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EVALUATION OF INCLUDING THE COST OF REPRODUCTION IN A GROWTH MODEL FOR BIGEYE TUNA IN THE EASTERN PACIFIC OCEAN, AND THE EFFECT ON STOCK ASSESSMENT RESULTS AND MANAGEMENT ADVICE

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ABSTRACT

Growth rate estimates are more important in stock assessments than is generally considered, particularly for assessments that fit to length-composition data. It is therefore important that growth is specified correctly in stock assessment models, in order to avoid bias in estimated management quantities. Tropical tunas typically show linear growth at young ages, after which the growth rate declines rapidly. The traditional von Bertalanffy growth curve, which has been used to model tropical tuna growth, is unable to adequately represent this growth pattern. Therefore, the more flexible Richards growth curve is now often used. In addition, the reduction in growth rates makes determining the age of older individuals problematic, resulting in a lack of length-at-age and maturity-at-age data for older individuals. We evaluate two growth curves for bigeye tuna in the eastern Pacific Ocean that include a proxy for the cost of reproduction. The growth curves are fitted to both age-length data derived from daily increment counts in otoliths and growth increment data from tagging, which together cover nearly the entire range of ages. The estimates of management quantities based on these growth curves are compared to those based on the von Bertalanffy and Richards growth curves as well as those using the current assessment growth assumptions. The growth models that included the proxy for cost of reproduction did not provide a substantial improvement over the currently used Richards growth model with age-length and tag-increment data included.

Keywords: maturity; growth model; tropical tunas; otoliths; tagging; age-at-length; stock assessment

1. INTRODUCTION

Individual fish growth is generally assumed to be one of the best understood and estimated processes in fisheries dynamics. However, individual growth is poorly estimated for most species when evaluated in the context of fisheries stock assessment and management, particularly when fitting to length composition data (Maunder *et al*. 2015). Furthermore, most studies in which hard parts, such as otoliths, have been used to estimate age at length have employed methods which have not been validated, so the significance of the temporal deposition rate of increments is unknown (Campana and Nielsen 1985). Small biases in the mean length at age, or possibly the variation of length at age, can result in meaningful biases in estimated biomass or fishing mortalities (Aires da Silva *et al*. 2015; Wang *et al*. 2015), which are commonly used to determine the status of fish stocks. These biases are a manifestation of fitting to length-composition data (Maunder and Piner 2015), and are compounded by the typical over-weighting of these data (Francis 2011).

Length-composition data can be very informative about absolute abundance and fishing mortality rates (Maunder and Piner 2015). If there are many old large fish in the catch, this implies that the fishing mortality is low and the abundance high. Therefore, the estimates of fishing mortality from a stock assessment model based on observed length-composition data will depend on how many large fish are expected. With respect to growth, this typically relates to how large the fish are expected to grow or, in the typical terminology, the asymptotic length. If the asymptotic length is biased, the estimates of fishing mortality and biomass will be biased. Unfortunately, there is often little information about the asymptotic length (*i.e.* there are few old fish available for sampling), and the asymptotic length becomes an extrapolation from younger fish based on the assumed model functional form (*e.g.* the von Bertalanffy curve).It is therefore important to get the form of the growth curve correct as well as to have information from old fish. Using information from multiple sources, such as age-length, tag growth increment, and modes in length-composition data, is important (Laslett *et al.* 2002; Aires da Silva *et al.* 2015; Carvalho *et al.* submitted).

The von Bertalanffy growth curve is the most commonly-used growth curve for fish stocks. It is simple and generally represents well the growth of the commonly-sampled ages of most fish species. However, it is often not adequate for stock assessment purposes when fitting to length-composition data, as the extrapolated asymptotic length can be substantially biased. Other growth curves that consider more complex growth dynamics, such as decreases in growth rates associated with maturation and reproduction (Roff, 1992. Stearns, 1992.), might better represent growth for many fish stocks.

One additional complication for fitting models to length-composition data is that the expected number of large fish is also a function of the variation of length-at-age. Most growth studies focus on estimating mean length-at-age and do not consider the assumptions made about the variation of length-at-age or the estimates. Therefore, growth studies need to consider estimation of the variation of length-at-age, but the estimates need to be consistent with the assumptions and data used in the stock assessment model.

