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Age and growth of the Argentine hake *Merluccius hubbsi* Marini, 1933 in the Brazilian South-Southeast Region during 1996-2001

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This is the first detailed study on the age and growth of the Argentine hake *Merluccius hubbsi* in Brazilian waters. A total of 3,651 specimens obtained from surveys and sampling landings using trawlers and long-lines in the South-Southeast Region (21°S to 34°S) between 1996 and 2001 were analyzed. Readings of sliced and burned otoliths were conducted on 686 individuals (397 females, 129 males and 160 young - sex not identified), identifying opaque and translucent zones. Marginal increment and edge type percentage methods were used for validation, resulting in one ring per year, formed during summer-autumn. Fish with no more than eight rings and six years of age were found, the two first rings after the core being formed during the first year. Back-calculation methods were applied to length/age data and the parameters of von Bertalanffy's growth model were fitted based on average length per ring. The value of maximum theoretical length varied between 470.27 mm and 807.40 mm; growth coefficient varied from 0.1657 to 0.3555 year^{-1} and the theoretical age at length zero between -1.2846 and -0.4552 years. Growth of females and males differed significantly. The techniques applied and the results obtained are discussed and compared with studies on hake conducted in Uruguay and Argentina, providing important information for the management of the species in Brazil, where it presents clear signs of overexploitation.

Este é o primeiro estudo detalhado sobre a idade e o crescimento da merluza *Merluccius hubbsi* no Brasil. Foram analisados 3.651 espécimes obtidos em cruzeiros de pesquisa e provenientes das frotas de arrasto e espinhel de fundo da região Sudeste-Sul do Brasil (21°S a 34°S) entre 1996 e 2001. Leituras de secções transversais de otólitos (corte, polimento e queima) foram realizadas para 686 indivíduos (397 fêmeas, 129 machos e 160 jovens com sexo não identificado), identificando-se zonas opacas e translúcidas. Foram calculados o incremento marginal e a porcentagem do tipo de borda, no tempo, para validação, resultando em um anel por ano, formado durante o verão-outono. Foram obtidos peixes com até oito anéis e seis anos de idade, sendo que os dois anéis depois do núcleo se formam durante o primeiro ano de vida. Foram aplicados métodos de retrocálculo aos dados de comprimento na idade e os parâmetros do modelo de von Bertalanffy foram estimados. O valor do comprimento máximo teórico variou entre 470,27 mm e 807,40 mm; a taxa de crescimento variou de 0,1657 a 0,3555 ano^{-1} e a idade teórica de comprimento zero entre -1,2846 e -0,4552 anos. O crescimento de fêmeas e machos difere significativamente. As técnicas aplicadas e os resultados obtidos foram discutidos, sendo comparados com estudos realizados no Uruguai e na Argentina e provendo informação importante para a gestão da espécie no Brasil, onde a merluza apresenta claros sinais de sobrepesca.

Key words: *Merluccius hubbsi*, Growth parameters, Otolith, Age structure, South-Southeastern region of Brazil.

Introduction

The Argentine hake, *Merluccius hubbsi* Marini 1933 (Gadiformes: Merlucciidae), is a demersal-pelagic species distributed in the West Atlantic from 21°S to 55°S (Figueiredo & Menezes, 1978; Menezes *et al.*, 2003; Cousseau & Perrotta, 2004). Due to its great economic importance, it has been widely studied in Uruguay and Argentina, where Angelescu *et al.* (1958) focused for the first time on its life history pattern. As with other hakes elsewhere in the world (Alheit & Pitcher, 1995), *M. hubbsi* is of great commercial importance in these two countries (Csirke, 1987), where many studies have been published about its reproductive habits and behavior (from Ciechomski, 1967 to Macchi *et al.*, 2006), feeding habits (Angelescu & Fuster de Plaza, 1965; Angelescu & Cousseau, 1969; Angelescu & Prenski, 1987; Prenski & Bezzi, 1991; Prenski & Angelescu, 1993; Ruiz & Fondacaro, 1997; Sánchez & García de La Rosa, 1999), identification of stocks (Bezzi & Perrotta, 1983; Perrotta & Sánchez, 1992; Gutiérrez *et al.*, 1995; Norbis *et al.*, 1999; Sardella & Timi, 2004); general biology

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and management (Rey *et al.*, 1996; Rey & Arena, 1999; Aubone *et al.*, 2000; Aubone *et al.*, 2004; Bezzi *et al.*, 2004; Sabatini, 2004) and biomass estimations (Arena *et al.*, 1987; Rey *et al.*, 1987; Bezzi & Ibáñez, 2003). Many growth studies have been undertaken by Otero (1977), Gaggiotti & Renzi (1990), Renzi & Pérez (1992), Villarino & Giussi (1992), Giussi *et al.* (1994), Torres *et al.* (1996), Norbis *et al.* (1999), Renzi *et al.* (1999), Lorenzo (2003) and Brown *et al.* (2004).

On the Brazilian coast *M. hubbsi* is found between 21°S and 34°S, at depths between 30 m and 700 m. It was traditionally fished by trawlers in small quantities prior to 2001, when commercial fleets expanded their fishing grounds to the shelf break and upper continental slope (Perez *et al.*, 2003; Vaz-dos-Santos, 2005; Perez & Pezzutto, 2006), starting to fish greater quantities of the species (Vaz-dos-Santos & Rossi-Wongtschowski, 2005). Since them, commercial landings of the Argentine hake in Brazil have grown by 197% (1996-2004) (Valentini & Pezzutto, 2006). Moreover, bottom trawl surveys conducted in the area have revealed high *M. hubbsi* concentrations in Brazilian waters (Haimovici *et al.*, 2005), closely related to the seasonal oceanographic characteristics of the region (Rossi-Wongtschowski & Paes, 1993; Seeliger *et al.*, 1998; Rossi-Wongtschowski & Madureira, 2006).

