INTER-AMERICAN TROPICAL TUNA COMMISSION

SCIENTIFIC ADVISORY COMMITTEE

13TH MEETING

(*by videoconference*)

16-20 May 2022

DOCUMENT SAC-13 INF-J

GROWTH ESTIMATES FOR SKIPJACK TUNA IN THE EASTERN PACIFIC OCEAN

Mark N. Maunder, Dan Fuller, and Kurt Schaefer

ABSTRACT

Growth is estimated for skipjack tuna in the eastern Pacific Ocean by fitting the growth cessation model to tagging data in a length-at-age context. Tagging data does not provide information on absolute age, so reasonable assumptions were made about the age of small skipjack to calibrate the age for the tagging data. Exploratory analysis showed that the tagging data exhibits linear growth and does not provide information about asymptotic length. Therefore, length frequency data from the fisheries were used to make alternative assumptions about asymptotic growth. Variation in estimated length-at-age was separated into measurement error and individual variation. The measurement error was estimated using short-term recoveries. Several alternative growth curves are provided that differ based on assumptions about the age of small skipjack and the asymptotic length.

INTRODUCTION

Growth estimates are needed for integrated age-structured stock assessments fit to length-composition data, which are commonly used for providing management advice. Age-length data (e.g., from otoliths) are most informative, but may not be available, particularly for hard-to-age species. Modes in length composition data can also be informative about growth, but the modes often merge for older ages and are less informative. Growth increments from tagging data are an alternative source of information that may be available for hard-to-age species, but need to be modelled appropriately and calibrated to age to define an age-based growth function. Some studies have combined two or more sources of information to increase precision (e.g., Laslett *et al*., 2002; Eveson *et al*., 2004; Aires-da-Silva *et al*., 2015). Others have integrated the data into stock assessment models to estimate the growth parameters simultaneously with the other model parameters in an attempt to reduce bias caused by selectivity or non-random sampling of otoliths (see Piner *et al*. 2016).

Aging of skipjack tuna has proven to be difficult due to no apparent consistent annual or daily rings (Wild and Foreman, 1980; Wild *et al*., 1995) and modes are often not apparent in length-composition data due to fast growth and year-round recruitment. Therefore, tagging growth increment data appears to be the only reliable source of information on growth. Several growth estimates have been conducted for skipjack based on tagging data, including studies in the eastern Pacific Ocean (EPO; e.g., Bayliff 1988, Maunder 2001). These approaches estimate growth as a function of length, which can be used in length-based stock assessments, but are not appropriate for use in age-structured models. Therefore, the approach of Laslett *et al.* (2002) should be used (e.g., Aires-da-Silva *et al.* 2015), which is based on the standard approach to estimate growth from age-length data but can be fit to tagging growth increment data. The main concept is to estimate the age at release so that each tag has two age-length data points that can be fit by the model, one at release and one at recapture, conditioned on the estimated age. The standard approach is to treat the age as a random effect and integrate over age to implement the estimation method (Laslett *et al.* 2002; Aires-da-Silva *et al.* 2015), but treating the age as a fixed effect has also been used (Maunder *et al.* 2018).

The approach of Laslett *et al.* (2002) requires at least some age-length data for one or more ages to scale the growth curve with respect to age. Since skipjack cannot be reliably aged, this type of information is not available. Fortunately, absolute age is not necessary for the skipjack age-based stock assessment. This is because recruitment is assumed to be independent of stock size and therefore knowing the lag between when spawning occurs and when the fish recruit to the fishery is not necessary. The growth curve can then be fit by making a reasonable assumption about the length at a given age (e.g., the age at recruitment to the fishery) or other similar assumption (e.g., setting the value of t_0 in the von Bertalanffy growth curve). Using length-based processes or the same aging assumptions in age-based processes (e.g., natural mortality, selectivity, and maturity) will adjust the stock assessment model appropriately for the assumed age at entry to the fishery. Sensitivity of the results from the stock assessment model to the assumptions about age can be used to check this concept.

Previous analyses of data from tropical tunas have had difficulty estimating the asymptotic length due to lack of data from old individuals (e.g., Aires-da-Silva *et al.,* 2015). This is due to difficulty aging tropical tunas using annual rings in otoliths, problems resolving daily increments in otoliths for individuals greater than about age 5 years, and very low recovery rates from old individuals. Therefore, assumptions may need to be made about the asymptotic length to ensure a reasonable value is obtained or whether convergence is even possible in the estimation algorithm.

Exploratory analysis showed that for the lengths of skipjack tagged in the EPO, there was little, if any, reduction in growth rates. Therefore, standard fisheries growth curves may not be appropriate to model the growth of skipjack. Therefore, we focus on using the growth cessation model (Maunder *et al*. 2018) that allows for linear growth for young individuals with a rapid cessation in growth rates at large sizes. This allows flexibility in assumptions about the growth curve beyond the range of the data, which may be useful in looking at the sensitivity of the stock assessment to assumptions about why no large skipjack are seen in the purse-seine catch (dome-shape selectivity, high rates of natural mortality for older individuals, high rates of fishing mortality, rapid cessation in growth, or a combination of these).

We fit the growth cessation model to tag growth increment data for skipjack tuna in the EPO using a modified version of the approach described in Aires-da-Silva *et al.* (2015). The model explicitly includes measurement error and individual growth variation.

METHODS

The approach is based on that presented in Aires-da-Silva *et al.* (2015), which can be separated into 1) a model that describes length-at-age, 2) a model that describes variation of length-at-age, 3) a model that describes the observation process, and 4) the inference procedure.

Length-at-age (growth) model

The growth cessation model (Maunder *et al.,* 2018), which may be more suitable for tunas, is used. This model allows for linear growth at young ages and a rapid reduction in growth at old ages, if required.

$$L_a = L_0 + r_{max}\left[\frac{\ln\left(e^{-ka_{50}}+1\right)-\ln\left(e^{k(a-a_{50})}+1\right)}{k}+a\right]$$

Where L_0 is the length at age 0, r_{max} is a parameter relating to the maximum growth rate, $k \geq 0$ is the steepness of the logistic function that models the reduction in the growth increment and a_{50} is the age of the logistic function's midpoint. L_0 can be defined based on the length at a given age (e.g., age at entry to the fishery).

$$L_0 = L_a - r_{max}\left[\frac{\ln\left(e^{-ka_{50}}+1\right)-\ln\left(e^{k(a-a_{50})}+1\right)}{k}+a\right]$$

The asymptotic length is a parameter of the von Bertalanffy and Richards models, but has to be derived for the growth cessation model. This can be done by integrating the growth equation over infinite time (pers. com. Ian Taylor).

$$\int_0^{\infty}\frac{r_{max}}{1+exp\left(k(a-a_{50})\right)}da = \frac{r_{max}ln\left(e^{ka_{50}}+1\right)}{k}$$

a_{50} can then be calculated as a function of L_{inf}.

$$a_{50} = \frac{ln\left(e^{\frac{k(L_\infty-L_0)}{r_{max}}}-1\right)}{k}$$

Reparametrizing the model by prespecifying both the asymptotic length and length at another age produces challenging or impossible algebra to find an algebraic solution for use in the model. However, since skipjack has constant growth for much of its life span, the formula for L_0 can be simplified to an approximation for a fixed length for a given young age.

$$L_0 = L_a - r_{max}a$$

Therefore, the reparameterization can be easily made:

$$a_{50} = \frac{ln\left(e^{\frac{k\left(L_\infty-L_{fix}+r_{max}a_{fix}\right)}{r_{max}}}-1\right)}{k}$$

Where L_{fix} is the specified length at a young age a_{fix}.

