

AGE AND GROWTH OF THE KING MACKEREL (*SCOMBEROMORUS CAVALLA*) OFF THE NORTHEASTERN COAST OF BRAZIL

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ABSTRACT

Age and growth of the king mackerel (*Scomberomorus cavalla*) were estimated for northeastern Brazil. A total of 405 sagittal otoliths from 140 males (24.4-112 cm), 73 females (28-114.8 cm) and 193 specimens of unknown sex (11.5-121 cm) were examined. Marginal increment analysis indicated an annual pattern for growth band deposition. The age classes ranged from 1 to 15 years. Length ranged from 11.5 to 121 cm. The Schnute model indicated that the von Bertalanffy growth model demonstrated the best adjustment, with $p=1/b$, and was therefore used for estimating growth. Back-calculated curves had smaller variances, giving the following estimated growth parameters for males: $L_{\infty}=116.8$ cm, $K=0.190$, $t_0=0.377$; and females: $L_{\infty}=132.7$ cm, $K=0.159$ and $t_0=0.387$. In order to compare the curves for males and females, the overlapping of 95% confidence intervals was performed for the parameters generated from the von Bertalanffy non-linear least square method. Specimens between 3 and 8 years of age represented 82.2% ($n=5,783$) of the catch composition, characterizing the species as a catchable stock in the region.

RESUMO

A idade e o crescimento da King mackerel (*Scomberomorus cavalla*) foram estimados na região nordeste do Brasil. Foram analisados 405 otólitos sagita, sendo 140 machos (24,4-112 cm), 73 fêmeas (28-114,8 cm) e 193 exemplares com sexo indeterminado (11,5-121 cm). A análise do incremento marginal indicou um padrão anual na deposição das bandas de crescimento. As classes de idade variaram entre 1 e 15 anos e os comprimentos de 11,5 a 121 cm. O modelo de Schnute indicou que o melhor ajuste é apresentado pelo modelo de von Bertalanffy com $p=1/b$, sendo, então, utilizado para as estimativas de crescimento. As curvas retrocalculadas apresentaram as menores variâncias e os parâmetros de crescimento foram estimados para machos: $L_{\infty}=116,8$ cm, $K=0,190$, $t_0=0,377$; para fêmeas: $L_{\infty}=132,7$ cm, $K=0,159$ e $t_0=0,387$. Para comparação das curvas de machos e fêmeas, foram construídas regiões de confiança de 95% para os parâmetros gerados pelo método de mínimos quadrados não linear de von Bertalanffy. Exemplares entre 3 e 8 anos representaram 82,2% ($n=5,783$) da composição das capturas, caracterizando assim, o estoque capturável da espécie na região.

Descriptors: *Scomberomorus cavalla*; King mackerel; Age and growth.

Descritores: *Scomberomorus cavalla*; cavala; Idade e crescimento.

INTRODUCTION

In a recent sampling program of landings from artisanal fisheries in northeastern Brazil, the king mackerel (*Scomberomorus cavalla*, Cuvier, 1829) accounted for 8.6% of the total recorded weight (LESSA, 2006), representing the fourth largest regional fishing resource in terms of economic importance (NÓBREGA; LESSA, 2007). The species occurs from the Atlantic coast of Massachusetts (USA) down to Rio de Janeiro (Brazil) (COLLETE; NAUEN, 1983), living in the epipelagic zone, mainly over the continental shelf.

From 1950 to 2004 (Fig. 1), catches of *S. cavalla* in its area of distribution rose from 4,743 t to

13,546 t (FAO, 2007). Between 1976 and 2004, the weight landed in northeastern Brazil (from the state of Piauí to the state of Bahia) rose from 10.9% to 29% (mean=19.4%) of the total catch throughout its entire area of occurrence (SUDEPE, 1976 to 1979 (SUDEPE, 1979); IBGE, 1980 to 1989 (IBGE, 1989); (IBAMA, 1990-2004) (Fig. 1). The states of Ceará (1,579 t) and Bahia (541 t) contributed the largest volumes in the northeastern region, accounting for 59% and 20.2% of the overall catch, respectively (IBAMA, 2004). The *S. cavalla* is also a major fishing resource in Trinidad (STURM; SALTER, 1990), Venezuela (GRIFFITHS, 1971), the Gulf of Mexico (ARREGUÍN-SÁNCHEZ, 1995) and off the US coast

(FINUCANE et al., 1986; COLLINS et al., 1989; Gold et al., 2002).

The economic importance of the king mackerel in its area of distribution has led to a large number of studies on its growth, the identification of stock units (BEAUMARIAGE, 1973; XIMENES et al., 1978; JOHNSON et al., 1983; MANOOCH et al., 1987; COLLINS et al., 1989; STURM; SALTER, 1990; ARREGUÍN-SÁNCHEZ et al., 1995; DEVRIES; GRIMES, 1997; DEVRIES et al., 2002), reproduction (IVO, 1972; BEAUMARIAGE, 1973; GESTEIRA; MESQUITA, 1976; FINUCANE et al., 1986; STURM; SALTER, 1990), mortality rates and exploitation status (FONTELES-FILHO, 1988; JOHNSON et al., 1983; AGUILAR-SALAZAR, 1991; ARREGUÍN-SANCHEZ et al., 1995; LESSA et al., 2004).

In northeastern Brazil, *S. cavalla* is exploited especially by the artisanal fleet, between the 20 and 200 m isobaths, catches undertaken with surface lines predominating (90.8%) and, in a lesser proportion, those with gillnets (9.2%), with the largest volumes being landed between January and April (LESSA, 2006). Lessa et al. (2004) assessed the exploitation status of the stock and estimated a mean annual biomass of 12,742 t for a mean yield of 3,307 t/year, indicating that, despite being underexploited, the stock is near its maximal exploitation limit.

