

Estimated growth rate of the skipjack tuna (*Katsuwonus pelamis*) from tagging surveys conducted in the senegalese area (1996-1999) within a meta-analysis framework

Jean-Pierre Hallier, Daniel Gaertner

► **To cite this version:**

Jean-Pierre Hallier, Daniel Gaertner. Estimated growth rate of the skipjack tuna (*Katsuwonus pelamis*) from tagging surveys conducted in the senegalese area (1996-1999) within a meta-analysis framework. Collective Volume of Scientific Papers, ICCAT, 2006, 59 (2), pp.411-420. <ird-00351399>

HAL Id: ird-00351399

<http://hal.ird.fr/ird-00351399>

Submitted on 9 Jan 2009

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

ESTIMATED GROWTH RATE OF THE SKIPJACK TUNA (*KATSUWONUS PELAMIS*) FROM TAGGING SURVEYS CONDUCTED IN THE SENEGALESE AREA (1996-1999) WITHIN A META-ANALYSIS FRAMEWORK

Jean Pierre Hallier¹, Daniel Gaertner²

SUMMARY

*Tagging data obtained during the research program called MAC are reanalyzed for skipjack tuna (*Katsuwonus pelamis*), using the von Bertalanffy-Fabens' growth model. Tagging surveys were initiated during 1996-1999 on-board commercial baitboats in Mauritanian and Senegalese waters. The analyses include the Francis' maximum likelihood estimation approaches accounting for growth variability as a function of the expected growth increment. Bearing in mind the generally high negative correlation between estimates of L_{∞} and K , and instead of fixing L_{∞} at an arbitrary level, we expressed L_{∞} as a simple function of K within a meta-analysis framework. Based on previous estimates of growth parameters for skipjack in the world ocean, the fit of this bioenergetic growth equation gave the following relationship: $L_{\infty} = 70.607 K^{-0.231}$. An alternative von Bertalanffy-Fabens' growth model was used in which to L_{∞} was substituted by this function of K . After the comparison of different error structure models, the estimates corresponding to the best fit under the AIC criteria were obtained for $K = 0.251$ and, after re-introducing this value in the bioenergetic equation, $L_{\infty} = 97.258$. These results are not in agreement with growth parameter estimates obtained previously in the same part of the Atlantic Ocean but are consistent with the majority of growth estimates obtained by other investigators using tagging, hard part or length-frequency data. The application of the Francis variance model suggests that the variability of the growth increment of skipjack is not constant.*

RÉSUMÉ

*Les données de marquage obtenues lors du programme de recherche intitulé « MAC » sont ré-analysées pour le listao (*Katsuwonus pelamis*), à l'aide du modèle de croissance von Bertalanffy-Fabens. Des campagnes de marquage ont été menées entre 1996 et 1999 dans les eaux de la Mauritanie et du Sénégal à bord de canneurs commerciaux. Les analyses incluent les approches d'estimation de la probabilité maximale de Francis qui tiennent compte de la variabilité de la croissance comme fonction de l'augmentation de croissance escomptée. Tenant compte de la corrélation négative généralement élevée entre les estimations de L_{∞} et K , et au lieu de fixer L_{∞} à un niveau arbitraire, nous avons exprimé L_{∞} comme une simple fonction de K dans le cadre d'une méta-analyse. Sur la base d'estimations antérieures des paramètres de croissance pour le listao dans l'océan mondial, l'ajustement de cette équation bioénergétique de croissance a fourni la relation suivante : $L_{\infty} = 70.607 K^{-0.231}$. Un modèle de croissance von Bertalanffy-Fabens alternatif a été utilisé dans lequel L_{∞} a été substitué par cette fonction de K . Après avoir comparé différents modèles de structure d'erreur, les estimations correspondant au meilleur ajustement selon les critères AIC ont été obtenues pour $K = 0,251$ et, après avoir réintroduit cette valeur dans l'équation bioénergétique, $L_{\infty} = 97.258$. Ces résultats ne coïncident pas avec les estimations des paramètres de croissance obtenues précédemment dans la même zone de l'océan Atlantique, mais ils concordent avec la majorité des estimations de croissance obtenues par d'autres chercheurs en utilisant des données de marquage, de pièces dures ou de fréquences de tailles. L'application du modèle de variance de Francis suggère que la variabilité de l'augmentation de croissance du listao n'est pas constante.*

RESUMEN

*Se vuelven a analizar los datos de marcado para el listado (*Katsuwonus pelamis*), obtenidos durante el programa denominado MAC, utilizando el modelo de crecimiento de von*