Variation of length-at-age

Following Aires-da-Silva *et al*. (2014), a linear relationship is assumed between the variation of length-at-age and length.

$$\sigma_L = \alpha + \beta L$$

To avoid numerical errors when $\sigma_L \leq 0$, it is assumed that σ_L increases with length so $\beta > 0$ and we also assume $\alpha > 0$.

Observation model

We include both measurement error and process variation in the growth model. Robust likelihoods were considered to deal with transcription and other errors following Maunder (2001), but initial analyses were unstable and we chose to explicitly remove outliers instead. Short-term recoveries can inform the measurement error. Unlike Maunder (2001), who only included a single measurement error due to the use of a length-based growth model, we included measurement error in both the release length and the recapture length. The measurement error parameters could differ between length at release and length at recapture. Length at release is usually measured by trained personal with the appropriate equipment, but the fish is alive, and measurements are taken quickly, which may induce error. Recaptured fish are typically measured dead, but other factors may create measurement errors, the measurer may be untrained or use an inappropriate tool.

We assume that the individual variation of length-at-age and the measurement error are both normally distributed.

$$L_{obs} = L_{pred} + \varepsilon_L + \varepsilon_m$$

Where $\varepsilon_L \sim N[0, \sigma_L^2]$ is the process variation and $\varepsilon_m \sim N[\mu_m, \sigma_m^2]$ is the measurement error. We assume that the measurement error is unbiased ($\mu_m = 0$).

The likelihood function is

$$\ell(\boldsymbol{\theta}|\boldsymbol{L}) = \frac{1}{\sqrt{2\pi(\sigma_L^2 + \sigma_m^2)}} exp\left(-\frac{\left(L_{obs} - L_{pred}\right)^2}{2(\sigma_L^2 + \sigma_m^2)}\right)$$

Where $\boldsymbol{\theta}$ represents the parameters to be estimated.

The total negative log-likelihood is simply the sum of the negative log-likelihood for all releases added to the sum of the negative log-likelihood for all recaptures.

Rather than formulating an integrated model for the measurement error, we simply evaluate the random error in short-term recoveries for which the growth is negligible, such that process error would also be negligible. When both measurement error and individual variation of length-at-age are both a linear function of length, then they will be completely confounded. The variation of length-at-age could be a function of age, but since in this study growth for the ages sampled is a linear function of age, then a standard deviation that is a linear function of growth is essentially identical to a linear function of age. Therefore, the measurement error standard deviation cannot be estimated simultaneously with the standard deviation for variation of length-at-age. We determine the measurement error standard deviation using a model that estimates three parameters 1) the length at release of each short-term recovery (L_{est}), 2) the growth rate as a function of the time at liberty, and 3) the standard deviation of the measurement error (σ_m). The observed length at release and length at recovery can be fit using the same likelihood function. For simplicity, we assume that the distribution (i.e., the standard deviation) for the measurement error in the length at release and in the length at recapture is the same.

$$\ell(\boldsymbol{\theta}|\boldsymbol{L}) = \frac{1}{\sqrt{2\pi(\sigma_m^2)}} exp\left(-\frac{\left(L_{obs} - L_{pred}\right)^2}{2(\sigma_m^2)}\right)$$

where $L_{pred} = L_{est}$ for the release length and $L_{pred} = L_{est} + \gamma t$ for the recapture length. t is the time at liberty.

The length at recapture was adjusted for shrinkage. We used the relationship with length developed for bigeye tuna by Schaefer and Fuller (2006):

$$L_f = 1.01814L_t + 0.1481$$

AIC adjusted for sample size (AICc) was used to choose the best model.

$$AIC_c = -2lnL + 2K + \frac{2K(K+1)}{n-K-1}$$

Initial analysis using tagged fish at liberty less than 20 days encountered convergence issues (high maximum gradient components). For this reason, we did a comprehensive analysis using fish at liberty less than 20 days and at liberty less than 50 days. We then chose the most appropriate model and estimated the parameters in addition for 10, 30, and 40 days at liberty. A linear regression was then applied to this model and the relationship was extrapolated to determine the measurement error for no days at liberty. Tagged fish at liberty for 20 days or more were then used in the growth analysis.

Inference procedure

The parameters are estimated using maximum likelihood by minimizing the negative log-likelihood in Template Model Builder (TMB, Kristensen *et al*., 2016). Rather than integrating across age, we simply estimate the age of each release as a parameter following Maunder *et al*. (2018). The number of parameters increases with the number of tagged fish, but there are two data points (length at release and length at recapture) for each parameter (age of the tagged fish). Also, the distribution of ages of released fish is unknown and could be complex (e.g., multi-modal, see Figure 1) and therefore difficult to represent with a distributional assumption. The age at recapture is simply the age at release plus the time at liberty.

Data

The tagging data was derived from IATTC tagging cruises conducted in the EPO during 2000 to 2020. Only data with recovery lengths measured by IATTC Field Office Personnel and for which the recapture date was considered of high confidence was used in the analyses. A few tags were eliminated due to missing data. We also eliminated three tags that had large negative annual growth rates. This resulted in a total of 337 tags of which 58 had a time at liberty of less than 50 days, which were used to estimate the measurement error, leaving 279 tags to use in the analysis.

We removed outliers including 10 negative values less than -0.1 and 4 positive values greater than 0.2 cm per day.

Scenarios

The size of first entry into the fishery is around 30 cm and the smallest skipjack in the tagging data to use in the analysis is 37 cm. The estimates of age are unreliable for skipjack tuna in the EPO (Wild and Foreman, 1980; Wild *et al*. 1995). Recent WCPO assessments estimated an age-class 1 quarter fish to be

23 cm (Vincent *et. al.,* 2019). Therefore, we assume that a 37 cm fish is about 2 quarters old. To test the sensitivity to this assumption we also looked at ages 3 quarters and 4 quarters.

Initial analyses indicated that convergence of the estimation method was an issue due to lack of information about the asymptotic length. Therefore, the scenarios were run with different assumptions about asymptotic length. A guess at the asymptotic length was made based on visual inspection of the length-composition data and assuming an asymptotic selectivity curve. The purse-seine fishery suggests using a range of 65-75 cm (Figure 4), while the longline fishery suggests using a range from 85-95 cm (Figures 5 and 6). However, the standard deviation of the variation of length-at-age should be taken into consideration (e.g., sd = 80 cm x 0.03 = 2.4 such that 2.5% of the lengths would be 80 + 2.4 x 2 = 84.8 cm and larger). Therefore, we choose values of 75, 80, 85 cm for the asymptotic length.

RESULTS

Measurement error

The models had convergence issues with high maximum gradient components, large standard errors and sensitivity to starting values when the data was restricted to tagged fish at liberty for less than 20 days (Table 1). There were only 27 fish (54 data points that include two measurements for each fish, the length at release and the length at recovery). The best model based on AICc included both the intercept of the linear relationship between the measurement error standard deviation and length and the growth rate. The second best model, which was 0.69 AICc units worse, only included the slope of the linear relationship and the growth rate. The third best model, which was 1.92 AICc units worse, included the slope of the linear relationship and the growth rate. The convergence issues did not occur when the data was restricted to tagged fish at liberty for less than 50 days. This data selection resulted in 58 fish (116 data points). The best model based on AICc included both the slope of the linear relationship and the growth rate and the second best model included just the slope and was 1.17 AICc units worse.

Due to the convergence issues of the model that only used tagged fish at liberty for less than 20 days, we used the results of the analysis that used tagged fish at liberty for less than 50 days to choose the best model, which estimated the slope of the linear relationship and the growth rate. This model then was applied to the other limits on the tagged fish days at liberty. The estimated slope parameters had a very strong linear relationship with the cutoff days at liberty (Figure 1). The extrapolated value for zero days at liberty that represents measurement error (i.e., the intercept of the linear relationship) is 0.0222. This value was used in the growth analysis.

