INTER-AMERICAN TROPICAL TUNA COMMISSION

SCIENTIFIC ADVISORY COMMITTEE

EIGHTH MEETING

La Jolla, California (USA)
8-12 May 2017

DOCUMENT SAC-08-09b

A GROWTH CURVE FOR SPECIES SHOWING A NEAR CESSATION IN GROWTH: APPLICATION TO BIGEYE TUNA (*THUNNUS OBESUS*) IN THE EASTERN PACIFIC OCEAN

Mark N. Maunder, Richard B. Deriso, Kurt M. Schaefer, Daniel W. Fuller, Alexandre M. Aires-da-Silva, Carolina V. Minte-Vera, Steven E. Campana

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ABSTRACT

We present a growth curve designed for species, such as some tropical tunas, that have an apparent linear relationship between length and age, followed by a marked reduction of growth after the onset of sexual maturity. The growth curve simply assumes linear growth for the youngest individuals and then uses a logistic function to model how the growth rate falls to zero at greater ages. One characteristic of the model is that, as t -> 0, the model converges to a linear regression. The range of ages for which a linear regression adequately represents the mean length at age depends on when the logistic function becomes influential. A beneficial characteristic of this model is that, unlike other growth models, a preponderance of younger fish does not overwhelm the information from older fish, which biases the estimates of mean length at age for older fish. We apply the growth curve to bigeye tuna (*Thunnus obesus*) data from the eastern Pacific Ocean (EPO), obtained from otolith daily increment counts and tagging experiments, and compare the results with those from the von Bertalanffy and Richards growth curves. The growth cessation curve fits the EPO bigeye tuna data better than do the von Bertalanffy and Richards growth curves. These results support the use of the growth cessation curve for bigeye tuna in the EPO, and possibly other tuna stocks.

1. INTRODUCTION

Individual growth is a fundamental process used in describing the dynamics of populations, and is important in the development of management advice for population management (Francis 2016; Maunder *et al*. 2016; Punt *et al*. 2016). For example, maximum sustainable yield in fisheries management is a tradeoff between increases due to recruitment and growth and losses due to fishing and natural mortality. In some applications, the average growth rate of the individuals of the most abundant ages in the catch is adequate. However, in other cases a more accurate representation of growth and how it changes with age is needed. For example, when fisheries stock assessment models are fitted to length-composition data, the mean size of the oldest individuals can have a large influence on estimates of absolute abundance (Maunder and Piner 2015; Zhu *et al*. 2016). This is important for many tropical tuna stocks because aging individuals is difficult and time-consuming, and many stock assessments are fitted to length-composition data (Kolody *et al*. 2016; *e.g.* Fournier *et al*. 1998; Maunder and Watters 2003).

Some tropical tuna stocks appear to have growth characterized by a linear relationship between length and age followed by a near cessation in growth (*e.g.* Aires da Silva *et al*. 2015; Kolody *et al*. 2016), ignoring growth for early ages. This relationship is difficult to represent with the growth curves typically used in fisheries stock assessment (*e.g.* the von Bertalanffy growth curve). Even the more flexible Richards growth curve tends to overestimate the average lengths of the oldest individuals because it cannot bend over quickly enough without distorting the growth of young fish (*e.g.* Aires da Silva *et al*. 2015). As mentioned above, the mean length of the oldest individuals can have a substantial influence on estimates of absolute biomass when stock assessment models are fitted to length-composition data, which is typical for tropical tuna stock assessments. Therefore, it is important to adequately represent growth in stock assessments of tropical tunas, so an alternative growth curve is needed.

Here we present a growth curve designed for species, such as tropical tunas, which have a linear relationship between length and age followed by a near cessation in growth, typically after the onset of sexual maturity. The growth curve is only an approximation, because it is based on cessation in growth and virtually all fish species are characterized by indeterminate growth (Sebens 1987). It is essentially the same as the logistic hockey stick stock-recruitment curve of Barrowman and Myers (2000). We then apply it to data for bigeye tuna (*Thunnus obesus*) in the eastern Pacific Ocean (EPO), and compare the results with those obtained using von Bertalanffy and Richards growth curves.