Despite its importance for fisheries, the biology of *M. hubbsi* has only been studied in the past by Haimovici *et al.* (1993), who focused on aspects of its reproductive and feeding habits in Southern Brazilian waters. After them, the following new studies have added to knowledge of the species: Vaz-dos-Santos (2002) on its growth, Vaz-dos-Santos & Rossi-Wongtschowski (2005) on population dynamics and catches, Vaz-dos-Santos *et al.* (2005) on length of first gonadal maturation, Honji *et al.* (2006) on ovarian development, Perez & Pezzutto (2006) on the exploitation of demersal species on the continental slope and Vaz-dos-Santos *et al.* (2006) on the management of its shared stock with Uruguay and Argentina. The above and Haimovici *et al.* (2006) study on the high numbers of juveniles taken in commercial landings have sought to call attention to the overexploitation of *M. hubbsi* in Brazil. According to this consensus, adequate management of the species and increased knowledge of the growth parameters of Brazilian stocks are urgently necessary.

Growth studies are the first step to a knowledge of population dynamics (Csirke, 1980) and permit the identification of stocks and catch structures (based on age composition), the longevity, mortality estimates and stock assessments whether for analytical considerations (Sparre & Venema, 1998) or ecological approaches (Gasalla & Rossi-Wongtschowski, 2004; Walters & Martell, 2004).

Weatherley & Gill's (1987) review shows that growth studies may be conducted in four ways: mark-recapture, cultivation, length-frequency analysis and ring interpretation of scales, otoliths, vertebrae and other structures. Considering that as: (i) Jones (1974 *apud* Podestá, 1990) postulated it is impossible to adopt mark-recapture procedures for hake, (ii) the longevity of this group exceeds twenty years (Alheit & Pitcher, 1995) and (iii) in Brazil there had been no commercial landing series of biological data, ring interpretation constitutes the only mean of investigation of the growth of the Argentine hake. This is an advantage, since it is the most accurate method and provides the best results (Bagenal & Tesch, 1978; FAO, 1981; King, 1995). In addition, the fact that Argentinian and Uruguayan hake growth studies have also been based on otolith analysis is well established, thus permitting comparisons.

The goal of this study was to provide a growth parameter estimate for *M. hubbsi* off the South-Southeast of Brazil and undertake the first detailed investigation related into its growth, time and patterns of ring formation, age validation techniques, age determination, application of back-calculation techniques and von Bertalanffy growth estimates.

Material and Methods

During the Brazilian National Program for the evaluation of the Economic Exclusive Zone Resources (REVIZEE Program), seasonal surveys and commercial landing samplings were conducted in the South-Southeast Brazilian region from 1996 to 2001, using bottom-trawls, mid-water trawls and bottom long-lines (Fig. 1). Commercial landing samples from bottom trawls and bottom long-line fishing gear were also used.

Total length (Lt) of each specimen was measured to the nearest millimeter and total weight (Wt) was recorded to the nearest gram. The sex was attributed on the basis of the macroscopic scale of Vazzoler (1996) and the maturity stages in accordance with Honji *et al.* (2006). Fish with incipient gonadal development, making the registration of sex difficult, were named as not identified (NI). The pair of otolith *sagitta* was removed from the auditive capsules, washed and dried (FAO, 1981; Secor *et al.*, 1991). Length, height and weight

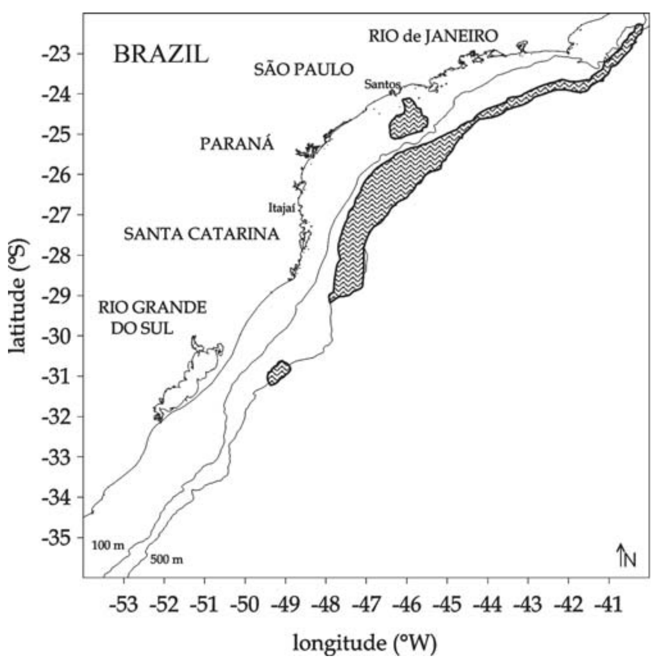

Fig. 1. Study area showing the location of *Merluccius hubbsi* samples collected during 1996-2001.

measurements (Lo, Ho and Wo, respectively) were taken from whole otoliths (Fig. 2). A paired t-test using otolith measurements was performed to ascertain left-right differences (α = 0.05%). Regression and residual analyses were conducted to describe otolith growth in relation to body growth and the relationship between otolith measurements, for males and females and pooled data. Covariance analysis was used to identify differences among regressions. All statistical procedures took Zar (1999) in account.

For otolith readings, sub-sampling was adopted in the attempt to obtain at least twenty hake of each sex and 30 mm length class. The otoliths were processed in accordance with FAO (1981), Secor *et al.* (1991) and Otero (1977); the last specific for *M. hubbsi*, who adopted transversal sections and burning (Christensen, 1964; Polat & Gumü^{o}, 1996) as the best technique for ring visualization. Otoliths greater than 15 mm were sectioned directly on a metallographic sharper. Otolith smaller than 15 mm were mounted in nautical resin before cutting, ensuring the integrity of the structure.

Transversal otolith sections were examined twice under a stereomicroscope applying reflected light by one reader, without giving any information about size, sex of the fish, area or sampling period (Bagenal & Tesch, 1978). The analysis was undertaken based on ICSEAF (1983) and Renzi & Pérez (1992) who established a criterion for ring interpretation adopted by other authors (Torres *et al.*, 1996; Renzi *et al.*, 1999; Norbis *et al.*, 1999; Lorenzo, 2003). A translucent band (TR – a narrow region of clear aspect, dark when burned and related to lower growth rates, intercalated with an opaque band – OP – a wide region related to faster growth rates) was considered as one ring. The otolith radius (Ro) and ring radius (Ra) were measured from the nucleus to the edge of the otolith (Fig. 3). Special attention was given to the two rings formed during the first year, named respectively the first and second demersal rings (after Buratti, 2003). The character (translucent or opaque) of the otolith edge was noted. When no agreement among number of rings, edge pattern and ring measurements was detected (more than 5% of variability), a third reading was taken. After that, if any doubt persisted, the otoliths were excluded from the analysis. All otoliths (whole and sliced) are preserved in the collection of the Laboratório de Ictiofauna, Instituto Oceanográfico da Universidade de São Paulo (from MEHU 000001/1 until MEHU 570812/3).