Growth estimates

A simple linear model of annual growth rate [(length at recovery – length at release)/time at liberty] versus the average length [(length at release + length at recovery)/2] was fit as an exploratory analysis. The results determined that the intercept is significant, but the slope is not. The mean increment is 27.49 cm per year.

The models have convergence issues with large maximum gradient components and in some cases the likelihood is larger indicating that the shape of the curve extending from the length of the last tagging data point to the asymptotic length is not well determined, although the standard errors are small (Table 2). The shape is controlled by the parameter K, which varies a lot among scenarios, while the other parameters do not. All models essentially estimate a linear increase in mean length with an average of

26.64 cm per year for the range of ages/lengths covered by the tagging data. Increasing the asymptotic length simply extends the model to larger lengths.

The estimates of individual variation are small indicating that there is little variation in growth rates among individuals, which is consistent with the low variation seen in otolith data despite the issues with aging (Wild and Forman 1980).

DISCUSSION

The model essentially estimates a linear increase in mean length for the range of ages/lengths fcovered by the tagging data (Figure 7). Therefore, there is no information to differentiate between the different values for the asymptotic length. Increasing the asymptotic length simply extends the model to larger lengths. The models have convergence issues with large maximum gradient components indicating that the shape of the curve extending from the length of the last tagging data point to the maximum length is not well determined. Essentially, the only parameter that is estimable is R_{max}, which is the linear growth rate, which is about 26.64 cm per year.

The growth rate for the lengths of individuals caught by the purse-seine fishery is well determined by the tagging data and can be used in stock assessments. However, there is no information on the growth rates of larger and older individuals, including asymptotic length and whether there is cessation with age. Any stock assessment will have to be robust to these assumptions.

Previous studies provide similar magnitude estimates of growth rates but estimate a decline with length over the range of lengths caught in the purse seine fishery (Table 3 and Figure 8). It is not clear why those studies show a decline in growth with length, while this study does not. These studies may have been less rigorous in the quality of the length measurements and the dates of recovery. In addition, they did not adjust for shrinkage. In future studies, shrinkage estimates specifically for skipjack should be used. Less than 10% of the data used in Maunder (2001) were at liberty 50 days or more, the quality of the data may be variable, captures were more coastal, and selectivity/vulnerability to the gear may have biased recaptures of larger individuals.

REFERENCES

Aires-da-Silva, A.M., M.N. Maunder, K.M. Schaefer, D.W. Fuller. 2015. Improved growth estimates from integrated analysis of direct aging and tag-recapture data: an illustration with bigeye tuna (Thunnus obesus) of the eastern Pacific Ocean with implications for management. Fisheries Research. 163:119-126.

Bayliff, W.H. 1988. Growth of skipjack, Katsuwonus pelamis, and yellowfin, Thunnus albacares, tunas in the eastern Pacific Ocean, as estimated from tagging data. Inter- American Tropical Tuna Commission, Bulletin, 19 (4): 307-385.

Eveson, J.P., Laslett, G.M., Polacheck, T., 2004. An integrated model for growth incorporating tag–recapture, length-frequency, and direct aging data. Can. J. Fish. Aquat. Sci. 61, 292–306.

Ianelli, J.N. 1993. Studies on the population structure of skipjack tuna, *Katsuwonus pelamis*, in the central and eastern Pacific Ocean. A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, University of Washington.

Joseph, J. and Calkins, T.P. 1969. Population dynamics of the skipjack tuna (*Katsuwonus pelamis*) of the eastern Pacific Ocean. Inter-American Tropical Tuna Commission, Bulletin, 13 (1): 1-273.

Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., Bell, B.M., 2016. TMB: automatic differentiation and laplace approximation. J. Stat. Softw. 70, 1–21.

Laslett, G.M., Eveson, J.P., Polacheck, T., 2002. A flexible maximum likelihood approach for fitting growth curves to tag–recapture data. Can. J. Fish. Aquat. Sci. 59, 976–986.

Maunder, M.N., 2001. Growth of skipjack tuna (Katsuwonus pelamis) in the eastern Pacific Ocean, as estimated from tagging data. Bull. Inter-Am. Trop. Tuna Commn. 21, 529–571.

Maunder, M.N., Deriso, R.B., Schaefer, K.M., Fuller, D.W., Aires-da-Silva, A.M., Minte-Vera, C.V., Campana, S.E. 2018. The growth cessation model: a growth model for species showing a near cessation in growth with application to bigeye tuna (Thunnus obesus). Marine Biology. 165(76).

Piner, K. R., Lee, H. H. and Maunder, M. N. 2016. Evaluation of using random-at-length observations and an equilibrium approximation of the population age structure in fitting the von Bertalanffy growth function. Fisheries Research. 180: 128-137.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Vincent, M.T., Pilling, G.M., Hampton, J. 2019. Stock assessment of skipjack tuna in the western and central Pacific Ocean. WCPFC-SC15-2019/SA-WP-05-Rev2

Wild, A., Foreman, T.J., 1980. The relationship between otolith increments and time for yellowfin and skipjack tunas marked with tetracycline. Inter-Amer, Trop. Tuna Comm. Bull. 17: 507-560

Wild, A., Wexler, J.B., Foreman, T.J., 1995. Extended studies of increment deposition rates in otoliths of yellowfin and skipjack tunas. Bulletin of Marine Science, 57(2), 555-562.

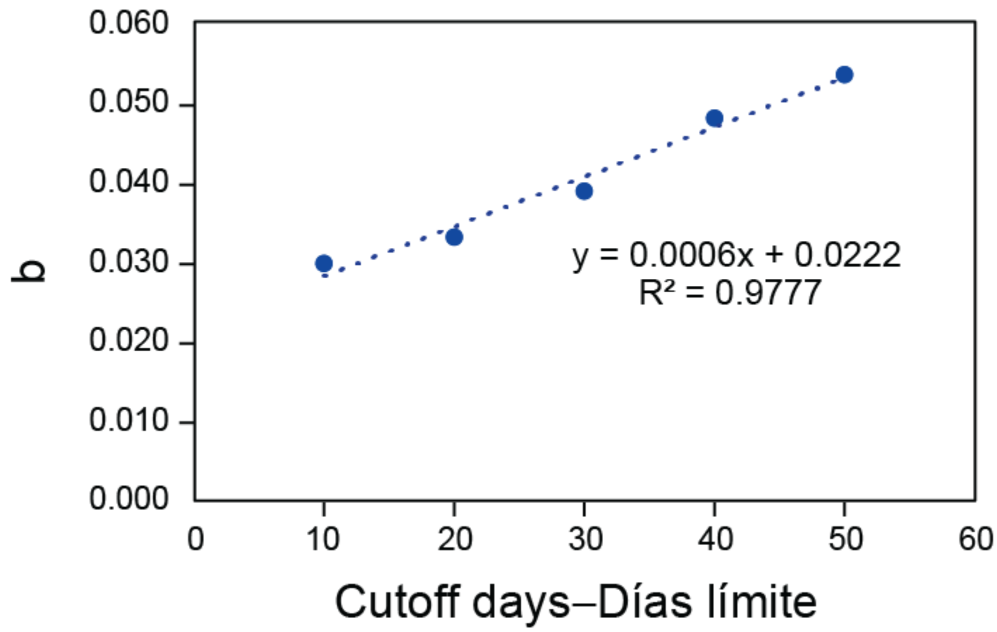

FIGURE 1. The estimated relationship between the number of days at liberty used to constrain the data and the estimate of the slope of the linear relationship between length and the measurement error standard deviation. The intercept (0.0222) is used to determine the length coefficient to estimate the measurement error (i.e., sd = 0.0222L) used in the growth analysis.

