 Col. Vol. Sci. Pap. ICCAT, 55(5): 1916-1925 (2003)

GROWTH MODELS FOR THE SKIPJACK TUNA (*Katsuwonus pelamis*) CAUGHT IN THE SOUTHEASTERN COAST OF SOUTH AMERICA

Humber Agrelli Andrade[1] *and Paul Gerhard Kinas*[2]

SUMMARY

*Growth models are an important component in the study of population biology and are generally required in fishery assessment. This paper is concerned with the fit of Schnute's general growth model to an age-length key of the skipjack tuna (*Katsuwonus pelamis*) caught off the southeastern coast of South America. We use the general framework of the model to investigate the effect of different error structures and the fit of specific submodels. Depending on the error structure different forms of the specialized von Bertalanffy growth curve arise as the final choice. We conclude that the classic von Bertalanffy model is adequate for the data at hand and present appropriate confidence intervals for the parameters. The existence of colinearity among parameter estimates and the implication on the precision of the estimates is discussed.*

RÉSUMÉ

*Les modèles de croissance constituent un élément important dans l'étude de la biologie des populations et sont généralement requis dans l'évaluation des pêcheries. Le présent document s'intéresse à l'ajustement du modèle de croissance général de Schnute à une clef d'identification âge-longueur du listao (*Katsuwonus pelamis*) capturé au large de la côte sud-ouest d'Amérique du Sud. Nous employons le cadre général du modèle pour rechercher l'effet de différentes structures d'erreurs et l'ajustement de sous-modèles spécifiques. Selon la structure d'erreurs, différentes formes de la courbe de croissance spécialisée de von Bertalanffy apparaissent comme choix final. Nous en concluons que le modèle classique de von Bertalanffy convient pour les données disponibles et présente des intervalles de confiance appropriés pour les paramètres. L'existence de colinéarité au sein des estimations de paramètre et l'implication sur la précision des estimations sont examinées.*

RESUMEN

*Los modelos de crecimiento son un componente importante en el estudio de la biología de la población y suelen ser necesarios para la evaluación de la pesquería. Este documento se ocupa del ajuste del modelo de crecimiento general de Schnute a la clave edad-talla del listado (*Katsuwonus pelamis*) capturado en las aguas de la costa suroriental de América del Sur. Hemos utilizado el marco general del modelo para investigar el efecto de las diferentes estructuras de error y el ajuste de submodelos específicos. Dependiendo de la estructura de error, las curvas de crecimiento especializadas de von Bertalanffy se plantean como la elección final. Concluimos que el modelo clásico de von Bertalanffy resulta adecuado para los datos disponibles y presenta intervalos de confianza apropiados para los parámetros. Se discute la existencia de una colinealidad entre estimaciones de parámetros y la implicación sobre la precisión de las estimaciones.*

KEYWORDS

Growth curves, Skipjack tuna, Population dynamics

[1] UNIVALI – CTTMar, C.P. 360, 88302-202, Itajaí-SC, BRAZIL. humber@cttmar.univali.br
[2] FURG – Depto. Matemática, C.P. 474, 96201-900, Rio Grande-RS, BRAZIL.

1 INTRODUCTION

Growth models are an important component in the study of population biology and are generally required in fishery assessment. Information about growth is necessary in several analytic fishery assessment models (*e.g.* Virtual Population Analysis (VPA)) (Hilborn and Walters, 1992; Quinn and Deriso, 1999). This paper examines the fit of growth models for the skipjack tuna (*Katsuwonus pelamis*) caught off the southeastern coast of South America.

There are two primary types of data used to fit empirical growth models: age-length keys and length-frequency distributions. While the latter are studied with modal progression techniques and with mixture distributions (Schnute and Fournier, 1980; Foucher and Fournier, 1982) the former are suited for growth models relating size and age directly. For skipjack caught off the southeastern coast of South America, an age-length key from the mid 1980's is available in the literature (Vilela 1990). There are no data from mark-recapture experiments. Therefore we concentrated our analysis on the available age-length key.

The traditional von Bertalanffy (1938) growth model was fitted to this age-length key by Vilela and Castello (1991). However, there is no *a priori* reason for this to be the most adequate model. In the context of a precautionary approach to fishery management, considering model uncertainty is recommended (Butterworth, Punt and Smith 1996; McAllister, Starr, Restrepo and Kirkwood 1999). Several other possibilities describe length as a function of increasing age in fishes (Ricker, 1979). However, to choose the more suitable model based on the available data, different alternatives must be compared by some criteria.