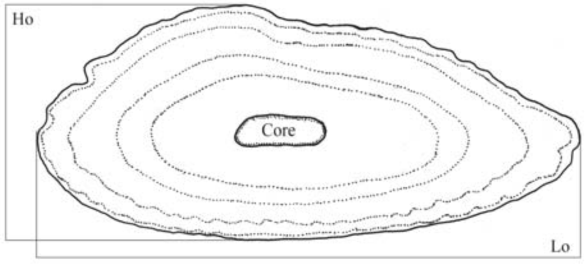

Fig. 2. *Merluccius hubbsi*: scheme of a whole right otolith showing core and length (Lo) and height (Ho) measurements.

The reliability of ring measurements was assessed by a plot of constancy based on the analysis of the measurements of each ring-group, undertaken with all the data and each sex. Differences between otolith ring averages were tested applying variance analysis, after data normality and homocedasticity had been checked (Zar, 1999).

Since one of the most important steps in aging studies is the validation, the establishment of timing and periodicity of ring formation (Beamish & McFarlane, 1983), marginal increment and percentage of edge pattern were calculated with data from the samples over time. Marginal increments were calculated using the equation proposed by Mio (1961):

$$MI = (Ro - Rmax) / Ro$$

where Ro is the otolith radius and Rmax is the outermost ring mark. This methodology, despite the availability of other formulations (Matsuura, 1961; Cadwallader, 1978; Tanaka *et al.*, 1981; Hyndes *et al.*, 1992), is widely applied in growth studies (Cotrina, 1977; Newberger & Houde, 1995; Bernardes, 2002; Amezcua *et al.*, 2006), though not for *M. hubbsi*. The average marginal increment values were compared as between seasons by variance analysis (Zar, 1999).

The back-calculation technique permits (i) the estimation of fish length at the time of ring formation, generating lengths at poorly represented ages, (ii) the magnification of quantities of length data, (iii) the corroboration of ring readings and (iv) greater accuracy for the estimation of parameters. The Fraser-Lee method (Bagenal & Tesch, 1978) has been applied traditionally as well as Francis's (1990) body and structure proportional hypothesis (BPH and SPH, respectively) and Campana (1990). The Fraser-Lee method uses the linear coefficient (a) derived from the regression between otolith radius and total length of the fish (Ro x Lt) in the equation:

$$La = a + [(Lt - a) / Ro] . Ra$$

where La is the total length at age a, Lt is the total length of the fish, Ro is the otolith radius and Ra is the radius of the otolith at age a. Francis's BPH hypothesis (1990) also uses the regression Ro x Lt to calculate the expected fish length in relation to its otolith radius. The correction factor (f) was calculated by dividing the observed by the expected total length and it was used to adjust the back-calculated lengths at the time of ring formation by multiplication. On the other

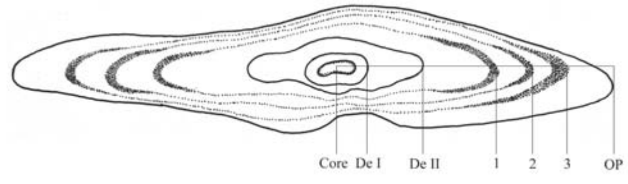

Fig. 3. *Merluccius hubbsi*: scheme of a sliced otolith showing core, demersal I (De I), demersal II (De II), 1 to 3 rings and opaque edge (OP).

hand, the SPH hypothesis based on the regression Lt x Ro permits the estimation of the expected otolith radius in relation to the fish's total length. Another correction factor (f') used to adjust the ring radius was calculated by dividing the observed by the expected otolith radius values.

Campana (1990) adapted Fraser-Lee's method based on the concept of the biological intercept (the starting point of the proportionality between fish length and otolith growth) using the equation:

$$La = Lt + \{ [(Ra - Ro) . (Lt - Lo')] / (Ro - Ro') \}$$

where La is the length at age a, Ra is the radius ring at age a, Ro is the total radius of the otolith, Lt is the fish's total length, Lo' and Ro' are the biological intercept considering here the values adopted by Vaz-dos-Santos (2002) for *M. hubbsi* in Brazil as 57 mm and 0.52 mm, respectively.

The von Bertalanffy growth model (VBGM) (von Bertalanffy, 1938) was fitted to age data using Solver in Microsoft Excel (Kelly *et al.,* 1997; Bellucco *et al.*, 2004; David *et al.*, 2005) for both observed and back-calculated lengths at age, for males and females separately and together, using the equation:

$$La = L_{inf} [1 - e^{-K(a - a_0)}]$$

where La is the predicted mean length at age a, L_{inf} is the maximum theoretical mean length, K is the growth coefficient and a_0 is the theoretical age at length zero. Comparisons among growth parameters obtained by different methods (observed and back-calculated) were made using the growth performance index (ϕ) developed by Munro & Pauly (1983):

$$\phi = \log K + 2 \log L_{inf}$$

The values obtained by this calculation were compared by means of a variance analysis (Zar, 1999).

Results

A total of 3,651 *M. hubbsi* specimens were caught during the surveys and from commercial landings between 1996 and 2001. The data were grouped in order to give a representative number and lengths for the analysis (Fig. 4). The minimum Lt was 24.00 mm and the maximum 647.00 mm (average 206.23 mm and median 200.00 mm). By sex 1,048 females (45.00 mm < Lt < 647.00mm), 809 males (97.00 < Lt < 575.00 mm) and 1,794 not identified (24.00 mm < Lt < 490.00 mm), were obtained in the samples.

The left and right otolith measurements did not present any differences (p > 0.05 for Lo, Ho and Wo), allowing the use of any of them. Regressions fitted and determination coefficients are presented in Table 1, for both sexes and all the fish. For all the otolith regressions analyzed, the difference between the sexes was significant (p < 0.001). Lt, Lo and Ho were described by both linear and logarithm models. The relationships involving otolith weight (Wo) were best described by power regressions. Thus, the otoliths of the Brazilian *M. hubbsi* can also be used for aging studies.