Age determination by means of growth bands is the most valuable means of obtaining the information used in virtual analyses of populations and catch curves (HILBORN; WALTERS, 1992). These estimates permit the adoption of management policies

and promote sustainable stock exploitation (LONGHURST; PAULY, 1987). The growth parameters of a species may present different values in distinct parts of its area of occurrence (SPARRE; VENEMA, 1997).

The production of a fish stock (discounting immigration and emigration) is a mixture of the recruitment of new specimens to the population and individual growth. Thus, there is a large volume of literature that addresses individual growth in the ecology of fisheries (HADDON, 2001). Regarding this literature, a number of models involve growth curve estimates based on age and length data, such as the Putter, von Bertalanffy, Richards, Gompertz, logistic, linear, quadratic and exponential models RICKER, 1975). Besides this diversity of models, others, such as those proposed by Walford (1946), Fabens (1965) and Allen (1966), are generally used to estimate von Bertalanffy growth parameters (SCHNUTE, 1981).

In the present study, we use the Schnute growth model (1981) to estimate four parameters, the parametric properties of which allow the systematic selection of an appropriate growth model for data on the age (readings of rings in whole otoliths) and size of *S. cavalla* specimens caught off northeastern Brazil. Through the model indicated as the most appropriate, we establish growth curves (for separate and combined sexes) and the age structure of the species, thereby contributing essential information (growth parameters) for future assessments of exploitation levels and sustainable catch rates for this important fishery resource in the region.

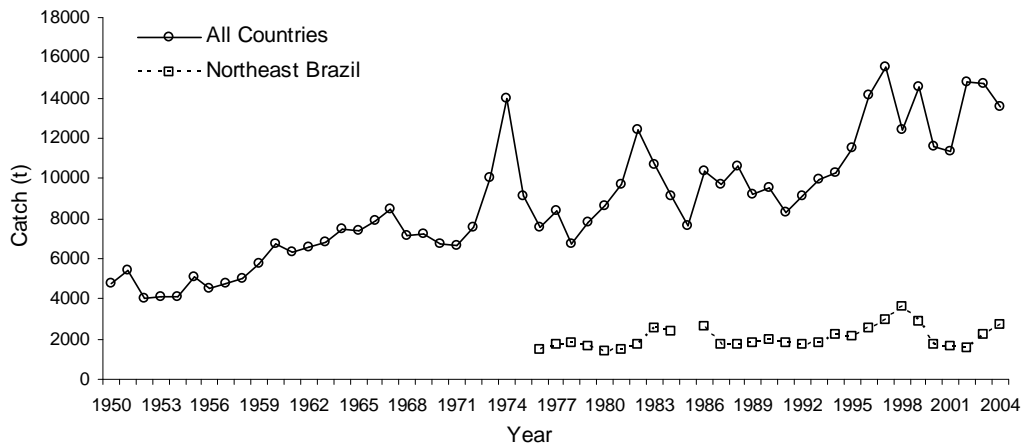


Fig. 1. Weight of *S. cavalla* landed between 1950 and 2004 throughout entire area of distribution and off northeastern Brazil between 1976 and 2004.

MATERIALS AND METHODS

Sampling

On the basis of daily samplings, the length (FL, cm) and weight (TW, g) of 7,019 specimens of *S. cavalla* caught with hand-lines and nets by the artisanal fleet, between January 1998 and April 2001, and landed in northeastern Brazil, were recorded. The fishing areas had depths of 4 to 216 m (mean=63.2 m; SD=31.5 m), with the distance from shore ranging from 1.37 to 68.65 Km (mean=22.2 Km; SD=14.6 Km) (Fig. 2). In the monthly samplings, otoliths were collected from 481 specimens; gonads were analyzed for the determination of gender.

Age determination

The right otolith of each pair was examined whole in vegetable oil on a black background under transmitted light. Otoliths were classified into age groups based on the number of translucent bands. Distances from the nucleus to the edge (otolith radius - OR) and between translucent bands were measured (Fig. 3) with a stereoscopic microscope equipped with ocular micrometer at 10x magnification (1 micrometer unit = 1 mm). The otoliths were examined by two

different readers with no previous knowledge of the individual's size or the other reading. Inter-examiner agreement on the age of whole otoliths was calculated using the average percentage error (1) described by Beamish and Fournier (1981). Marginal increment analysis was performed to determine the periodicity of growth band formation, using the equation (2) proposed by Cadvallader (1978):

$$APE = \frac{1}{N} \sum \left(\frac{1}{R} \sum (X_{ij} - X_j | X_j) \right) \cdot 100 \tag{1}$$

in which *N* = the number of fish aged; *R* = the number of readings; *X_{ij}* = the mean age of *jth* fish at the *ith* reading; and *X_j* = the mean age calculated for the *jth* fish, and

$$PMI = \left(\frac{OR - r_n}{r_n - r_{n-1}} \right) \cdot 100 \tag{2}$$

in which, *OR* = otolith radius; *r_n* = distance between otolith nucleus and the last band; and *r_{n-1}* = distance between otolith nucleus and the penultimate band.

