SCRS/1976/071 Col.Vol.Sci.Pap. ICCAT, 6 (1): 117-123 (1977)

A REVIEW AND EVALUATION OF ESTIMATES OF NATURAL MORTALITY RATES OF TUNAS

by

T. C. Murphy, G. T. Sakagawa

SUMMARY

A review of estimates of natural mortality rate (M) of tunas in published records is made. The review indicates that reasonable estimates are available for albacore, bluefin and yellowfin tuna only. The estimates are used to generate a relationship with K, parameter of the von Bertalanffy growth equation, and the relationship used to estimate M for tunas with known K values. The range of estimates of M are: Albacore, 0.13-0.40; bigeye tuna, 0.44-0.68; bluefin tuna, 0-0.24; skipjack tuna, 0.69-0.93; and yellowfin tuna, 0.67-0.91.

RESUME

Le présent rapport passe en revue les estimations du taux de mortalité naturelle (M) qui figurent dans les travaux publiés. Cet examen permet d'observer qu'il n'y a d'estimations raisonnables disponibles que sur le germon, le thon rouge et l'albacore. Ces estimations sont utilisées pour une mise en corrélation avec K, paramètre de l'équation de von Bertalanffy sur la croissance, et la relation employée pour estimer M pour les thonidés dont les valeurs de K sont connues. La gamme des estimations de M est: germon 0,13-0,40 -thon obèse 0,44-0,68 -thon rouge 0-0,24 -listao 0,69-0,93 -albacore 0,67-0,91.

RESUMEN

Presenta un análisis de las estimaciones de tasas de mortalidad natural (M) procedentes de publicaciones. Dichas estimaciones sólo son fiables en lo que respecta al atún blanco, atún (BF) y rabil. Se emplean para establecer una relación con K, parámetro de la ecuación de crecimiento de von Bertalanffy, y con la relación utilizada para estimar M en el caso de túnidos cuyos valores de K son conocidos de antemano. La gama de estimaciones de M es como sigue: Atún blanco: 0,13-0,40; patudo: 0,44-0,68; atún (BF): 0-0,24; listado: 0,69-0,93; rabil: 0,67-0,91.

INTRODUCTION

Losses in an exploited fish population can be attributed to natural and fishing mortalities, concepts that are easy to visualize but whose parameters are more difficult to estimate. Natural mortality, in particular is the more difficult to estimate accurately. Methods such as those described by Heincke (1913), Ricker (1958), and Robson and Chapman (1961) among others, utilize the catch curve of virgin stocks or of stocks with beginning stages of fishery development to estimate the coefficient of natural mortality (M). In developed fisheries, where fishing is intense, Silliman (1943), Beverton and Holt (1956, 1967), and Paloheimo (1961) have introduced various techniques for estimating M. Recently with the advent of computers, intricate algorithms to simulate the catch history of fish populations have been introduced to determine mortality coefficients as well as other useful parameters. For tuna, this approach was used by Silliman (1966), Ishii (1968; 1969) and Suda (1970).

Tag-recapture has long been a technique used to estimate coefficients of fishing and natural mortalities. This technique places great demands on the data since errors due to the effects of tagging must be considered as well as errors due to the usual methods of catch sampling.

The purpose of this paper is to review published estimates of coefficient of natural mortality for some species of tuna, and to draw inferences about M for species in which M is not known. We do this by evaluating the data and techniques used in published estimates for (1) whether the assumptions needed to derive the estimate are met or nearly met, and (2) whether the estimate generally agrees with other estimates for the same species. When few comparative values were available for a species, we used the principle that short-lived species have relatively high natural mortality rates and long-lived species have low natural mortality rates (Beverton and Holt, 1959) to judge the reasonableness of an estimate. Because of these criteria, we reviewed estimates only if they were original and actually estimated from data.