The alternative explored in this paper is the four parameters model formulated by Schnute (1981), which contains many specific growth models (*e.g.* generalized and restricted von Bertalanffy, Gompertz, etc.) as special cases. Schnute´s general formulation is attractive because it allows for a smooth transition between models of different functional form (*i.e.* specific submodels) and because of the statistical stability of the resulting parameter estimates (in the sense of numerical convergence).

Given a specific functional form the appropriate estimation of growth parameters also depends on the error structure assumed for the data. If the variability in size is constant as a function of age, an additive error structure is suitable. However, if the variability in size increases with age a multiplicative error is appropriate (Quinn and Deriso, 1999). The analysis of residuals can be used to empirically choose the most appropriate error structure.

Vilela (1990) constructed an age-length key using samples of skipjack landings collected in the mid 80's. In a preliminary analysis the author had concluded that growth of male and female were not statistically different and therefore presented the data lumped by sex.

In this paper we investigate which growth model is more suitable for skipjack tuna caught in the southeastern coast of South America by analyzing the age-length key of Vilela (1990). We do this within the framework of Schnute´s general growth model, investigating the effect of assuming an additive or a multiplicative error structure as well. Interesting features that arise from the data analysis are examined and the implications of structural uncertainty in model choice are discussed.

2 MATERIALS AND METHODS

2.1 Data and Growth Model

The age-length key constructed by Vilela (1990) included 613 spines sampled between 1986 and 1988 (**Tables 1 and 2**).

The growth model of Schnute (1981) relates age t to some measure of size $Y(t)$ (here taken as furcal length) according to the following equation:

$$Y(t)=\left[\gamma_1^b+\left(\gamma_2^b-\gamma_1^b\right)\frac{1-e^{-a(t-\tau_1)}}{1-e^{-a(\tau_2-\tau_1)}}\right]^{1/b} \quad (1)$$

Parameters τ_1 and τ_2 are fixed ages specified in advance with the restriction $\tau_1<\tau_2$. There are four parameters to be estimated: a, b, γ_1 and γ_2. Parameters γ_1 and γ_2 are sizes expected at ages τ_1 and τ_2 respectively, with restriction $0<\gamma_1<\gamma_2$. Various special models known in the literature are related to specific values of parameters *a* and *b* (see Schnute, 1981). For instance, if $a>0$, and $b=1$ the model reduces to the von Bertalanffy growth model for length in which case *a* is the intrinsic growth parameter usually represented by k in the fishery literature.

2.2 Error Structure in the Models

To fit the model to observed data an appropriate error structure must be assumed. An additive error structure is appropriate when the variability of size $Y(t)$ is constant as a function of age t (homoscedasticity). In this case, the observed length of fish i (y_i) is related to its age t_i according to the expression

$$y_i=f(t_i,\phi)+\sigma\varepsilon_i \quad (2),$$

where $\phi=(a,\ b,\ \gamma_1,\gamma_2)$ is the parameters vector of the growth model $f(\ )$ defined by the right-hand side of equation (1), and ε_i is the error term, assumed to be a normal random variable with mean zero [$E(\varepsilon_i)=0$] and variance $V(\varepsilon_i)=\sigma^2$.

If the variability of size increases as a function of age (*i.e.* heteroscedasticity), then it is more adequate to use a multiplicative error structure (Quinn and Deriso, 1999). In this case the length of an individual fish should be modeled as

$$y_i=f(t_i,\phi)\cdot\exp(\sigma\varepsilon_i) \quad (3)$$

with parameters and error distribution as defined above.

2.3 Parameter Estimation

The estimation of the parameter vector ϕ can be reduced to a standard problem in non-linear minimization (Press, Flannery, Teukolsky and Vetterling 1986). Finding maximum likelihood estimates of ϕ under the additive error structure of expression (2) is equivalent to minimizing the function

$$S(\phi)=\sum\left[y_i-f(t_i,\phi)\right]^2 \quad (4).$$

Alternatively, if the multiplicative error structure (3) is assumed, the function to be minimized is

$$S(\phi)=\sum\left\{\ln\left[\frac{y_i}{f(t_i,\phi)}\right]\right\}^2 \quad (5).$$

After choosing appropriate starting values, the search for the point of global minimum denoted ϕ_{mle} is obtained in two stages. First a simplex algorithm searches the parameter space to escape any eventual local minima. After convergence, current estimates are used as starting values in a more refined Quasi-Newton procedure to get to the final estimates. The covariance matrix of the estimated parameters is obtained in the usual way from the Hessian matrix of second derivatives of the likelihood function evaluated at ϕ_{mle} (Lehmann, 1983).