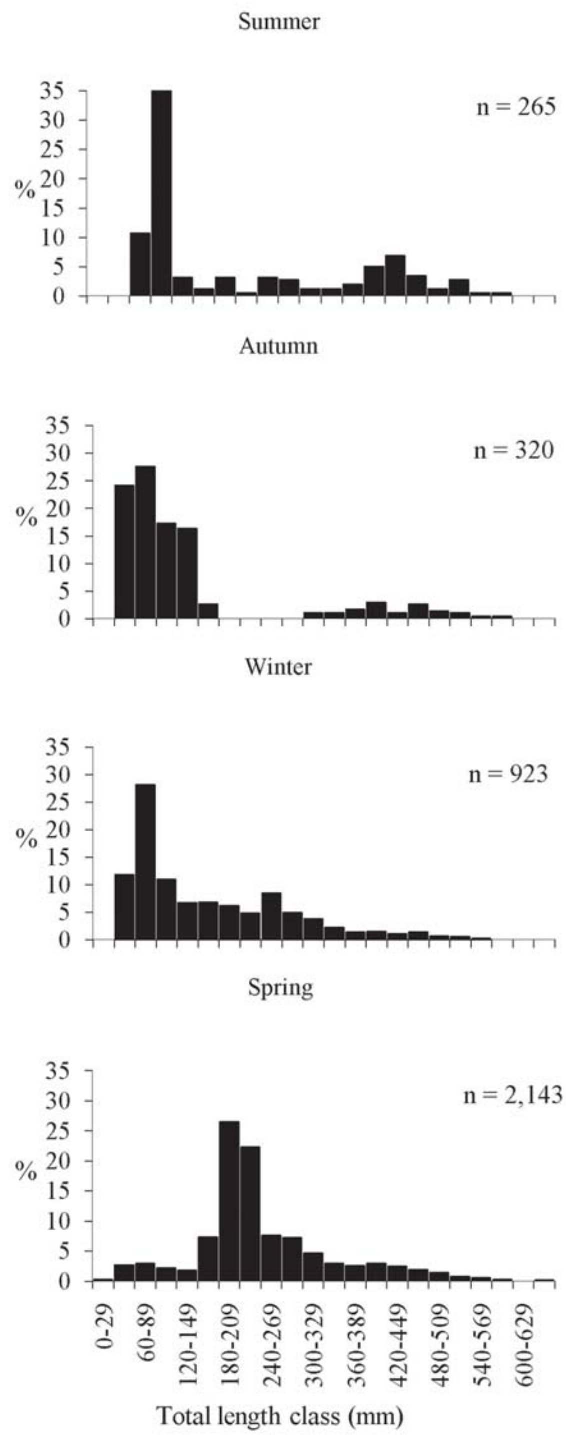

Fig. 4. *Merluccius hubbsi*: seasonal length class distribution obtained from surveys and commercial landings during the period 1996-2001.

A total of 705 otolith sections were examined and 70.0% of agreement was found as between the first and the second readings. After the third reading, this percentage grew to 97.3%

Table 1. *Merluccius hubbsi*: parameters of the fits related to otolith measurements, determination coefficient (r^2) and sample sizes (n).

Model Fitted	Sex	a	b	r^2	n
Lt-Lo	all fishes	0.5693	0.0446	0.9902	1.036
linear	Female	0.5060	0.0446	0.9914	889
	Male	0.2370	0.0469	0.9849	614
Lt-Wo	all fishes	$9\ .10^{-8}$	2.4200	0.9767	848
power	Female	$9\ .10^{-8}$	2.4155	0.9782	716
	Male	$5\ .10^{-8}$	2.5616	0.9512	438
Lt-Ho	all fishes	-12.417	3.2420	0.9639	1.074
logarithm	Female	-12.404	3.2478	0.9666	924
	Male	-10.088	2.7345	0.9371	637
Lo-Wo	all fishes	0.0001	2.5409	0.9866	981
power	Female	0.0001	2.5360	0.9867	849
	Male	0.0001	2.6048	0.9687	571
Lo-Ho	all fishes	-2.6629	3.2872	0.9541	1.126
logarithm	Female	-2.6465	3.3066	0.9584	975
	Male	-1.7326	2.6736	0.9301	695
Ho-Wo	all fishes	0.0007	2.7724	0.9867	990
power	Female	0.0007	2.7741	0.9867	856
	Male	0.0007	2.6699	0.97	573

with the sub-sample (686 sections, being 397 females, 129 males and 160 young of unidentified sex remaining to the next steps). No fish was found with more than eight rings in the otoliths. Based on the criteria adopted, the first one after the core was identified as demersal I, the second as demersal II and the others were numbered from one to six. The number of fish by ring-group is presented in Table 2.

The constancy plot showed little overlap among ring measurements whether for females or males together (Fig. 5) and separately. The ANOVA applied to the average ring radius showed significant differences for the sexes analyzed together ($F = 15{,}185.35$, $p < 0.001$, $r^2 = 0.9782$) and separately ($F = 12{,}897.71$, $p < 0.001$, $r^2 = 0.9786$ for females and $F = 3{,}233.76$, $p < 0.001$, $r^2 = 0.9717$ for males).

The marginal increment calculated for the fish with two (Fig. 6) and three (Fig. 7) rings, which were the most frequent in the samples, showed that rings are formed annually. However, the time of the ring formation of these two groups did not match: group two presented ring formation in autumn and group three during summer. No significant differences were found in the marginal increment averages as between

Table 2. *Merluccius hubbsi*: specimen frequency by edge pattern and ring-group.