¹ IOTC, PO Box 1011, Victoria, Seychelles

² IRD (UR Thétis) CRH BP 171, 34203 Sète Cedex, France

Bertalanffy-Fabens. Las prospecciones de marcado se iniciaron durante 1996-1999 en aguas mauritanas y senegalesas a bordo de barcos de cebo vivo comerciales. Los análisis incluyen enfoques de estimación de máxima verosimilitud de Francis, que tienen en cuenta la variabilidad en el crecimiento como una función del incremento previsto del crecimiento. Teniendo en mente la correlación generalmente muy negativa entre las estimaciones de L_∞ y K , en vez de fijar L_∞ en un nivel arbitrario expresamos L_∞ como una función simple de K , en un marco de meta-análisis. Sobre la base de anteriores estimaciones de parámetros de crecimiento para el listado en el océano mundial, el ajuste de esta ecuación bioenergética de crecimiento proporcionó la siguiente relación: $L_\infty = 70,607 K^{-0,231}$. Se utilizó un modelo alternativo de crecimiento de von Bertalanffy-Fabens en el que L_∞ fue sustituida por su función de K . Tras una comparación de los diferentes modelos de estructura de error, se obtuvieron las estimaciones correspondientes al mejor ajuste según los criterios AIC para $K = 0,251$ y, tras reintroducir este valor en la ecuación bioenergética, se obtuvo $L_\infty = 97,258$. Estos resultados no concuerdan con las estimaciones de parámetros de crecimiento obtenidas anteriormente en la misma parte del océano Atlántico, pero coinciden con la mayoría de las estimaciones de crecimiento obtenidas por otros investigadores que utilizaron datos de marcado, partes duras y frecuencias de tallas. La aplicación del modelo de varianza de Francis sugiere que la variabilidad del incremento del crecimiento del listado no es constante.

KEYWORDS

Growth, Skipjack, Tagging, Tropical tuna

1 Introduction

Different methods are commonly used to obtain growth estimates: (1) analysis of tag and recapture data, (2) analysis of the hard parts of the fish (e.g., otoliths, vertebrae, etc.), and (3) analysis of cohort progressions in length-frequency distributions. However, it was showed that Skipjack (*Katsuwonus pelamis*) spawns in an opportunistic manner throughout the year and over large areas of the Atlantic Ocean, so the cohorts cannot easily be identified (Cayré and Farrugio, 1986). Furthermore, skipjack growth parameters may vary with latitude (Bard and Antoine, 1986) and direct estimates of age have been hampered by the lack of consistent check marks on hard parts of the fish.

For all of these reasons and bearing in mind the amount of tagging data accumulated since the implementation of the research program called MAC (for “Mattes de thons Associées aux Canneurs”) on the bait boat fishing technique and its consequences (Hallier et al., 2001), it has been considered suitable to re-evaluate the growth rate of skipjack in the Senegalese area from tagging data.

2 Materials and Methods

Tagging took place on board commercial baitboats mainly in the north of Mauritania from 1996 to 2000. Skipjacks were tagged in schools associated with baitboats, and recaptures were registered in schools associated with baitboats (very few were recovered in free schools fished by purse seiners or outside of the bait boat area). In addition to the conventional “spaghetti” tag, another type of tag (commonly used for opportunistic tagging of tunas and billfishes by the sport fishermen) was used during the Bigeye Tuna Year Program (BETYP) of the International Commission for the Conservation of Atlantic Tunas (ICCAT). However, the lower efficiency of the new tag type, specifically for the recapture rate of bigeye tuna (*Thunnus obesus*), was showed in previous studies (Hallier and Gaertner, 2002; Gaertner et al, 2004). Accordingly, and even if has not yet been evidenced whether Betyt tags stunted the growth rate for skipjack or not, only the spaghetti tag type (including oxy-tetracycline injected fish) was used in the present analysis.

Measurements of the fish were made from the tip of the snout to the fork of the tail to the nearest centimetre or half-centimetre with calipers. Only fish with accurate size and known dates and positions at tagging and at recapture are used for growth study. Recapture for fish at liberty for less than 20 days have not been considered as well as fish with growth less than -2 cm. The first limitation is to take into account a possible stress of the fish that will disrupt the growth and slight measurement errors as tuna were measured directly on the tagging cradle. The second limitation is directly related to measurement’s errors that can be done negatively or positively.