REVIEW AND EVALUATION OF PUBLISHED ESTIMATES

It is well accepted that M varies over the entire life span of a cohort, being effected by environmental and population factors in different degrees as the fish matures. However, M is frequently treated by biologists as a constant or an "average" that describes the natural mortality coefficient of a population as a whole, perhaps underestimating M for younger individuals and overestimating it for older fish. In order to achieve the purpose of this paper, we assumed that for each species of tuna, a single constant M exists and that discrepancies between estimates of M are due to lack of suitable data or to failures in meeting required assumptions, neither of which constitutes random errors. Differences in estimated M values will be treated as real differences even though the values themselves may be considered by some as so close to one another as to be indistinguishable.

Albacore (*Thunnus alalunga*)

Suda (1966a) obtained $M=0.2$ for immature to 6-year-old North Pacific albacore using fishery data of the Japanese longline fleet. In a later analysis, he (Suda, 1966b) assumed M increases by increments of 0.2 for older fish, i.e., $M=0.4$ for age 6, $M=0.6$ for age 7 and $M=0.8$ for age 8. This increment apparently is based on the difference between $M=0.2$ for age 5 and $Z=0.4$ (coefficient of total mortality) for age 6, which Suda (1963) estimated from fishery data during early years when the stocks were lightly exploited. Z is therefore assumed to be essentially equal to M.

Wetherall and Yong (MS[1]) re-analyzed data from the Japanese longline fleet and concluded that Suda's estimates for albacore 6 years and older were too high. They proposed that M increases by increments of 0.1 for those ages.

For Atlantic albacore, Beardsley (1971) and Bard (MS[2]) estimated M from fishery data. Beardsley used a technique that utilized changing fishing and natural mortality rates to reproduce the catch history of 4-year-old albacore from catches of 3-year olds. He obtained estimates of $M=0.23$ and 0.32 for estimates of Z's of 0.96 and 0.50, respectively. Beardsley felt that $Z=0.96$ for the North Atlantic stock was more reasonable and therefore, he concluded $M=0.23$ was his best estimate.

Bard (MS[2]) also estimated M using data for 3- and 4-year olds. He used the technique of Silliman (1943) and obtained $0<M<0.3$. He concluded that $M=0.2$ was most likely, based on the implicit assumption that the estimate of $M=0.2$ of Suda (1966a) is accurate and representative for albacore in general.

If we include Suda's estimate of $M=0.4$ for 6-year-old albacore, the last age group for which there is a direct estimate, the range of reasonable estimates of M is between 0.2 and 0.4 for albacore. The most frequently reported estimate for average M is 0.2 or 0.23.

---

[1] Wetherall, J.A., and M.Y.Y. Yong. 1975. A cohort analysis of the North Pacific albacore stock and an assessment of yield per recruit in the American and Japanese fisheries. Southwest Fisheries Center, Honolulu, Hawaii 96812. Admin. Rept. No. 16H, 1975.

[2] Bard, F.X. 1974. Etude sur le germon (Thunnus alalunga, Bonnaterre, 1788) de l'Atlantique nord elements de dynamique de population. Inter. Comm. Conserv. Atlantic Tunas, Collective Vol. Sci. Pap. 2 (SCRS-1972): 198-244.

Bigeye Tuna (*Thunnus obesus*)

Suda and Kume (1967) applied the method of Paleheimo (1961) to obtain M=0.36 for Pacific Ocean bigeye tuna older than 5 years, the first age of complete recruitement to the fishery during the period 1957-1964. Ishii (1968) applied various recruitment schemes to simulate variable recruitment of bigeye from age 2 to 5 years. Basically, his method consisted of comparing the observed and simulated catch history of the bigeye fishery studied by Suda and Kume using a steepest descent approach to minimize the chi-square value as a measure of goodness of fit. His estimates of M ranged between 0.35 and 0.56.

An M value of 0.73 for Indian Ocean bigeye was obtained by Suda (1970) by assuming a linear relation between fishing effort and the reciprocal of nominal catch-per-unit-effort. He considered the bigeye fishery to be in a steady state during the period 1959-1963 and assumed recruitment to be stable and growth to be the same as in Pacific bigeye tuna.