Estimating growth for tropical tunas is particularly problematic because, unlike temperate species that experience seasonal changes in temperature or distinct spawning periods, they typically do not exhibit annual increments in hard parts that could be used for aging. Aging often relies on counting daily increments in otoliths, and becomes problematic at older ages (4-5 years) as the increments become compressed along the counting path and difficult to resolve even at high magnifications with microscopes (Wild 1986; Schaefer and Fuller 2006). Therefore, information on the growth of old individuals from other sources (*e.g.* growth increments from tag-recapture data) needs to be combined with the otolith daily increment data to extend the ranges in lengths and ages so as to reliably estimate the growth curve and the asymptotic length (*e.g.* Aires da Silva *et al.* 2015).

We develop growth curves for bigeye tuna in the eastern Pacific Ocean (EPO), taking into consideration the cost of reproduction and fitting to both tagging and age-length data. The implications of these growth curves for stock assessment and management is evaluated by including them in the stock assessment and comparing the results with those using the current growth curve and with the von Bertalanffy and Richards models.

1.1. Application to bigeye tuna in the EPO

The growth rate of bigeye tuna in the EPO used in previous stock assessments was based on a growth model derived from counts of daily increments in 254 sagittal otoliths from fish between 30 and 149 cm long (Schaefer and Fuller 2006; Aires-da-Silva and Maunder 2011). Because of the inability to resolve the daily increments after about 4 years of age, this method is unable to provide validated age estimates for older fish, and the asymptotic length was extrapolated based on the assumed growth function from smaller fish. Recently, growth increment data from tagging (length at release, length at recapture, and time at liberty) have been combined with the age-length data from otolith counts to provide information on growth from throughout the length range in the fishery (Aires da Silva *et al* 2015). The Richards growth model, which has an additional parameter making it more flexible, is now commonly used (*e.g.* Aires-da-Silva and Maunder 2011). In addition, information on the variation of length-at-age from growth studies has generally not been used in the assessments.

It has been suggested that the growth of topical tunas slows as they mature, but this has not been demonstrated by the studies on age and growth and reproductive biology of yellowfin or bigeye from the EPO (Wild 1986; Schaefer 1998; Schaefer *et al.* 2005; Schaefer and Fuller 2006). Since tropical tunas are highly fecund, and spawn batches of eggs at close to a daily frequency throughout the year after reaching maturity, provided the water temperature is above about 24°C (Schaefer 2001), it is reasonable to assume that growth may be impacted by reproductive costs. It is also possible that growth differs between males and females, since their maturity schedules and reproductive energetic costs differ (Schaefer 2001). However, for bigeye up to about 4 years of age there was no significant difference in the growth rates between males and females (Schaefer and Fuller 2006).

Minte-Vera *et al.* (submitted) proposed two growth models that take reproductive costs into consideration. One model is based on first principles and reduces growth based on the proportion of individuals mature (or equivalently, the probability of being mature) at a given length. The second model treats the asymptotic length parameter as a function of the proportion of individuals mature. The reason for choosing the asymptotic length over the growth rate (as used by Laslett *et al.* 2002) may be unintuitive, but makes sense based on first principles (see Minte-Vera *et al.* submitted). Both models rely on information about maturity-at-age (or length as described below) and assume a logistic curve for the relationship. Our study differs from Minte-Vera *et al.* (submitted) in that it applies the models to a different species (bigeye tuna), uses both otolith age-length data and tag growth-increment data, uses maturity-at-length rather than maturity-at-age data, and evaluates the management consequences of the different growth curves.

Due to the inability to age older individuals from hard parts, it is desirable to use both the age-length data and the tag growth increment data, if available, to estimate the parameters of growth curves for tropical tunas (Aires da Silva *et al.* 2015). The appropriate approach to combining these two data sets is that developed by Lasslet *et al.* (2002), which treats the two data sets in a consistent statistical framework. This requires treating the age-at-release from the tagging data as a random effect, and involves high-order integrals using specialized software.

Variation of length-at-age in a stock assessment model is different than variation of length-at-age in growth models. In a stock assessment model, the variation of length-at-age is used to predict the catch-at-length that is used to fit to the observed catch-at-length. This catch-at-length distribution is the sum of catch-at-length over a specified time period (quarterly in our applications), and is influenced by (unmodeled) temporal variations in growth and selectivity. Therefore, the variation of length-at-age in a stock assessment model differs from (and is probably larger than) that observed in the age-length data (in daily increment data, age is expressed in days) or growth-increment data for a point in time. Therefore, it may not be appropriate to use estimates of the variation of length-at-age from the growth analysis in the stock assessment, but rather estimate the parameters representing the variation of length-at-age inside the stock assessment. Zhu *et al.* (submitted) demonstrated, using simulation analysis, that under conditions close to ideal, estimation of the variation of length-at-age parameters inside the stock assessment model is feasible, and that the values of those parameters are less critical than those of the parameters of the growth model with respect to the estimation of common management quantities.