Ring-group	Edge Pattern	Absolute Frequency	Total
0	OP	143	236
	TR	93	
1	OP	63	103
	TR	40	
2	OP	60	115
	TR	55	
3	OP	76	155
	TR	79	
4	OP	34	64
	TR	30	
5	OP	6	11
	TR	5	
6	OP	2	2
	TR	---	
Total			686

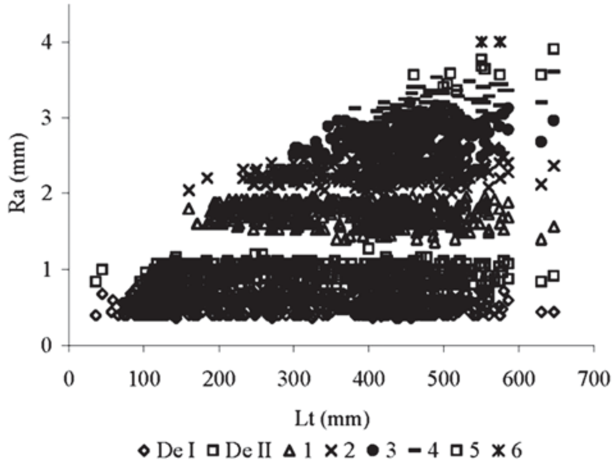

Fig. 5. *Merluccius hubbsi*: plot for total length (mm) and ring radius (mm) showing the constancy of otolith readings.

seasons for ring-group two ($F = 1.35$, $p = 0.262$) and for ring-group three ($F = 1.41$, $p = 0.241$). It was not possible to analyze the sex data separately due to the low number of males caught. In this way, females showed the same graphic shape, illustrated in Figs. 6 and 7. Concerning the analysis of the edge pattern by season, conducted on ring-groups two and three (Fig. 8 and Fig. 9, respectively), the results showed the same aspects described for periodicity and seasonality. The highest percentages of translucent edge were found during autumn for ring-group two and during the summer for ring-group three.

Since one year was obtained after the validation of the rings, an age-length distribution table was prepared (Table 3). For the back-calculation procedures of Fraser-Lee and the BPH hypothesis, power regressions between otolith radius (Ro) and total length were fitted to the data of all the fish ($Lt = 99.7\ Ro^{1.2576}$, $r^2 = 0.9536$, $p < 0.001$), both females ($Lt = 101.26\ Ro^{1.259}$, $r^2 = 0.9603$, $p < 0.001$) and males ($Lt = 102.71\ Ro^{1.1062}$, $r^2 = 0.9488$, $p < 0.001$). The regressions between total length and otolith radius were also fitted for all the fish ($Ro = -5.7642 + 1.4558 \ln Lt$, $r^2 = 0.9456$, $p < 0.001$), females ($Ro = -5.7172 + 1.4489 \ln Lt$, $r^2 = 0.9408$, $p < 0.001$) and males ($Ro = -5.2744 + 1.3583 \ln Lt$, $r^2 = 0.9457$, $p < 0.001$).

Observed lengths and mean back-calculated lengths at ages (Table 4) were used to fit the growth parameters of the VBGM. The maximum theoretical length varied between 470.27mm and 807.40mm; the growth coefficient varied between 0.1657 and 0.3555 $year^{-1}$; the theoretical age at length zero varied between -1.2846 and -0.4552 years and the growth performance index continued at between 4.88 and 5.05 ($F = 28.63$, $p = 0.001$, $r^2 = 0.7816$) (Table 5). Growth curves are shown for females (Fig. 10) and males (Fig. 11).

Discussion

This study is the first detailed growth analysis of *M. hubbsi* in Brazilian waters showing that otolith ring counting is a satisfactory method for the assessment the species age, as

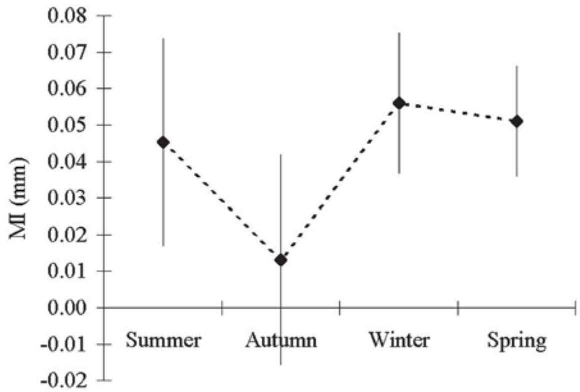

Fig. 6. *Merluccius hubbsi*: seasonal average marginal increment (MI, mm) and confidence limits obtained for all fish with two rings.

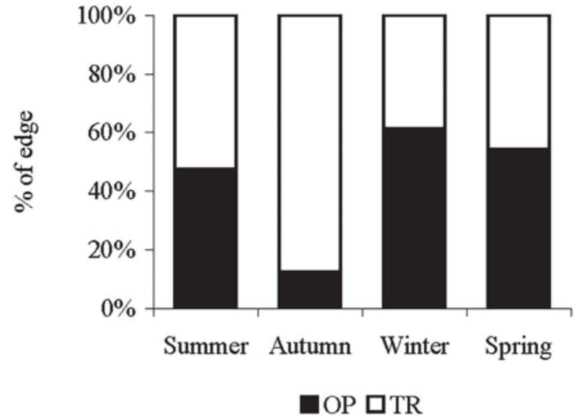

Fig. 8. *Merluccius hubbsi*: seasonal frequency of opaque (OP) and translucent (TR) edges for fish otoliths with two rings.

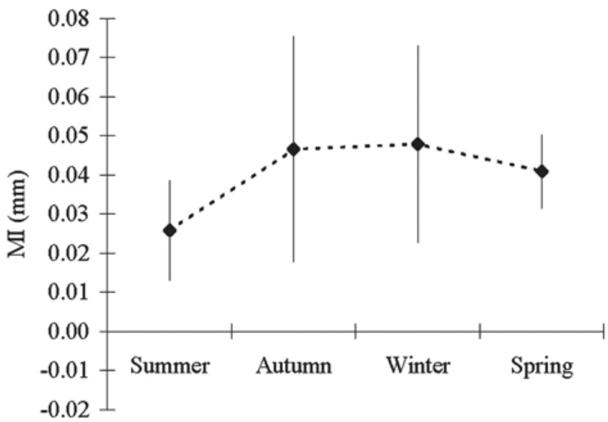

Fig. 7. *Merluccius hubbsi*: seasonal average marginal increment (MI, mm) and confidence limits obtained for all fish with three rings.

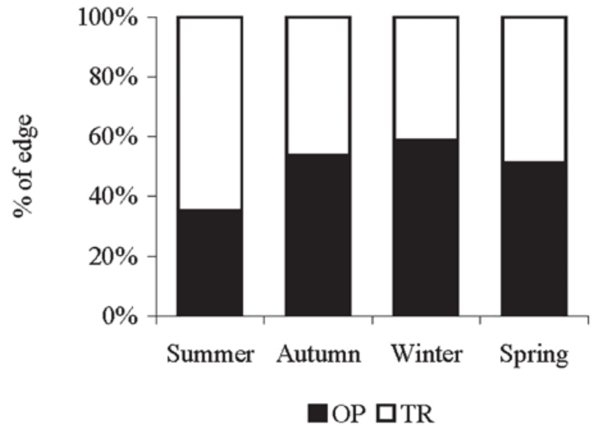

Fig. 9. *Merluccius hubbsi*: seasonal frequency of opaque (OP) and translucent (TR) edges for fish otoliths with three rings.