FIGURA 1. La relación estimada entre los números de días en libertad utilizados para delimitar los datos y la estimación de la pendiente de la relación lineal entre la talla y la desviación estándar del error de medición. El intercepto (0.0222) se utiliza para determinar el coeficiente de la talla para estimar el error de medición (es decir, sd = 0.0222L) utilizado en el análisis de crecimiento.

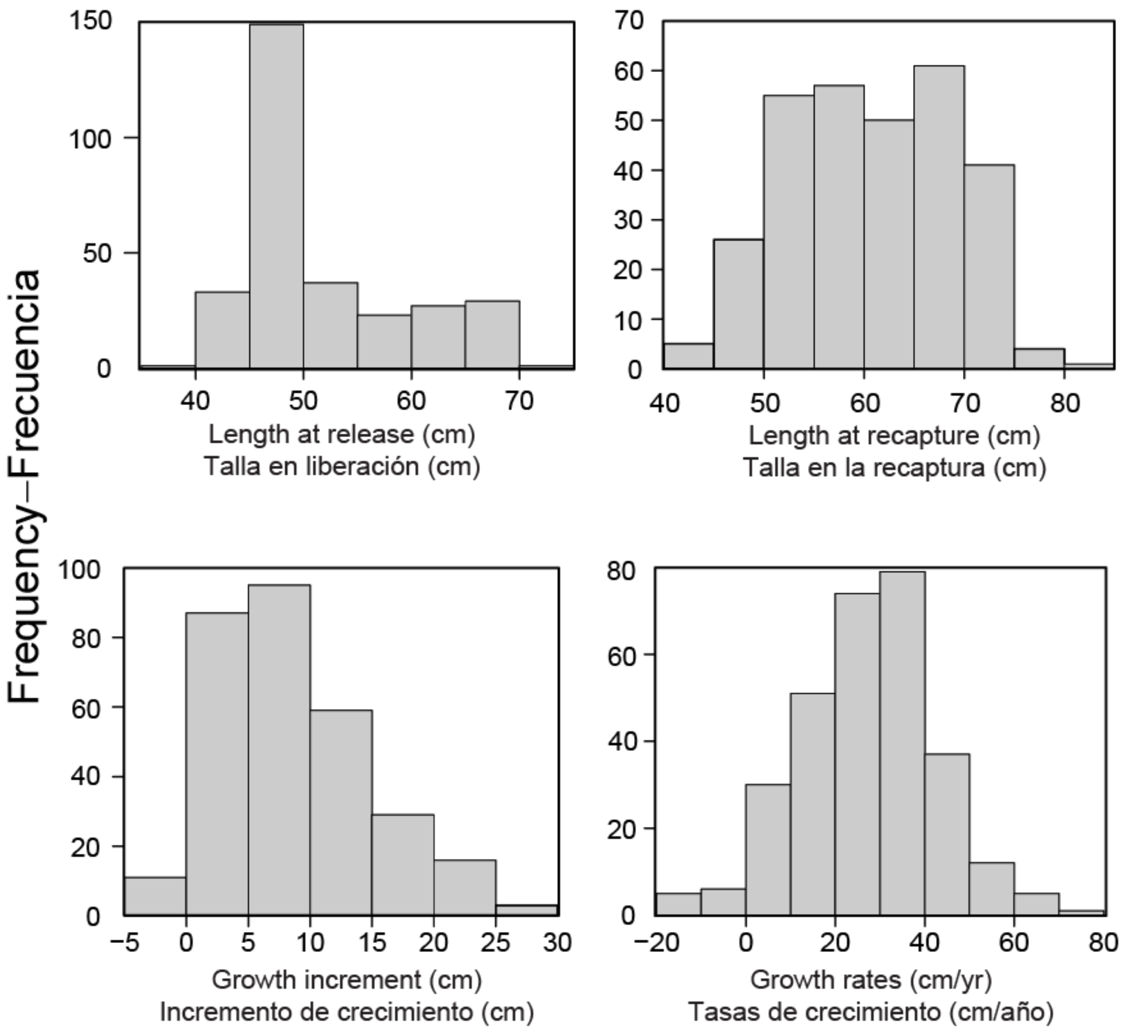

FIGURE 2. Frequency distributions of the lengths at release, lengths at recapture, growth increment, and annual growth rates.

FIGURA 2. Distribuciones de frecuencias de la talla de liberación, talla de recaptura, incremento de crecimiento y tasas de crecimiento anual.

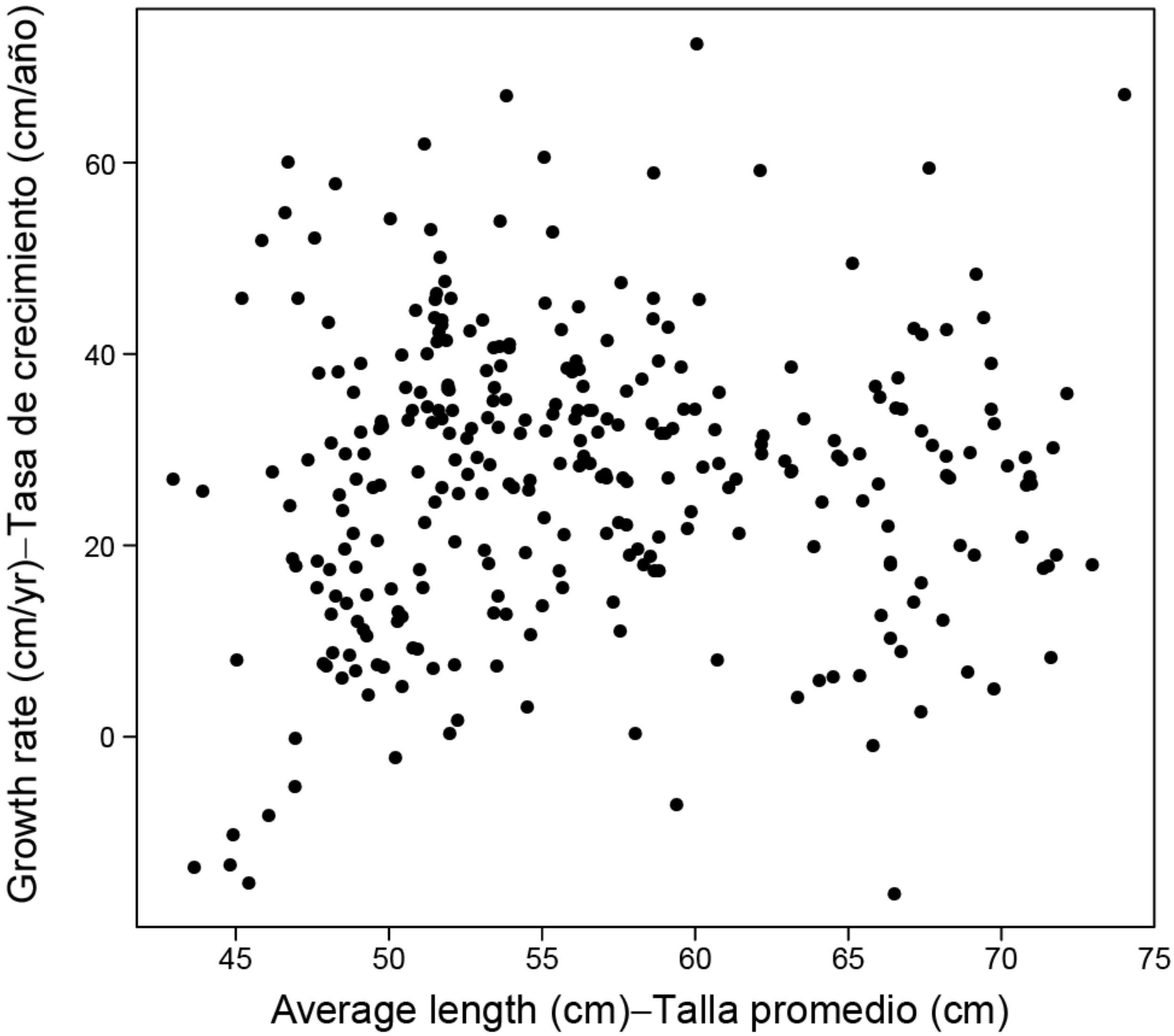

FIGURE 3. Plot of the annual growth rate versus the average length [(release length + recapture length)/2].
FIGURA 3. Gráfica de la tasa de crecimiento anual frente a la talla promedio [(talla de liberación + talla de recaptura)/2].