The standard error of the assymptotic length L_∞ (which is defined as a function of the parameter vector ϕ whenever $a>0$) and the construction of confidence regions was obtained with a parametric bootstrap (Efron and Tibshirani, 1993) by simulating from a multivariate Gaussian density centered at

ϕ_{mle} and with the estimated covariance matrix.

The stability of parameter estimates within Schnute´s parameterization was verified by specifying different starting values for the unknown parameters and using different pairs of fixed ages τ_1 and τ_2.

2.4 Comparing Growth Models

As pointed out in Quinn and Deriso (1999) two types of comparisons among growth models are needed. First, there is the need to select some best model for a particular data set. Second, there is the need to compare growth models obtained from different data sets. In this study we analyze only one data set, hence we can only make the first type of comparison.

We will perform our analysis by first fixing an error structure (additive or multiplicative) and, given that structure, search for the most appropriate growth model. The simple regression between the absolute residuals (*observed – predicted*) and age (Glejser, 1969) will be used to confront the additive and multiplicative error structures.

There are several statistical tests to compare nested growth models (*e.g.* Hotelling, Fisher´s *F*, and likelihood-ratio tests). We used the *F*-statistic presented in Schnute (1981) to decide between the general four parameter model and some nested submodel of interest. Cerrato (1990) showed that this simple *F*-statistic could be successfully used in the generalized von Bertalanffy growth model if the sample size is large. We used this test statistic to compare specific growth models nested within the generic Schnute formulation. For some sample of size n this *F*-statistic is given by the expression

$$F = \frac{\left(\frac{S(\phi_2) - S(\phi_1)}{\kappa - \upsilon}\right)}{\left(\frac{S(\phi_1)}{n - \kappa}\right)} \quad (6).$$

κ and υ ($\kappa > \upsilon$) are the number of free parameters in models with parameter vectors ϕ_1 and ϕ_2 respectively. Under the null hypothesis that all κ-υ parameters that ϕ_1 has in excess to ϕ_2 are zero, this statistic has approximately a Fisher distribution with parameters (κ-υ, n-κ).

The selection of some "best" model starts by choosing the maximum likelihood fit for the full model given by equation (1). The next step is an inspection of parameter estimates for *a* and *b* in the context of some submodel (for example, with a parameter restriction like *b*=1). After obtaining parameter estimates for the submodel, the *F* statistic (6) is calculated. If there is no evidence for rejecting the submodel (null hypothesis) this simpler model is a justified choice by the principle of parsimony.

All calculations and bootstrap simulations were performed with the statistical software Statistica© version 5.1.

3 RESULTS

The distribution of skipjack tuna samples between December 1983 and March 1989 is shown in **Table 1** suggesting that there is no change in the sampled length range over the period. Overall sample sizes and variances in length are calculated from the age-length key (**Table 2**) and displayed by age in **Figure 1**. There is no clear trend in variance by age. While variances of length tend to increase until age 3, the pattern is erratic for older age classes, which were poorly sampled.

We fitted Schnute´s general growth model using several pairs of fixed ages τ_1 and τ_2 together with different starting values for the unknown parameters but the estimated parameters were always the same. For the results presented here we fixed the ages $\tau_1 = 1$, $\tau_2 = 4$ and the starting values (a, b, γ_1, γ_2) = (0.1, 0.1, 30, 60).

The results of the analysis are summarized in **Table 3**. Case 1 refers to the fit of the four parameters model while Case 2 refers to the submodel selected for comparison in each situation.

The predicted length for skipjack tunas of ages 1 and 4 are very similar in all four cases (full and submodels, with additive and multiplicative erros) with values close to 43 cm and 64 cm, respectively. In the most general models (Case 1) the estimated values for the parameters a and b are sensitive to the choice of an additive or multiplicative error structure. With an additive error the maximum likelihood estimates of a and b are about 0.2 and 1.3 respectively. When a multiplicative error is assumed, the estimates of a and b are both about 0.3. While the model with multiplicative error structure points to the von Bertalanffy model usually adopted for growth in weight (b =1/3) the additive error structure favors the von Bertalanffy model usually adopted for growth in length (b =1). These three-parameter submodels are denoted as Case 2 and the estimates are listed in **Table 3** as well. The strong negative correlation between estimates of *a* and *b* for both Case 1 models indicate high colinearity between these parameters. This explains the considerable gain in precision in the estimates when going from Case 1 to Case 2 regardless of the assumed error structure.

