SCRS/1978/037 Rev. Col.Vol.Sci.Pap. ICCAT, 8 (2): 356-366 (1979)

ASPECTS OF THE GROWTH OF ATLANTIC BLUEFIN TUNA DETERMINED FROM MARK-RECAPTURE DATA

by

M. L. Parrack, P. L. Phares

SUMMARY

Three models fit to mark-recapture data defined the general pattern of growth. The von Bertalanffy and Richards models best fit the growth data, the logistic model did not. Estimates made from mark-recapture data of parameters of the von Bertalanffy model compare closely to those developed by other investigators from studies based upon vertebral and otolith data. Temporal trends were noted in functions developed to transform weight into length.

RESUME

Trois modèles ajustés aux données de récupération de marques ont servi à définir quelles étaient les caractéristiques générales de la croissance. Contrairement aux modèles de von Bertalanffy et de Richards, qui donnent le meilleur ajustement, le modèle logistique ne s'adapte pas aux données. Les estimations obtenues, à partir des données de récupération de marques, par les paramètres du modèle de von Bertalanffy sont très voisines de celles qui avaient été obtenues par d'autres chercheurs au moyen de l'étude des vertèbres et des otolithes. Des variations dans le temps ont été observées dans les relations longueur/poids.

RESUMEN

Tres modelos ajustados a los datos de marcado y recaptura, definen la pauta general de crecimiento. El mejor ajuste a los datos de crecimiento era el de los modelos de von Bertanlanffy y Richards; el modelo logístico no se ajustaba. Las estimaciones de parametros del modelo de von Bertalanffy realizadas a partir de datos de marcado y recaptura, se asemejan mucho a las desarrolladas por otros investigadores partiendo de estudios basados en datos de vertebras y otolitos. Se observaron tendancias temporales en las funciones desarrolladas para transformar el peso en talla.

Introduction

Previous studies of the growth of Atlantic bluefin tuna, Thunnus thynnus thynnus (Linnaeus), have been based upon the size and age of individual tuna, where age was inferred by counting annuli on vertebrae or otoliths (Mather and Shuck 1960, Rodriguez-Roda 1964, Butler et al. 1977, Berry et al. 1976, Butler 1971, Butler 1975, Butler 1976, Caddy and Butler 1976, Caddy et al. 1976). The results of such age determination have been modeled by several workers (Butler et al. 1977), Rodriguez-Roda 1971, Sakagawa and Coan 1974, Bard et al. 1978). In this study, we used mark-recapture data to model growth. Such data affords a direct measure of the change in size per change in time, thus eliminating the possibility of error introduced by incorrect age determination. We estimated parameters of the von Bertalanffy (Bertalanffy 1938), Logistic (Pearl and Reed 1920) and Richards' (Richards 1959) growth models to define length-age functions.

Methods

We analyzed mark-recapture data collected by the U.S.A. from 1966 to 1977. Those data include the sizes of individuals when released and recaptured and the dates of release and recapture. Size measures varied in nature because of diverse field methods and conditions at the time of release and recapture. Although recapture size was usually recorded as length, only weight was recorded in many cases. Size was not actually measured in 30% of all cases, but estimates were made by visual approximation (Table 1). We treated these approximations the same as actual measurements in this analysis.

Growth models were defined as length-age functions rather than weight-age functions because we believe that the weights of individuals at a particular age are much more variable than lengths at age. That phenomenon was first hypothesized by Mather and Shuck (1960) in their analysis of vertebral and scale data to define growth. Observations of the size and number of annuli on vertebrae of individual fish collected by the U.S.A. from 1974 to 1977 substantiate that hypothesis. We therefore believe that length-age functions are likely more precise representations of growth than are weight-age functions.

For cases in the mark-recapture data where only weight was recorded and length was not, weight was transformed to length according to the model: caliper fork length = a (total weight)^b. The parameters of the model were estimated separately for each month from May through October from samples sized by U.S.A. scientists from 1974 to 1977. These data contain lengths and weights of 3545 individuals ranging from 45 to 300 cm in length and from 2 to 545 kg in weight (Table 2). Nonlinear least squares estimates of the parameters were determined by using Marquardt's algorithm (Marquardt 1963) to minimize the expression:

$$\sum_{i=1}^{n} (L_i-L_i')^2$$

where L_i is the length of an individual defined by the model, L_i' is the observed length, and n is the number of observations for a particular month.