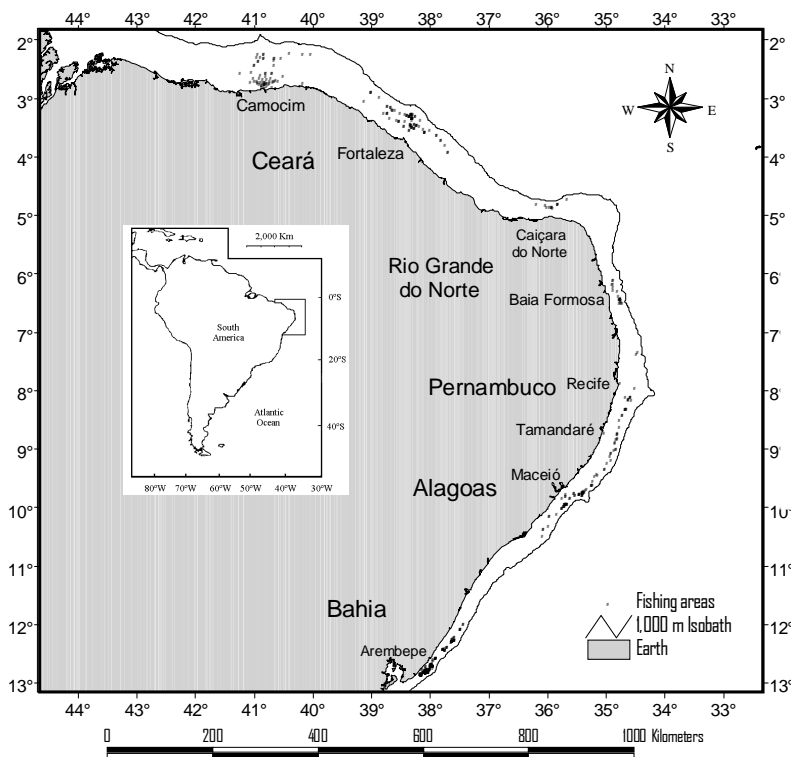


Fig. 2. Sampling locations and fisheries areas of king mackerel (*S. cavalla*) collected off northeastern Brazil: Arembepé (Bahia); Maceió (Alagoas); Recife and Tamandaré (Pernambuco); Baía Formosa and Caçara do Norte (Rio Grande do Norte); Fortaleza and Camocim (Ceará).

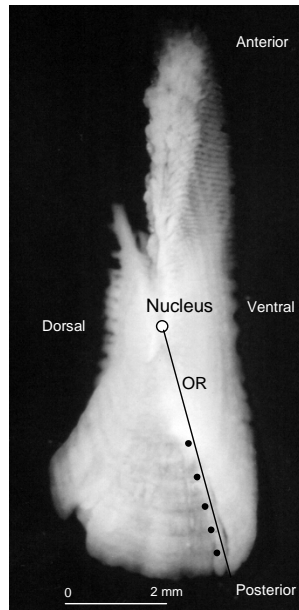


Fig. 3. Characteristics of whole otoliths from king mackerel observed under transmitted light for age determination. Male specimen, five years of age, measuring 63 cm FL (OR = otolith radius; ● = translucent bands).

To determine whether the periodicity of the bands reveals a similar pattern between adults and juveniles, marginal increment analysis was made separately for groups with 1 to 4 bands (juveniles) and 5 to 15 bands (adults), using the maturity scale proposed by Gesteira and Mesquita (1976). Marginal increment analyses for juveniles and adults were tested with one-way fixed-effects analysis of variance ($\alpha = 0.05$). Tukey's studentized range (HSD) test was used for *a posteriori* comparisons ($\alpha = 0.05$).

Backcalculation

Linear and multiplicative correlations between OR and FL were calculated for males, females and combined sexes, determining the adjustment to normal distribution compared by analysis of variance. The residual dispersion diagram, determination coefficient and *F* value (Fisher) were used to find the regression model best adjusted to the data. Analysis of covariance ($\alpha = 0.05$) was applied to compare correlations between the OR and FL of males and females.

Measurements of the distance between the otolith nucleus and the last band were back-calculated using the Monastyrsky equation (3) for the body proportionality hypothesis (BPH) (FRANCIS, 1990).

Mean backcalculated and observed lengths were compared and subsequently tested by analysis of covariance ($\alpha = 0.05$) in order to determine whether there were differences between these two methods as well as to validate the growth marks in the otoliths.

$$L_i = (S_i / S_c)^b \cdot L_c \quad (3)$$

in which L_i = the back-calculated length at last age; S_i = otolith radius at the time of the last band; S_c = the otolith radius at capture; L_c = the length at capture; and b = the slope coefficient of the relationship between OR and FL (multiplicative relationship for combined sexes).

Estimation of Growth Parameters

In order to determine which growth model had the best adjustment to lengths and ages of males, females and combined sexes, the growth equation formulated by Schnute (1981) was employed, using the nonlinear least squares methods (4). Relative growth rates z_1 and z_2 were also calculated (5 and 6), in accordance with the same author.

$$L_t = \left[y_1^b + (y_2^b - y_1^b) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right]^{1/b} \quad (4)$$

$$z_1 = \frac{((y_2^b - y_1^b)/b) \cdot e^{-a\tau_1}}{((e^{-a\tau_2} - e^{-a\tau_1})/a) \cdot y_1^b} \quad (5)$$

$$z_2 = \frac{((y_2^b - y_1^b)/b) \cdot e^{-a\tau_2}}{((e^{-a\tau_2} - e^{-a\tau_1})/a) \cdot y_2^b} \quad (6)$$

in which L_t is predicted length at age t ; τ_1 = first specified age; τ_2 = second specified age; a = constant relative rate of relative growth rate; b = incremental relative rate of relative growth rate; y_1 = size at age τ_1 , y_2 = size at age τ_2 ; z_1 = relative growth rate at age τ_1 ; z_2 = relative growth rate at age τ_2 .