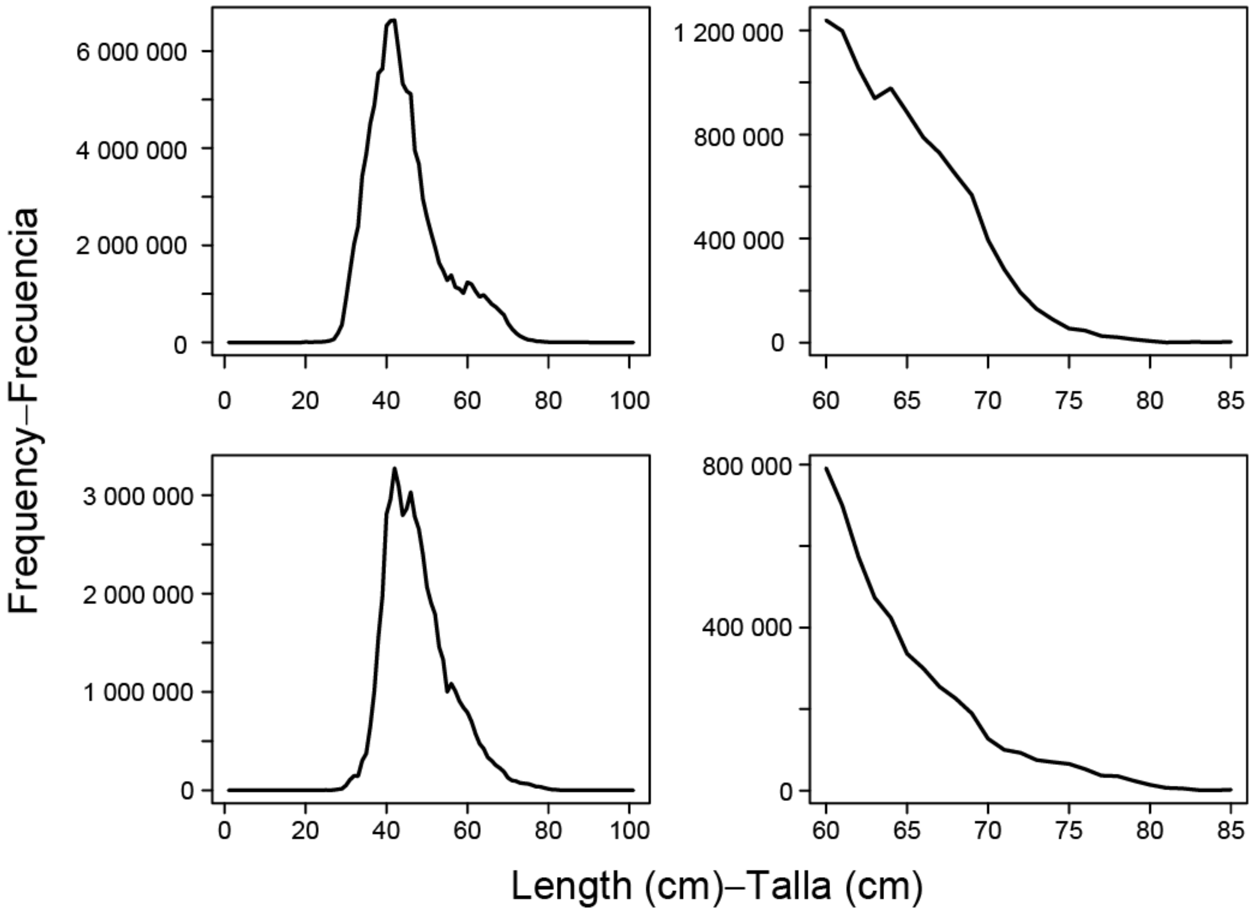

FIGURE 4. Skipjack tuna length (cm) frequency distributions in the EPO from the OBJ (top) and NOA (bottom) fisheries for 2000-2019. The right figures simply change the x-axis to show the larger fish in more detail.
FIGURA 4. Distribuciones de frecuencias de la talla del atún barrilete (cm) en el OPO de las pesquerías OBJ (arriba) y NOA (abajo) de 2000 a 2019. Las figuras de la derecha simplemente cambian el eje 'x' para mostrar los peces más grandes con mayor detalle.