Table 3. *Merluccius hubbsi*: age-length distribution obtained from ring-counts of the otoliths.

Total length class (mm)	0	1	2	3	4	5	6	Total
0-29								
30-59	4							4
60-89	30							30
90-119	68							68
120-149	68							68
150-179	33	2	1					36
180-209	20	19	1					40
210-239	12	31	2					45
240-269	1	23	11					35
270-299		17	23					40
300-329		7	25	5				37
330-359		3	12	11				26
360-389		1	7	18	2			28
390-419			13	34	5			52
420-449			9	33	11			53
450-479			5	27	12	1		45
480-509			3	10	12	4		29
510-539			3	11	11	2		27
540-569				5	7	2	1	15
570-599				1	4		1	6
600-629								
630-659						2		2
Total	236	103	115	155	64	11	2	686

Table 4. *Merluccius hubbsi*: average total length at age from otolith rings and back-calculation analysis.

Method	Sex	Age-group						
		0	1	2	3	4	5	6
Rings	All fishes	131.10	245.00	340.00	430.30	483.90	537.00	562.50
	Females	122.70	245.80	362.10	435.30	483.90	540.70	550.00
	Males	125.30	239.82	288.15	348.78	540.00	500.00	575.00
Fraser-Lee	All fishes	153.11	263.65	335.92	401.63	457.86	513.12	546.80
	Females	155.44	272.39	344.42	404.69	458.18	516.55	536.93
	Males	132.28	229.67	283.59	354.61	474.03	496.67	556.84
BPH	All fishes	67.26	201.32	291.78	373.77	438.53	498.40	538.63
	Females	66.73	203.62	296.75	376.24	439.27	502.90	529.91
	Males	71.78	199.81	266.04	337.71	452.08	482.59	550.59
SPH	All fishes	87.70	174.67	251.68	336.13	405.00	467.16	519.00
	Females	85.94	171.89	252.28	337.39	406.12	473.23	513.40
	Males	84.31	178.77	242.98	301.15	388.24	432.20	522.86
Campana	All fishes	82.51	221.59	308.68	385.56	447.41	505.61	542.90
	Females	81.60	225.67	314.89	388.24	447.91	509.54	533.57
	Males	78.62	204.62	269.31	340.81	456.64	485.95	552.23

has been done by Uruguayan and Argentinian scientists.

Relationships between otolith length, height and weight presented high values for the coefficient of determination (r^2), indicating that otoliths represent fish growth adequately. Only Ruarte (1997) presented these relationship values for *M. hubbsi* from Argentina and his results were similar to those of the present study, although higher values were found in

Table 5. *Merluccius hubbsi*: growth parameters and growth performance index obtained in the present study.

Method	Sex	L_{inf}	K	a_0	ϕ
Rings	All fishes	782.92	0.1991	-0.9129	5.09
	Females	660.95	0.2871	-0.7080	5.10
	Males	797.75	0.1523	-1.1395	4.99
Fraser-Lee	All fishes	737.00	0.1863	-1.2846	5.01
	Females	674.94	0.2231	-1.2099	5.01
	Males	614.42	0.2000	-1.2365	4.88
BPH	All fishes	725.51	0.2091	-0.4881	5.04
	Females	685.82	0.2332	-0.4552	5.04
	Males	470.27	0.3555	-0.4796	4.90
SPH	All fishes	807.40	0.1657	-0.6845	5.03
	Females	743.53	0.1924	-0.6259	5.03
	Males	533.11	0.2667	-0.6592	4.88
Campana	All fishes	697.23	0.2279	-0.5854	5.04
	Females	656.91	0.2584	-0.5415	5.05
	Males	474.89	0.3497	-0.5320	4.90

Brazil, associated with warmer water temperatures. The Argentine hake occurs in Brazil in the upper portion of the Brazilian Current, which is composed of Tropical Water (temperature above 20°C) and the South Atlantic Central Water (SACW, 6°-20°C) (Castro *et al.*, 2006). These temperatures are higher than those of the water masses that flows on the Argentinian continental shelf, a mixture of Malvinas (Falklands) Current with Sub-Antarctic and continental waters (Guerrero & Piola, 1997). In this area, surface temperatures vary between 7°C and 8°C in winter and 10°C and 11°C in summer (Boltovskoy, 1981; Piola & Rivas, 1997). Moreover, Lombarte & Lleonart (1993) have proved higher temperatures accompany higher rates of otolith growth, especially for Gadiform fish.

Sliced otoliths are the best way to investigate the rings in the Argentine hake. Otero (1977) and Gaggiotti & Renzi (1990) compared whole and sectioned otoliths, but since Renzi & Pérez (1992) established a trustworthily criteria for ring-counts based on sliced otoliths, this methodology has traditionally been used for the species (Villarino & Giussi, 1992; Giussi *et al.,* 1994; Torres *et al.*, 1996; Norbis *et al.,* 1999; Renzi *et al.*, 1999; Lorenzo, 2003).

The percentage of agreement among counts was highly satisfactory. Gaggiotti & Renzi (1990), Renzi & Pérez (1992), Villarino & Giussi (1992) and Giussi *et al.* (1994) normally made otolith analyses with two readers simultaneously, discarding those for which there was no consensus, but in none of the papers cited was the percentages of coincidence among counts presented.

This paper introduces a new classification for the ring arrangement since many authors have been referring to the rings formed during the first year as pelagic and demersal, respectively (Torres *et al.*, 1996; Norbis *et al.*, 1999; Lorenzo, 2003). Buratti (2003), based on otolith microstructure analysis, showed that the "pelagic ring" is formed two months after birth, when younglings migrated from the pelagic to the demersal habitat, with approximately 30 mm of total length. Thus, "pelagic ring" is not an appropriate designation and we have called it demersal ring I. The second is the demersal ring II, previously named demersal. The reasons for demersal ring formation are still unknown according to the most recent studies on *M. hubbsi*'s growth (Lorenzo, 2003; Brown *et al.*, 2004).