2. MATERIALS AND METHODS

2.1. Growth cessation curve

The four-parameter growth cessation curve simply assumes linear growth for the youngest individuals and then uses a logistic function to model how the growth rate falls to zero at greater ages. Since growth at very young ages is often different from growth at older ages, it is prudent to have a parameter to simply adjust the mean length at age zero using a parameter (L_0) rather than further complicate the model.

$$L_t = L_0 + \int_0^t \frac{r_{max}}{1+exp[k(x-t_{50})]}dx \qquad \text{e.q. 1}$$

The solution to the integral equation is

$$L_t = L_0 + r_{max}\left[\frac{ln\left(e^{-kt_{50}}+1\right)-ln\left(e^{k(t-t_{50})}+1\right)}{k}+t\right] \qquad \text{e.q. 2}$$

where:

t is age

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;

t_{50} is the age of the logistic functions midpoint.

The constant of integration is subsumed within L_0.

One characteristic of the model is that, as t -> 0, the model converges on a linear regression with slope r_{max} and intercept L_0. The range of ages for which a linear regression adequately represents the mean length at age will depend on when the curve bends over (related to t_{50}) and how rapidly it bends over (k). A beneficial characteristic of this model is that, unlike other growth models, a preponderance of younger fish does not overwhelm the information from older fish, which biases the estimates of mean length at age for older fish. In addition, information from young fish can be used to estimate r_{max} and L_0, using a linear regression, while the other parameters can be estimated by fixing r_{max} and L_0 when fitting to data for older fish.

2.2. Parameter estimation

The contemporary approach to estimate growth curves is to use as much available information as possible to improve the estimates, particularly if different data sets provide information on different ages (*e.g.* Eveson *et al*. 2004). For example, this involves fitting the growth model simultaneously to age-length data from otoliths and length-increment data from tagging (Laslett *et al*. 2002; Eveson *et al*. 2004; Aires da Silva *et al*. 2015; Francis *et al*. 2016). Here we use a method similar to that of Aires da Silva *et al*. (2015). However, rather than treating age as a random effect, we simply estimate the age of each tagged individual as a separate parameter. The reason for this is threefold: 1) to avoid complications and convergence issues with the implementation of random effects in this illustration; 2) to avoid having to assume a distribution for the ages, which is unknown; and 3) all the tag release lengths were within the range of the otolith age-length data, so the age at release should be well estimated. The model is fitted to the observed lengths using a normal distribution based likelihood function with a constant coefficient of variation for both the age-length data and the tagging data. The von Bertalanffy and Richards growth curves are also fitted to the data for comparative purposes. To evaluate whether the Richards growth curve can adequately represent the near-cessation in growth, the Richards growth curve is also fitted under three additional scenarios:

1) The likelihood function for the tagged fish recaptured at 180 cm or greater multiplied by 100;
2) The age-length likelihood down-weighted by a factor of 0.01;
3) The age-length likelihood down-weighted by a factor of 0.1.

2.3. Data

The growth curve is illustrated using data from bigeye tuna in the EPO similar to those used by Aires da Silva *et al*. (2015). The age-at-length data are from direct readings of otolith daily increments, which cover mostly young bigeye up to four years of age (<150 cm). Length-increment data from tagging experiments are also dominated by young bigeye less than 150 cm, but some observations from larger bigeye are also available. A detailed description of these data sources is found in Schaefer and Fuller (2006). The tag-recapture data were updated with additional tag-recapture observations collected in recent years.

3. RESULTS AND DISCUSSION

The growth cessation model (See Table 1 for parameter estimates) fits well to both the otolith age-length data and the growth-increment data from tagging for bigeye tuna in the EPO (Figure 1). It fits the data better than the von Bertalanffy and Richards growth curves (Table 2) by 100.6 and 15.6 log-likelihood units, respectively, which is a better fit under all standard statistical tests. Neither the von Bertalanffy nor the Richards growth curves is able to bend over quickly enough, and they both overestimate the average recapture length of the oldest individuals in the tagging data, as seen in the residuals (Figure 2). The growth cessation model fits the tagging data best, and the von Bertalanffy model fits the age-length data best. The growth cessation model fits both the age-length data and the tagging data better than the Richards model. Putting more weight on the tagging data with recaptures greater or equal to 180 cm, or down-weighting the age-length data, allows the Richards growth curve to bend over (Figures 3 and 4) and fit the tagging data better, but at the expense of a worse fit to the age-length data (Table 1), resulting in a strong residual pattern (Figure 5).