Growth was modelled using the translation of the von Bertalanffy curve formalized by Fabens (1965) to account for the sort of information obtained from tagging programmes (i.e., tag release and recapture lengths and time at liberty data):

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

$$\Delta L = L_{t+\Delta t} - L_t$$

where the increment in length ΔL through the period Δt (i.e., the time at liberty) is calculated as the difference between the size at recapture $L_{t+\Delta t}$ minus the size at tagging L_t ; K and L_{∞} are the conventional growth rate coefficient and the asymptotic average maximum length of the von Bertalanffy curve respectively (Haddon, 2001).

Assuming normal random errors (thereafter, called Model A), the likelihood function L can be represented by

$$L = \prod \left(\frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(\Delta L - \Delta \hat{L})^2}{2\sigma^2}} \right)$$

where σ^2 is the constant variance of the residuals between the observed and expected ΔL values. The maximum likelihood estimates of L_{∞} , K , and σ were obtained by minimising the negative logarithm of L (LL), which is

$$LL = - \sum \ln \left(\frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(\Delta L - \Delta \hat{L})^2}{2\sigma^2}} \right)$$

It can be argued, however that this approach makes no attempt to model variability in individual growth rate. For instance, one can expect that growth variability is a function of the size at tagging and the time at liberty (e.g., the greater the expected growth, the greater the variability in growth). To account for this assumption, Francis (1988) proposed different functional forms between residual variance and expected growth:

$$\sigma = \nu(\Delta \hat{L}), \text{ Model B}$$

$$\sigma = \nu(\Delta \hat{L})^{\tau}, \text{ Model C}$$

$$\sigma = \tau \left(1 - e^{-\nu(\Delta \hat{L})} \right), \text{ Model D}$$

Models selection can be done with the aid of the Akaike's information criteria. This criterion gives a good trade-off between the extremes of under-fitting and over-fitting: $AIC = 2LL + 2p$, where LL is the negative log-likelihood and p is the number of parameters. The model with the smallest AIC (the parsimonious model) is used for estimating the likelihood of the observed growth increment in terms of size at tagging and time at liberty.

It is generally admitted that (1) there is a high negative correlation between the estimates of K and L_{∞} and, (2) these estimates are sensitive to the size range of the population sampled. That is to say that analysing growth parameters from a sample composed mainly by young fishes one can expect a reasonable estimate of K and a weak estimate of L_{∞} (and vice versa). In the case of tagging data, methods to overcome the fact that the proportion of short-term returns can be very large compared with long-term returns of tagged fish has been proposed by Joseph and Calkins (1969). When there are some doubts, there is still the possibility to perform

sensitivity analysis, e.g., fixing one parameter and calculating the objective function for different values of the second (Bayliff, 1988) or based on expert knowledge fixing the asymptotic length at a value corresponding to an average maximum size observed in the catch (Bard and Antoine, 1986).

Nevertheless, we prefer a “meta-analysis” approach based on Beverton and Holt’s considerations about several patterns in growth and mortality parameters across fish species. Following these authors, Jensen, (1997) stated that the relation between asymptotic length and the growth coefficient might occur as the result of a constraint on growth, and consequently can be expressed as a simple bioenergetic growth equation, such as:

$$L_{\infty} = C K^{-h}$$

where C and h represent metabolic and growth parameters whose interpretation is beyond the scope of this paper.

In spite, these metabolic considerations were originally used for the comparison of life history parameters across species or across taxonomic groups, we considered that estimates of the growth parameters of skipjack obtained from different sources reflect the variability across the different stocks of skipjack in the world ocean, and consequently can be useful to estimate the parameters C and h .

A modification to the Fabens’ equation can be done by substituting L_{∞} by this function of K, such as:

$$\Delta L = \left((C K^{-h}) - L_t \right) \left(1 - e^{-K \Delta t} \right)$$

The alternative Fabens’ equation has one less parameter and one can expect a better estimate of K after removing of the high correlation between the conventional growth curve parameters.

3 Results

The frequency distributions of skipjack for length at release and at length at recapture are given in **Figure 1** (approximately 40-60 cm and 45-65 cm, respectively). The assumptions of the model used, the different parameters, the overall likelihood and the associated AIC are presented in **Table 1**. Only models A and D provided realistic growth parameters estimates (for model B and C, convergence was reached for L_{∞} larger than 1000 and K lower than 0.01 !). One possible explanation for the lack of reasonable estimation might be the relative sensitivity of the Fabens’ growth curve formulation to the negative values of some observed growth increments in the tagging data. A significant improvement in fit was achieved from introducing a relative complex relationship between the variability in growth and the expected value of the length increment. According to Model D, the best fit was obtained with $L_{\infty} = 119.123$; $K = 0.172$; $\nu = 0.693$; $\tau = 3.233$.

