

AGE AND GROWTH OF BRAZILIAN SARDINELLA, *Sardinella brasiliensis* (STEINDACHNER) (OSTEICHTHYES:CLUPEIDAE), IN SOUTHEASTERN BRAZIL

Idade e crescimento da sardinha-verdadeira, *Sardinella brasiliensis* (Steindachner) (Osteichthyes:Clupeidae), no Sudeste do Brasil

Antonio Aduato Fonteles-Filho¹, Maria Odete Ximenes-Carvalho¹, Melquíades Pinto Paiva², Miguel Petrere Júnior³

ABSTRACT

New estimates of the growth parameters of Brazilian sardinella, *Sardinella brasiliensis* (Steindachner), have been obtained, based on readings of age rings on scales collected in the period from April, 1999 through March, 2000, off southeastern Brazil. The hypothesis of the existence of isometry in fish/scale growth was confirmed and the ageing techniques were validated by monthly variations in the marginal increment and in the mean back-calculated length, indicating birthday dates in April and November. Two cohorts are supposed to be produced by spawnings taking place about six months apart. The weight-length relationship is given by the regression equation $W = 0.0000867 L^{2.570}$. Growth equations in length (mm) and weight (g) are: $L_t = 286 [1 - e^{-0.462(t + 1.3)}]$ and $W_t = 178.2 [1 - e^{-0.462(t + 1.3)}]^{2.570}$, with a growth performance index $\phi = 4.58$. The first ring in scales of Brazilian sardinella should be formed when individuals are actually 1.8 year old, within a life span that reaches $t_{max} = 7.7$ yr. The natural mortality coefficient was estimated as $M = 0.769$ and the ratio $M/K = 1.66$ is within the order of magnitude for Clupeidae species, being consistent with the behavior of small carnivorous species.

Key words: Brazilian sardinella, *Sardinella brasiliensis*, age, growth, weight-length relationship, southeastern Brazil.

RESUMO

Novas estimativas de parâmetros do crescimento da sardinha-verdadeira, *Sardinella brasiliensis* (Steindachner) foram obtidas com base na identificação e medição de anéis etários e zonas de crescimento em escamas coletadas no período de abril de 1999 a março de 2000, na região Sudeste do Brasil. A hipótese da existência de isometria na relação peixe/escama foi confirmada e a periodicidade na formação dos anéis etários foi validada através da variação mensal no incremento marginal e no comprimento retrocalculado, indicando datas de aniversário das coortes em abril e novembro. Portanto, devem existir duas coortes produzidas a partir de desovas que ocorrem com intervalo de seis meses. A relação peso/comprimento é dada pela equação $W = 0,0000867 L^{2,570}$. O crescimento em comprimento (mm) e em peso (g) é representado pelas seguintes equações: $L_t = 286 [1 - e^{-0,462(t + 1,3)}]$ e $W_t = 178,2 [1 - e^{-0,462(t + 1,3)}]^{2,570}$, com índice de desempenho do crescimento $\phi = 4,58$. O primeiro anel em escamas da sardinha-verdadeira deve formar-se quando os indivíduos têm 1,8 ano de idade, para uma expectativa de vida, $t_{max} = 7,7$ anos. O coeficiente de mortalidade natural foi estimado em $M = 0,769$ e a razão $M/K = 1,66$ se encontra dentro da ordem de magnitude para espécies da família Clupeidae, confirmando seu nicho trófico como o de pequenas espécies carnívoras.

Palavras-chaves: sardinha-verdadeira, *Sardinella brasiliensis*, idade, crescimento, relação peso/comprimento, Sudeste do Brasil.

¹ Instituto de Ciências do Mar; Universidade Federal do Ceará, Av da Abolição, 3207 - Fortaleza, CE 60165-081. E-mail: afontele@labomar.ufc.br; ximenes@labomar.ufc.br

² Departamento de Biologia Marinha, Universidade Federal do Rio de Janeiro, Cidade Universitária, Rio de Janeiro, RJ 21944-970. E-mail: mappaiva@uol.com.br

³ Departamento de Ecologia, UNESP, Rio Claro.

INTRODUCTION

The Brazilian sardinella, *Sardinella brasiliensis* (Steindachner), is a fish endemic to the southeastern Brazilian coast and geographically isolated from other species of the genus *Sardinella* in the Atlantic Ocean. It is the most abundant marine fishery resource in Brazil, exploited by purse-seiners since the late 1950s. Its population is confined to the Brazilian Bight, it does not migrate extensively and its abundance is limited by the productivity of the region from São Tomé Cape (22° S – Rio de Janeiro State) down to Santa Marta Grande Cape (29° S – Santa Catarina State), having reached its maximum yield of 243,000 t in 1973 (Cergole, 1995). Since then the annual yield showed a continuous downward trend leading to a minimum in 1990, with 33,037 t, wherefrom there have been signs of recovering which caused yield to reach values around 120,000 t in 1997, but which did not actually proved true in more recent years (Dias Neto, 2002). That decreasing trend seems to be a result of the combined interaction of overfishing, and economic and environmental instability, the latter one specially caused by failures in recruitment ascribed to a lack of intrusion of the South Atlantic Central Water, which must have caused high larval mortality (Matsuura, 1995). This scenario of collapse by an otherwise productive fishery has called for periodical reviews of age and growth estimates because of their relevance to the understanding of population dynamics processes.