It is important to use the best possible growth estimates in fisheries stock assessments, particularly if they are fitted to length-composition data. The expected size of the oldest individuals relative to the largest fish observed in the data influences the estimates of the exploitation rates and absolute abundance levels (Maunder and Piner 2015). The model must increase fishing mortality to avoid allowing fish to live longer and grow larger than the fish observed in the data. This is particularly problematic for tropical tuna stock assessments that rely heavily on length-composition data. The growth cessation model fits the EPO bigeye tuna data better than do the von Bertalanffy and Richards growth curves. These results support the use of the growth cessation curve over the currently-used Richards growth model for the assessment of bigeye tuna in the EPO. If the Richards curve is used, then the model estimated by putting more weight on the tagging data with recaptures greater or equal to 180 cm appears to most closely resemble the growth cessation model, particularly for the oldest individuals (Figure 3).

Virtually all fish species are characterized by indeterminate growth, whereby growth persists throughout the entire lifetime without the genetically-imposed, predetermined limits characteristic of mammals (Sebens 1987). Growth rate reductions become increasingly evident after the onset of sexual maturity (Haino and Kaitala 1999), due to both the energetic (physiological) costs of sexual maturity and limitations in food availability. In many species, the combination of cumulative mortality rate and variability in food supply results in an average growth trajectory of individuals in the population that never appears to completely flatten. In many long-lived fish species, however, growth curves that flatten out to the point where growth is almost undetectable are common, due to the increased energetic costs of a larger body size in a habitat with a limited or stable food supply (Karkach 2006). This is particularly evident in long-lived deep-sea fishes such as *Pristipimoides filamentosus* (Andrews *et al*. 2012) and *Sebastes* spp (Campana *et al*. 2016), but has also been observed in long-lived species in other habitats (*e.g. Cheilodactylus spectabilis* (Ewing *et al*. 2007). Therefore, the growth-cessation model may be applicable to a wide range of species and stocks.

The growth-cessation model can be viewed as a simplification of Minte-Vera *et al*.'s (2016) cost of reproduction (COR) model. In the COR model, the parameters of the logistic function are those that represent the maturity schedule. The COR model has two additional parameters, one of which describes the loss in energy due to reproduction, and therefore individuals can continue growing after they reach maturity. It is not clear if the near cessation or slowing of growth is related to maturity in tropical tunas, which is represented by the logistic function in the COR model, and estimating the parameters of the logistic function might be desirable. Therefore, the additional parameters of the COR model, and the fact that the formula for growth uses an iterative procedure over age, makes estimation problematic compared to the fewer parameters of the growth-cessation model. The parameters t_{50} and k of the growth-cessation model could be fixed based on the maturity ogive, as suggested by Minte-Vera *et al*. (2016) for the cost of reproduction (COR) model. Laslett *et al*. (2002) proposed the von Bertalanffy growth curve with logistic growth rate as a special case of Wang's (1998) generalization of the von Bertalanffy growth curve to model the apparent two-stage growth of southern bluefin tuna. However, their model has more parameters, and may be less able to model the linear growth for young individuals. Lopez *et al*. (2000) showed that the generalized Michaelis-Menten equation, with its variable inflection point, was able to adequately describe sigmoidal growth in a wide variety of animals.

Despite the growth-cessation model being composed of two completely different growth patterns (linear growth and cessation in growth), the logistic transition from linear growth to cessation in growth allows for the smooth curvature in length-at-age similar to the von Bertalanffy growth curve. An additional parameter could be added to equation 1 to allow growth to continue at a low rate for old fish, but estimation of this additional parameter is likely to be problematic, and the growth curve would not continue to bend over towards an asymptote like other commonly-used growth curves (see Minte-Vera *et al*. (2016) for a review of other two-stage growth models). The few data that are available for EPO bigeye tuna indicate that growth effectively stops, or nearly stops, at old ages, supporting the use of the growth-cessation model, but more data are needed to confirm the appropriateness of the model. Other tuna stocks show similar linear growth followed by near cessation (Kolody *et al*. 2016), suggesting general applicability of the model.

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TABLE 1. Parameter estimates and standard errors for the growth cessation model fitted to data for bigeye tuna in the eastern Pacific Ocean.

L_0	18.85	0.42
r_{max}	37.24	0.79
K	0.89	0.08
t_{50}	4.57	0.09
CV	0.038	0.001

TABLE 2. Likelihood values and derived quantities from the fit of the models to the data. The likelihoods presented for the Richards model scenarios with different data weightings are based on the likelihood without weighting included.