Assuming an additive error, comparisons between the four parameters free Schnute model (Case 1) and the model with b =1 (Case 2) showed no significant differences in the model fit (F = 0.031; p > 0.85) (**Table 4**). Similarly, there is no significant difference between the four parameters model (Case 1) and the three parameters model with b =1/3 (Case 2), when a multiplicative error is assumed (F = 0.001; p > 0.95). Within the range of ages available in the data set both models with three free parameters (Case 2), give an almost indistinguishable fit (**Figure 2**). The residual plot (**Figure 3**) further confirms the similarity between these two fits.

For all growth models considered here, estimates of the assymptotic length L_∞ and the age at length zero t_0 can be obtained as functions of ϕ (for appropriate expressions see Schnute´s paper) and are also displayed in **Table 3** in both Case 2 models. The additive error structure suggests an assymptotic length of about 90 cm, exceeding by roughly 10 cm the estimate obtained for the multiplicative error. The overlap of the bootstrap confidence intervals suggest that this difference is unclear from a statistical standpoint.

4 DISCUSSION

Within the framework of Schnute's general growth model and assuming additive error, the traditional von Bertalanffy growth model (b = 1) is an acceptable choice with parameters given in **Table 4**. However, the assumed error structure proved to be essential to elect this growth model for the available skipjack tuna data. Additive and multiplicative errors point to different most suitable growth models (*i.e.* both Case 2 models). The inspection of the shapes (**Figure 2**) and of the residuals (**Figure 3**) suggest that the practical difference is minor within the range of observed ages. The effect of model structure on the final estimates can also be analyzed by comparing the confidence intervals for L_∞; showing that most of the region is shared by both models. However, the possible effect of using any of these models to estimate catch at age (or even optimized age-length keys) in the stock assessment approach, should be verified in the future.

Conceptually the increase of variance in length as a function of age is an expected pattern for a natural fish population favoring a multiplicative error structure. However, small sample sizes or even some effects of gear selectivity (*e.g.* Rosa-Lee effect) can preclude the observation of an increase in the variability of length in relation to the age.

There is high colinearity between parameters estimates *a* and *b* (Case 1) as indicated by the estimated correlation of –0.987 resulting in low precision in the estimates (large confidence intervals). After fixing *b* (Case 2) the precision in the estimate of *a* increases more then six times (0.25÷0.04 = 6.25) regardless of the chosen error structure. It is interesting to notice that the precision in estimates of γ_1 and γ_2 is almost unaffected by the choice between Cases 1 and 2, although the multiplicative erros structure provides slightly more precise estimates.

A previous analysis by Villela and Castello (1991), using Marquart´s procedure, provided point estimates similar to the maximum likelihood estimates obtained for our Case 2 with additive error structure. Those authors however did not provide confidence intervals. The confidence intervals of *a* and L_∞ presented here (Case 2) give a wrong idea about the range of possible pairs of values because of a hidden but strong non-linear correlation among these parameters. This feature becomes apparent in the scatterplots of **Figure 4**. This is a remainder that marginal (one-dimensional) confidence intervals can be misleading if carelessly used.

REFERENCES

VON BERTALANFFY, L. 1938. A quantitative theory of organic growth (Inquires on growth laws II). Human Biol. 10: 181-213.

BUTTERWORTH, D. S., A. E. Punt and A. D. M. Smith. 1996. On plausible hypotheses and their weightings, with implications for selection between variants of the Revised Management Procedure. Rep. Int. Ehal. Commn. 46: 481-491.

CERRATO, R. M. 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. Can. J. Fish. Aquat. Sci. 47: 1416-1426.

EFRON, B. and R. Tibshirani. 1993. An Introduction to the Bootstrap. New York: Chapman and Hall. 436 pp.

FOUCHER, R. P. and D. Fournier. 1982. Derivation of Pacific cod age composition using length-frequency analysis. N. Amer. J. Fish. Manage. 2: 276-284.