After transforming weights to lengths, the usable mark-recapture data included 354 individuals ranging in release length from 42 to 280 cm and in recapture length from 53 to 295 cm. Four individuals were at large 9.7, 7.5, 5.9, and 4.9 years, 6 about 3 years, 31 approximately 2 years, 170 about 1 year, and the remaining 143 at large less than 1 year.

Since mark-recapture data were employed, growth functions of interest were expressed in terms of the change in age rather than absolute age following the method of Fabens (1965) for the von Bertalanaffy model, and Parrack (1978) for the logistic model. Each recaptured individual was of some unknown age on the date marked and on the date recaptured so that the change in age is equivalent to the time at large. Expressed in these terms the logistic function changes

from
$$S_a = S_\infty/(1 + be^{-ka}) \tag{1a}$$

to
$$S_r = S_\infty/\left(1 + \left[(e^{-k(\Delta a)})\ (S_\infty - S_m)/S_m\right]\right) \tag{1b}$$

by substitution and rearrangement of terms. Likewise, the von Bertalanffy

equation
$$S_a = S_\infty\ (1-be^{-ka}) \tag{2a}$$

becomes
$$S_r = S_\infty - (S_\infty - S_m)\ e^{-k(\Delta a)} \tag{2b}$$

The Richards' model can be transformed from

$$S_a = \left[S_\infty^{1-\phi} - (S_\infty{}^{1-\phi} - b^{1-\phi})e^{-(1-\phi)\lambda a}\right]^{\frac{1}{1-\phi}}_{\quad 1-\phi} \tag{3a}$$

to
$$S_r = \left[S_\infty^{1-\phi} - (S_\infty{}^{1-\phi} - S_m^{1-\phi})\ e^{-(1-\phi)\lambda(\Delta a)}\right] \tag{3b}$$

following the general algebraic methods employed to convert the logistic and von Bertalanffy models. Definitions of symbols employed above are:

S_a = size at age a,

S_r = size when recaptured,

S_m = size when marked,

S_∞ = an equation parameter, the asymptotic size,

b = an equation parameter related to the size at birth,

a_r = age of an individual on the date recaptured,

a_m = age on the date marked and released,

$\Delta a = a_r - a_m$ = time at large,

and λ, ϕ and k are equation parameters related to the rate of growth.

Equation parameters S_∞, k, ϕ, and λ were estimated by utilizing the Marquardt algorithm to minimize the residual sum of squares:

$$\sum^{n}(S_r - S_r')^2 \tag{4a}$$

where n = the number of observations,

S_r' = the observed size, and

S_r = the size as estimated by the growth equation. In this case sizes are recapture lengths and the numbers observed refer to individuals marked and recaptured.

We estimated the parameter b in each model from auxiliary size-at-age data. Fabens (1965) presented a method using the length at birth (size at age zero) to estimate b in the von Bertalanffy function. We have used a different procedure based upon more than a single known size at age. Here, we employed length-frequency data from the monthly U.S.A. purse seine catches for the years 1974-1977. These multimodal length frequencies exhibit several non-overlapping unimodal distributions. We interpreted each unimodal distribution to be a sample of the length distribution of a single year class (i.e., of fish of the same age). Only unimodal distributions clearly disjoint from all others were used; if doubt existed we did not utilize the data. Each of the 20 distinct unimodal distributions are approximately symmetrical, and we used the average length of each distribution to estimate the most probable length at age.

Determination of age in months required not only the date of catch but also the annual birth date of each individual. Collection dates of larval Atlantic bluefin tuna from the western North Atlantic (Richards 1976, 1977) indicate spawning begins during the last of April, extends through May and is completed during the first week of June. We assumed that the small fish in the monthly samples of the U.S.A. purse seine catch were residents of the western Atlantic nursery area and were not migrants from eastern Atlantic nursery areas where the time of spawning may be different. We assumed a May 1 birthdate for fish in these length frequencies and aged the average length in each monthly sample accordingly.