We fitted the two growth models that include maturity schedule information and the von Bertalanffy and Richards growth models) to age-length and tag growth increment data for bigeye tuna in the EPO. The suitability of these models is compared, using AIC and a qualitative evaluation of the realism of the parameter estimates and residuals. These growth curves are then used in the current stock assessment model (Aires-da-

Silva and Maunder 2014), and the estimates of relevant management quantities compared.

2. MATERIALS AND METHODS

2.1. Data sources

2.1.1. Age-at-length data

Age-at-length data are obtained from direct readings of daily increments in the sagittal otoliths of bigeye tuna from the EPO. A detailed description of the data, methodology, and results is found in Schaefer and Fuller (2006). Aires-da-Silva *et al.* (2015) used those age estimates in their analysis of bigeye tuna growth. These data cover fish up to 4 years of age (about 150 cm), or about one-quarter of the apparent longevity of bigeye, based on an estimated maximum age of at least 15 years from annual age estimates and from information on the tagged fish that were at liberty for the longest periods (Aires-da-Silva *et al.* 2015).

2.1.2. Tagging growth-increment data

Length-increment data are from from tagging experiments on bigeye tuna in the EPO. A detailed description of the data sources is found in Schaefer and Fuller (2006). The data were updated to include additional tagging growth-increment observations collected in recent years. The tagging growth-increment data are dominated by bigeye less than 150 cm, although some observations from larger bigeye up to about 190 cm fork length (FL)are also available, due to the recapture of some individuals that were at liberty for up to 8 years. Aires-da-Silva *et al.* (2015) used a similar data set for their analysis of bigeye tuna. The release and recapture lengths are assumed to be measured without error.

2.1.3. Maturity-at-length data

Due to the difficulty of aging older tropical tunas, reliable maturity-at-age data are not available, and inferences about maturity have to be made based on maturity-at-length data. Data on proportion mature, batch fecundity, and frequency of spawning at length are available for yellowfin tuna (Schaefer 1998). All three of these contribute to the cost of reproduction. Therefore, their product should be used as a proxy for the relative cost of reproduction used in the growth models. Other factors (*e.g.* behavior) may also impact the costs of reproduction, but data on these are generally not available. Information on the maturity-at-length is available for female bigeye tuna only (Schaefer *et al.* 2005), and therefore the relative cost of reproduction is assumed to be equal to the proportion mature at age times the cube of mean length–at-age. The cube of length is a commonly-used proxy for weight, and weight is a commonly used as a proxy for relative egg production.

2.2. Analytical methods

2.2.1. Growth models

2.2.1.a Von Bertalanffy

$$L_a = L_\infty(1 - \exp(-K(a - t_0))) \qquad (1)$$

2.2.1.b Richards

$$L_a = L_\infty\left(1 + \frac{1}{p}\exp(-K(a - t_0))\right)^{-p} \qquad (2)$$

2.2.1.c Von Bertalanffy Log-Linf

Equation (1) where

$$L_\infty(a) = L_{\infty,1} + \varphi(a)\left(L_{\infty,2} - L_{\infty,1}\right) \qquad (3)$$

where $\varphi(a)$ is the proportion mature at age a (see equation 9)

2.2.1.d Cost of reproduction (CoR) Model

Growth is modelled by explicitly including a term that takes into account the cost of reproduction in the growth increment; this equation represents the average growth of a population, rather than the individual growth, and is based on the differential equation:

$$\frac{dL}{da} = \alpha - \beta L \quad - \gamma \tau_a \qquad (4)$$

where

L is length

a is age

τ_a is the relative cost of reproduction

α, β, and γ are parameters.

The relative cost of reproduction may be a function of several factors, including fecundity and frequency of spawning. We assume that these factors that influence the relative cost of reproduction, in combination with the proportion mature at age, represent the average (over all individuals in the population) relative (the oldest individuals are generally assumed to have the highest costs) age-specific energetic costs associated with reproduction, and not the absolute cost of reproduction. Costs related to behavior are ignored, since there is generally no information available for them, but the model implies that they are either constant, proportional to length, or proportional to the measure of reproductive costs from the other factors. This relative value is then scaled to an absolute value by an estimated parameter. In data-limited cases it might simply be assumed that the relative cost of reproduction is a function of the proportion mature at age and individual weight as represented by length cubed.