Silliman (1966), using a method developed by him for analog computers, combined recruitment and yield-per-recruit relations to simulate the Pacific bigeye tuna fishery for the years 1953-1963. Recruitment was assumed to occur at about age 3 years and an average Z=0.4 was assumed. Nominal fishing effort for 1953-1963 was used and M was varied until the minimum sum of square of the difference between actual and estimated catches was achieved. He obtained the best results with M=0.1.

The majority of estimates of M for bigeye are between 0.35 and 0.56, and the "outliners" are M=0.1 and M=0.73 (Table 1). The estimate of M=0.1 of Silliman (1966) is based on assumptions concerning growth and recruitment curves that do not agree with the findings of Suda and Kume (1967). Also, M values as low as 0.1 are generally found in very long-lived fish and not in fish with maximum age of 7 years or so, such as for bigeye tuna (Table 2).

The estimate of M=0.73 falls outside the majority of values, but does not appear to be unreasonably high compared to M=0.8 for yellowfin tuna (see section on yellowfin tuna), which has a life span similar to bigeye tuna (Table 2). Consequently, we conclude that M for bigeye tuna probably lies in the lower portion of the range, 0.35 to 0.73.

Bluefin Tuna (*Thunnus thynnus*)

Two species of bluefin tuna, northern and southern bluefin tuna occur in the world oceans. In this report we review only estimates for the northern species. Sakagawa and Coan (MS)[3] assumed that the relation of M and K, of the von Bertalanffy growth equation, is constant. They calculated the constant for tunas from estimates of M=0.8 and K=0.36 for Pacific yellowfin. Using a known K for Atlantic bluefin tuna and the constant, they estimate M of 0.1-0.2 for bluefin tuna. They also used data from the northwestern Atlantic purse seine fishery and the method of Paloheimo (1961) to obtain estimates of M=0.1 to 1.9. Confidence limits for these estimates were wide, however, and Sakagawa and Coan placed little faith in the results from the fishery data.

Mather, et al. (1972), used tagging data of young fish to estimate a combined natural mortality plus losses due to migration (M+X) of 0.68. They were unable to segregate the natural mortality component but felt that it was about 0.1 to 0.2.

From these published estimates, it appears that M for northern bluefin tuna most likely lies between 0.1 and 0.2.

Skipjack Tuna (*Katsuwonus pelamis*)

Fink (1965) used tagging data of yellowfin and skipjack tunas tagged in 1955-1960 in the eastern Pacific to estimate Z' (=M+F+Q), F and Q (mortality coefficient due to tag shedding and other causes). Only 1957 releases produced enough returns to obtain reliable estimates. For skipjack tuna tagged in 1957, Fink obtained Z'=6.98 and F=2.10. Q was estimated for only yellowfin tuna tagged in 1957. With the assumption that Q for yellowfin tuna (1.06) is the same as for skipjack tuna, we subtracted Q and F from Z' and obtained M=3.82 for skipjack tuna.

Joseph and Calkins (1969) also used tagging data of skipjack tuna from the eastern Pacific to estimate natural mortality. They used a combination of procedures, and obtained M=1.68.

The catch history of the eastern Pacific surface fishery for skipjack tuna was simulated by Silliman (1966) using assumed values for M and F. His best results were obtained with M=0.3.

Published estimates of M for skipjack tuna ranges between 0.30 and 3.82 (Table 1), which is extremely broad. If the life span of skipjack tuna is about 5 years,then M of 0.3 is too low and M of 3.82 or even 1.68 is too high. The M should be close to that of yellowfin tuna. The reason for these poor estimates are many, but a few important factors can be identified. The estimates of Fink and Joseph & Calkins included effects of emigration; therefore, their estimates overestimate actual M. Silliman's estimate was derived from a method that is dependent on the assumed ranges over which the parameters are allowed to vary and F and M

---

[3] Sakagawa, G.T., and A.L. Coan. 1974. A review of some aspects of the bluefin tuna (Thunnus thynnus thynnus) fisheries of the Atlantic Ocean. Intern. Comm. Conserv. Atlantic Tunas, Collective Vol. Sci. Pap. 2 (SCRS-1972): 259-313.

in the method are not derived from unique solutions. We therefore conclude that the estimate of M for skipjack tuna probably lies in the higher portion of the range of 0.3 and 1.68.