From these data of average length at age we estimated the remaining parameter, b, in the three models (equations 1a, 2a, and 3a). We used values of S_∞, k, ϕ and λ estimated from the mark-recapture data and then solved for b such that expression 4a was minimized, as before, using Marquardt's algorithm. In this case the sizes referred to in expression 4a are average lengths at age, and the numbers observed refere to 20 such lengths derived from the length frequencies.

The Richards' equation is equivalent to the von Bertalanffy and the logistic equations for certain values of ϕ. Thus of the three equations, the Richards' must necessarily produce the best least squares fit (i.e., the smallest residual sum of squares). We fitted all three equations, however, in order to compare them to each other and to those of previous workers.

The shapes of age-length curves generated by the three growth models are determined by the parameters S_∞, k, ϕ and λ, which were estimated from the mark-recapture data. These data did not include inferred age but rather only actual measures of change in size per change in time. The parameter b, estimated from age-size data where age was inferred from modes in length frequencies, determines only the location of the curves on the age axis, i.e., it sets the origin for age. The actual growth information was derived from the mark-recapture data.

Results

In anticipation that the length-weight relations might differ temporally, we fit separate models to each set of monthly data (Table 3). Although the 95% support plane confidence intervals (Conway et al. 1970) on parameters overlap between months, point estimates exhibit definite temporal trends. Separate monthly models were therefore employed to transform weights to lengths to achieve maximum estimation accuracy from the available data.

U.S.A. purse seine length-frequency samples (Figure 1) show from two to three discrete unimodal distributions. We interpret the first distinct distribution of lengths (47-64 cm) to represent the size frequency of age one plus fish, the second (66-92 cm) of age two plus, the third (84-111 cm) of age three plus, and the fourth (110-134 cm) of age four plus. Twenty calculations of monthly average size of fish of ages one to four from these length-frequencies (Table 4) were used to estimate the parameter b in each model.

All three growth models (Table 5) exhibit similar predicted growth patterns (Figure 2) particularly for young, small fish. The relative abilities of the three functions to model Atlantic bluefin tuna growth can be evaluated by comparing the residual sum of squares generated from mark-recapture data (Table 6) and by judging the estimates of asymptotic length to realistically reflect the average maximum attainable size. The Richards' model must produce the smallest residual sum of squares, so by that criterion best models growth. However, the residual sums of squares produced by all three models are about the same. Although we could not test these sums of squares for significant differences, we observed that the residual sum of squares of the Richards' is but 2% smaller than that of the von Bertalanffy and but 4% smaller than that of the logistic, so that all three models generally fit these data. The three models define asymptotic size quite differently, however. The asymptote is estimated by the logistic to be 259 cm, the von Bertalanffy to be 313 cm, and the Richards' to be 279 cm. Since that parameter theoretically defines the average maximum size attained, these estimates were compared with maximum sizes in catch samples. Tiews (1963) reports maximum sizes caught to be from 280 to 330 cm fork length. Fish from 290 to 295 cm composed 0.017% of the Spanish "madrague" catch at Barbate in 1976 (Aloncle et al. 1977). The asymptotic size defined by the logistic model seems unrealistic; that of the Richards' model does better reflect observations. Of the three, however, asymptotic size modeled by the von Bertalanffy model seems most accurate.

The ability of the von Bertalanffy model to fit the observations is visible from plots of the observed lengths about the growth model (Figure 3). Data points were plotted by first calculating the age at release from the fitted model, adding the time at large to compute the age at recapture, then plotting that age and the recapture size. Although the observed data do not fall extremely close to the modeled line, the scatter is not severe.

Discussion

We cannot determine conclusively from these data that any of these growth models are or are not correct for Atlantic bluefin tuna. The residual sums of squares generated by the Richards' and von Bertalanffy models are approximately equivalent and the estimates of asymptotic size generated by both models in general reflect observed phenomena. We feel that the poorer fit of the logistic model to the mark-recapture data (as indicated by the larger residual sum of squares) and the unrealistic predicted asymptotic size lend evidence that this model does not adequately model growth. Although neither the Richards' nor von Bertalanffy model is clearly best, we recommend the von Bertalanffy model be used because of its international acceptance and previous use by other investigators.