Being a short-lived fish, the growth rate of Brazilian sardinella is high and it is supposed to have an important bearing upon variations in the species' asymptotic length. Therefore, age and growth have been its most studied aspects in population dynamics, but the variety of methods used (length frequency distribution, age annuli in otoliths and scales, the Compleat ELEFAN, modal progression analysis and FISAT package) have yielded accordingly a wide array of estimates of K (0.31.yr⁻¹ to 0.87.yr⁻¹), L_{∞} (230 mm to 335 mm), and t_0 (-0.15 to -2.00 yr. (Richardson *et al.*, 1960; Santos & Frantzen 1965; Rijavec *et al.*, 1977; Matsuura, 1977 and 1983; Vazzoler *et al.*, 1987; Cergole & Valentini, 1994; Cergole, 1995; Cergole *et al.*, 1999).

Most environmental abiotic and biotic factors all have some sort of effect on the actual growth rate or the way rings formed on hard structures of fish can be interpreted during age determination studies. Otoliths are thought to be more reliable than scales in age studies (Vazzoler *et al.*, 1982) but the use of computer methods has come to be more and more frequent to that end. In the Subtropical Zone, such factors as temperature, spawning season and food supply should

be held accountable for the occurrence of the effects of growth changes on the fish body, specially hard structures. Spawning of Brazilian sardinella is multiple and protracted, spanning the period of October-April, with different peaks over the fishing area. Age rings are formed on early August and the first ring in otoliths appears after 6 to 8 months. Validation of age has been established by means of isometric growth of the fish and their hard structures, and the periodicity in ring formation (Magro *et al.*, 2000).

A vital question on the population dynamics of Brazilian sardinella has somehow remained unanswered, that is the one dealing with the time span of its age groups, thought to be annual by some authors and half-yearly by others. Therefore, this paper intends to throw some further light upon the question raised as to the hypothesis of two cohorts being formed within a twelve-month period as a result of two spawnings occurring on the northern and southern parts of the distribution region (22°–29° S) and, hence, giving rise to semestral age groups. The database consists of information gathered from scale reading in a year's period which is amenable to comparison with similar ones got from otolith reading.

MATERIAL AND METHODS

The biological material studied was made up of scales collected from individuals of Brazilian sardinella in commercial landings at Angra dos Reis fishing harbor (Rio de Janeiro State) by purse-seiners operating on the continental shelf of southeastern Brazil in the period April, 1999 through March, 2000. All individuals were caught by a standard method (purse seining) over a narrow depth range, so that no adjustment needed being made to correct possible bias arising from depth specific size distribution. Furthermore, purse-seine is supposed to be a non-selective gear so that no bias is expected to exist in the stock length distribution.

The sample was comprised of 480 individuals of both sexes ranging in size from 140 mm to 299 mm TL, whose scales varied from 3.2 mm to 7.2 mm, as measured from the focus to the outer edge. The age structure is composed of age groups varying from 1 year (130 mm TL) identified in scales of 480 individuals, to 6 years (238 mm TL) identified in scales of 5 individuals. In addition, the length-weight relationship was fitted through the equation $W = aL^b$, where W is weight of an individual in grams and L is total length (mm), using least-squares regression on log-transformed data consisting of 2,279 fish randomly selected from the landings, ranging from 124 mm to 280 mm TL. The width of each growth zone was measured as the distance from the focus to its distal

edge by means of an Eberbach projector. The maximum of eight rings was identified on a single 299 mm-long individual, but the corresponding data had to be left out of the calculations because of the bias they brought into the growth parameters estimates. Thus, the working database consisted of 479 individuals with up to six rings in their scales. However, the back-calculated length at age 6, that is 238 mm TL, is very near most of the estimated values of L_{∞} in previous research works, what ascribes high credibility to the new estimates of L_{∞} and K .

The periodicity of ring formation was evaluated through the analysis of the monthly variation of: (1) the mean marginal increment, calculated as the difference between the scale radius and the measurement from the focus to the last ring; to take into account effects of large within age variability observed in scale radiuses, all marginal increments were expressed as a fraction of their total radius (relative marginal increments – RMI, according to the methodology developed by Ehrhardt, 1992); (2) the mean of back-calculated lengths of age rings 1 to 6 years, those with values in all months of the studied period.

Growth was analyzed by back-calculation of growth histories. For this purpose a power curve was assumed to exist between scale size and total length (TL). Parameters of that function were estimated by linear least squares fits to the logarithmically transformed data. This relationship and the distance from the focus to successive rings were used to back-calculate lengths at presumed age from the equation:

$$\text{Log } L_n = [\text{Log } S_n (\text{Log } L - \text{Log } a) / \text{Log } S] + \text{Log } a$$

where $L = TL$ at the time of capture, $L_n = TL$ when ring n was formed, $S =$ scale size, $S_n =$ distance from scale focus to ring n , and $a =$ antilog of the intercept of the straight line fitted to transformed scale size-TL data. **Log a** is supposed to represent the length of fish when scales first appear on the body, and helps usually to correct results of back-calculation (Lee, 1920).