$$\tau_a = \varphi(a)\gamma L^3 \qquad (5)$$

where

$\varphi(a)$ is the proportion of fish mature at each age a

We approximated the differential equation by a difference equation with small time steps (*e.g.* days), so that the growth increment is:

$$G_a = \alpha - \beta L_{a-1} - \varphi(a)\gamma L_{a-1}^3 \qquad (6)$$

The length at age a is:

$$L_a = L_{a-1} + G_a \qquad (7)$$

The model is started from L_0, the length at age a_0, which is also a parameter. Age a_0 can be chosen to be an age close to the minimum age in the data, well before the onset of maturity; we chose a_0 to be equal to age zero for convenience. We also reparameterized the model in terms of the length when growth is zero (the asymptotic length in certain formulations of the model), which is conventionally termed L_∞. This parameterization makes choosing initial parameter values and bounds constraining the possible parameter values more intuitive.

$$\alpha = \beta L_\infty + \varphi(a)\gamma L_\infty^3 \qquad (8)$$

The growth function was also reparameterized so that $\beta = \exp(\ln\_\beta)$, $\gamma = \exp(\ln\_\gamma)$ $L_\infty = \exp(\ln\_L_\infty)$ and $L_0 = \exp(\ln\_L_0)$

The proportion mature-at-age $\varphi(a)$ is modelled using a logistic function:

$$\varphi(a) = \frac{1}{1+e^{\frac{-\ln(19)*(a-t_{50})}{(t_{95}-t_{50})}}} \qquad (9)$$

where t_{50} is the age at which 50% of the individuals are mature, and t_{95} the age at which 95% of the individuals are mature, which is parameterized as $t_{95} = t_{50} + \exp(\ln\_\delta_{t_{95}})$.

The maturity-growth model depends on six parameters: $\ln\_\beta$, $\ln\_\gamma$, $\ln\_L_\infty$, $\ln\_L_0$, t_{50}, and $\ln\_\delta_{t_{95}}$.

2.2.2. Model fitting

2.2.2.a Length-at-age likelihood

The observed length of fish *i* at age *t* was assumed to be:

$$L_{obs,t,i} = \widehat{L_t} + e_i \qquad (10)$$

where $\widehat{L_t}$ is the predicted average length-at-age *t*, and e_i is a normally-distributed random variable $e_i \sim N(0, \sigma_i^2)$. The likelihood is

$$\mathcal{L}_i[L|a,\theta] = N\left((L_i - \hat{L}_{a_i}), \sigma_{a_i}^2\right) \qquad (11)$$

Where θ is the parameters of the growth model.

The standard deviation of the error, which is assumed to be process error (*i.e.* the variation in the lengths of individuals of a given age in the population, and not the observation (*e.g.* measurement error)), was modeled as proportional to the average length-at-age:

$$\sigma_i = \beta_\sigma L_t \qquad (12)$$

2.2.2.b Tagging data likelihood

To ensure that the likelihood for the tag growth-increment data is consistent with the age-length data, the likelihood is formulated in terms of length given age. However, age is not observed, and is therefore treated as an unknown random variable, and the likelihood is calculated by integrating over age:

$$\mathcal{L}_{Ltag,Lrec,\delta} = \int p(a) * N\left((L_{tag} - \hat{L}_a), \sigma_a^2\right) * N\left((L_{rec} - \hat{L}_{a+\delta}), \sigma_{a+\delta}^2\right) da \qquad (13)$$

where

a is age in days

A is the maximum age in days

p(a) is the prior distribution for age at release (uniform(1,A) in our application)

L_{tag} is the length at tagging

L_{rec} is the length at recovery

δ is the time at liberty in days

2.2.2.c Maturity-at-length likelihood

We assume that maturity is a function of age, but we have only maturity-at-length data. Therefore, the maturity-at-length likelihood becomes somewhat complicated. Similar to the tag growth-increment data, we integrate over age and fit to both the length data and the maturity data.

$$\mathcal{L}(mat|l) = \int P(mat|a)p(a|l)da \qquad (14)$$

$$p(a|l) = \frac{N((L - \hat{L}_a), \sigma_a^2)p(a)}{p(l)} \qquad (15)$$

$$p(l) = \int p(l|a)p(a)da \text{ is a constant} \qquad (16)$$

The likelihood for the maturity-at-length data is therefore:

$$\mathcal{L}_{mat} = \int p(a) * P(mat|a) * N\big((L - \hat{L}_a), \sigma_a^2\big) da \quad (17)$$

where

a is age in days

A is the maximum age in days

p(a) is the prior distribution for each age (uniform(1,A) in our application)

L is the observed length

$P(mat|a)$ is the probability of being mature at age, $P(mat|a) \sim$ Bernoulli (φ), where φ comes from the equation for maturity-at-age (Equation 6).