The constancy graph permits the analysis of a biological and a methodological aspect. In the first case, it is possible to conclude that there is no absorption or decalcification of the otoliths. In the second case, the counts presented no tendency. These present authors have found no published papers that use this kind of analysis for *M. hubbsi*.

In relation to the time formation of rings, the Uruguayan and Argentinian studies have all used the aspect of the edge for validation. Otero (1977) and Lorenzo (2003) verified annual ring deposition, a wide and conspicuous translucent zone. These authors also refer to a second translucent mark, not identified in the present study. Norbis *et al.* (1999) also observed the predominance of one translucent edge during the year. The two methods used here also showed the annual deposition of rings in otoliths, occurring during summer-autumn for *M. hubbsi* from Brazilian waters.

The variations in the average marginal increment did not differ significantly (ANOVA, $p > 0.05$), due to the presence of fish with an opaque and translucent edge throughout the year. This variability was also found in Argentinian and Uruguayan studies. Otero (1977) determined October (spring) as the period of ring formation, disregarding secondary rings in his analysis. Gaggiotti & Renzi (1990) found ring formation

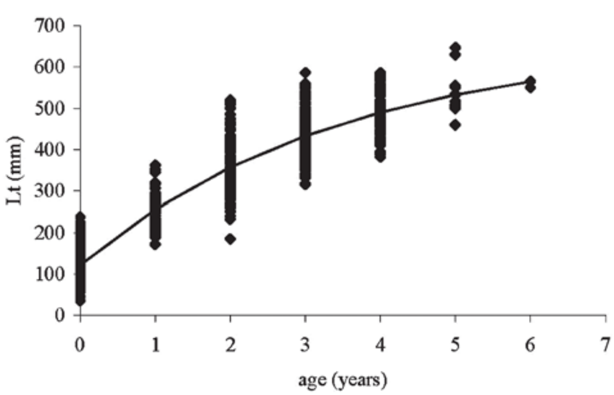

Fig. 10. *Merluccius hubbsi*: age-size data and growth curve fitted applying Campana back-calculated method for females.

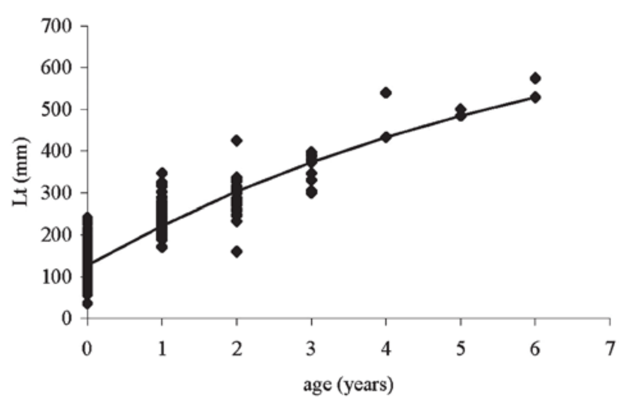

Fig. 11. *Merluccius hubbsi*: age-size data and growth curve fitted applying Campana back-calculated method for males.

during the second semester. Lorenzo (2003) indicated late winter and early spring as the seasons of ring formation. However, Norbis *et al.* (1999) evidenced high frequencies of translucent bands in fish caught during the spring and summer with opaque bands increasing in the autumn and predominant in the winter, thus agreeing with our results.

Ring formation implies alterations in somatic growth (Bagenal & Tesch, 1978; Weatherley & Gill, 1987; Lombarte & Lleonart, 1993). Reproduction and feeding modify the organism's physiology (Vazzoler, 1996; Zavala-Camin, 1996) and explain ring formation, in association with environmental conditions such as fluctuations of productivity and food availability. In Brazil, Honji *et al.* (2006) showed that the Argentine hake is a multiple spawning species and spawning females are caught in the Southeast-South region throughout the year. Besides, Lessa *et al.* (2006) recently showed that validation through marginal increments in multiple spawners is affected by the extensive period of oocyte liberation. These facts might be related to the ring formation in otoliths, it being reasonable to hypothesize that reproduction (spawning) is responsible for the time variability found in ring formation.

Concerning age structure, Argentine hake of four, five and six years of age were sporadic in the samples, males being rare. These ages were lower than those observed in Uruguay and Argentina. At the beginning of the Argentine hake fishery, Angelescu *et al.* (1958) identified fish of between one and seven years old. After them, reports summarizing results of surveys conducted during the later sixties and the earlier seventies record fish of between one and thirteen years old (Rojo & Silvosa, 1969; Odemar & Silvosa, 1971). Otero (1977) found both males and females with no more than nine years of age. Gaggiotti & Renzi (1990) again found fish of up to thirteen years of age. Nevertheless, these studies were conducted before the establishment of the criteria for otolith ring counts in *M. hubbsi* established by Renzi & Pérez (1992). So an overestimation of the age by two years as regards the interpretation of the first rings may have occurred, it being acceptable that these studies recorded fish of up to eleven years of age. After the publication of Renzi & Pérez's (1992) criteria, Giussi *et al.* (1994) recorded fish of from one to ten years old. Lorenzo (2003) and Bezzi *et al.* (2004), giving the most recent data about age and growth of the species in Uruguay and Argentina, reported females of eleven years of age and males of eight.

All the above studies present similar mean lengths for age as this present one in Uruguayan and Argentinian waters. A tendency to a reduction in length has been detected over the years, due to overexploitation (Aubone *et al.*, 2000; Bezzi *et al.*, 2004). These studies also confirm that females grow bigger and live longer than males, as has also been found in Brazil. However, only earlier ages have been found in Brazil, as historical observations of commercial landings have shown that more than fifteen years ago larger and older hake were common. This fact suggests that the Argentine hake is overexploited, corroborating the same diagnosis made by Vaz-dos-Santos & Rossi-Wongtschowski (2005) and Haimovici *et al.* (2006) based on the large number of juveniles (of less than 356.80 mm L_{50}, according to Vaz-dos-Santos *et al.*, 2005) present in the commercial landings.