The various estimates of the parameters of growth of skipjack obtained in different oceans with different methods such as tagging, hard part and length frequency analysis are listed in **Table 2**. As expected there is a strong negative correlation between the estimates of K and L_{∞} (**Figure 2**). The relationship between the asymptotic length and the growth coefficient (fitted by a nonlinear least squares regression) can be represented as follow:

$$L_{\infty} = 70.607 K^{-0.231}$$

New parameter estimates are then made from the modified Fabens’s equation (**Table 3**). From the bioenergetic growth equation the L_{∞} values corresponding to the different models can be easily calculated. Among the different functional forms of the relationship between residual variance and expected ΔL , model C is the best under the AIC criteria. This result suggests that $\sigma = \nu \left(\Delta \hat{L} \right)^{\tau}$ would be the most appropriate error structure for this data set. Even so the fit of this model could be improved by removing some outliers, there are not significant trends in residuals which may indicate substantial bias in the parameter estimates (**Figure 3**). This model appears to fit reasonably well the growth increment for skipjack in the Senegalese and Mauritanian waters. We obtained 0.251 for K, 1.640 for ν and 0.368 for τ . Introducing the new value of K into the bioenergetic equation gives $L_{\infty} = 97.258$.

4 Discussion and conclusion

This new estimate of the asymptotic length obtained from the alternative Fabens' equation seems to be more consistent than in the conventional Fabens' equation in which L_{∞} and K were both estimated during the minimization of the objective function.

The estimates of L_{∞} and K from this tagging data set are consistently higher and lower, respectively, than those reported by Cayré et al. (1986) in the same area (62 cm for L_{∞} and 2.080 for K ; **Table 2**). In contrast, growth parameters obtained in the gulf of Guinea (Chur and Zharov, 1983; Bard and Antoine, 1986) and in the Western Atlantic (Vilela and Costello, 1991; Pagavino and Gaertner, 1995), as well as in other oceans, are consistent with the results from this analysis (**Table 2**); at least given the limitations due to the heterogeneity in the data sets and the methods used.

The application of the Francis variance model suggests that the variability of the growth increment of skipjack is not constant. This model assumes that growth variation is based on growth increment which corresponds to a combination of the length at recapture and the time at liberty (**Figure 4**). Others models relating variance in growth to different factors have been proposed: Baker et al, (1991) on predicted length at recovery, Hampton (1991) on the time at liberty, Maunder (2001) on a combination of time at liberty and length at release. This last author analysing tagging data of skipjack in the Eastern Pacific conclude that variance in growth can better be explained by time at liberty than length at release.

References

- ADAMS, M. S. 1999. Population Dynamics and Assessment of Skipjack Tuna (*Katsuwonus pelamis*) in the Maldives. PH. D dissertation, Renewable Resources Assessment Group. Centre for Environmental Technology, T. H. Huxley School of Environment, Earth Sciences and Engineering, Imperial College of Science Technology and Medicine, Univ. of London, 304 p.
- AMARASIRI, C. and L. Joseph. 1987. Skipjack tuna (*Katsuwonus pelamis*) - aspects on the biology and fishery form the western and southern coastal waters of Sri Lanka. IPTP. Col. Vol. Work. Docs. 2: 1-10.
- BAKER, T.T., R. Lafferty and T. J. II Quinn. 1991. A general growth model for mark-recapture data. Fish. Res. 11(3-4): 257-281.
- BARD, F.X., and L. Antoine. 1986. Croissance du listao dans l'Atlantique Est. In: Symons, P.E.K., Miyake, P.M., Sakagawa, G.T. (Eds.), Proc. ICCAT conference on the international skipjack year program, Madrid, pp. 301-308.
- BAYLIFF, W. H. 1988. Growth of skipjack, *Katsuwonus pelamis* and yellowfin, *Thunnus albacares*, tunas in the Eastern pacific Ocean, as estimated from tagging data. Bull. Inter. Amer. Trop. Tuna Comms. 19(4): 311-358.
- BROCK, V. E. 1954. Some aspects of the biology of the aku (*Katsuwonus pelamis*) in the Hawaiian Islands. Pac. Sci. 8: 94-104.
- BROUARD, F., R. Grandperrin and E. Cillaurren. (1984). Croissance des jeunes thons jaunes (*Thunnus albacares*) et des bonites (*Katsuwonus pelamis*) dans le Pacifique tropical occidental. ORSTOM de Port-Vila, Notes et Documents d'Océanographie, 10, 23 p.
- CAYRÉ, P. and H. Farrugio. 1986. Biologie de la reproduction du listao (*Katsuwonus pelamis*) de l'Océan Atlantique. In: Symons, P.E.K., Miyake, P.M., Sakagawa, G.T. (Eds.), Proc. ICCAT conference on the international skipjack year program, Madrid, pp. 252-272.
- CHI, K. S. and R.-T. Yang. 1973. Age and growth of skipjack tuna in the waters around the southern part of Taiwan. [Summ. in Chin.] Nat. Taiwan Univ. Sci. Rep. Acta Oceanogr. Taiwanica (3): 199-221.
- CHUR, V. N. and V.L. Zharov. 1983. Determination of age and growth of the skipjack tuna, *Katsuwonus pelamis* (Scombridae) from the southern part of the Gulf of Guinea. J. Ichthyol. 23(3): 53-67.
- FABENS, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth (29): 265-289.
- FRANCIS, R. I. C. C. 1988. Maximum likelihood estimation of growth and growth variability from tagging data. New Zealand Journal of Marine and Freshwater Research. 22: 42-51.