GLEJSER, H. 1969. A new test for heteroscedasticity. J. Amer. Statist. Assoc. 64: 316-323.

HILBORN, R. and C. J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York.

LEHMANN, E. L. 1983. Theory of Point Estimation. New York: Wiley.

McALLISTER, M. K., P. J. Starr, V. Restrepo and G. P. Kirkwood. 1999. Formulating quantitative methods to evaluate fishery management systems: what fishery processes should we model and what trade-offs do we make? ICES J. Marine Science 56: 900-916.

PRESS, W. H., B. P. Flannery, S. A. Teukolsky and W. T. Vetterling. 1986. Numerical Recipes: The Art of Scientific Computing. New York: Cambridge University Press.

QUINN, T. J., II and R. B. Deriso. 1999. Quantitative Fish Dynamics. Oxford University Press, New York.

RICKER, W. E. 1979. Growth rates and models. In: Hoar, W. S. and Randall, D. J. (Eds.). Fish Physiology. Vol III. Chapter 11. 677-743.

SCHNUTE, J. and D. A. Fournier. 1980. A new approach to length frequency analysis: growth structure. Can. J. Fish. Aquat. Sci. 37: 1337-1351.

SCHNUTE, J. 1981. A versatile growth model with statiscally stable parameters. Can. J. Fish. Aquat. Sci. 38(9): 1128-1140.

VILELA, M. J. A. and J. P. Castello. 1991. Estudio de la edad y del crecimiento del barrilete (Katsuwonus pelamis) en la región sur y sudeste de Brasil. Frente Maritimo 9(sec. a):29-35.

VILELA, M. J. A. 1990. Idade, crescimento, alimentação e avaliação do estoque de bonito listado, *Katsuwonus pelamis* (Scombridae: Thunnini), explorado na região sudeste-sul do Brasil. MSc. Thesis. Fundação Universidade do Rio Grande, RS, Brasil. 81 pp.

Table 1. Date, range length and number of spines used to construct the age-length key for skipjack tuna (*Katsuwonus pelamis*) caught in the southeastern South America. (Redraw from Vilela, 1990).

Date	Length Range in the Sample (cm)	Number of Spines
December/1983	35 – 60	154
December/1985	46 – 53	27
January/1986	46 – 65	93
February/1986	48 – 67	31
April/1986	37 – 51	30
May/1988	34 – 69	134
July/1988	41 – 68	123
September/1988	42 – 63	81
November/1988	47 – 70	76
February/1989	44 – 58	116
March/1989	43 – 64	100

Table 2. Age-length for skipjack tuna (*Katsuwonus pelamis*) caught in the southeastern South America. (Redraw from Vilela, 1990).

Length/Age	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5
36	2								
37	1	1							
38	1	5							
39	2	7							
40	2	1							
41	2	5							
42		1	1						
43		4	5						
44		6	5						
45		3	14						
46		2	24	2					
47		1	30	9					
48			23	16					
49			22	15					
50			13	25	2				
51			7	34	10				
52			5	42	12				
53			4	27	14				
54				25	21	5			
55				14	18	4			
56				10	13	5			
57				1	7	4			
58					10	3	2		
59					7	3			
60					4	5	4	2	
61					1	9	4	1	
62						2	1	1	
63						3	4	1	
64						3	2	1	
65							1	1	
66								1	
67									1
68									1
69									
70								2	

Table 3 - Schnute model parameters estimates for the skipjack tuna (*Katsuwonus pelamis*) caught in the southeast of South America. Case 1 represents the four parameter model, and case 2 represents the three parameter model with restrictions b = 1 (additive error structure), and b = 1/3 (multiplicative error structure).