Yellowfin tuna (*Thunnus albacares*)

Hennemuth (1961) estimated Z from length frequency data of yellowfin tuna caught in the eastern tropical Pacific. He then subtracted F, derived from Schaeffer's (1957) estimate of the coefficient of catchability and estimates of fishing effort, to obtain M of 0.64 to 0.92 (average 0.77). In 1967, Schaeffer updated Hennemuth's estimates and obtained M of 0.55-1.05 with $Z = 1.72$.

Fink (1965) used tagging data to estimate Z', F and Q for yellowfin tuna released in the eastern tropical Pacific during 1955-1960. His Q was estimated as the difference between Z' for the tagged population and Z for the untagged population (from Hennemuth, 1961). Estimates of M derived from Fink's data ranges between 0.11 and 4.75 with a mean of 1.3.

Honma, Kamimura, and Hayasi (1971) estimated an M of 1.2 for yellowfin tuna of the entire western and central equatorial Pacific using Paloheimo's (1961) technique. Their estimates for the separate regions were 2.5 for the western region and 1.1 for the central region. Ishii (1969) applied a method which allows for variable natural mortality by age and migration and obtained M=0.92 for age 3 and older yellowfin tuna. Pianet and LeHir (1971) estimated apparent natural mortality coefficients for yellowfin tuna caught by Point Noire baitboats and seiners in the eastern tropical Atlantic. They assumed that Z from 1967 landings of yellowfin tuna is approximately equal to M', the apparent natural mortality, or M=1.58 and 2.61 for baitboats and seiners, respectively.

Most of the published M values for yellowfin range between 0.6 and 1.2. Fink (1965) noted that while his estimates of total mortality were reasonable, the corrections and assumptions necessary to derive F, and then M, clouded the results. He was not able to measure directly the losses due to effects other than fishing and natural mortality, nor to estimate the rate of emigration. Pianet and LeHir were unable to accurately determine the age structure of the catch and noted that the M values derived were crude. We therefore conclude that the "best" estimates of M for yellowfin tuna is around 0.8 based mainly on the studies of Hennemuth and Schaeffer.

RELATIONSHIP OF M, K AND T_{max}

The above review of published estimates of M showed that only for albacore, bluefin tuna and yellowfin tuna are there reasonable estimates of average M that agree from one study to another or with life history information of the species. Estimates for bigeye and skipjack tuna, on the other hand, are quite variable and inconsistent with other information on these species. To more accurately estimate an average M for bigeye and skipjack tunas, we utilized the method of Beverton and Holt (1959) of constructing relationships between M, K, and T_{max}, the maximum age.

Data from Beverton and Holt (1959) on M and K for [illegible] of fishes were plotted against maximum age (Figure 1). Both M and K vary with age in a similar manner, although K is generally smaller than M for a particular species. Both decline in an exponential manner with increased T_{max}. Hence, we conclude that both M and K is curvilinearly related to T_{max} in fishes in general.

Coan (1976) reviewed estimates of the von Bertalanffy growth equation for Atlantic albacore, bluefin, yellowfin and skipjack tunas and selected the most reasonable estimates, K=0.14 for albacore, K=0.053 for bluefin tuna, K=0.42 for yellowfin tuna and K=0.431 for skipjack tuna (Table 2), based on recent studies that included a large sample size and a wide range of fish sizes. These estimates are representative for the respective species. The K values are plotted on $1/T_{max}$ (Table 2) for the four species (Figure 2). T_{max} for the four species (Table 2) are approximate maximum ages. A regression line was fitted to the points and the intercept proved not significantly different from zero. A line was then fitted through the origin and K for bigeye tuna was estimated as 0.30 using $1/T_{max} = 0.143$ with maximum age of 7 years. This value of K has a 95% confidence limit of about 0.2 to 0.4, which is within the range of estimates of K for Pacific bigeye tuna (Shomura, 1966), but is higher than the point estimate, 0.10, derived by Champagnat and Pianet (MS[4]) for Atlantic bigeye tuna caught by baitboats and seiners.