These mark-recapture data show growth to be slow as compared to other tunas, corroborating previous studies based upon vertebral and otolith data. Our estimates of equation parameters for the von Bertalanffy model compare closely to those estimated by Rodriguez-Roda (1971) for fish captured in the eastern Atlantic (Table 7) and are similar to those estimated in the western Atlantic by Bu er et al. (1977) from otolith data, by Bard et al. (1978) from vertebral data, and by Mather et al. (1973) from mark-recapture data.

Rodriguez-Roda (1971), ourselves, and several other investigators (Table 7) estimate the parameter t_o to be about minus 1 year or less. Birth size as modeled here and by Rodriguez-Roda (1971) in the von Bertalanffy function is about 27 cm. The logistic function models birth size at 38 cm and the Richards' at 33 cm. Bluefin tuna larvae are observed to be from 0.284 to 0.304 cm at birth (Sanzo 1932). The difference between modeled and observed size at birth can be explained two ways: either growth during the first year of life is not correctly represented by any of the three models used, or ages were incorrectly determined from vertebral marks and length-frequency data. In the case of studies based upon vertebral marks, fish may not lay down the first annulus until the second winter rather than during the first winter as commonly assumed. In this study if fish are not available to the U.S.A. purse seine fishery during the first year of life, the first mode in the length frequency samples may represent the distribution of lengths of fish which are age two plus rather than age one plus, the second mode of fish which are age three plus rather than age two plus, and so on. This study and that of Rodriguez-Roda (1971) do model zero length to occur about 1 year before the assumed birth date.

We have chosen, as have other investigators, simply to assume that the models do not correctly reflect the age-length relation during the first year of life. That assumption is not based upon evidence we developed in this study but rather upon the views of those who have extensively studied Atlantic bluefin tuna life history. Until data is gathered, either by mark-recapture experiments or by some other means, to investigate the growth of very young fish the reason for this discrepancy between observed and calculated birth size shall remain unclear. The shapes of the growth curves, however, are not affected by that discrepancy because the equation parameters that define the actual rates of growth were estimated from direct measures of the change in size per change in time (i.e., from mark-recapture data).

Derivation of these models allowed us to study aspects of the growth of Atlantic bluefin tuna. We did not attempt to develop estimators of age at length; these models should not be considered as such. Although stochastic procedures were employed to fit these models, the models are deterministic. If these length-age relationships are used as estimators, there will be inaccuracies due to annual variation in general growth patterns and variations in growth rates among individual fish. A comparison of the average length and range of length at age deduced from length frequency samples (Table 4) with growth models (Figure 2), however, do indicate that such variation in growth patterns may not be great for small, young fish, so that age can be accurately deduced from these models for fish less that 100 cm in length.

Acknowledgements

The mark-recapture data we employed were collected by two separate programs and not by us. Special thanks are extended to Frank Mather and John Mason of the Woods Hole Oceanographic Institute. That program, under the direction of Frank Mather, has given us data from fish they marked which were caught by both sport and purse seine fishermen. We also employed data collected by the National Marine Fisheries Service program at the Miami, Florida, laboratory from fish they marked on U.S.A. purse seine vessels in recent years.

We are also indebted to William Richards, Raymond Baglin, and Emma Henderson of the National Marine Fisheries Service, and to Frank Mather for their help in editing and reviewing the manuscript.

Literature Cited

Aloncle, J. H., J. Rodriguez-Roda and K. Tiews. 1977. Report of the bluefin tuna working group. Observations on the size composition of bluefin tuna catches from 1976. ICES Document C. M. 1977/J:3.

Bard, F. X., J. L. Cort and J. C. Rey. 1978. Commentaries sur la composition démographique des pêcheries de thon rouge (*Thunnus thynnus*) de l'est Atlantique et de la Méditerranée, 1960-76. ICCAT Col. Vol. Sci. Pap. VIII(2):355-365.

Berry, F. H., D. W. Lee and A. R. Bertolino. 1977. Progress in Atlantic bluefin tuna ageing attempts. ICCAT Col. Vol. Sci. Pap. VI(2): 305-317.