2.2.3. Parameter estimation

The reproductive cost growth model of Minte-Vera *et al.* (2015) is implemented by modelling the growth on a small time increment (*e.g.* day) using a recursive approach, which is not conducive to random effect implementation in AD Model Builder (Fournier *et al.* 2012) or Template Model Builder (Kristensen *et al.* 2014), which are the preferred tools for non-Bayesian implementation of random-effect models involving high dimensional integrals. We therefore use a brute force approach to integrate across age, by constructing the objective function that sums the likelihood evaluated at a range of ages on a daily basis.

$$\mathcal{L}_{Ltag,Lrec,\delta} = \sum_{a=1}^{A} p(a) * N\big((L_{tag} - \hat{L}_a), \sigma_a^2\big) * N\big((L_{rec} - \hat{L}_{a+\delta}), \sigma_{a+\delta}^2\big) \quad (18)$$

$$\mathcal{L}_{mat} = \sum_{a=1}^{A} p(a) * P(mat|a) * N\big((L - \hat{L}_a), \sigma_a^2\big) \quad (19)$$

A further complication arises because, when the predicted maturity is zero, the Bernoulli probability is equal to zero for mature individuals, thus eliminating the contribution of the length component of the likelihood. Therefore, the model prefers to estimate a high age at maturity. To avoid this bias, we use a two-step iterative process.

1. Estimate the growth parameters (including for the variation of length-at-age) conditioned on fixed values of the maturity parameters and using only the age-length and tag growth-increment likelihood components.
2. Estimate the maturity parameters conditioned on fixed values of the growth parameters and using only the maturity likelihood component.

The parameter estimates from step 1 are used in step 2, and those from step 2 are used in step 1. Good estimates of both the growth and maturity parameter values should be obtained before starting step 1 for the first time. The steps are iterated until the parameter values no longer change.

3. RESULTS

The model fits to the data are evaluated by using AIC, which takes into consideration the different number of parameters among the four models. The four models are not fitted to the same data sets, so the overall likelihood is not comparable, and the Von Bertalanffy and Richards models are not fitted to the maturity data. However, the models can be compared from the fits to the combined age-length and tag growth-increment data, although the two models that include the cost of reproduction are disadvantaged because the fit to these two data sets is traded off with the fit to the maturity data. The CoR model has a lower AIC than the log-L_{inf} model, and the Richards model has a lower AIC than the von Bertalanffy model (Table 1). Despite the disadvantage of fitting to the maturity data, the CoR model has a lower AIC than the other models if the AIC is based only on the age-length and the tag growth-increment data. The CoR model fits the tagging growth-increment data and the maturity data best (lowest negative log-likelihood), and the von Bertalanffy model fits the age-length data best.

The growth curves are all similar for ages less than about 4 years and fit the data similarly, however the log-L_{inf} and von Bertalanffy models estimate higher asymptotic lengths and are a worse fit to the greater lengths-at-recovery (Figure 1). The influence of the cost of reproduction in the CoR model occurs only for the last few ages in the age-length data (Figure 2).

The estimated spawning biomass ratio (SBR: the spawning biomass divided by the virgin spawning biomass) using the CoR and Richard growth models is similar to that of the current assessment, which uses the Richards growth model from Aires da Silva *et al.* (2015) (Figure 3). The assessments using the log-L_{inf} and von Bertalanffy growth models estimate higher depletion levels (lower SBR), presumably because they have higher asymptotic lengths, which interact with the length-composition data.

4. DISCUSSION

Growth rate is an essential parameter in stock assessment models, particularly those that are fitted to length-composition data. Length-composition data have generally been given too much weight in stock assessment models (Francis 2011), and moderate model misspecification can result in substantial bias in estimated management quantities (Maunder and Piner 2015; Lee *et al.* 2014). It is therefore important that growth is correctly specified in stock assessment models. This is particularly true for tropical tuna assessments, which lack the luxury of survey-based indices of abundance and regular catch-at-age data, as well as catch-induced contrast in indices of abundance, and are therefore largely dependent on length-composition data to provide information about absolute abundance and fishing mortality rates.