The most likely range of M for albacore, bluefin tuna and yellowfin tuna is also plotted against $1/T_{max}$ in Figure 2. M seems to be consistently higher than K as is also the case for fish in general (Figure 1).

A regression line was computed to define the limits within which the natural mortality coefficients might fall given a linear relation between M and K (Figure 3). The straight line in Figure 3 assumes M increases proportionally with K and is described by

$$M = -0.0195 + 1.9388K \qquad (1)$$

The intercept of this equation is not significantly different from zero; consequently, a line through the origin is more appropriate in describing the relation. The relation is described by

$$M = 1.879K$$

The 95% confidence limits of M predicted from this equation using appropriate K values for five species of tunas are shown in Table 2. Admittedly the equation is based on few data points (three points) and on an unverified assumption of linearity in the M and K relation to be very reliable. However, the estimated ranges of M agree well with "best" estimates reported in the literature and with life history information on the species.

---

[4] Champagnat, C., and R. Pianet. 1974. Croissance du patudo (Thunnus obesus) dans les regions de Dakar et de Pointe-Noire. ICCAT Collective Vol. Sci. Pap., 2(SCRS-1973): 141-144.

LITERATURE CITED

Beardsley, G.L. 1971. Contributions to the population dynamics of Atlantic albacore with comments on potential yields. Fish. Bull. 69: 845-857.

Beverton, R.J.H., and S.J. Holt. 1956. A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer., 140: 67-83.

______________. 1959. A review of lifespans and mortality rates of fish in Nature, and their relation to growth and other physiological characteristics. *In* G.E.W. Wolstenholme and M. O'Conner (Eds.). CIBA Foundation Colloquia on Ageing, 5: 142-181. J.& A. Churchill, Ltd., London.

Coan, A. 1976. Length, weight and age conversion tables for Atlantic tunas. Intern. Comm. Conserv. Atlantic Tunas, Collective Vol. Sci. Pap. 5(SCRS-1975) (1): 64-66.

Fink, B.D. 1965. Estimation, from tagging experiments, of mortality rates and other parameters respecting yellowfin and skipjack tuna. Inter-Amer. Trop. Tuna Comm., Bull. 10: 1-82. (In English & Spanish).

Heincke, F. 1913. Investigations on the Plaice. General report 1. The plaice fishery and protective measures. Preliminary brief summary of the most important points of the report. Cons. Intern. Explor. Mar. Rapp. et Proc. - Verb., 16: 67p.

Hennemuth, R.C. 1961. Year class abundance, mortality and yield per recruit of yellowfin tuna in the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull. 6: 1051. (In English and Spanish.)

Honma, M., T. Kamimura and S. Hayasi. 1971. Compilation of catch records for assessment of yellowfin tuna stocks in longline fishery in the Pacific Ocean, and application to date for the years of 1950 to 1964. Bull. Far Seas Fish. Res. Lab., 4: 1-25.

Ishii, T. 1968. Studies on estimating parameters of fish populations supplied by sequential recruitment, III. Simultaneous estimation of parameters of Pacific bigeye tuna by the tracing method. Bull. Jap. Soc. Sci. Fish., 34(6): 488-494.

________. 1969. Studies on estimating parameters of a fish population supplied by sequential recruitment V. Simultaneous estimation of parameters with the transfer effect of Pacific yellowfin tuna. Bull. Jap. Soc. Sci. Fish., 35(6): 537-545.

Joseph, J., and T.P. Calkins. 1969. Population dynamics of the skipjack tuna (*Katsuwonus pelamis*) of the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull. 13: 7-119. (In English and Spanish.)

Mather, F.J. III, B.J. Rothschild, G.J. Paulik, and W.H. Lenarz. 1974. Analysis of migration and mortality of bluefin tuna, *Thunnus thynnus*, tagged in the northwest Atlantic Ocean. Fish. Bull., 72: 900-914.