- GAERTNER, D., J. P. Hallier and M. N. Maunder. 2004. A tag-attribution model as a means to estimate the efficiency of two types of tags used in tropical tuna fisheries. *Fish. Res.* 69:171–180.
- HADDON, M. 2001. Modelling and quantitative methods in fisheries. Chapman and Hall/CRC, Boca Raton (USA). 406p.
- HAFIZ, A. 1987. Skipjack fishery in the Maldives. IPTP. Col. Vol. Work. Docs. 2: 11-22.
- HALLIER, J.-P. and D. Gaertner. 2002. Comparative efficiency between BETYP tags and conventional tags. Col. Vol. Sci. Pap. ICCAT 54(1): 17–32.
- HALLIER, J.P., T. Diouf, A. Hervé and C. Peignon. 2001. Le Programme MAC: Etat des opérations et des analyses. Doc. multigraphié, CRODT, IRD, CNROP. 90 p.
- HAMPTON, J. (1991). Estimation of southern bluefin tuna *Thunnus maccoyii* growth parameters from tagging data, using von Bertalanffy models incorporating individual variation. *Fish. Bull.* 89(4): 577-590.
- JENSEN, A. L., (1997). Origin of the relation between K and Linf and synthesis of relations among life history parameters. *Can. J. Fish. Aquat. Sci.* (54): 987-989.
- JOSEPH, J. and T. P. Calkins. 1969. Population dynamics of the skipjack tuna *Katsuwonus pelamis* of the Eastern Pacific Ocean. *Bull. Inter. Amer. Trop. Tuna Comms.* 13(1): 273 p.
- JOSSE, E., J. C. Le Guen, R. Kearney, A. Lewis, A. Smith, L. Marec and P. K. Tomlinson. 1979. Growth of skipjack. Occasional Papers, SPC, (11): 83.
- MAUNDER, M. N. 2001. Growth of skipjack tuna (*Katsuwonus pelamis*) in the Eastern Pacific Ocean, as estimated from tagging data. *Bull. Inter. Amer. Trop. Tuna Comms.* 22(2): 131p.
- MARCILLE, J. and B. Stéquert. 1976. Etude préliminaire de la croissance du listao (*Katsuwonus pelamis*) dans l'ouest de l'Océan Indien tropical. *Cah. ORSTOM (Ser. Oceanogr.)*, 51(44): 201-206.
- MOHAN, M. and K. K. Kunhikoya. 1985. Age and growth of *Katsuwonus pelamis* (Linnaeus) and *Thunnus albacares* (Bonnaterre) from Minicoy waters, In: E. G. Silas, (ed.) Tuna Fisheries of the Exclusive Economic Zone of India: Biology and Stock Assessment. 36, CMFRI, 143-148 pp.
- PAGAVINO, M. and D. Gaertner. 1995. Ajuste de una curva de crecimiento a frecuencias de tallas de atún Listado (*Katsuwonus pelamis*) pescado en el Mar Caribe suroriental. Col. Vol. Sci. Pap. ICCAT, 44(2): 303-309.
- SIBERT, J. R., R. E. Kearney and T. A. Lawson. 1983. Variation in growth increments of tagged skipjack *Katsuwonus pelamis*. Tuna and Billfish Assessment Programme. South Pacific Commission, Nouméa, Technical Report No. 10. 43 pp.
- SIVASUBRAMANIAM, K. 1985. Tunas and their fishery in the EEZs of Maldives and Sri Lanka. BOBP/WP/31, Bay of Bengal Programme (BOBP), Madras.
- TANABE, T., S. Kayama and M. Ogura. 2003. An outline of the growth study on skipjack tuna (*Katsuwonus pelamis*) in the Western Pacific. Doc. IOTC., WPTT-03-17, 14 p.
- UCHIYAMA, J. H. and P. Struhsaker. 1981. Age and growth of skipjack tuna *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, as indicated by daily growth increments of sagittae. *Fish. Bull.*, 79: 151-162.
- VILELA, M. J. A. and J. P. Castello. 1991. Estudio de la edad y del crecimiento del barrilete *Katsuwonus pelamis*, en la region Sur y Sudeste de Brasil. *Frente Maritimo*, 9: 29-35.
- WANKOWSKI, J. W. J. 1981. Estimated growth of surface schooling skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, from the Papua New Guinea Region. *Fish. Bull.*, 79(3): 517-532.
- WILD, A. and J. Hampton. 1994. A review of the biology and fisheries for skipjack tuna, *Katsuwonus pelamis*, in the Pacific Ocean. *FAO Fish. Tech. Pap.*, 336(2): 1-51.
- YAO, M. 1981. Growth of skipjack tuna in the western Pacific Ocean. *Bull. Tohoku Reg. Fish. Res. Lab.*, (43): 71-82.