Bertalanffy, L. von. 1938. A quantative theory of organic growth (Inquiries on Growth Laws II). Hum. Biol. 10(2):181-213.

Butler, M. J. 1971. Biological investigations on aspects of the life history of the bluefin tuna 1970-71. Newfoundland and Labrador Tourist Development Office, Report (Contr. No. 162, Dept. of Biology, Memorial Univ., St. John's, Newfoundland), 169 pp.

Butler, M. J. 1975. Prince Edward Island Bluefin Tuna Research Program, 1974. Mimeographed, 165 pp.

Butler, M. J. 1976. Prince Edward Island Bluefin Tuna Research Program, 1975. Mimeographed, 18 pp.

Butler, M. J., J. F. Caddy, C. A. Dickson, J. J. Hunt, and C. D. Burnett. 1977. Apparent age and growth, based on otolith analysis, of giant bluefin tuna (*Thunnus thynnus thynnus*) in the 1975-76 Canadian catch. ICCAT Col. Vol. Sci. Pap. VI(2):318-330.

Caddy, J. F., and M. J. Butler. 1976. Recent catch trends and age composition in Canadian coastal fisheries for giant bluefin tuna (*Thunnus thynnus*), and their relevance to assessment of the Northwest Atlantic large fish stocks. ICCAT Col. Vol. Sci. Pap. V (2):244-257.

Caddy. J. F., C. A. Dickson, and M. J. Butler. 1976. Age and growth of giant bluefin tuna (*Thynnus thynnus thynnus*) taken in Canadian waters in 1975. Fish. Res. Bd. Canada, MS Rept. Ser., No. 1395, 17 pp.

Conway, G. R., N. R. Glass, and S. C. Wilcox. 1970. Fitting nonlinear models to biological data by Marquardt's algorithm. Ecology 51(3): 503-507.

Fabens, A. J. 1965 Properties and fitting of the Bertalanffy growth curve. Growth 29:265-289.

Marquardt, D. W. 1963. An algorithm for least squares estimation of nonlinear parameters. J. Soc. Ind. App. Math. 11:431-441.

Mather, F. J., III, and H. A. Shuck. 1960. Growth of bluefin tuna of the western North Atlantic. U.S. Dept. of the Interior, Fish and Wildlife Series, Fisheries Bulletin, 61(179):39-52.

Mather, F. J., III, B. J. Rothschild, and G. J. Paulik. 1973. Preliminary analysis of bluefin tagging data. ICCAT Col. Vol. Sci. Pap. I: 413-444.

Parrack, M. L. 1978. Aspects of brown shrimp, *Penaeus aztecus*, growth in the northern Gulf of Mexico. Fish. Bull. In press.

Pearl, R., and L. J. Reed 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. Proc. Nat. Acad. Sci. USA 6:275-288.

Richards, F. J. 1959. A flexible growth function for empirical use. J. Exp. Botony 10(29):290-300.

Richards, W. J. 1976. Spawning of bluefin tuna (Thunnus thynnus) on the Atlantic Ocean and adjacent seas. ICCAT Col. Vol. Sci. Pap. V(2): 267-278.

Richards, W. J. 1977. A further note on Atlantic bluefin tuna spawning. ICCAT Col. Vol. Sci. Pap. VI(2):335-336.

Rodriguez-Roda, J. 1964. Biología del atún, Thunnus thynnus (L.), de la costa sudatlantica de España. Invest. Pesq., 25:33-146.

Rodriguez-Roda, J. 1971. Investigations of tuna (Thunnus thynnus) in Spain. ICCAT Rept. for the biennial period, 1970-71. Part II:110-113.

Sakawaga, G. T., and A. L. Coan. 1974. A review of some aspects of the bluefin (Thunnus thynnus thynnus) fisheries of the Atlantic Ocean. ICCAT Col. Vol. Sci. Pap. II:259-313.

Sanzo, L. 1932. Uova e primi stadi larvali di tonno (Orcynus thynnus Ltkn.). Mem. Com. talassogr. ital., 189:1-16.

Tiews, K. 1963. Synopsis of biological data on bluefin tuna Thunnus thynnus (Linnaeus) 1758 (Atlantic and Mediterranean). Proc. World. Sci. Meet. Biol. Tunas and relat. Spec., FAO Fish. Rept. 6(2):443-481.