Paloheimo, J.E. 1961. Studies on estimation of mortalities I. Comparison of a method described by Beverton and Holt and a new linear formula. J. Fish. Res. Board Can. 18: 645-662.

Pianet, Y., and Y. LeHir. 1971. La campagne thoniere 1970 a Pointe-Noire. Doc. Sci. Cent. ORSTOM., Pointe-Noire Nour. Ser. 17: 1-15.

Ricker, W.E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119; 300p.

Robson, D.S., and D.G. Chapman. 1961. Catch curves and mortality rates. Trans. Amer. Fish. Soc., 90: 181-189.

Schaeffer, M.B. 1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull. 2: 245-285. (In English and Spanish.)

______________. 1967. Fishery dynamics and present status of the yellowfin tuna population of the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. 12: 87-135. (In English and Spanish.)

Shomura, R.S. 1966. Age and growth studies of four species of tunas in the Pacific Ocean. *In*: T.A. Manar (ed), Proceedings of the Governor's Conference on Central Pacific Fisheries Resources. State of Hawaii, p. 203-219.

Silliman, R.P. 1943. Studies on the Pacific pilchard or sardine (*Sardinops caerelea*). 5. A method of computing mortalities and replacements. Fish Wildl. Serv., Spec. Sci. Rep., 24: 10p.

______________. 1966. Estimates of yield for Pacific skipjack and bigeye tunas. *In*: T.A. Manar (ed.), Proceedings of the Governor's Conference on Central Pacific Fisheries Resources. State of Hawaii, p. 231-249.

Suda, A. 1963. Catch variations in the North Pacific albacore, IV. The survival rate in the fishing grounds of the Northwest Pacific. Rep. Nankai Reg. Fish. Res. Lab. 17: 103-110.

______________. 1966a. Catch variation in the North Pacific albacore VI. The speculations about the influences of fisheries on the catch and abundance of the albacore in the Northwest Pacific by use of some simplified mathematical models (continued paper-I). Rep. Nankai Reg. Fish. Lab., 24: 1-14.

______________. 1966b. Catch variations in the North Pacific albacore VII. Considerations on the sustainable yield. Rep. Nankai Reg. Fish. Lab., 24: 103-114.

______________. 1970. Approximate estimation of parameters in dynamics of fish populations utilizing effort and catch statistics with little information on biological features. Bull. Far Seas Fish. Lab., 3: 1-14.

Suda, A., and S. Kume. 1967. Survival and recruitment of bigeye tuna in the Pacific Ocean, estimated by the data of tuna longline catch. Rep. Nankai Reg. Fish. Res. Lab., 25: 91-103.

Table 1. Published estimates of coefficients of natural mortality (M) for some species of tunas

Species	Ocean	Source	M (Yearly basis)
ALBACORE	Atlantic	Bard (MS)[1]	0 - 0.30
	Atlantic	Beardsley (1971)	0.23, 0.32
	Pacific	Suda (1963; 1966a)	0.20 - 0.40
BIGEYE	Indian	Suda (1970)	0.73
	Pacific	Ishii (1968)	0.35 - 0.56
	Pacific	Silliman (1966)	0.10
	Pacific	Suda and Kume (1967)	0.36
NORTHERN BLUEFIN	Atlantic	Mather, et al (1974)	0.10 - 0.20
	Atlantic	Sakagawa and Coan (MS)[2]	0.10 - 1.90
SKIPJACK	Pacific	Fink (1965)	3.82
	Pacific	Joseph and Calkins (1969)	1.68
	Pacific	Silliman (1966)	0.30
YELLOWFIN	Atlantic	Pianet and LeHir (1971)	1.58, 2.61
	Pacific	Fink (1965)	0.11 - 4.57
	Pacific	Hennemuth (1961)	0.64 - 0.92
	Pacific	Honma et al (1971)	1.1, 2.5
	Pacific	Ishii (1969)	0.92
	Pacific	Schaeffer (1967)	0.55 - 1.05

[1] Bard, F.X. 1974. Etude sur le germon (Thunnus alalunga, Bonnaterre, 1788) de l'Atlantique nord elements de dynamique de populations. Inter. Comm. Conserv. Atlantic Tunas, Collective Vol. Sci. Pap. 2(SCRS-1972): 198-224.