The von Bertalanffy growth function was fitted to the back-calculated size at age data using the working formula by Beverton & Holt (1957):

$$L_t = L_{\infty} [1 - e^{-K(t-t_0)}],$$

extrapolated to $L = 0$, where $L_t =$ mean TL at age t , $L_{\infty} =$ asymptotic length, $K =$ growth coefficient and $t_0 =$ relative age at birth. Using the Ford-Walford plot:

$$L_{t+\Delta t} = L_{\infty} (1 - e^{-K\Delta t}) + e^{-K\Delta t} L_t$$

which correlates successive back-calculated length-at-age, the intercept and slope values were fed into the

following formulae:

$$L_{\infty} = a / (1-b)$$

$$t_0 = t + \{(1/K) \cdot \ln [(L_{\infty} - L_t) / L_{\infty}]\}$$

$$K = - \ln b / \Delta t \text{ (being } \Delta t = 0.5 \text{ yr)}$$

so as to provide estimates of growth equation parameters. Wald confidence intervals were calculated for L_{∞} , K and t_0 using a non-linear regression model by means of seven interactions.

The longevity was estimated as $t_{\text{max}} = t_0 + 3.0/K$ (Pauly, 1980). A growth equation in weight is also presented, the asymptotic weight being calculated using the weight-length relationship. The natural mortality coefficient (M) was estimated by the Pauly (1983) equation: $\log M = -0.0066 - 0.279 \log L_{\infty} + 0.6543 \log K + 0.4627 \log T$, where T is the environmental temperature set at 22° C. This parameter was used to evaluate its relationship to the growth coefficient through the ratio M/K . The empirical equation $\phi' = \log_{10} K + 2 \log_{10} L_{\infty}$ for "growth performance" by Pauly & Munro (1984) was also employed.

RESULTS

Age validation – Although there are numerous methods available to establish the seasonal (or annual) nature of the growth of age rings on hard parts of fish, marginal increments have been extensively used for this purpose. The method assumes that time of ring formation corresponds to the time when marginal increments were minimum. Marginal increments, however, vary considerably according to several sources of variance among which age, size within age, sex and time are the most important.

Relative marginal increments were estimated by age and month and their mean values are presented in Table I. A reduced number of observations were available for older ages, precluding the use of relative marginal increments for fish with more than 6 rings in their scales in the age validation analysis. Omission of older ages, however, does not affect the results of the age validation approach adopted since marginal scale growth at older ages is considerably reduced and at those ages measurement error becomes more significant relative to seasonal changes in marginal scale growth.

Monthly trends of mean relative marginal increments (RMI) at age for Brazilian sardinella are shown in Figure 1. Negative exponential functions of the form $\text{RMI} = a (\exp[-(bt)])$ (where, a and b are regression parameters) were fitted to full RMI on age data sets corresponding to a few selected months, from August (month 8) to January (month 1). Estimated

slopes (b) and anti-logarithms of intercepts (a) are plotted by months in Figure 2. A good correspondence was found between slopes and intercepts, which may be indicative of the consistency of the data regarding temporal dynamics of RMI growth patterns. The observed trend in slopes is interpreted as the seasonal

change in the rate of growth relative to marginal increments per unit change in age for ages 1 to 6 for a given month, while the trend in intercepts is interpreted as the seasonal change in relative marginal increment for individuals exhibiting 0-ring, and, therefore, it represents the maximum deposition of

Table 1 – Mean relative marginal increment by age on scales of Brazilian sardinella, *Sardinella brasiliensis*, from April, 1999 through March, 2000.

MEAN RELATIVE MARGINAL INCREMENT												
	4	5	6	7	8	9	10	11	12	1	2	3
1			0,377	0,341	0,392	0,335	0,159					
2	0,191	0,169	0,169	0,175	0,164	0,179	0,082	0,155	0,161	0,168		
3	0,123	0,109	0,156	0,109	0,105	0,112	0,071	0,1	0,095	0,111	0,109	0,107
4	0,098	0,084		0,095	0,109	0,083		0,079	0,058	0,084	0,082	0,119
5	0,067	0,06			0,061	0,053						0,073
6					0,036							0,046
LOG (RMI)												
	4	5	6	7	8	9	10	11	12	1	2	3
1			-0,97551	-1,075873	-0,936493	-1,093625	-1,838851					
2	-1,65548	-1,77786	-1,77786	-1,742969	-1,807889	-1,720369	-2,501036	-1,86433	-1,82635	-1,78379		
3	-2,09557	-2,21641	-1,8579	-2,216407	-2,253795	-2,189256	-2,645075	-2,302585	-2,35388	-2,19823	-2,21641	-2,23493
4	-2,32279	-2,47694		-2,353878	-2,216407	-2,488915		-2,538307	-2,84731	-2,47694	-2,50104	-2,12863
5	-2,70306	-2,81341			-2,796881	-2,937463						-2,6173
6					-3,324236							-3,07911
SLOPE AND INTERCEPT OF THE LOG-TRANSFORMED DATA												
	4	5	6	7	8	9	10	11	12	1	2	3
b	-0,337	-0,33672	-0,44119	-0,430745	-0,424809	-0,445622	-0,403112	-0,336989	-0,51048	-0,34657	-0,28463	-0,30212
a	-1,01474	-1,14264	-0,6547	-0,770418	-0,735787	-0,749059	-1,522097	-1,224108	-0,81107	-1,11326	-1,36252	-1,15544
r	-0,99338	-0,9949	-0,90411	-0,963732	-0,967982	-0,99236	-0,93754	-0,985281	-0,99981	-0,99367	-1	-0,90567