	Additive Error		Multiplicative Error	
	Case 1	Case 2	Case 1	Case 2
$\hat{\gamma}_1 \pm 1$ SE	42.742 ± 0.251	42.737 ± 0.251	42.648 ± 0.213	42.649 ± 0.208
95% CI for $\hat{\gamma}_1$	(42.249;43.235)	(42.246;43.229)	(42.230;43.066)	(42.241;43.057)
$\hat{\gamma}_2 \pm 1$ SE	64.187 ± 0.524	64.142 ± 0.460	63.932 ± 0.646	63.943 ± 0.538
95% CI for $\hat{\gamma}_2$	(63.159;65.214)	(63.240;65.044)	(62.666;65.198)	(62.890;64.997)
$\hat{a} \pm 1$ SE	0.176 ± 0.249	0.220 ± 0.040	0.333 ± 0.258	0.325 ± 0.040
95% CI for $\hat{a}$	(-0.311;0.664)	(0.141;0.298)	(-0.172;0.839)	(0.246;0.404)
$\hat{b} \pm 1$ SE	1.288 ± 1.624	1	0.281 ± 1.610	1 / 3
95% CI for $\hat{b}$	(-1.896;4.472)		(-2.874;3.436)	
$\hat{L}_\infty \pm 1$ SE		87.078 ± 7.359		79.757 ± 4.339
95% CI for $\hat{L}_\infty$		(78.143;105.260)		(73.213;90.335)
$\hat{t}_o$		-2.071		-4.135
Correlations				
$(\hat{\gamma}_1, \hat{\gamma}_2)$	0.175	0.147	0.190	0.090
$(\hat{\gamma}_1, \hat{a})$	-0.209	-0.573	-0.282	-0.483
$(\hat{\gamma}_1, \hat{b})$	0.124		0.209	
$(\hat{\gamma}_2, \hat{a})$	-0.593	-0.799	-0.647	-0.822
$(\hat{\gamma}_2, \hat{b})$	0.488		0.544	
$(\hat{a}, \hat{b})$	-0.987		-0.987	

Table 4 - Statistics and hypothesis tests from the Schnute growth model for the skipjack tuna (*Katsuwonus pelamis*) from the southeast South America.

	Additive Error (AE)		Multiplicative Error (ME)	
	Case 1	Case 2	Case 1	Case 2
Residual sum of squares	3812.408989	3812.602856	1.470810	1.470812
Residual mean square ($\hat{\sigma}^2$)	6.260113	6.250169	0.002415	0.002411
$\hat{\sigma}$	2.502022	2.500034	0.049144	0.049104
F (case1 x case2)	0.031	(P > .85)	0.001	(P > .95)

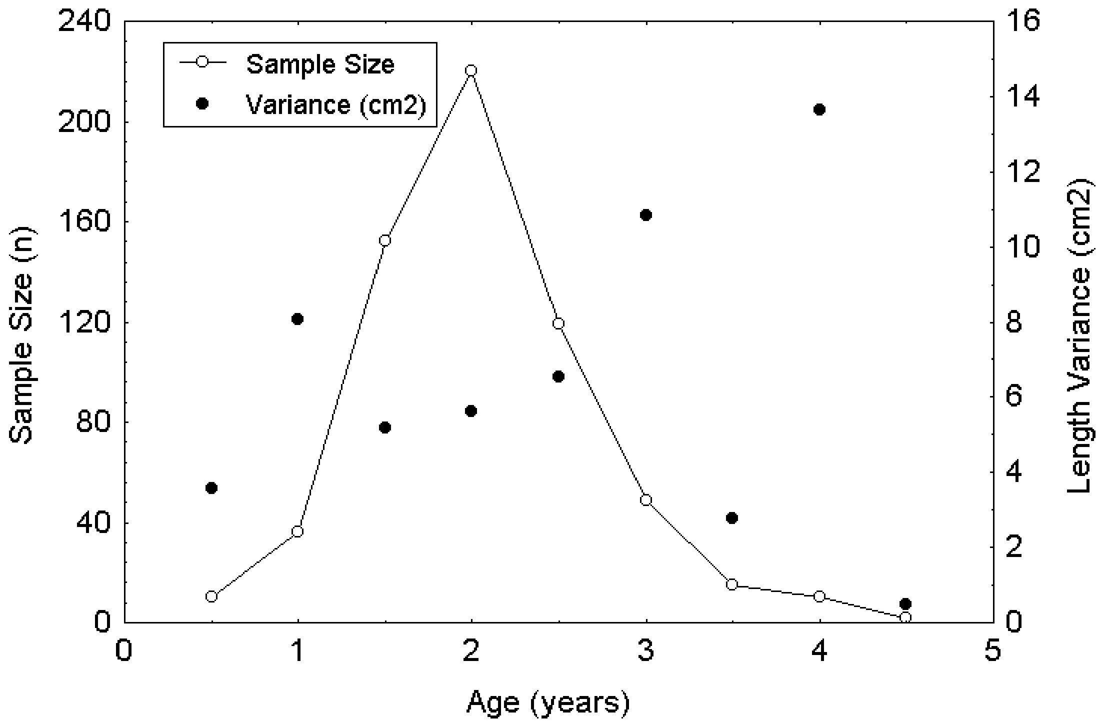

Fig. 1 - Sample size and length variance in relation with age as calculated from the age-length key for skipjack tuna (*Katsuwonus pelamis*) presented in Vilela (1990).