[2] Sakagawa, G.T., and A.L. Coan. 1974. A review of some aspects of the bluefin tuna (Thunnus thynnus thynnus) fisheries of the Atlantic Ocean. Intern. Comm. Conserv. Atlantic Tunas, Collective Vol. Sci. Pap. 2(SCRS-1972): 259-313.

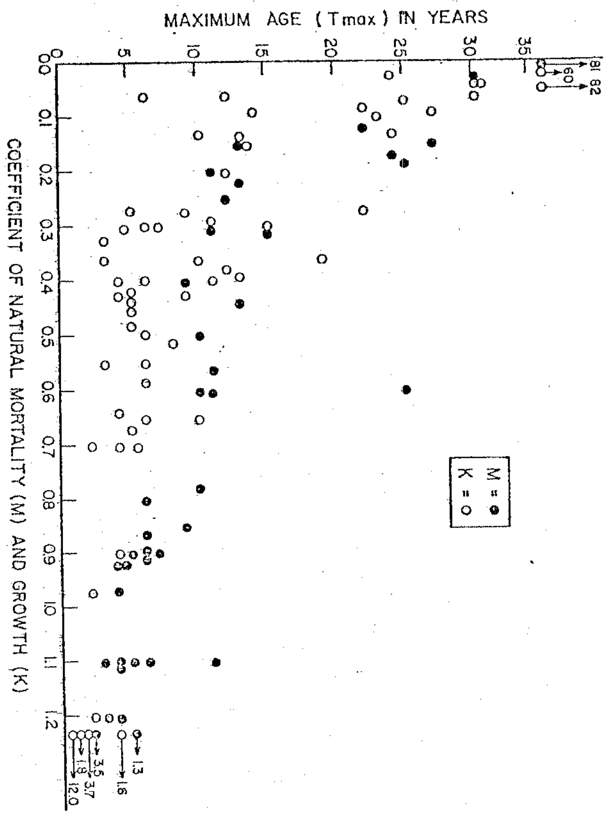

Figure 1. Coefficients of natural mortality (M) and growth (K) plotted against maximum age (T_{max}) in years. (Data from Beverton and Holt, 1959)

Table 2. Maximum age (T_{max}), K and M for some species of Atlantic tunas. Confidence limit (C.L.) of $\hat{M}$ determined from equation in text.

Species	T_{max} (yrs)	$1/T_{max}$	K	M	95% C.L. $\hat{M}$
Albacore	9	0.111	0.14[1]	0.23	0.13-0.40
Bigeye	7	0.143	0.30[2]	(none)	0.44-0.68
Bluefin	25	0.040	0.053[1]	0.10	0 -0.24
Skipjack	5	0.200	0.43[1]	(none)	0.69-0.93
Yellowfin	6	0.167	0.42[1]	0.80	0.67-0.91

[1] Coan (1976)

[2] Estimated from K = 2.117 ($1/T_{max}$)