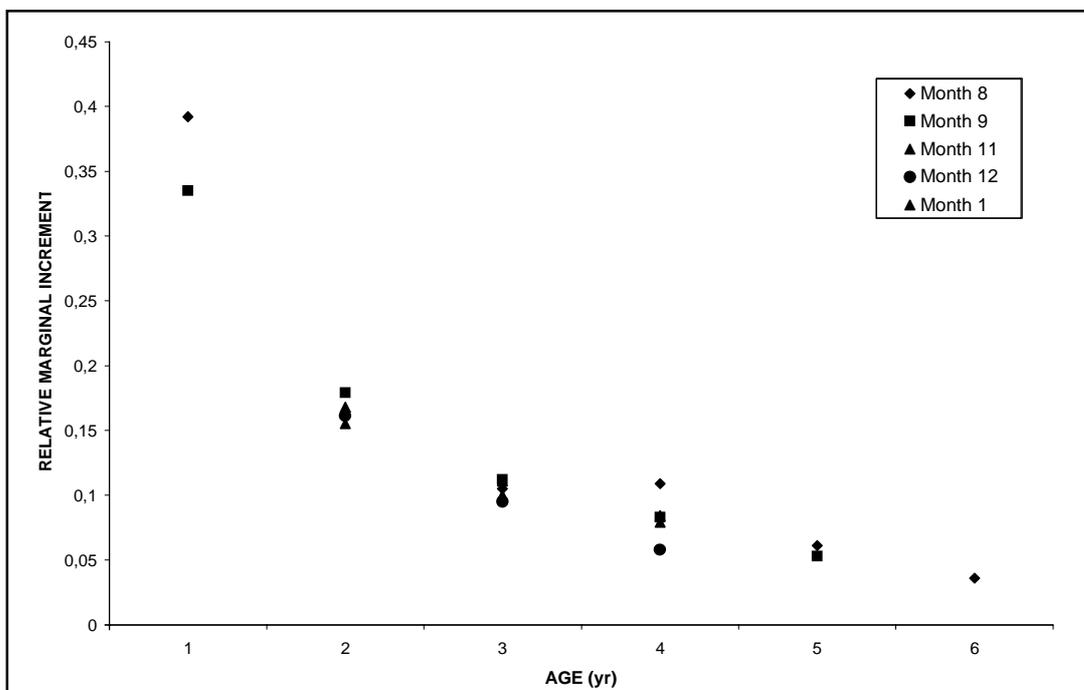


Figure 1 – Monthly trends of RMI of Brazilian sardinella, *Sardinella brasiliensis* (Steindachner) at age for months 8 (August) through 1 (January).

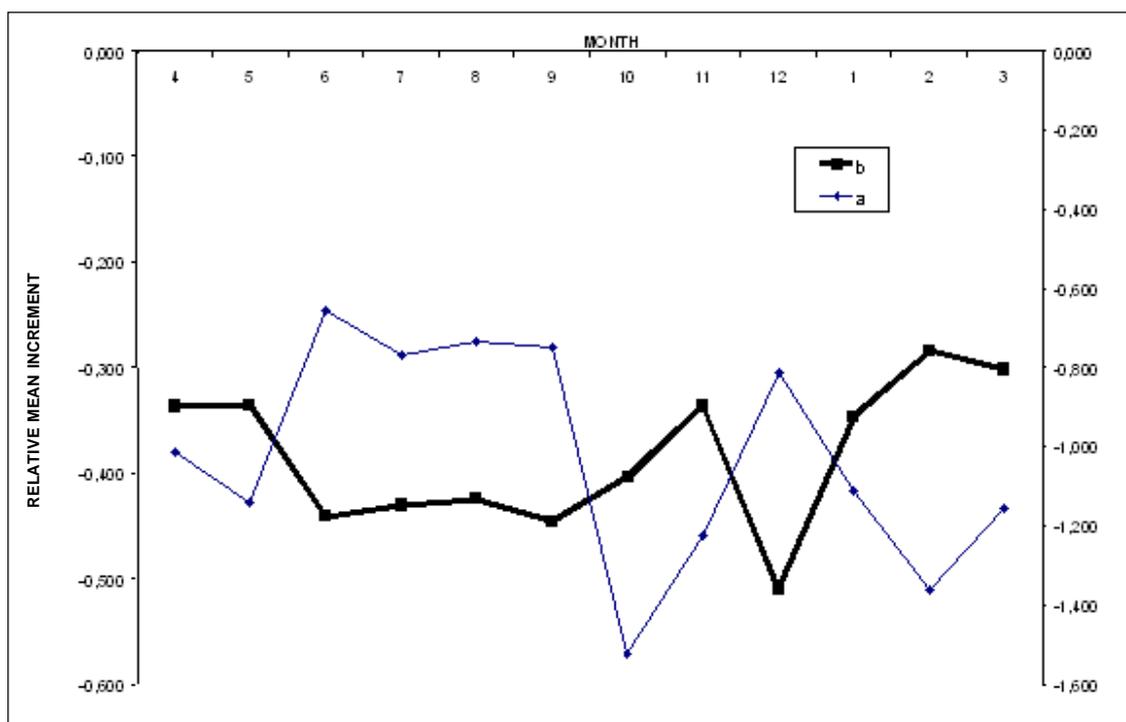


Figure 2 – Seasonal evolution of slopes (b) and intercepts (a) functions fitted to logarithmically transformed RMI on age of Brazilian sardinella, *Sardinella brasiliensis* (Steindachner).

seasonal relative marginal increment for any age (Ehrhardt, 1992).