Growth parameters were also calculated for separate and combined sexes, using the von Bertalanffy equation, with $p=1/b$ (7), with individual observed lengths and back-calculated lengths to the last band of each specimen (Francis, 1990). The method with the best adjustment to the data (direct and back-calculated) was chosen based on the comparison of variances and adjustments of the residuals to normal distribution.

$$L_t = L_{\infty} \left(1 - e^{-k(t-t_0)}\right)^{1/b} \tag{7}$$

in which L_t is predicted length at age t ; L_{∞} = mean asymptotic fork length; K = growth rate constant; t_0 = the age when length is theoretically zero; b = incremental relative rate of relative growth rate.

Data Analysis

Growth parameters for back-calculated lengths of males and females were compared by the overlapping of 95% confidence intervals, using the bi-dimensional normal distribution model described by Kimura (1980) and Cerrato (1990). In order to compare estimated growth parameters of males and females, Hotelling's T^2 test (CERRATO, 1990) was applied (8) and its graphic representation was demonstrated using overlapping 95% confidence intervals for differences between the vectors of parameters L_{∞} and K .

$$\theta_{female} = \begin{pmatrix} L_{\infty} \\ K \end{pmatrix} \quad \text{and} \quad \theta_{male} = \begin{pmatrix} L_{\infty} \\ K \end{pmatrix} \tag{8}$$

$$\delta = \theta_{female} - \theta_{male} \quad H_0 : \delta = 0 \quad H_1 : \delta \neq 0$$

The ϕ parameter (PAULY; MUNRO, 1984) – which expresses growth performance and allows the determination of how environmental and latitudinal differences cause changes in growth rates (K) and, consequently, changes in asymptotic length (L_{∞}) for a given species – was estimated (9) for the growth parameters (von Bertalanffy) established in the present study for males, females and combined sexes. The estimated parameters within the same area and other areas of *S. cavalla* distribution were then compared. The adjustment to normal distribution of the frequencies of the ϕ parameter for the different

areas of occurrences was tested using the Kolmogorov-Smirnov test ($\alpha = 0.05$).

$$\phi = \log_{10} K + 2 \log_{10} L_{\infty} \tag{9}$$

A distribution of age structure for the entire sample was established. The inverted von Bertalanffy growth curve was used to estimate the longevity of *S. cavalla* in northeastern Brazil.

RESULTS

Length Frequency

Length ranged from 11.5 to 136 cm FL for the entire sample (n=7,019) (mean=73.8 cm; SD=18.13 cm). The smallest specimens occurred in February, April, June and August, whereas the largest occurred in August and September (Fig. 4). Female and male lengths ranged from 28 to 127 cm (mean=63.9 cm; SD=23.9 cm) and 24.4 to 126 cm (mean=66.9 cm; SD=21.18), respectively. There was no significant difference between males and females regarding length (ANOVA; P=0.28) (Fig. 5).

Age Determination

A total of 84.2% (n=405) of the collected otoliths (n=481) were used for the growth study, as 76 otoliths were broken and not suitable for measurements or band counts. Of the 405 otoliths used, 140 were male (24.4-112 cm), 73 female (28-114.8 cm) and 193 specimens were of undetermined sex (11.5-121 cm).

The number of translucent bands in the otoliths ranged from 1 to 15, with size estimates ranging from 11.5 to 121 cm FL. The average percentage error between the two readers ranged from 0% to 15.9% on 1 to 15 bands, with an APE of 8.96% for the entire sample.

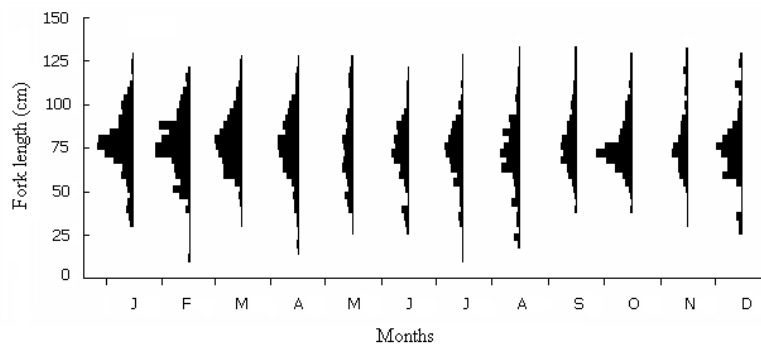


Fig. 4. Frequency distribution of monthly lengths (grouped years) of *S. cavalla* off northeastern Brazil.

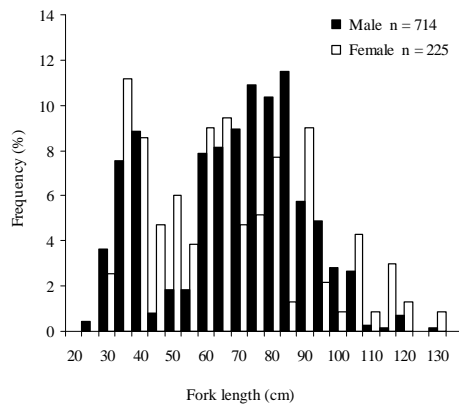


Fig. 5. Frequency distribution of male and female lengths of king mackerel off northeastern Brazil

The relative marginal increment for the juvenile group had the smallest values from November to March (Fig. 6a), suggesting the formation of translucent bands in this period. There was a significant difference in mean increments throughout the year ($P < 0.05$) and the *post-hoc* test indicated significant differences in November, December, January, February and March in relation to the other months. Marginal increment for the adult group had the smallest values between September and April (Fig. 6b), also with significant differences in monthly means ($P < 0.05$); the *post-hoc* test demonstrated that the monthly means of June, July and August were statistically different from those of the remaining months. Based on these results, an annual pattern extending from September to April was considered for the deposition of growth bands in the region.