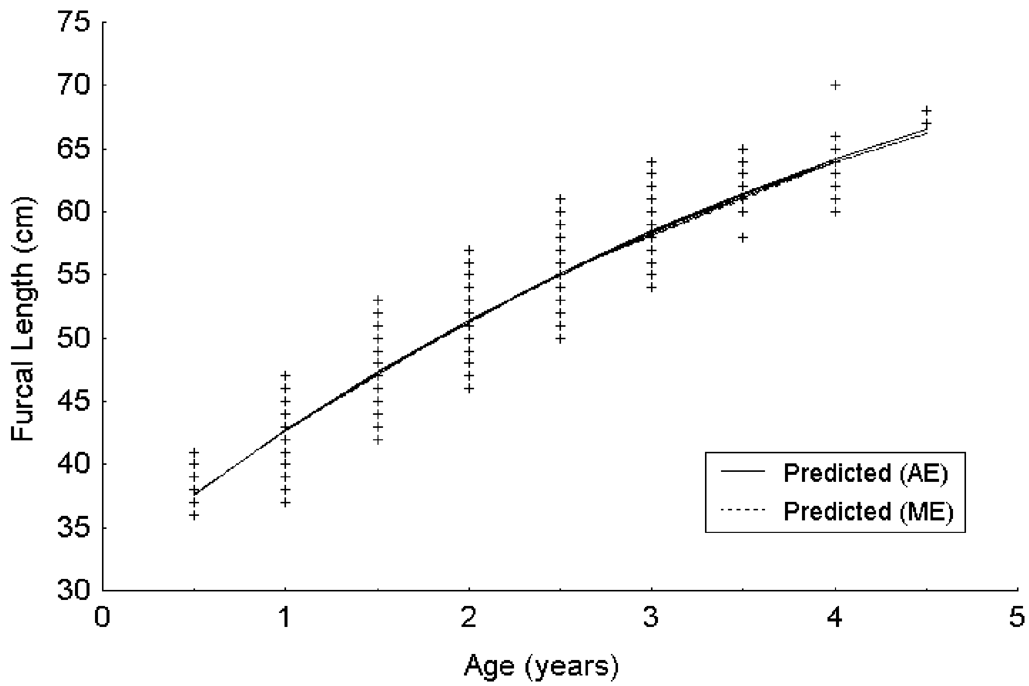

Fig. 2 – Schnute model fitted to data from skipjack tuna (*Katsuwonus pelamis*) caught in the southeast South America. Continuous line represents the fit with $b = 1$ pointed as the suitable model when assumed additive error (AE) structure. Dotted line represents the fit with $b = 1/3$ pointed as the suitable model when assumed multiplicative error (ME) structure.