If in fact rings seen on scales are valid indicators of age, then they should be formed during a short period and at the same time every year. The observed trend of the monthly slopes clearly shows the growth progression of relative marginal increments towards a maximum growth period from January to May, indicating the completion of growth rings in the scales at that time. Conversely, regressive trends towards minimum values of the slope is indicative that rings of rapid growth in the scales of sardine are most probably formed twice within a twelve-month period, in June (month 6) and December (month 12), which should be taken as the times of age change and probably the birthday dates of the corresponding cohorts (Figure 2). Species of the same genus, namely *Sardinella aurita* and *Sardinella eba*, from Angola, form two hyaline rings in the otolith (Baptista, 1977 in Thomas, 1983).

The appearance of the December cohort should coincide with the time of peak spawning, in December-January (Matsuura, 1977 and 1988), but for the June cohort there should be other causing factors, probably related to reduced temperatures and evasion of the nutrient-rich South Atlantic Central Water (SACW) during the austral winter (Rossi-Wongtschowski *et al.*, 1996). Inasmuch as rings in *S. brasiliensis* otoliths and scales could not be associated only with

reproduction for they have been observed both in sexually mature and immature individuals, they have been very useful in indicating age changes in that species whatever the causes of their formation (Saccardo *et al.*, 1988).

A rigorous statistical treatment was accomplished by means of the ANCOVA, despite the small sample size in a few age rings, but in this case it was vital because of the need for defining the occurrence of more than one cohort in a year's span.

Growth – The scales of Brazilian sardinella are of the cycloid type characterized by a neat focus and growth rings marked on its foremost section and



Figure 3 – Seasonal evolution of slopes (b) and intercepts (a) functions fitted to logarithmically transformed RMI on age.

turned quite evident by the diminishing distance between *circulli* as age progresses (Figure 3).

The hypothesis of the existence of isometry in the growth of fish and their scales was confirmed by the following, statistically-significant regression equation: $\log L = 3.53 + 0.815 \log S$ ($r = 0.952$; $P < 0.01$). According to Lee (1920), the back-calculated lengths at age 1 tend to be overestimated when the intercept of the 'fish length/scale length' relationship is positive. The introduction of the value of the intercept $\log a = 3.53$ into the original back-calculation formula and the weighing of back-calculated lengths at age by their respective sampling numbers have been useful in minimizing this effect.

By feeding the coefficients of the Ford-Walford fitted regression equation $L_{t+\Delta t} = 59.3 + 0.793 L_t$ ($r =$

0.994 ; $P < 0.01$) into the fore-mentioned formulae, the estimated growth parameters are: $L_\infty = 286$ mm, $K = 0.232$ and $t_0 = -1.3$ yr. Age was interpreted according to the timing of annulus formation and assuming that two cohorts are present in the fishing area produced by as many spawnings about six months apart, so that being the calculated K that of a half-year period, the annual value was estimated as $K = -\log_e 0.793 / 0.5 = 0.462$. Using these estimates as initial points for the interaction, whose correlation was measured by $r = 0.997$ ($P < 0.01$), new ones were arrived at and have been used as the best to represent the growth of Brazilian sardinella. Thus, the growth equation in length (mm) is (Figure 4):

$$L_t = 284 [1 - e^{-0.462(t+1.68)}]$$

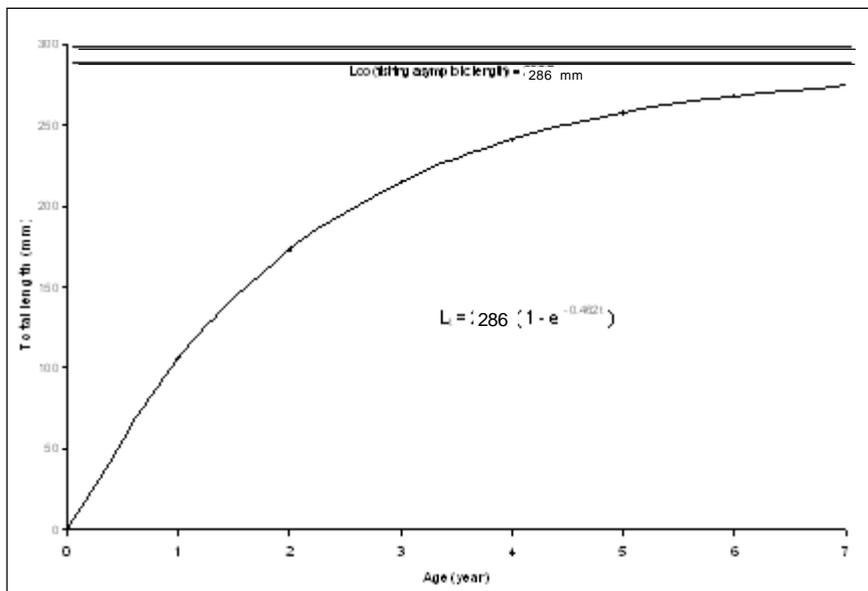
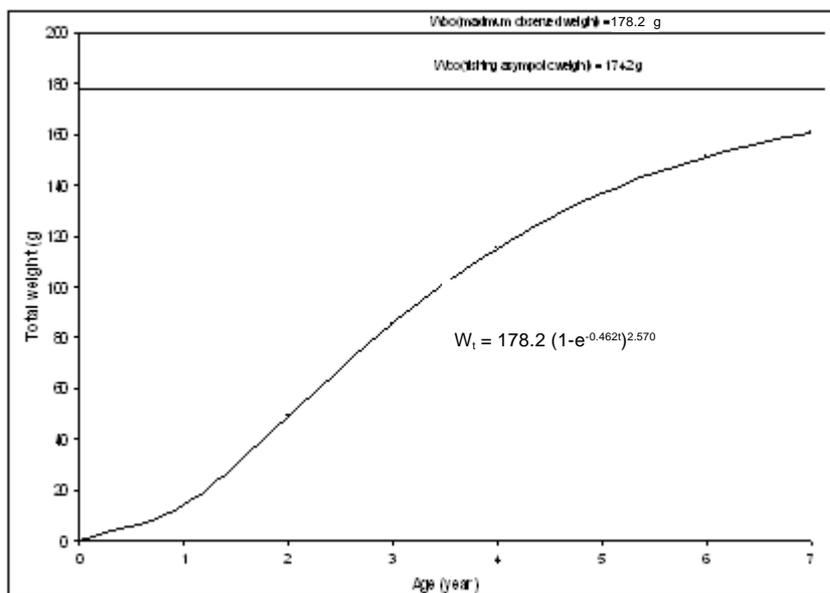