Backcalculation

Correlations between OR and FL demonstrated the best adjustments to the

multiplicative regression model (Table 1 - Fig. 7a). There were no significant gender differences in OR and FL correlations (ANCOVA; $P = 0.10$). Mean observed and backcalculated lengths for the ages exhibited similarities (Fig. 7b), with no significant differences (ANCOVA; $P = 0.13$). These findings indicate that the bands interpreted on the otoliths may be used to estimate growth and establish the age structure of the *S. cavalla* caught off northeastern Brazil.

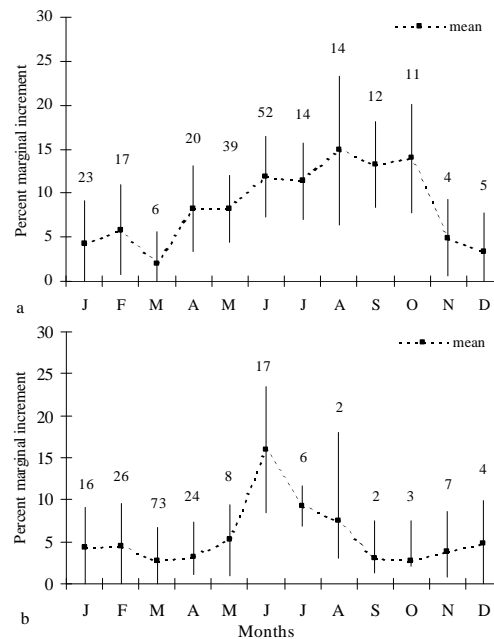


Fig. 6. Relative marginal increment with minimal, maximal and mean values (\pm standard error) for young specimens (a) and adults (b) of *S. cavalla* off northeastern Brazil.

Table 1. Linear and multiplicative relationship between otolith radius (OR) and fork length (FL) for sexes both separately and combined, tested through ANOVA.

Sex	Model	Relationship	<i>n</i>	<i>F</i>	<i>P</i>	<i>r</i> ²
Female	Linear	FL=17.604OR-16.312	73	1,121	$P < 0.01$	0.940
Male	Linear	FL=17.755OR-15.945	140	2,921	$P < 0.01$	0.954
Combined	Linear	FL=17.688OR-15.442	405	10,744	$P < 0.01$	0.964
Female	Multiplicative	FL=8.8329OR ^{1.2923}	73	1,222	$P < 0.01$	0.945
Male	Multiplicative	FL=8.7813OR ^{1.3086}	140	3,437	$P < 0.01$	0.961
Combined	Multiplicative	FL=8.3421OR ^{1.3434}	405	13,181	$P < 0.01$	0.970

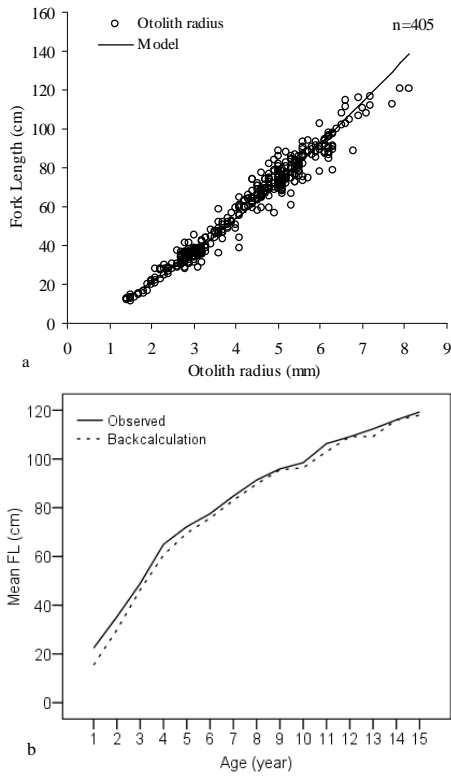


Fig. 7. Relationship between OR and FL (combined sexes) showing adjusted multiplicative model (a); mean observed and backcalculated lengths (b) for *S. cavalla* at different catch ages (combined sexes).

Growth Parameters

Absolute ages were calculated taking January as the month when the species changes its age.

Table 2. Growth parameters calculated from observed lengths (OL) and back-calculated (BC) lengths, using Schnute model (1981). τ_1 = first specified age; τ_2 = second specified age; a = constant relative rate of relative growth rate; b = incremental relative rate of relative growth rate; y_1 = size at age τ_1 ; y_2 = size at age τ_2 ; z_1 = relative growth rate at age τ_1 ; z_2 = relative growth rate at age τ_2 (S – variance, r^2 - coefficient of determination).

Methods	Sex	n	y_1	y_2	a	b	τ_1	τ_2	z_1	z_2	S	r^2
OL	Male	140	20.04	107.55	0.143	1.020	1.25	13.9	1.243	0.037	26.64	0.939
	Female	73	32.9	118.37	0.170	0.993	2.25	13.9	0.872	0.034	41.35	0.924
	combined	405	15.37	115.69	0.139	1.018	1	15.5	2.316	0.040	31.61	0.949
BC	Male	140	12.27	104.32	0.170	1.022	1	13	2.926	0.043	23.03	0.953
	Female	73	26.5	111.16	0.115	1.038	2	13	0.355	0.023	24.84	0.957
	combined	405	13.02	109.3	0.151	1.026	1	15	3.123	0.043	21.03	0.970

The growth model proposed by Schnute (1981) estimated values of $a > 0$ and $b \geq 1$ for separated and combined sexes in the northeastern region (Table 2), which indicates that the most suitable model for describing the growth of the species is that of von Bertalanffy, specialized with $p=1/b$. Moreover, growth rates (z_1, z_2) for τ_1 and τ_2 exhibited wide variation, indicating an extremely high increase in the ages established for τ_1 and very low increase for older specimens (τ_2), with a being an estimate of relative constant growth rate (Table 2).