Table 1. Von Bertalanffy parameters estimates of skipjack from the Fabens' growth curve. Model A assumes a constant variance, whereas models B, C, and D are based on different functional forms between residual variance and expected growth (see text).

<i>Model</i>	L_∞	K	σ	ν	τ	LL	p	AIC
A	115.100	0.190	2.339	NA	NA	503.600	3	1013.200
B		not realistic	$f_b(\Delta \hat{L})$				3	
C		not realistic	$f_c(\Delta \hat{L})$				4	
D	119.123	0.172	$f_d(\Delta \hat{L})$	0.693	3.233	480.186	4	968.371

Table 2. Estimates of growth parameters for skipjack in the world ocean.

<i>Area</i>	L_∞	K	<i>Method</i>	<i>Reference</i>
E. Atlantic G. of Guinea	80	0.322	Tagging	Bard and Antoine, 1986
E. Atlantic N. trop	80	0.601	Tagging	Bard and Antoine, 1986
E. Atlantic G. of Guinea	86.7	0.307	Spines	Chur and Zharov, 1983
E. Atlantic Senegal	62	2.080	Tagging	Cayré et al, 1986
E. Atlantic Cap Vert	60	1.537	Tagging	Cayré et al, 1986
W. Atlantic Caribbean sea	94.9	0.340	Length-freq	Pagavino and Gaertner, 1995.
W. Atlantic Brasil	87.12	0.219	Spines	Vilela and Costello, 1991
Indian Ocean	60.6	0.930	Length-freq	Marcille and Stequert, 1976
Indian Ocean Maldives	64.3	0.550	Tagging	Adams, 1999
Indian Ocean Maldives	82	0.450	Length-freq	Hafiz, 1987, in Adams 1999
Indian Ocean Sri Lanka	85	0.620	Length-freq	Amarasiri and Joseph, 1987;
Indian Ocean Sri Lanka	77	0.520	Length-freq	Sivasubramanium, 1985; in Adams, 1999
Indian Ocean Minicoy	90	0.490	Length-freq	Mohan and Kunhikoya, 1985; in Adams, 1999
E. Pacific	75.5	0.770	Tagging	Sibert et al, 1979
E. Pacific	79	0.640	Tagging	Josse et al, 1979
E. Pacific N	96.3	0.515	Tagging	Bayliff, 1988
E. Pacific S	66.5	1.806	Tagging	Bayliff, 1988
E. Pacific	73	0.820	Tagging	Joseph and Calkins, 1969
E. Pacific	107	0.420	Length-freq	Joseph and Calkins, 1969
W. Pacific	61.3	1.250	Tagging	Sibert et al, 1979
W. Pacific	65.5	0.945	Tagging	Josse et al, 1979
W. Pacific Vanuatu	60	0.750	Length-freq	Brouard et al, 1984
W. Pacific Trop. & Jap.	93.6	0.430	Otolith	Tanabe et al, 2003
W. Pacific Japan	76.6	0.600	Length-freq	Yao, 1981; in Wild and Hampton, 1994
W. Pacific Taiwan	103.6	0.302	Vertebrae	Chi and Yang, 1973; in Wild and Hampton, 1994
Central Pacific	102.2	0.550	Otolith	Uchiyama and Struhsaker, 1981
Central Pacific	80	0.950	Grouped L-freq	Brock, 1954; in Adams, 1999
Central Pacific West	74.8	0.515	Length-freq	Wankowski, 1981