Figure 4 – Growth curve in length (mm) of Brazilian sardinella, *Sardinella brasiliensis* (Steindachner).

Figure 5– Growth curve in weight (g) of Brazilian sardinella, *Sardinella brasiliensis* (Steindachner).



which was converted to the equation in weight, in grams (Figure 5):

$$W_t = 174.2 [1 - e^{-0.462(t + 1.68)}]^{2.570}$$

through the weight-length relationship:

$$W = 0.0000867 L^{2.570} \quad (r = 0.930; P < 0.01).$$

The asymptotic standard error values for the above-cited parameter were 17.640 cm, 0.045 yr.⁻¹ and 0.347 yr., yielding the corresponding 95% Wald lower and upper intervals: $L_\infty = 227.4 - 339.7$ cm; $K = 0.088 - 0.375$ yr.⁻¹ and $t_0 = -2.784 - (-0.575)$ yr. Despite the fact that sardines grow very quickly during the first year of life, standard von Bertalanffy's equation expresses growth trends correctly. The corresponding growth performance index was estimated as $\phi' = 4.58$, a value similar to that obtained for scaled sardine, *Harengula jaguana*, a clupeoid that inhabits the same grounds as Brazilian sardinella off southeastern Brazil (Hubold & Mazzetti, 1982).

DISCUSSION

One problem in estimating the asymptotic length for most species is that it is frequently outrun by the size of larger individuals occurring in the catch. For Brazilian sardinella this has been often the case since all previous estimates of that parameter fall short of the observed maximum values of a 300-mm TL fish reported by Nomura (1962) and an eight-ring, 299-mm TL fish, in this research work. The latter one was discarded because its inclusion in the calculations would bring about an

overestimation of the asymptotic length ($L_\infty = 503$ mm) coupled with an underestimation of the growth coefficient ($K = 0.080$). Moreover, it is a common fact that large sardinella fish (over 260 mm TL) are rarer and rarer in the catches on account of the high rate of fishing mortality to which its population has been submitted for the past 20 years (Magro *et al.*, 2000). In this case, a "fishing asymptotic length" was adopted which would correspond with the catchable stock and would be sufficient for the purposes of determining age compositions to be used in population dynamics studies.

The length-at-age data calculated through the growth equation show that the first and second annuli, with mean lengths 31 mm TL and 84 mm TL, were not represented in the scales so that in fact the first marked annulus (average 126 mm TL) should stand for the third half-year age group. Moreover, our collections did not yield fish small enough to ascertain the time of the year when the first annulus is formed because those were obtained through the sampling of commercial landings where the catchable stock ranges from 90 to 240 mm TL (Cergole *et al.*, 1999).

The distribution of the back-calculated lengths is shown to be multimodal, with overlapping subdistributions corresponding with seven age groups whose mean lengths are quite similar to the back-calculated ones (Figure 6). This bears out the existence of two cohorts in a year's period assuming its maximum length and age in the catchable stock to be 240 mm TL and 3.9 yr. Comparatively, the longevity of a cohort, meaning the oldest age at which nearly all of its individuals will have died, is $t_{\max} = 7.7$ yr.