Growth curves established for combined and separate sexes demonstrate that the estimates generated for back-calculated lengths obtained higher determination coefficients, lower variances and better adjustments of the residuals to normal distribution, whether using the Schnute model (Table 2) or the von Bertalanffy equation (Table 3). The latter method was, therefore, used to describe the growth of *S. cavalla* in northeastern Brazil. Growth parameters estimated for males (Table 3) indicated a higher growth rate compared to females and exhibited a smaller L_∞ (Fig. 8), whereas females had a higher L_∞ (Table 3).

Data Analysis

The overlapping of confidence intervals for males and females indicate no significant differences between these curves (Fig. 9a). These confidence intervals provide a measure for the variability of estimated parameters through the von Bertalanffy nonlinear least squares method, generating the following estimates of intervals for females: L_∞ (118.33 - 147.06 cm) - K (0.133 - 0.183 year⁻¹) and for males: L_∞ (106.39 - 127.20 cm) - K (0.164 - 0.215 year⁻¹).

Table 3. Von Bertalanffy growth parameters calculated from observed lengths (OL) and back-calculated (BC) lengths of king mackerel collected off northeastern Brazil (SE - standard error; CV - coefficient of variation; r^2 - coefficient of determination).

Methods	Sex	n	L_{inf} (cm)	SE	CV	K (/year)	SE	CV	t_0 (year)	SE	CV	r^2
OL	Male	140	118.6	7.300	0.061	0.171	0.021	0.128	0.098	0.129	1.319	0.939
	Female	73	141.2	12.75	0.090	0.129	0.022	0.176	0.180	0.215	1.192	0.935
	combined	405	124.9	3.435	0.027	0.165	0.009	0.060	0.270	0.075	0.277	0.935
BC	Male	140	116.8	6.500	0.056	0.190	0.020	0.110	0.377	0.085	0.226	0.952
	Female	73	132.7	8.507	0.064	0.159	0.02	0.127	0.387	0.127	0.328	0.957
	combined	405	123.9	2.395	0.019	0.171	0.007	0.039	0.302	0.041	0.137	0.969

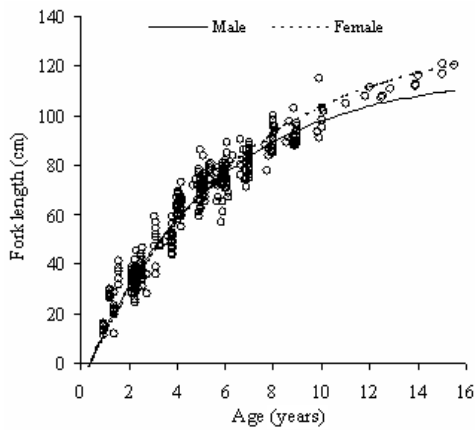


Fig. 8. Von Bertalanffy growth curves using back-calculated lengths for *S. cavalla* collected off northeast Brazil.

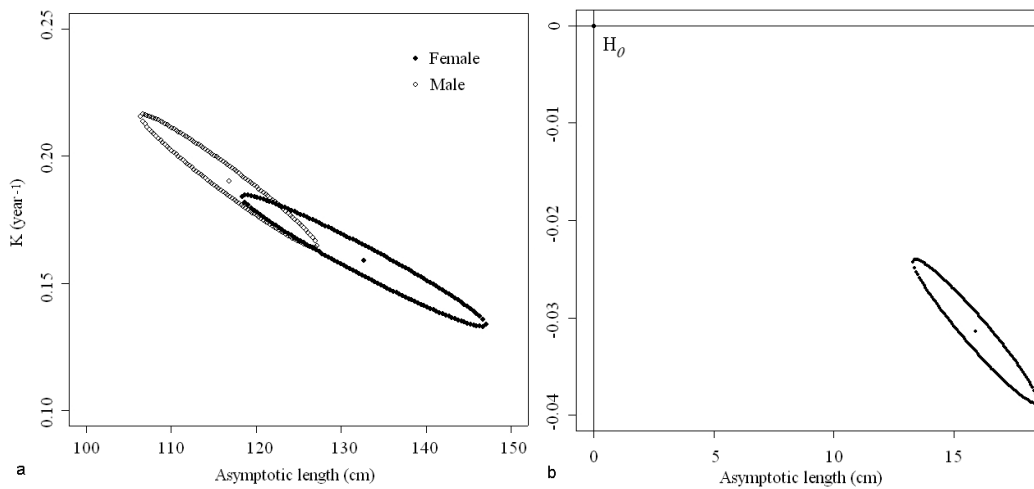


Fig. 9. Cross sections of approximate 95% confidence regions around least squares estimates (L_{∞} , K) for growth parameters of males and females: (a) 95% confidence intervals calculated by the difference between the vectors of the growth parameters (L_{∞} , K) (T^2 of Hotelling) for females and males, (b) of *S. cavalla* off northeastern Brazil.

On the other hand, Hotteling's T^2 test and 95% confidence intervals calculated for differences between the vectors of the growth parameters (L_∞ , K) of females and males demonstrated significant differences ($T^2 = 455.74$; $F = 226.79$; $df = 3.03$; $P < 0.001$) for growth between sexes. The test result is shown graphically in Figure 9b, in which the point H_0 ($\delta = 0$) stands out from the constructed confidence intervals ($\delta \neq 0$).

The distribution of the ϕ parameter had similar values over the whole area of occurrence (Table 4), revealing a similar growth pattern throughout the distribution of *S. cavalla* (mean=3.423; SD= 0.043) and normal distribution (Kolmogorov Smirnov-P=0.592) (Fig. 10a).