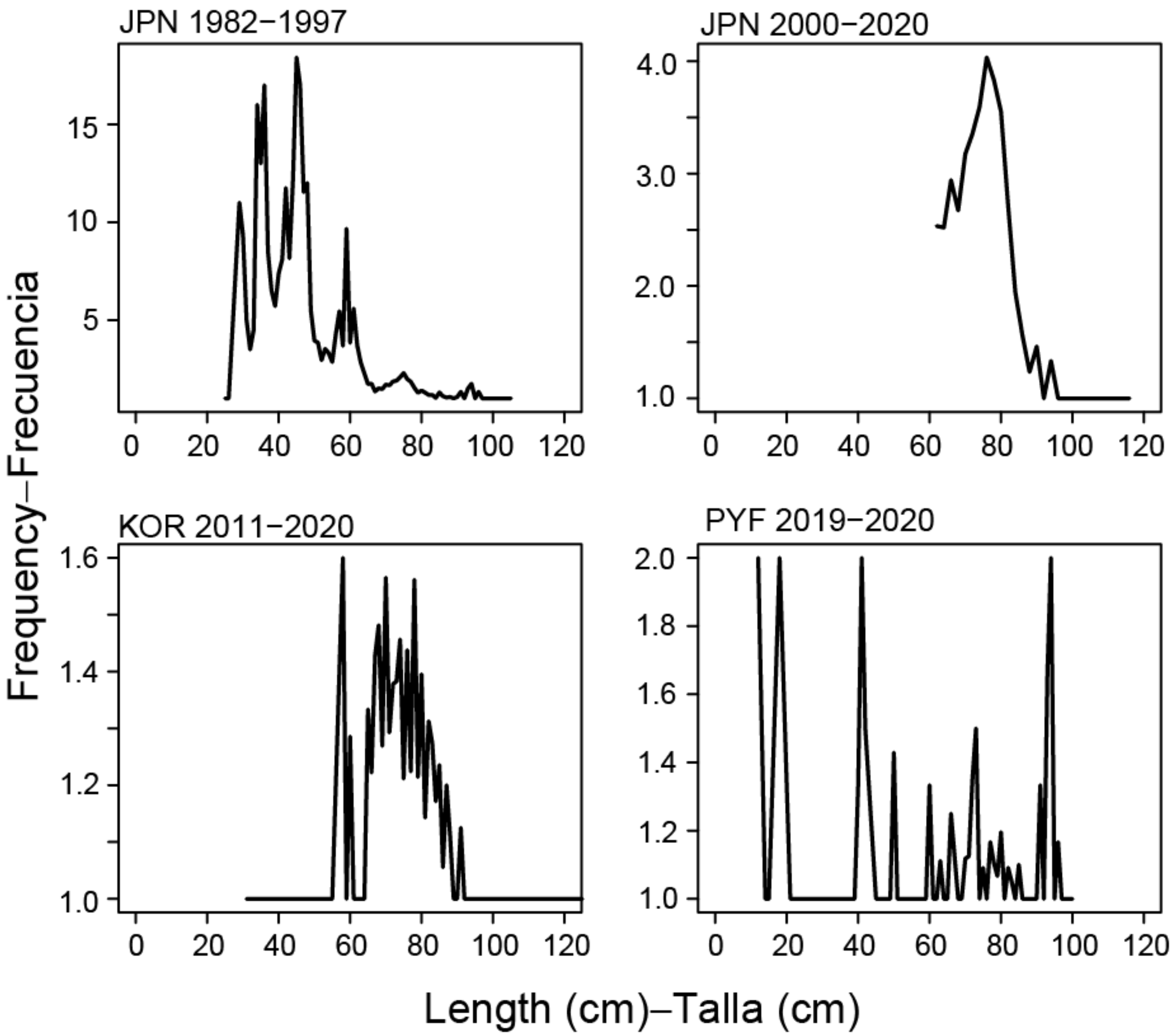

FIGURE 5. Skipjack tuna length (cm) frequency distributions in the EPO from the longline fisheries: JPN = Japan, KOR = Korea, PYF = French Polynesia.

FIGURA 5. Distribuciones de frecuencias de la talla del atún barrilete (cm) en el OPO de las pesquerías palangreras: JPN = Japón, KOR = Corea, PYF = Polinesia Francesa.

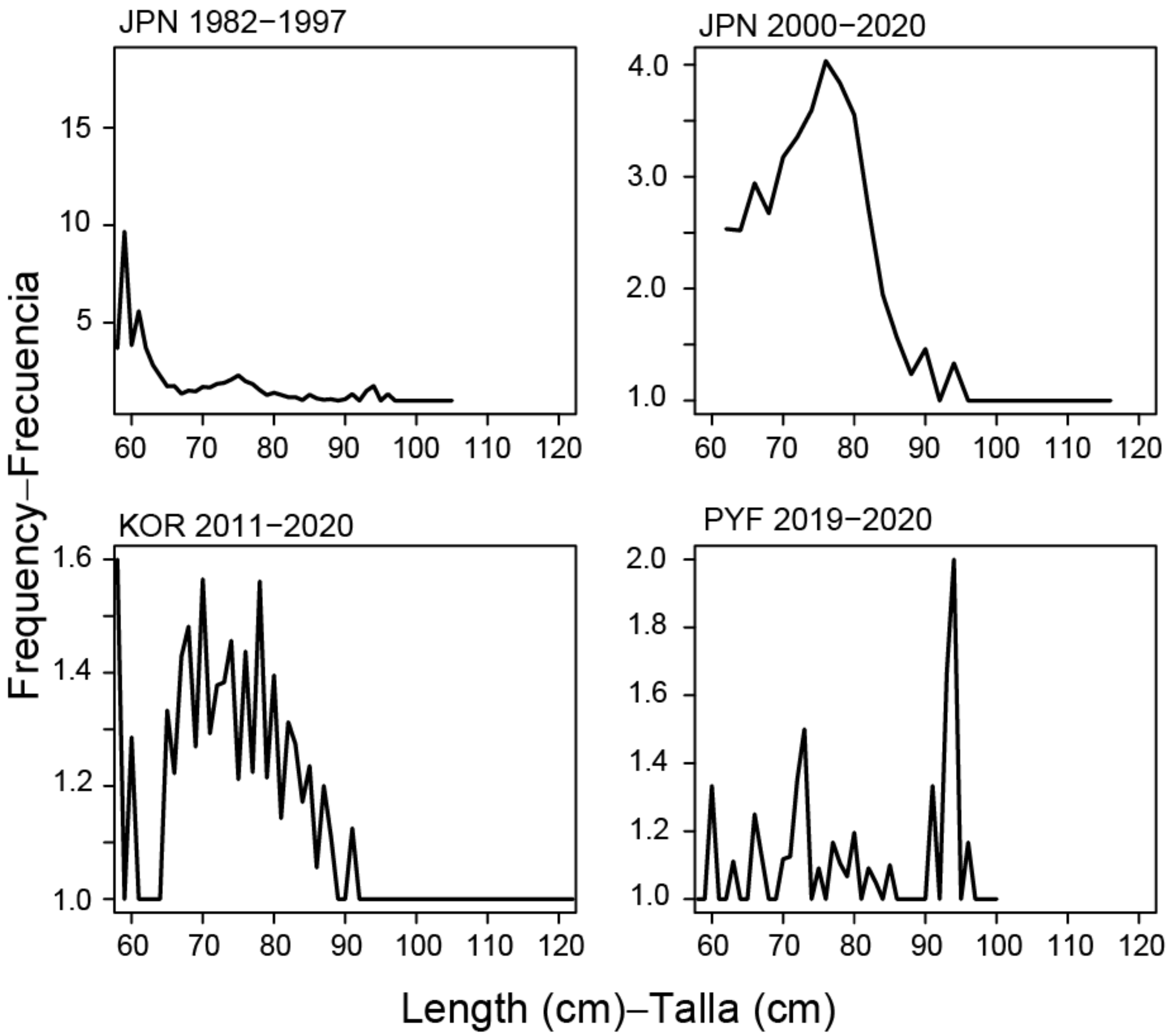

FIGURE 6. Skipjack tuna length (cm) frequency distributions in the EPO from the longline fisheries: JPN = Japan, KOR = Korea, PYF = French Polynesia. X-axis reduced to show details.

FIGURA 6. Distribuciones de frecuencias de la talla del atún barrilete (cm) en el OPO de las pesquerías palangreras: JPN = Japón, KOR = Corea, PYF = Polinesia Francesa. El eje 'x' se ha reducido para mostrar detalles.