Growth models for tropical tunas have been greatly improved by combining age-length and tag growth-increment data into a single analysis (Laslet *et. al.* 2002; Aires da Silva *et al.* 2015). We have further improved these models over the standard von Bertalanffy model by including the cost of reproduction, as represented by the proportion mature and cube-of-length proxy, in the bigeye tuna growth model (Minte-Vera *et al.* submitted). However, the Richards growth curve provides a similar fit to the data and is less complicated to implement. Both of these developments have reduced the impact of extrapolating the size of old individuals from information about intermediate-aged individuals, reducing the bias caused by fitting to length-composition data. We believe that this will result in major improvements in the reliability of stock assessment results and estimated management quantities for tropical tunas compared to using the von Bertalanffy growth curve fitted to age-length data only. Further developments could be made in growth modelling, such as more detailed modelling of energy expenditure, but it is not clear whether the available data will support such detailed modelling. A major improvement would be to include sex-specific information, since the cost of reproduction in tunas differs between males and females (Schaefer 2001). In our application we used the female maturity schedule for bigeye from the EPO, but it should be noted that the maturity schedule for males is expected to be quite different, with males reaching maturity at smaller sizes and younger ages, as was found for yellowfin in the EPO (Schaefer 1998).

We assumed in our analysis that maturity is a function of age, which complicated the calculations because we had only maturity-at-length data. Assuming that maturity was a function of length may have simplified the computations, but it is not clear which of these assumptions is correct and whether it would make a difference.

It is well known that the particular parameterization of a growth model can influence the ability to estimate the model's parameters. We implemented some forms of reparameterization of the growth models, but these were based on intuition and convenience and are not necessarily optimal. Optimization of the objective function was difficult, and additional reparameterization might improve estimation performance (*e.g.* Schnute 1981). The maturity likelihood was problematic to implement, and further refinement of that component of the model may be beneficial.

There is a general lack of understanding about the importance of growth, as well as maturity, in stock assessment models, especially when estimating such values as spawning biomass. It is commonly thought that a reasonable approximation of the mean length-at-age of the fish of the most common age is adequate, but this is not the case for stock assessment modelling, particularly when fitting to length-composition data. We encourage a more thorough evaluation of the data collection for growth estimation and consequent analysis of the data, so that growth analysis provides the information required for contemporary stock assessment models. For example, Piner *et al.* (submitted) show that the sampling design (*e.g.* sampling by length group), which is not taken into consideration in this modelling approach, can also negatively bias the estimates of the variation of length-at-age. Francis *et al.* (submitted) explain how ignoring the correlation between the length at release and the length at recapture of tagged fish can bias the estimates when using the methods designed to treat the age-length and tagging growth-increment data more consistently. Schaefer and Fuller (2006) also reported that there is a shrinkage error introduced by death, freezing, and thawing of tunas, which should be accounted for by adjusting the recapture lengths of tagged tunas and thus making data input into growth rate models using age-length and tag-increment data comparable. Shrinkage in the lengths of tunas following capture and death has routinely been ignored in studies of growth, and in the length- composition data used in stock assessments, but should be considered in future evaluations of such data sets.

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TABLE 1. Negative log likelihoods for the four models tested. The von Bertanlanffy and Richards growth curves do not include the maturity data component. The component likelihoods and AIC are given as differences from the model with the lowest value. The AIC difference is calculated separately for the von Bertanlanffy and Richards growth curves. *these quantities cannot be compared with the CoR and logLinf models.

	CoR	**log-L_{inf}**	**VB**	**Richards**
f	-13820.40	-13782.96	-6902.87*	-6918.29*
age	4.33	0.58	0.00	3.60
tag	0.00	25.81	30.36	11.34
mat	0.00	15.38		
age+tag	0.00	22.06	26.03	10.61
pars	7	7	4	5
AIC	0.00	74.89	28.84*	0.00*
AIC age+tag	0.00	44.12	46.06	17.23

TABLE 2. Parameter estimates for the four models.

	CoR	**log-L_{inf}**	**VB**	**Richards**
L_{inf}	199	236	288	212
K		0.00058	0.00044	0.00100
t_0		-115	-131	396
p				-2.48
L_{inf2}		254		
β	0.00019			
γ	0.00890			
L_0	19			
A50	1191	1315		
A95	1460	1711		
sd	0.050	0.053	0.053	0.051