Using the age-length key for all the specimens analyzed in the growth study (n=405), the age structure for the entire sample was calculated, of the total of which specimens between 3 and 8 years of age represented 82.2% (Fig. 10b). According to the estimated parameters for separate sexes, females and

males have an approximate longevity of 32 and 26 years, respectively.

DISCUSSION

Whole otoliths of *S. cavalla* were used in the present study, as they offered good visibility of the bands (Fig. 3) and an acceptable average percent error (8.96%) between readings (CAMPANA, 2001). This APE reflects a moderately high level of precision in otolith readings and indicates that the aging protocol adopted is replicable. According to Campana and Jones (1992), measures of percent agreement vary substantially both among species and among ages within a species. Beamish and Fournier (1981) state that 95% agreement to within one year between two age readers of the Pacific cod (*Gadus macrocephalus*) constitutes poor precision, given the few classes in the fishery, but 95% agreement within five years would constitute good precision for the spiny dogfish (*Squalus acanthias*), given its sixty-year longevity.

Table 4. Parameters of von Bertalanffy growth equation for king mackerel (*S. cavalla*). L_∞ in fork length; ϕ' growth index of performance from Pauly and Munro (1984); M=males; F=females; B=both sexes combined.

Area	L_∞	K (/year)	t_0 (year)	ϕ'	Sex	Source
NE Brazil	116	0.180	0.22	3.38	M	Nomura and Rodríguez, 1967
	137	0.150	0.13	3.45	F	
	141.2	0.140	0.14	3.45	B	
NE Brazil	113.3	0.229	1.5	3.47	M	Ximenes et al., 1978
	131.7	0.164	2	3.45	F	
	124.9	0.185	1.8	3.46	B	
Florida (USA)	111	0.208	1.48	3.41	M	Manooch et al., 1987
	142	0.136	1.98	3.44	F	
	148	0.115	2.36	3.40	B	
Trinidad	112.3	0.180	-1.79	3.36	M	Sturm and Salter, 1990
	140.1	0.150	-1.52	3.47	F	
Atlantic ocean (USA)	96.4	0.262	-1.98	3.39	M	DeVries and Grimes, 1997
	126.7	0.145	-3.15	3.37	F	
E. Gulf of Mexico	102.6	0.247	-1.84	3.41	M	
	137.8	0.172	-1.83	3.51	F	
W. Gulf of Mexico	102.8	0.203	-2.74	3.33	M	
	134.1	0.150	-2.69	3.43	F	
	116.8	0.190	0.37	3.41	M	
NE Brazil	132.7	0.159	0.38	3.45	F	this study
	123.9	0.171	0.30	3.42	B	

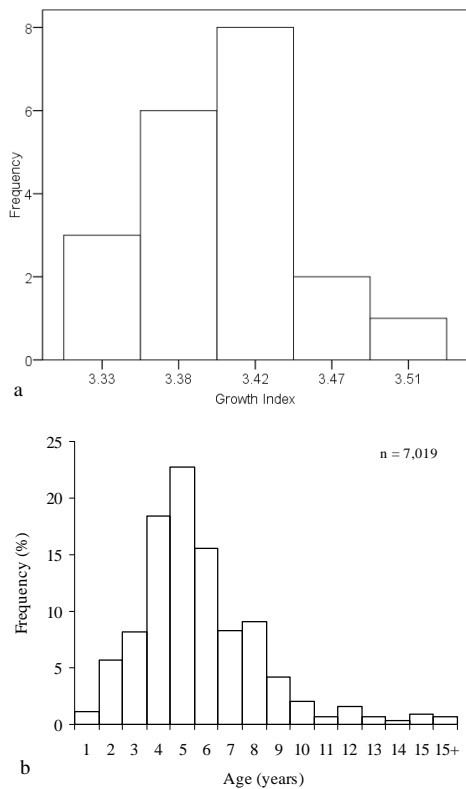


Fig. 10. Frequency distribution of growth index (ϕ) calculated for king mackerel growth parameters in different areas of the species distribution (a). Age composition for king mackerel (*S. cavalla*) collected off northeastern Brazil.

Whole otoliths have been used by a large number of authors (NOMURA; RODRIGUES, 1967; BEAUMARIAGE, 1973; JOHNSON et al., 1983; MANOOCH et al., 1987; COLLINS et al., 1989) to estimate the age of *Scomberomorus* species due to the ease in the reading of growth bands (MANOOCH et al., 1987). High average percentage errors and low matching between band readings in sectioned otoliths have been found for *S. queenslandicus* and *S. munroi* off the east coast of Australia (BEGG; SELLIN, 1998). Likewise, low matching between readings of whole and sectioned otoliths, with a tendency toward overestimating age using sectioned otoliths, have been reported for the king mackerel (*S. cavalla*) off the Atlantic coast of the USA (Collins et al., 1989).

In the monthly marginal increment analysis, juveniles and adults exhibited similarities related to the period of the year when the smallest distances from the last growth band to the otolith edge were recorded. However, a shorter period was observed in juveniles, which may be related mainly to the endogenous control of growth band formation

(LONGHURST; PAULY, 1987). An extensive period of growth band formation was found in adults, suggesting that there may also be a strong influence of reproduction activity, promoting a redirection of energy to gonad maturity and reproduction, with a consequent reduction in somatic growth and possibly leading to the formation of translucent bands. In northeastern Brazil, *S. cavalla* exhibits full spawning, which is more intense between September and March (FONTELES-FILHO, 1988), coinciding with the period of smaller marginal increments, as observed in the otoliths of adult specimens in the present study.