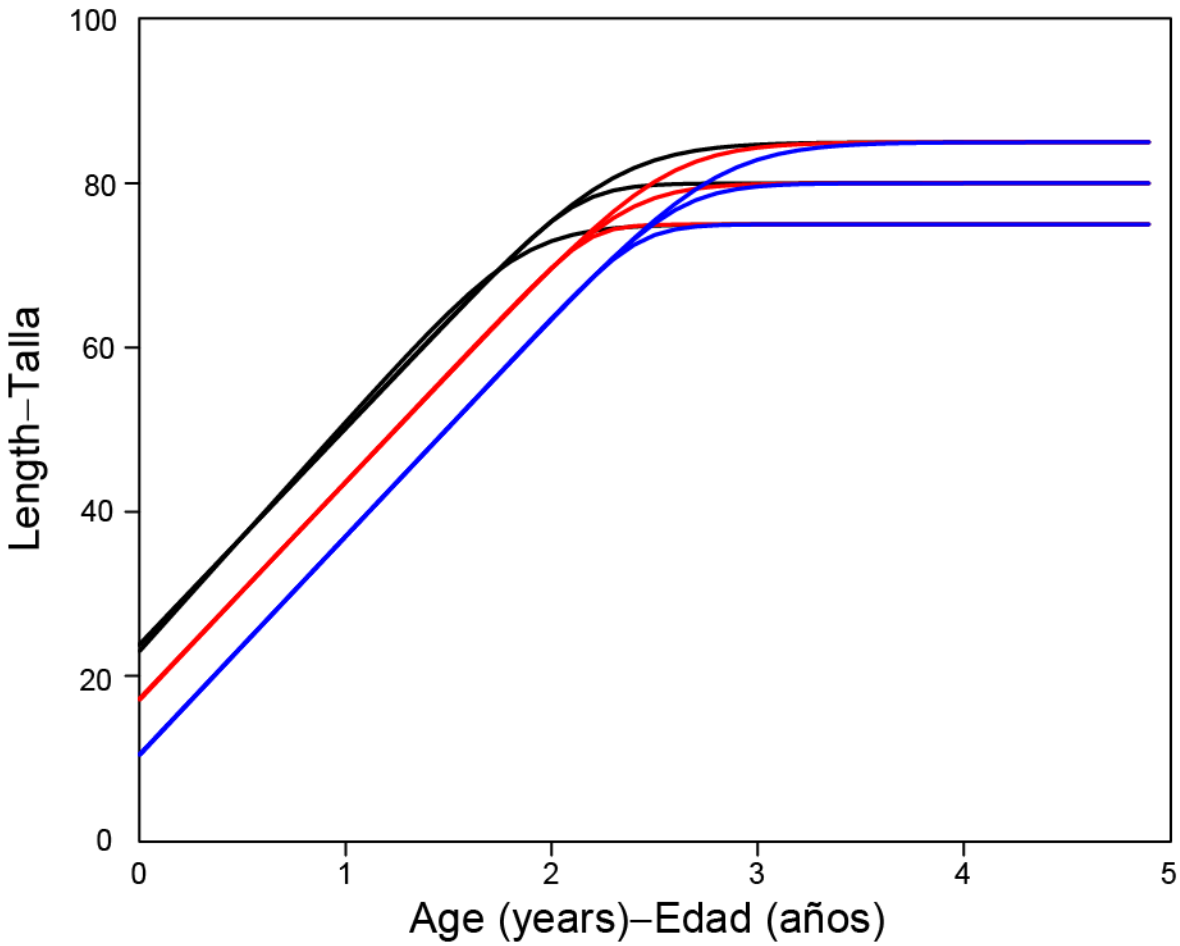

FIGURE 7. Estimated growth curves with asymptotic length fixed at 75, 85, 95 and 105cm (lower to upper lines) for different ages at 37cm (red = 0.25, black = 0.5, and blue = 0.75).

FIGURA 7. Curvas de crecimiento estimadas con la talla asintótica establecida en 75, 85, 95 y 105 cm (de la línea inferior a la superior) para diferentes edades a 37 cm (rojo = 0.25, negro = 0.5 y azul = 0.75).

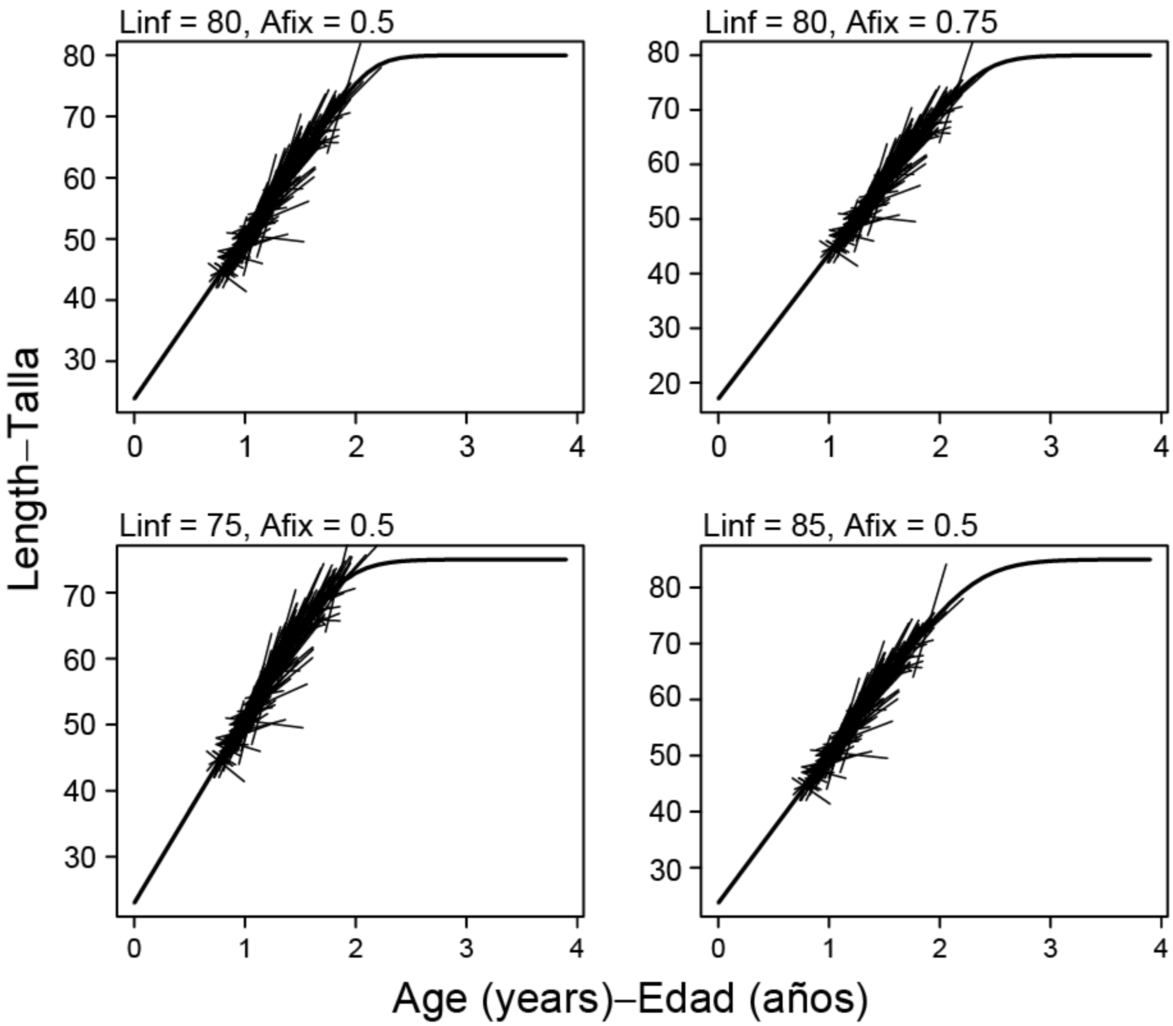

FIGURE 8. Example fits to the tagging data. The lines link the observed length at release to the observed length at recapture for the estimated age of each tagged fish.

FIGURA 8. Ejemplos de ajustes a los datos de marcado. Las líneas relacionan la talla de liberación observada con la talla de recaptura observada para la edad estimada de cada pez marcado.