Table 3. Von Bertalanffy parameters estimates of skipjack from the alternative von Bertalanffy-Fabens's equation. * Estimated *a posteriori*, as $L_\infty = 70.607 K^{-0.231}$. Model A assumes a constant variance, whereas models B, C, and D are based on different functional forms between residual variance and expected growth (see text).

<i>Model</i>	L_∞^*	K	σ	ν	τ	LL	p	AIC
A	(94.902)	0.278	2.340	NA	NA	503.782	2	1011.564
B	(107.976)	0.159	$f_b(\Delta \hat{L})$	1.665	NA	525.367	2	1054.733
C	(97.258)	0.251	$f_c(\Delta \hat{L})$	1.640	0.368	479.904	3	965.807
D	(96.639)	0.257	$f_d(\Delta \hat{L})$	0.709	3.216	480.358	3	966.716

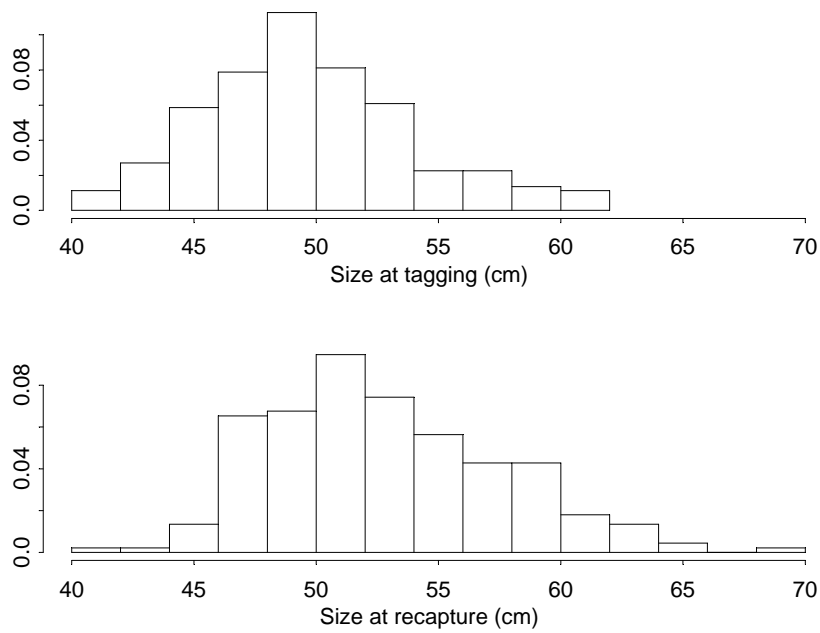


Figure 1. Frequency of recoveries for different lengths at release (top) and lengths at recapture (bottom).

Skipjack Growth parameters

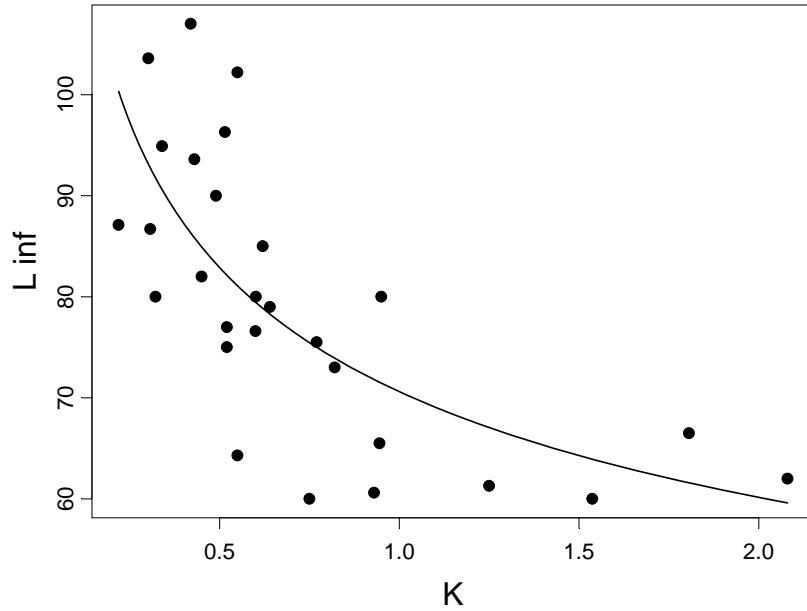


Figure 2. Distributions of combinations of estimates of L_{∞} and K for skipjack tuna from different studies.