Ximenes et al. (1978) found similar results in northeastern Brazil, with reductions in the translucent margins occurring in the otoliths from December to March, corresponding to the period of intense reproduction (GESTEIRA; MESQUITA, 1976). In Trinidad, bands are formed from November to February (STURM; SALTER, 1990), matching the period of reproductive activity (September to March). Similarly, in the northern hemisphere, translucent bands are formed from April to June (BEAUMARIAGE, 1973; JOHNSON et al., 1983; MANOOCH et al., 1987), when the reproduction season begins (FINUCANE et al., 1986). Thus, the reproduction process may be related to the formation of growth bands in *S. cavalla*.

The reasonable adjustment between the OR and FL resulting from the multiplicative model (Table 1- Figure 7a) and the similarity between the mean observed and backcalculated lengths (Fig. 7b) confirm the presupposition of proportionality between otolith size and length of the specimens (CARLANDER, 1981). Furthermore, the satisfactory adjustment of the backcalculated method to the data must be particularly attributed to the identification of the regression model that best described the relationship between the OR and FL, with the subsequent use of the Monastyrsky model suggested by Francis (1990). Backcalculation is widely used to validate marks interpreted on otoliths from species of *Scomberomorus* for age determination (NOMURA; RODRIGUES, 1967; XIMENES et al., 1978; COLLINS et al., 1989; STURM; SALTER, 1990; SCHMIDT et al., 1993).

No significant difference in growth was observed between sexes using visual analyses with overlapping between confidence intervals. However, this methodology is not characterized by a formal hypothesis test and does not give a *P* value. It is therefore conservative in demonstrating significant differences (BEALE, 1960; CERRATO, 1990). Despite these limitations, 95% confidence intervals provided a measurement for the variability of estimated growth parameters using the von Bertalanffy nonlinear least squares methods.

Hotelling's T^2 hypothesis test indicated a significant difference in growth for males and females,

and was the most accurate in the present study. Differences in growth pattern between sexes is typical of *Scomberomorus* species (BEAUMARIAGE, 1973; POWELL, 1975; STURM, 1978; JOHNSON et al., 1983; FABLE et al., 1987; MCPHERSON, 1992; BEGG; SELLIN, 1998), with females reaching larger sizes (L_{∞}) than males.

The Schnute growth model was used to examine which model achieved the best adjustment to *S. cavalla* growth in northeastern Brazil. According to the values obtained for parameters a and b , the specialized von Bertalanffy model is the best model for describing the growth of the species in the region. The Schnute model employed in the present study was motivated by a concise biological principle and the four parameters nearly always have stable statistical estimates with reasonable biological interpretations (SCHNUTE, 1981).

The growth index (ϕ) values estimated in the present study correspond precisely to the means of the observed frequencies for the parameters reported for different areas of distribution of the species (Table 4 - Figure 10a) taking into consideration the estimate generated for combined sexes. According to Longhurst and Pauly (1987), there is a close relationship between the surface areas of the gills of a fish, its capacity to absorb oxygen, its size, longevity and growth parameters; environmental and latitudinal differences may also affect the growth of fish.

The stock structure of the king mackerel has frequently been the target of a variety of studies in the Gulf of Mexico and along the southeastern coast of the USA. Johnson et al. (1994) found differences in the stocks in the eastern and western Gulf of Mexico based on enzymatic electrophoresis. More recently, Gold et al. (2002) concluded that allele variations are consistent with the hypothesis of two highly distinguished stocks in Florida, separated by the peninsula. DeVries and Grimes (1997) found differences in growth for the king mackerel on the eastern side of the Gulf of Mexico and the Atlantic Ocean (USA). Analyses of otolith shapes in specimens from the Atlantic coast of the USA and the eastern Gulf of Mexico were efficient in classifying individuals from both locations; 99.8% of the species landed in southeastern Florida in winter originated from the Atlantic stock, compared to just 0.2% from the eastern Gulf of Mexico (DEVRIES et al., 2002).

Differences in growth between sexes indicate that males have faster growth until approximately five years of age. Beginning at six years of age, females have larger sizes for the same age (Fig. 8). According to Gesteira and Mesquita (1976), this species is ready for reproduction at 63 cm FL off the coast of the state of Ceará, Brazil (4.5 years for males; 4.4 years for females). At ages of first sexual maturity, females begin to have larger sizes

than males for the same age and reach larger asymptotic sizes (Table 3-Figure 8). Off the coast of Ceará, greater growth rates for females beginning in the adult phase stem from their greater voracity – as determined through studies on feeding habits (FONTELES-FILHO, 1988) – which may explain the inversion in growth rates found in the present study beginning in the adult phase.

The accentuated growth rate of males in relation to females at early ages is also verified by the τ_1 parameters estimated from the younger ages τ_1 by the Schnute model, which resulted in considerably higher values for males using both the direct and backcalculated methods (Table 2). This accelerated growth may be related to a greater proportion of males in relation to females (Fig. 5) in catches of *S. cavalla* in northeastern Brazil, as males would be more rapidly recruited to areas and fishing gear than females. This characteristic is a positive factor for the maintenance of the *S. cavalla* stock in northeastern Brazil, as the preservation of females is more important to the reproduction of the species than the preservation of males (NIKOLSKY, 1978; HELFMAN et al., 1997).

The growth parameters and characteristics estimated in the present study and the age structure for *S. cavalla* caught by the artisanal fleet in northeastern Brazil represent an important contribution to our knowledge of the species. The present study updates essential information for assessing the stock of this important resource, for which the last growth studies in the region were carried out approximately thirty years ago (XIMENES et al., 1978). Likewise, studies on the age structure, reproduction, stock composition and exploitation levels of *S. cavalla* in northeastern Brazil should also be undertaken permanently in order to promote sustainable catches and the maintenance of this important fishery resource.

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