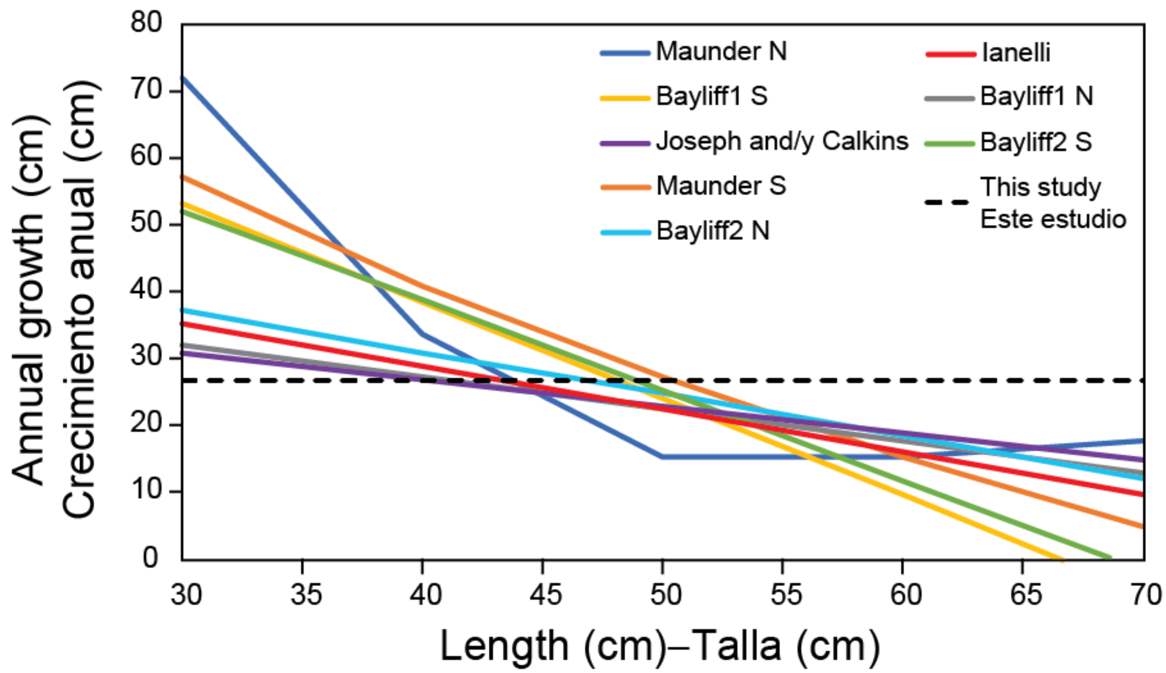

FIGURE 9. Estimates from other studies reported in Table 4 of Maunder (2001) compared to the average of R_{max} estimates across all the scenarios reported in this study.

FIGURA 9. Estimaciones de otros estudios, presentadas en la Tabla 4 de Maunder (2001), frente al promedio de las estimaciones de R_{max} para todos los escenarios examinados en este estudio.

TABLE 1. Parameter estimates, their standard errors, and the objective function value for the measurement error model under different model assumptions.

TABLA 1. Estimaciones de parámetros, sus errores estándar y el valor de la función objetivo para el modelo de error de medición bajo diferentes supuestos para el modelo.

Less than 20 days at liberty

mgc	like	g	se	ln_a	se	a	ln_b	se	b	Npar	AICc	dAICc
1.33E+00	108.73			0.353	0.317	1.424				28	338.42	0.69
2.92E+00	108.56			0.417	0.253	1.518	-5.090	1.226	0.006	29	347.63	9.90
2.09E+01	103.62	25.918	23.507	0.497	0.117	1.643				29	337.73	0.00
3.82E-04	111.23						-3.268	0.096	0.038	28	343.42	5.69
3.83E+00	104.58	42.565	22.339				-3.399	0.108	0.033	29	339.65	1.92
8.21E-01	103.51	26.627	23.627	0.477	0.143	1.611	-6.934	2.842	0.001	30	347.89	10.16

Less than 50 days at liberty

mgc	like	g	se	ln_a	se	a	ln_b	se	b	Npar	AICc	dAICc
2.49E-04	291.92			1.098	0.066	2.997				59	828.28	9.42
1.14E-01	287.80			-6.626	26.665	0.001	-2.879	0.067	0.056	60	828.69	9.83
2.53E-01	290.36	22.581	7.958	1.084	0.066	2.957				60	833.81	14.96
1.25E-03	287.80						-2.879	0.066	0.056	59	820.02	1.17
1.22E-04	282.88	24.796	7.735				-2.921	0.066	0.054	60	818.86	0.00
1.64E-01	282.89	25.369	7.735	-6.201	13.539	0.002	-2.922	0.066	0.054	61	827.86	9.00

TABLE 2. Maximum gradient component (mgc), negative log-likelihood (nlnL), parameter estimates and their standard errors (se) for different ages at 37cm (Afix) and asymptotic length
TABLA 2. Componente de gradiente máximo (mgc), log-verosimilitud negativa (nlnL), estimaciones de parámetros y sus errores estándar (se) para diferentes edades a 37 cm (Afix) y a la talla asintótica (Linf).

(Linf).Afix	Linf	mgc	nlnL	ln_rmax	se	rmax	ln_k	se	K	ln_sd_b	se	sd_b
0.5	75	35.88	1338.22	3.33	0.03	27.94	1.67	0.19	5.33	-4.01	0.07	1.81E-02
0.5	80	0.57	1329.44	3.27	0.02	26.26	2.03	0.45	7.64	-4.04	0.07	1.76E-02
0.5	85	32.03	1329.96	3.28	0.02	26.53	1.47	0.24	4.36	-4.04	0.07	1.76E-02
0.75	75	6.59	1331.04	3.27	0.02	26.34	2.43	0.38	11.34	-4.03	0.07	1.77E-02
0.75	80	8.60	1329.99	3.28	0.02	26.56	1.74	0.26	5.71	-4.04	0.07	1.76E-02
0.75	85	11.41	1329.65	3.27	0.02	26.38	1.57	0.29	4.78	-4.04	0.07	1.76E-02
1	75	28.02	1331.92	3.28	0.02	26.62	2.17	0.24	8.72	-4.03	0.07	1.78E-02
1	80	17.14	1329.77	3.28	0.02	26.54	1.82	0.27	6.18	-4.04	0.07	1.76E-02
1	85	13.34	1329.83	3.28	0.03	26.59	1.49	0.30	4.42	-4.04	0.07	1.76E-02

TABLE 3. Estimates from other studies reported in Table 4 of Maunder (2001) compared to the average of R_{max} estimates across all the scenarios reported in this study.

TABLA 3. Estimaciones de otros estudios, presentadas en la Tabla 4 de Maunder (2001), frente al promedio de las estimaciones de R_{max} para todos los escenarios examinados en este estudio.

Study	30	40	50	60	70
Maunder N	72	33.6	15.2	15.2	17.6
Maunder S	57.2	40.8	27.2	15.2	4.8
Bayliff1 N	32	27.2	22.4	17.6	12.8
Bayliff1 S	53.2	38.4	24	9.6	-5.2
Bayliff2 N	37.2	30.8	24.8	18.4	12
Bayliff2 S	52	38.8	25.2	11.6	-2
Joseph and Calkins	30.8	26.8	22.8	18.8	14.8
Ianelli	35.2	28.8	22.4	16	9.6
This study	26.64	26.64	26.64	26.64	26.64

APPENDIX A: ALTERNATIVE GROWTH MODELS

Other growth models could be used in the analysis that assumes a length at a given age. These were not used in the skipjack analysis but here we provide information for the Richards growth model (Schnute, 1981) used by Aires-da-Silva *et al.* (2014).

$$L_a = L_\infty \left(1 + \frac{1}{p} e^{-K(a-t_0)}\right)^{-p}$$

Where L_a is the mean length at age a, L_∞ is the asymptotic length, K is the growth coefficient, t_0 is the inflexion point, and p is the shape parameter that is related to the ratio L_a/L_∞ at the inflection point. This model represents the von Bertalanffy growth model when p=-1. t_0 can be defined based on the length at a given age (e.g., age at entry to the fishery).

$$t_0 = \frac{ln\left[p\left(\sqrt[p]{\frac{L_\infty}{L_a}} - 1\right)\right]}{K} + a$$