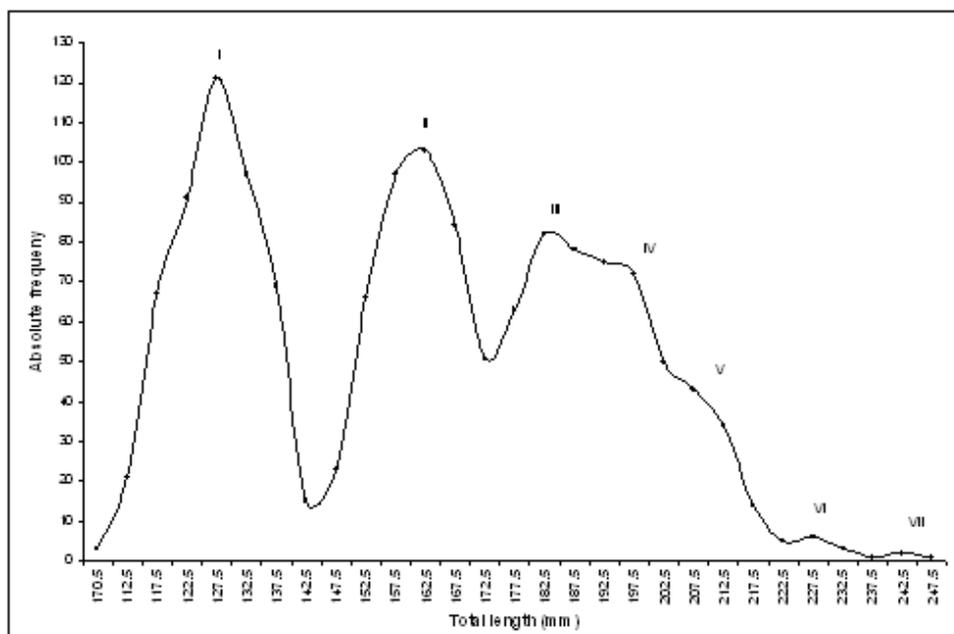


Figure 6 – Back-calculated length distribution of Brazilian sardinella, *Sardinella brasiliensis* (Steindachner).

Therefore, it may be assumed that individuals with one annulus in their scales have a real mean age of 1.8 yr. so that those born at the beginning of the spawning season, say in October, will have their first half-year annulus formed in July; likewise, those born at the end of the spawning season, say in April, will have its first half-year annulus formed in January. This finding is supposed to have an important bearing on future calculations of age structures and hence, on stock assessment, so that the catch data from now on should be arranged by half-year instead of yearly intervals.

The annual value of the growth coefficient (K) calculated in this paper is within the range of most estimates come up with in the existing papers and summarized by Cergole (1995), but with one big difference, namely the annual values were calculated by doubling the estimated value by the Ford-Walford method, under the assumption that its periodicity is half-yearly and not annual. There is some controversy about this finding since Saccardo *et al.* (1988) at first considered two groups per year, one composed by fish that were born in the beginning of the spawning season and the other by fish born at the end of it. When the average length for each age class was plotted on a graph against the year, its points were connected following the cohorts and it seemed there to be a large range of values within the same age group, resulting in two cohorts. Later, by application of the Bhattacharya method to the length frequency distribution, a conclusion was drawn to the effect that a single cohort is formed each year, what agrees with the growth curves obtained by the ELEFANI method, under the assumption that despite the reproductive season being very long (October-March), the intensive spawning takes place within a relatively short period, generally in December-January.

The natural mortality coefficient, estimated as $M = 0.769$, is supposed to hold an inverse correlation with growth rate which is supposed to be the result of a host of factors causing stress while maintaining a close direct relationship to temperature and an inverse relationship to longevity. The ratio $M/K = 0.769/0.462 = 1.66$ is within the order of magnitude for short-lived, highly-preyed upon Clupeidae species (Pauly, 1983).

Buesa (1987) stated that the smaller the maximum length (L_M) value for a given species, the faster is the relative growth rate, so that during the first year of life species with L_M in the ranges of < 51 cm, 51-100 cm and > 100 cm are able to attain up to 65%, 44% and 29% of this parameter, respectively. For Brazilian sardinella, this growth limit was found to be 57.3%, a trait that should be held accountable for the vulnerability of the stock to fishing pressure and environmental changes.

Acknowledgements: Our warmest thanks are due to the fishing company Castro Indústria e Comércio de Pescados Ltda. (Angra dos Reis, Rio de Janeiro State, Brazil) and its chairman, Isake de Castro, for their constant and ever-present attention, and the donation of the biological material that supports this paper.

REFERENCES

- Beverton, R. J. H. & Holt, S.J. On the dynamics of exploited fish populations. *Fish. Invest. ser. 2*, London, v.19, p. 1- 533, 1957.
- Buesa, R. J. Growth rate of tropical demersal fishes. *Mar. Ecol. Progr. Ser.*, v.36, p. 191-199, 1987.
- Cergole, M.C. Stock assessment of the Brazilian sardine, *Sardinella brasiliensis*, of the southeastern coast of Brazil. *Scien. Mar.*, v. 59, p. 597-610, 1995.
- Cergole, M.C.; Saccardo, S.A.; Rossi-Wongtschowski, C.L.B. & Valentini, H. Composição etária das capturas de sardinha-verdadeira após o colapso da pescaria em 1987-1993. *XIII Encontro Brasileiro de Ictiologia*, p. 573, 1999.
- Cergole, M.C. & Valentini, H. Growth and mortality estimates of *Sardinella brasiliensis* in the southeastern Brazilian bight. *Bol. Inst. Oceanogr.*, São Paulo, n.42, p. 113-127, 1994.
- Dias Neto, J. *Gestão do uso dos recursos pesqueiros marinhos do Brasil*. Dissertação de Mestrado, Centro de Desenvolvimento Sustentável, Universidade de Brasília, xiii + 164 p., Brasília, 2002.
- Ehrhardt, N.M. Age and growth of swordfish, *Xiphias gladius*, in the Northwestern Atlantic. *Bull. Mar. Sci.*, Miami, v. 50, p. 292-301, 1992.
- Hubold, G. & Mazzetti, M.V. Growth, morphometry, and aspects of the life history of the scaled sardine *Harengula jaguana* Poey, 1865 in the Guanabara Bay, Brazil. *Rep. Mar. Res.*, v.29, p. 80-88, 1982.
- Lee, R. A review of the methods of age and growth determination in fishes by means of scales. *Fish. Invest. ser. 2*, London, n.4, p.1-32, 1920.
- Magro, M.; Cergole, M.C. & Rossi-Wongtschowski, C.L.B. *Síntese dos conhecimentos dos principais recursos pesqueiros costeiros potencialmente exploráveis na costa sudeste-sul do Brasil: peixes*. Grafline Editora, 143 p., 2000.
- Matsuura, Y. O ciclo de vida da sardinha-verdadeira (Introdução à Oceanografia Pesqueira). *Publ. Esp. Inst. Oceanogr.*, São Paulo, n.4, p. 1-146, 1977.
- Matsuura, Y. *Estudo comparativo das fases iniciais do ciclo de vida da sardinha-verdadeira, Sardinella brasiliensis, e da sardinha-cascuda, Harengula jaguana*