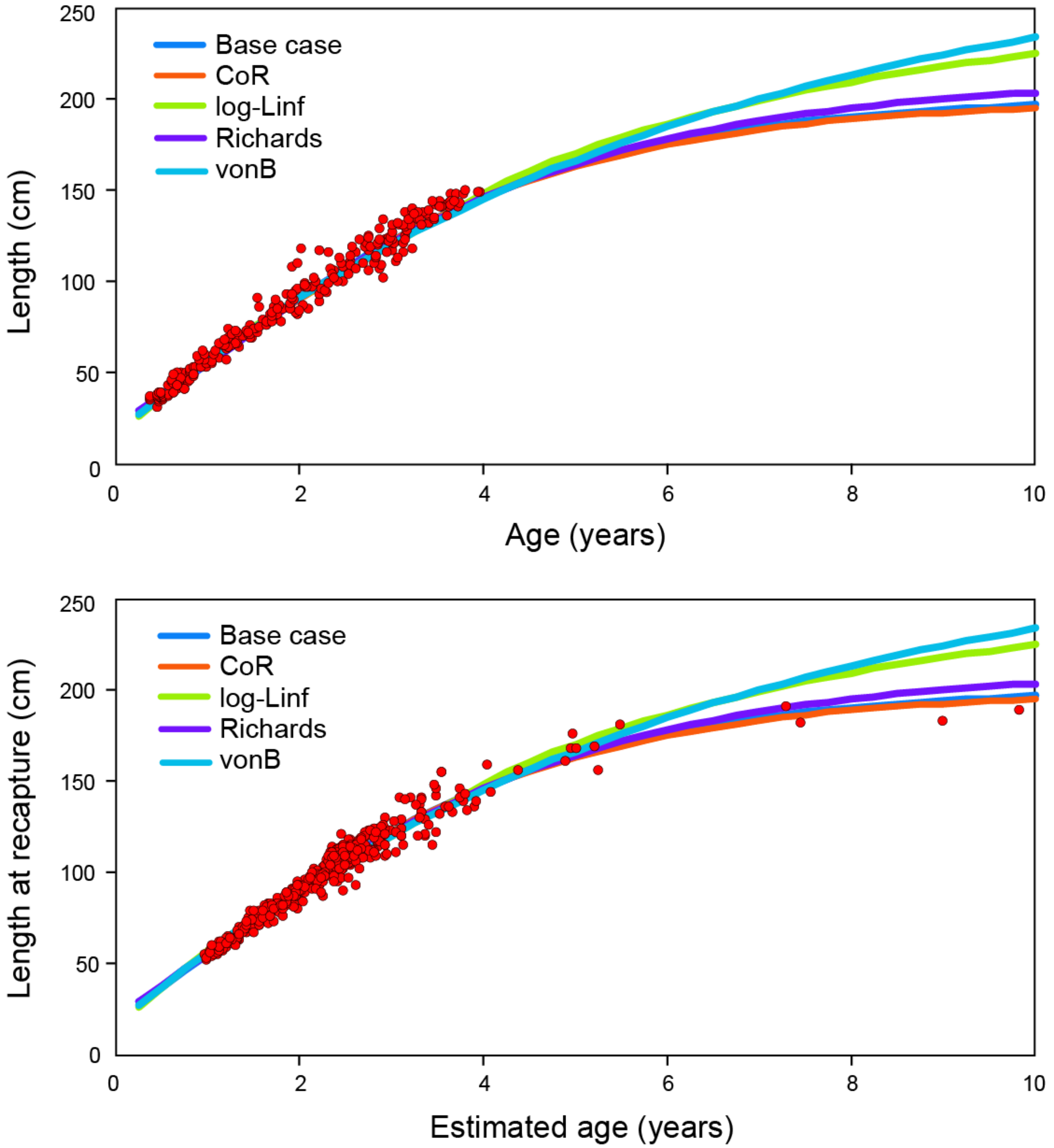

FIGURE 1. Fit to the bigeye tuna age-length data (upper panel) and to the length at recapture based on the estimated age (lower panel). The estimated age at recapture is based on predicting the age at release from the growth curve estimated using the CoR growth model.