Fraser-Lee's back-calculation method is based on the linearity of the relationship between otolith radius and total length, with the straight line not intersecting the origin (Bagenal & Tesch, 1978; Campana, 1990). This fact could have led to the abandonment of the use of this methodology. However, Hile (1970) reviewed the relations between the otolith radius and the length of the fish, checking on many studies presenting non-linear fits. Particularly, Monastyrsky (1930 *apud* Hile, *op. cit.*) was one of the first authors who fitted a non-linear relationship and obtained satisfactory results. Francis (1990) also agrees that the non-linear fits may be used. Power relationships obtained between otolith radius and total length reflect the behavior of the whole otolith in the height axis, presuming that this pattern will be maintained in the transversal section. Proportional methods (BPH and SPH) had been considered initially by Whitney & Carlander (1956) and reconsidered by Francis (1990), who recommended the application of both techniques. The difference between the two estimations results in a degree of imprecision. Campana (1990) proposed his back-calculation method as a modification of Fraser-Lee's, minimizing bias by applying the biological intercept concept, the starting-point of the otolith and fish length relationship. The main problem of this relates to the determination of the values of Lo' and Ro'. Francis (1995) had criticized it, pointing out that this assertion was only a conjecture and dependent on detailed knowledge of early growth. Brown *et al.* (2004) calculated Lo' and Ro' in larvae of *M. hubbsi* from Argentina, obtaining 2.0 mm and 7.7 mm, respectively. We have considered it inappropriate to use these values for Brazilian hake, since it is better to use values calculated for the same area; so in the present study the biological intercept was adopted from the values obtained from the smallest fish ever captured in our samples, used earlier with success by Vaz-dos-Santos (2002).

Except for the Fraser-Lee method for ages zero and one, all other methods applied underestimated mean total lengths for age in relation to those calculated from ring counts. Lorenzo (2003) was the only one who used back-calculation (Campana method) for Argentine hake. According to Bagenal & Tesch (1978), length underestimation could be related to the Lee phenomenon and may be attributed to various factors: (i) incorrect back-calculation, (ii) no random sample (larger fish advantage), (iii) natural selection (favoring younger fish) and (iv) fish mortality. The first two hypotheses can certainly be discarded because different back-calculation methods had been used to prevent model failures and a variety of fishing gear had been used for sampling. It is impossible anyway to quantify the effect the mortality rates exert on the population analyzed.

As for back-calculation functions, already commented on Material and Methods, we consider that their application gave support to ring reading and accuracy for parameter estimation. Analyzing VBGM parameter estimates and comparing them with mean lengths obtained from rings counts, attention must be draw to two points: the lowest values of t_0 may be assumed to be the closest to reality, because the fish hatch five days after fertilization (Bezzi *et al.*, 2004); L_{inf} values must be close to the maximum total lengths observed. Thus the best VBGM parameter fit derive from Campana back-calculated lengths, fortunately the method that has the best biological basis and is the same as that adopted in Uruguay for *M. hubbsi* (Lorenzo, 2003). Attention must be given to male parameter estimations based on mean lengths obtained from ring-counts, the values of which are far too high, greatly exceeding the true ones. Besides, only growth parameters whose values for the growth coefficient (K) of the males are higher than those for the females can be biologically acceptable.

The growth performance index takes the natural relationship between the maximum theoretical length and the growth coefficient into consideration (Munro & Pauly, 1983) and may reflect the diet of a species (Isaac-Nahum, 1990). According to this latter author, ϕ values near group five (found in *M. hubbsi*) represent an active carnivorous species on a high trophic level. The results of the present study showed males already in group four (approximating to five) and females in group five. This reflects the smaller lengths attained by males, as a consequence of differential growth. In a trophic approach, males occupy lower depths than females, having other feeding ground (Angelescu & Prenski, 1987), thus also justifying differences in ϕ values as between sexes. Comparing the growth parameters obtained here with those from the relevant literature after Renzi & Pérez (1992) (Table 6) it is possible to diagnose the same situation as is described above. Older and larger specimens of *M. hubbsi*, especially females, are still present in the most recent Uruguayan and Argentinian landings and surveys (Lorenzo, 2003; Bezzi *et al.*, 2004), reflected in the greater values of maximum theoretical mean length.

Summarizing, the growth parameters based on Campana back-calculation method obtained for *M. hubbsi* are the most adequate, being L_{inf} = 656.91 mm, K = 0.2584 year^{-1} and t_0 = -0.5415 year for females and L_{inf} = 474.89 mm, K = 0.3497 year^{-1} and t_0 = -0.5320 year for males. If no sex information is available, parameters estimated for sex pooled may be used (L_{inf} = 697.23 mm, K = 0.2279 year^{-1} and t_0 = -0.5854 year). The drastic reduction in the number of fish of above three years of age clear demonstrates the overexploitation of the Argentine hake in Brazil.

It seams that Brazilian *M. hubbsi* growth does not occur in the same way of that observed in Uruguay and Argentina, but studies that are being finished showing that Argentine hake in the South Brazilian area is a shared species between these countries.

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Table 6. *Merluccius hubbsi*: growth parameters and growth performance index obtained from the relevant literature.

Study	Method	Sex	L_{inf}	K	a_0	ϕ	Area / Period
Bezzi	Rings	Females	885.5	0.1883	-0.27	5.17	Argentina,
et al.		Males	616.6	0.3960	-0.38	5.18	northern stock, 2003
(2004)		Females	980.0	0.1458	-0.42	5.15	Argentina,
		Males	542.9	0.3852	0.01	5.06	southern stock, 2003
Lorenzo	Rings	Females	933.50	0.1610	-0.727	5.15	
(2003)		Males	539.30	0.3630	-0.442	5.02	Uruguay,
	Campana	Females	806.40	0.1790	-0.537	5.07	Autumn, 1994
		Males	519.10	0.3200	-0.661	4.94	
	Rings	Females	826.80	0.1890	-0.598	5.11	
		Males	487.40	0.4430	-0.266	5.02	Uruguay,
	Campana	Females	761.60	0.2080	-0.344	5.08	Spring, 1994
		Males	487.90	0.3480	-0.345	4.92	
	Rings	Females	889.40	0.1600	-0.777	5.10	
		Males	509.90	0.3850	-0.661	5.00	Uruguay,
	Campana	Females	810.20	0.1800	-0.493	5.07	Autumn, 1995
		Males	493.00	0.3700	-0.380	4.95	
Giussi	Rings	Females	757.03	0.217	-0.333	5.09	Argentina,
et al.		Males	506.80	0.33	-0.881	4.93	Summer, 1983
(1994)		Females	757.67	0.247	-0.525	5.15	Argentina,
		Males	514.31	0.323	-1.080	4.93	Winter, 1983

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