- (Pisces:Clupeidae). Tese de Livre Docência, Universidade de São Paulo, 150 p., 1983
- Matsuura, Y. Synopsis on the reproductive and early life history of the Brazilian sardine, *Sardinella brasiliensis*, and related environmental conditions. *IOC Work. Rep.*, n.65, p.1-8, 1988.
- Matsuura, Y. *Os ecossistemas brasileiros e os principais macrovetores de desenvolvimento: subsídios ao planejamento da gestão ambiental*. Ministério do Meio Ambiente, 104 p., Brasília, 1995
- Nomura, H. Length-weight tables of some fish species from southern Brazil. *Contr. Avul. Inst. Oceanogr.*, São Paulo, n.3, p.1-4, 1962.
- Paiva, M.P. *Recursos pesqueiros estuarinos e marinhos do Brasil*. Edições UFC, 286 p., Fortaleza, 1997
- Pauly, D. Gill size and temperature governing factors in fish growth: a generalization of von Bertalanffy's growth formula. *Berich. Inst. Meeres. Univer. Kiel*, v.63, p.1-156, 1979.
- Pauly, D. Theory and management of tropical multispecies stocks: a review, with emphasis on the Southeast Asia demersal fisheries. *ICLARM Stud. Rev.*, Manila, n.1, p.1-3, 1980.
- Pauly, D. On the interrelationships between natural mortality, growth parameters, and environmental temperature in 175 fish stocks. *J. Cons. Perm. Intern. Explor. Mer*, Copenhagen, v. 29, p.175-192, 1983.
- Pauly, D. & Munro, J.B. Once more on growth comparison in fish and invertebrates. *Fishbyte*, Manila, n. 2, p.21, 1984.
- Richardson, I.D.; Vazzoler, A.E.A.M.; Faria, A. & Moraes, M.N. Report on sardine investigations in Brazil. *FAO Proceedings of Sardine Meeting 3*, p.1051-1079, 1960.
- Rijavec, L.; Jablonski, S.; Simon, A.S.C.B.; Rodrigues, L.F. & Pires, M.R.Q. Contribuição ao conhecimento da biologia e dinâmica da sardinha (*Sardinella brasiliensis*) em águas brasileiras (resultados preliminares). *SUDEPE/PDP, Doc. Ocas.*, Rio de Janeiro, n.24, p.1-36, 1977.
- Rossi-Wongtschowski, C.L.B.; Saccardo, S.A. & Cergole, M.C. Are fluctuations in Brazilian sardine catches related to global-scale climate changes? *An. Acad. Brasil. Ciên.*, Rio de Janeiro, v.68, p.239-250, 1996.
- Saccardo, S.A.; Rossi-Wongtschowski, C.L.B.; M.C. Cergole, M.C. & M.M. Bittencourt, M.M. Age and growth of the southeastern Brazilian sardine, *Sardinella brasiliensis*, 1981-1983. *Bol. Inst. Oceanogr.*, São Paulo, n.36, p.17-35, 1988.
- Santos, E.P. & Frazten, F.M. Growth of sardines: quantitative aspects. *An. Acad. Brasil. Ciên.*, Rio de Janeiro, v.37, p. 360-362, 1965.
- Thomas, R.M. Back-calculation and time of hyaline ring formation in the otoliths of the pilchard off Southwest Africa. *South Afr. J. Mar. Sci.*, v.1, p.3-18, 1983.
- Valentini H. & Cardoso, R.D. Análise da pesca da sardinha-verdadeira, *Sardinella brasiliensis*, na costa sudeste do Brasil. *Atlântica* 13: 45-54, 1991.
- Vazzoler A.E.A.M.; Rossi-Wongtschowski, C.L.B. & Braga, F.M.S. Estudos sobre a estrutura, ciclo de vida e comportamento de *Sardinella brasiliensis* (Steindachner, 1879), na área entre 22° S e 28° S, Brasil. II. Determinação da idade individual e crescimento dos otólitos. *Bol. Inst. Oceanogr.*, São Paulo, n.31, p.77-94, 1982.
- Vazzoler A.E.A.M.; Rossi-Wongtschowski, C.L.B. & Braga, F.M.S. Estudos sobre a estrutura, ciclo de vida e comportamento de *Sardinella brasiliensis* (Steindachner, 1879), na área entre 22° S e 28° S, Brasil. IV. Crescimento: aspectos quantitativos. *Bol. Inst. Oceanogr.*, São Paulo, n.35, p. 53-63, 1987.