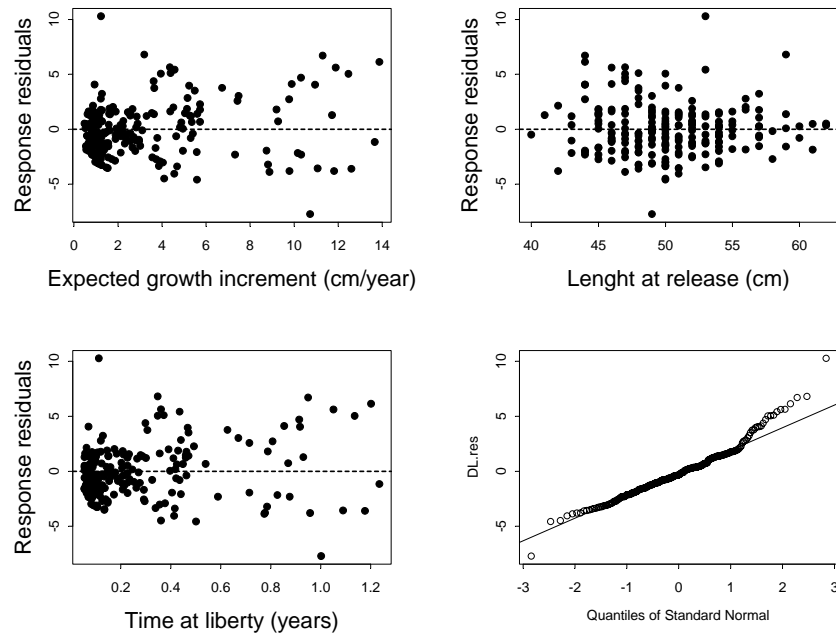


Figure 3. Diagnostic plots from the alternative von Bertalanffy-Fabens's growth model.

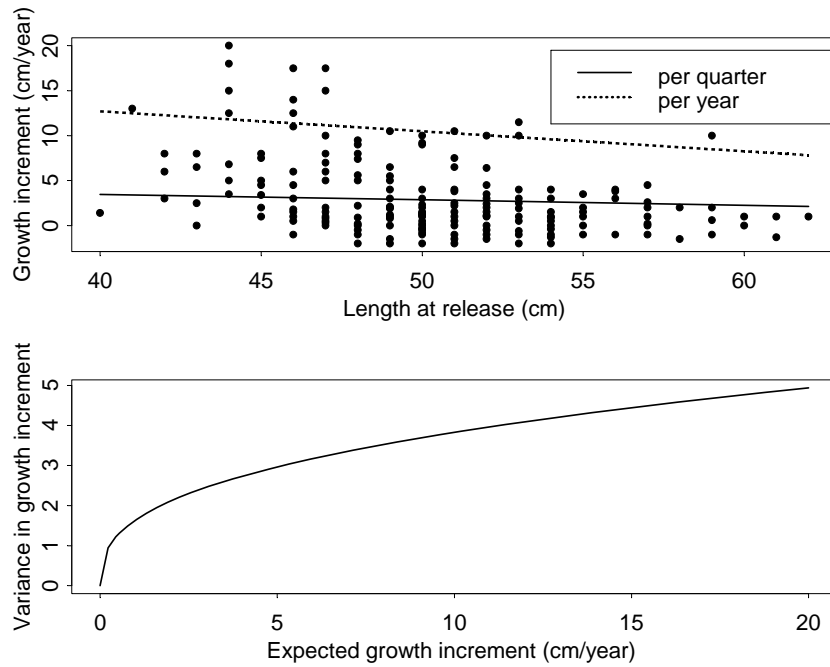


Figure 4. Expected growth increment from the alternative von Bertalanffy-Fabens's model for different lengths at release and times at liberty: one year and a quarter (top). Changes in growth variability over the growth increment as described by the Francis variance model C (bottom).