Table 1. Summary of mark-recapture data collected by the U.S.A. from 1966-1977

	Numbers of Fish Returned	
	Size Actually Measured	Size Visually Approximated
Release		
Length Recorded	264	42
Weight Recorded	0	48
Recapture		
Length Recorded	201	38
Weight Recorded	26	90

Table 2. Summary of length-weight data collected by the USA during 1974-1977.

Month	Numbers of Individuals Measured	Range of Length (fork length, cm)	Range of Weight (total weight, kg)
May	204	52 - 284	2.2 - 417.2
June	730	21 - 267	2.6 - 372.3
July	727	52 - 298	2.6 - 465.4
August	1069	22 - 372	2.9 - 486.3
September	644	20 - 334	4.5 - 545.2
October	171	138 - 278	22.7 - 409.1
Total	3545	20 - 372	2.2 - 545.2

Table 3. Length-weight conversion constants estimated from samples of the USA catch from the Western North Atlantic. The model employed is $L = a(W)^b$ where L is caliper fork length (cm), W is body weight (kg) and both a and b are equation constants.

	a		b	
Month	Estimate	*Confidence Interval	Estimate	*Confidence Interval
May	34.8503	33.7690 - 35.9310	0.3521	0.3462 - 0.3581
June	35.6896	35.3130 - 36.0660	0.3425	0.3397 - 0.3454
July	36.3418	35.4070 - 37.2770	0.3414	0.3368 - 0.3460
August	35.6537	34.9880 - 36.3200	0.3420	0.3386 - 0.3453
September	41.1558	38.4380 - 43.8740	0.3129	0.3014 - 0.3245
October	43.7946	38.0150 - 49.5740	0.3002	0.2770 - 0.3234
All Data	36.2854	35.8910 - 36.6790	0.3381	0.3361 - 0.3401

*Support plane confidence limits were calculated at the 95% significance level according to the method of Conway et al. (1970).

Table 5. Atlantic bluefin tuna growth models; size (S) is in cm caliper fork length and age (a) is in years

Model	Equation
Logistic	$S = 259.1/(1.0 + 5.7462\ e^{-A(0.3945)})$
von Bertalanffy	$S = 313.0\ (1.0 - 0.9169\ e^{-A(0.0903)})$
Richards	$S = (4.7757 - 2.1334\ e^{-A(0.1797)})^{3.6025}$

Table 4. Average length at age inferred from length frequency samples of USA purse seine catches, 1974-1977.

Year	Month	Age (years)	Average Length (cm)	Range of Length
1974	July	1	53.4	47-60
		2	77.5	70-83
		3	93.5	85-107
	August	1	55.4	50-60
		2	82.3	73-89
		3	97.9	90-111
	September	1	59.6	54-64
		2	85.9	79-92
		3	101.4	96-108
1975	July	1	56.4	50-61
		2	74.5	66-87
	August	1	57.3	53-64
		2	76.0	66-85
1976	July	2	77.5	68-84
		3	96.1	86-110
1977	June	2	76.7	69-85
		3	102.0	92-108
		4	121.6	110-134
	July	1	57.3	53-60
		2	79.4	70-90

Table 6. Residual sums of squares for three Atlantic bluefin tuna growth models fit to mark-recapture data.

Model	Residual Sum of Squares
Logistic	46330
von Bertalanffy	45337
Richards	44935

Table 7. A comparison of parameter estimates for the von Bertalanffy growth model of Atlantic bluefin tuna.

Source	L_∞	k	t_o
Rodriguez-Roda (1971)	356	0.09	-0.89
Sakagawa and Coan (1974)			
from Mather and Schuck data	437	0.06	-1.49
from Mather and Jones data	447	0.05	-1.59
Mather et al. (1973)	296	0.10	-
Butler et al. (1977)			
males	287	0.13	-0.33
females	277	0.12	-0.80
Bard et al. (1977)	318	0.11	-0.62
Present Study	313	0.09	-0.96

Figure 1. Monthly length-frequency samples from the U.S.A. purse seine catch, 1974-1977.