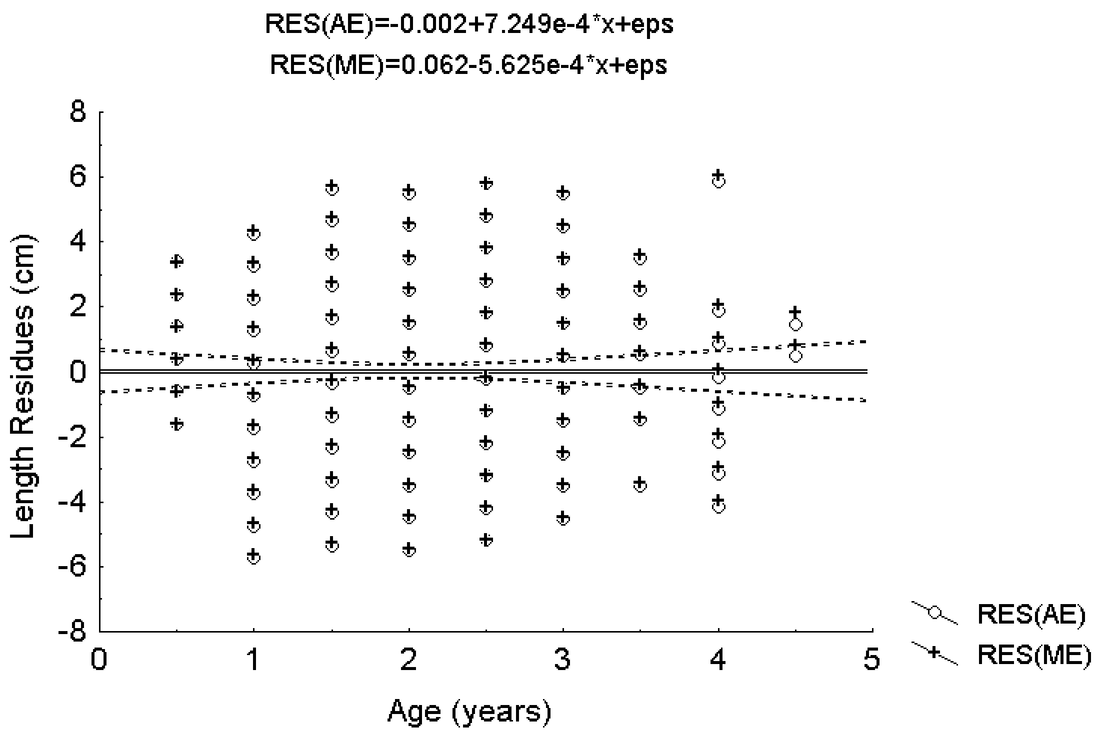

Fig. 3 – Residuals when assumed additive (RES_AE) or multiplicative error (RES_ME) structure to fit the Schnute model.

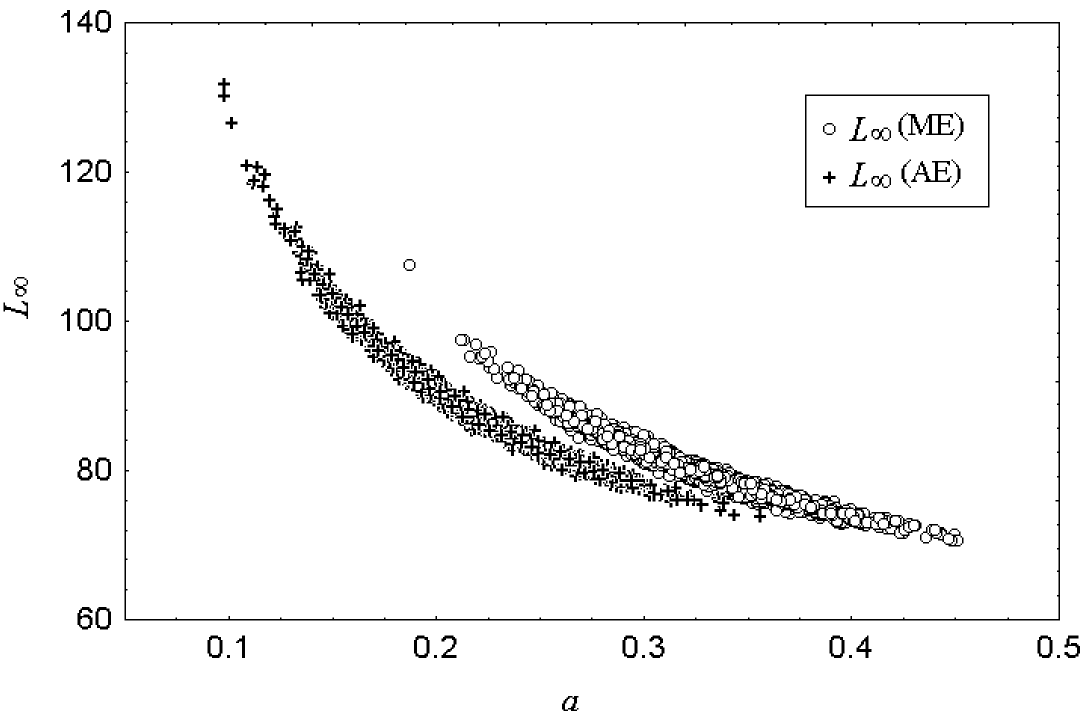

Fig. 4 – Scatterplots for the parameters $L\infty$ and a (related to k of the traditional von Bertalanffy formulation) from a parametric bootstrap for the skipjack tuna (*Katsuwonus pelamis*) caught in the southeastern coast of South America. (AE) Additive error; (ME) Multiplicative error.