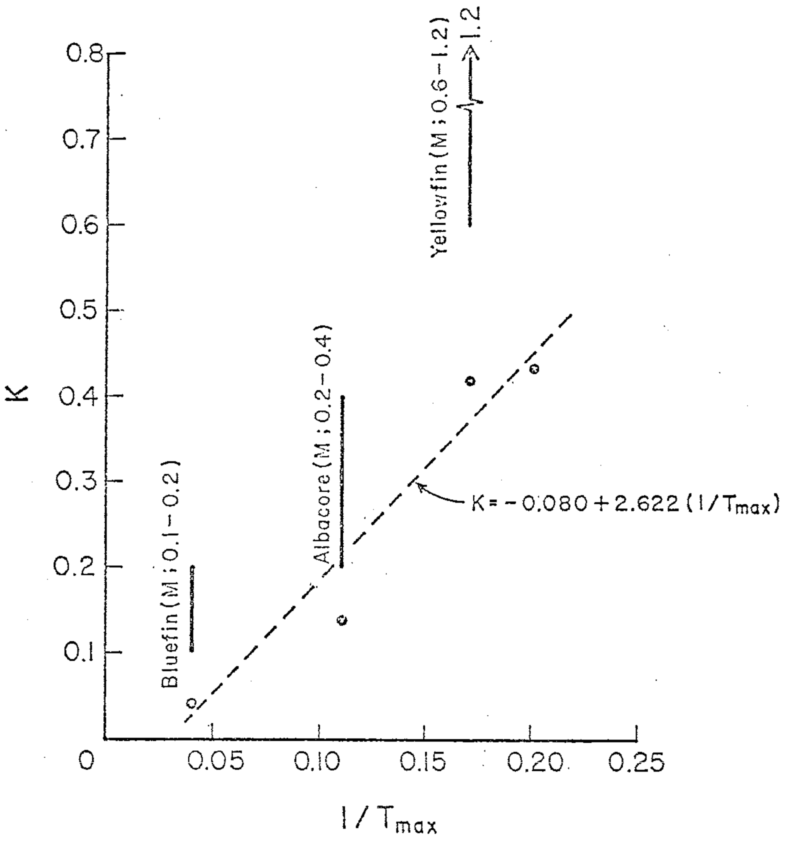

Figure 2. Coefficient of growth (K) on maximum age (T_{max}) for tunas. The ranges of estimated coefficient of natural mortality (M) are also shown.

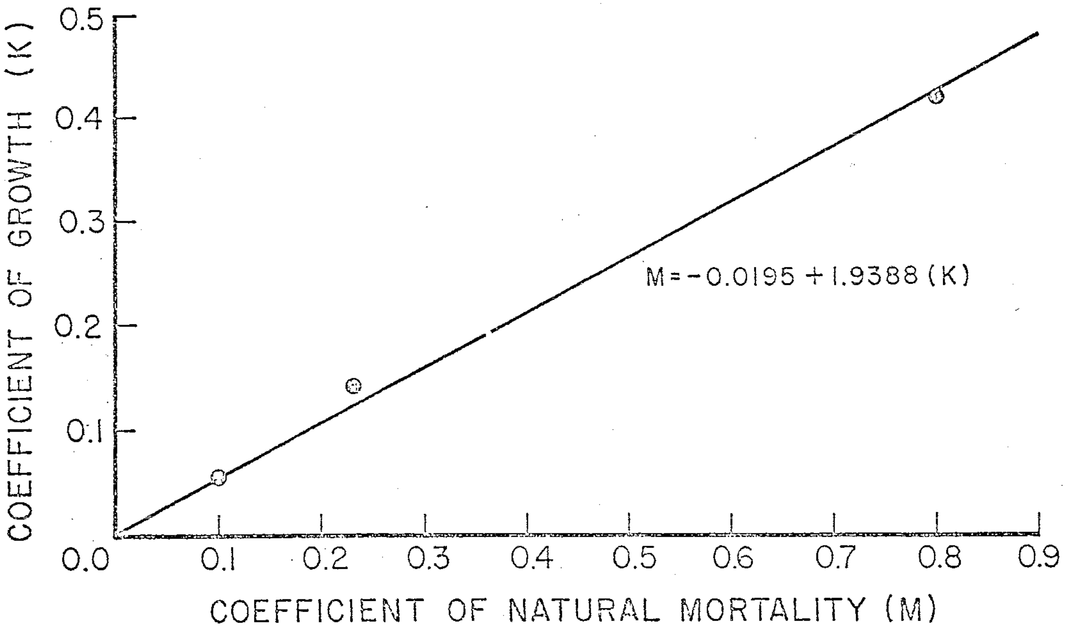

Figure 3. Relation between the coefficient of growth (K) and the coefficient of natural mortality (M) for tunas