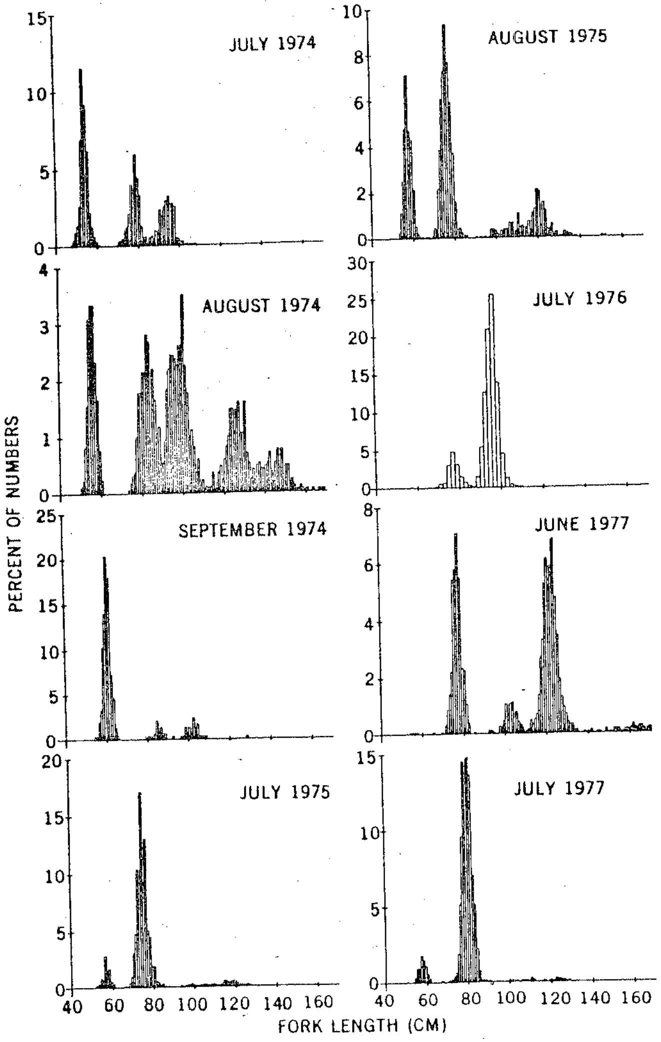

Figure 2. Three models of Atlantic bluefin tuna growth.

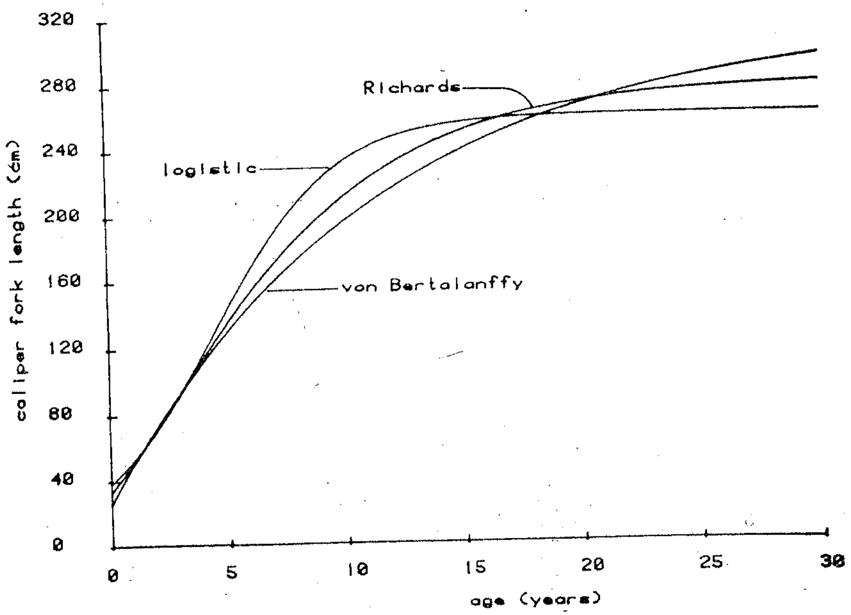

Figure 3. The von Bertalanffy growth model for Atlantic bluefin tuna derived from mark-recapture data.