalities. The growth of *M. atricauda* has increased in the last four decades, most noticeably for adult females over three years old and males over two years old. A threefold decrease in its density and the demersal fish community as a whole are the most likely causes of the growth increase.

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