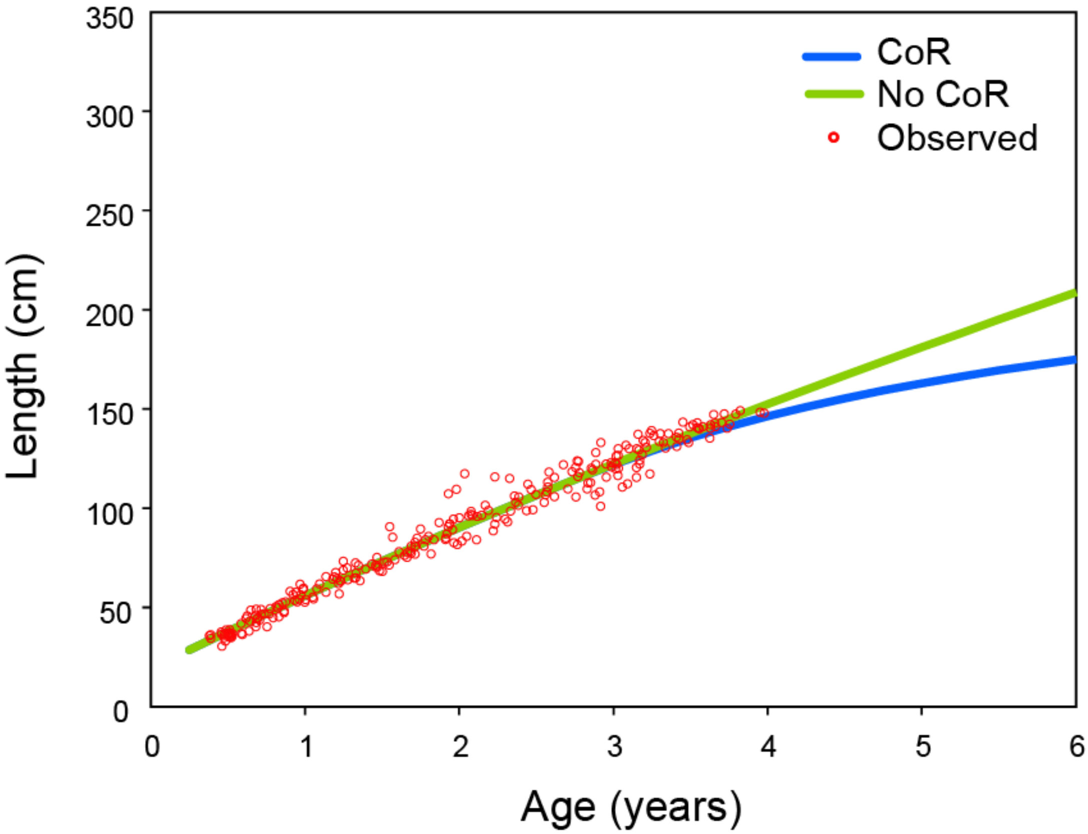

FIGURE 2. Fit to the bigeye tuna age-length data of the CoR growth model and the CoR growth model with the parameters fixed at their best estimates, but with the CoR component removed (No CoR).

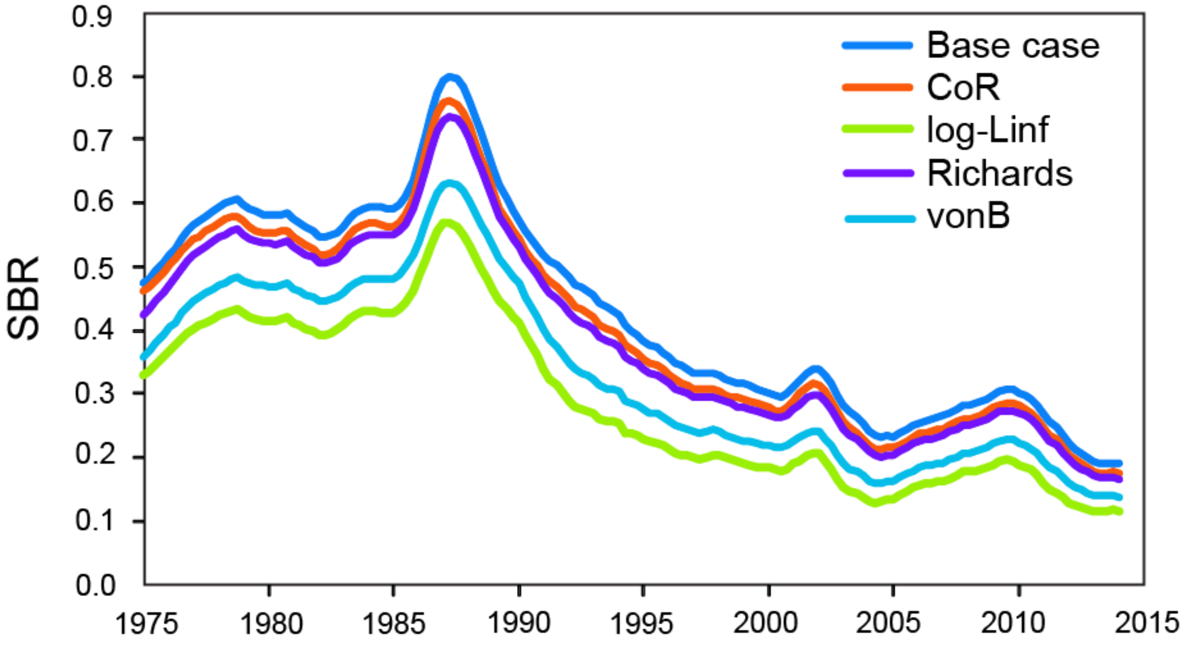

FIGURE 3. Estimates of bigeye tuna spawning biomass ratio (SBR: spawning biomass divided by virgin spawning biomass) using the different growth curves.