		Growth cessation	Von Bertalanffy	Richards	Richards up-weight tag recaptures ≥180 cm	Richards down-weight age-length data (0.01)	Richards down-weight age-length data (0. 1)
Number of parameters		466	465	466	466	466	466
Negative log likelihood	Age	617.8	610.6	620.1	828.2	1399.8	969.7
	Tag	1356.2	1464.0	1369.5	1309.8	1240.7	1260.2
	Total	1974.1	2074.6	1989.7	2138.0	2640.5	2229.8
Difference in negative log likelihood from the minimum	Age	7.2	0.0	9.5	217.6	789.2	359.0
	Tag	115.5	223.3	128.8	69.0	0.0	19.4
	Total	0.0	100.6	15.6	163.9	666.4	255.8
Length at age 10		189.4	214.6	195.8	191.0	188.6	190.9
sd at age 10		7.3	9.0	7.6	5.8	5.2	5.7
75^{th} percentile		194.3	220.7	201.0	194.9	192.1	194.7

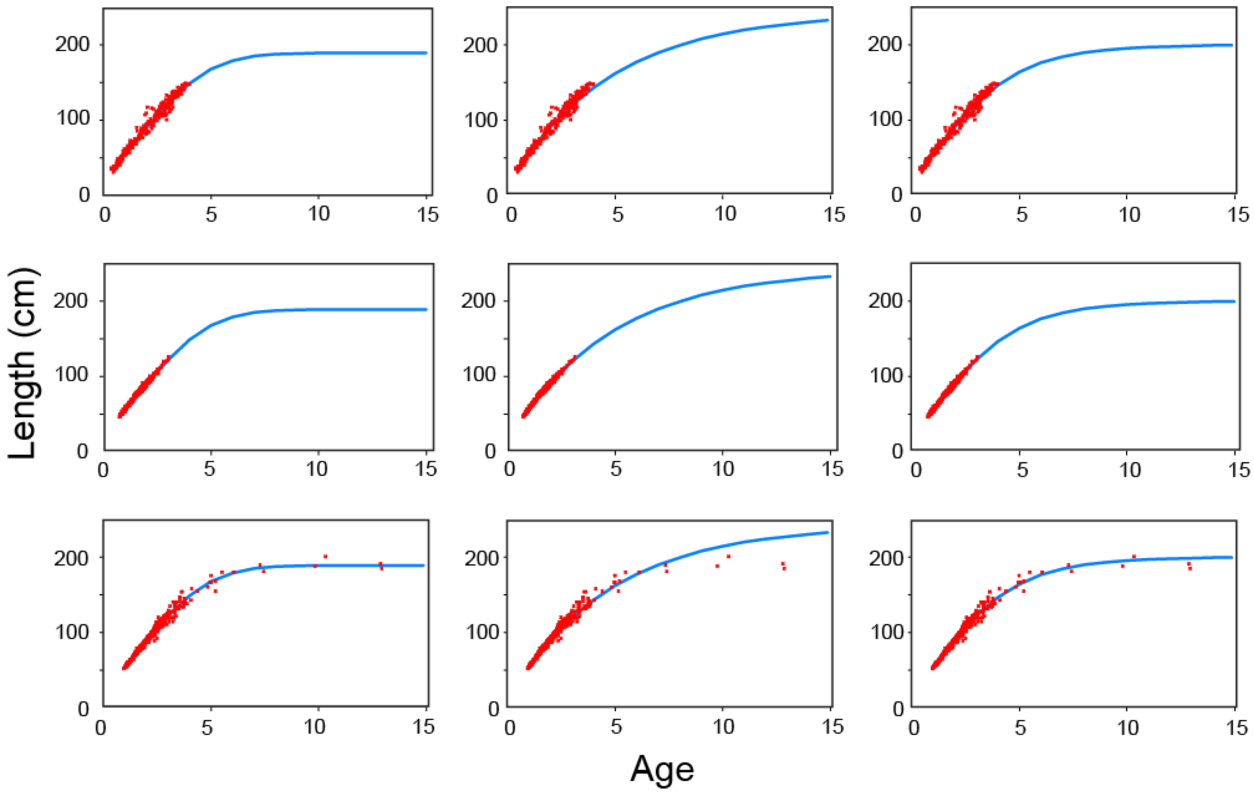

FIGURE 1. Fit of the growth-cessation model (left panels) to the otolith age-length data (top), tagging length at release (middle), and tagging length at recapture (bottom) for bigeye tuna in the eastern Pacific Ocean compared to the von Bertalanffy (middle panels) and Richards (right panels) models.

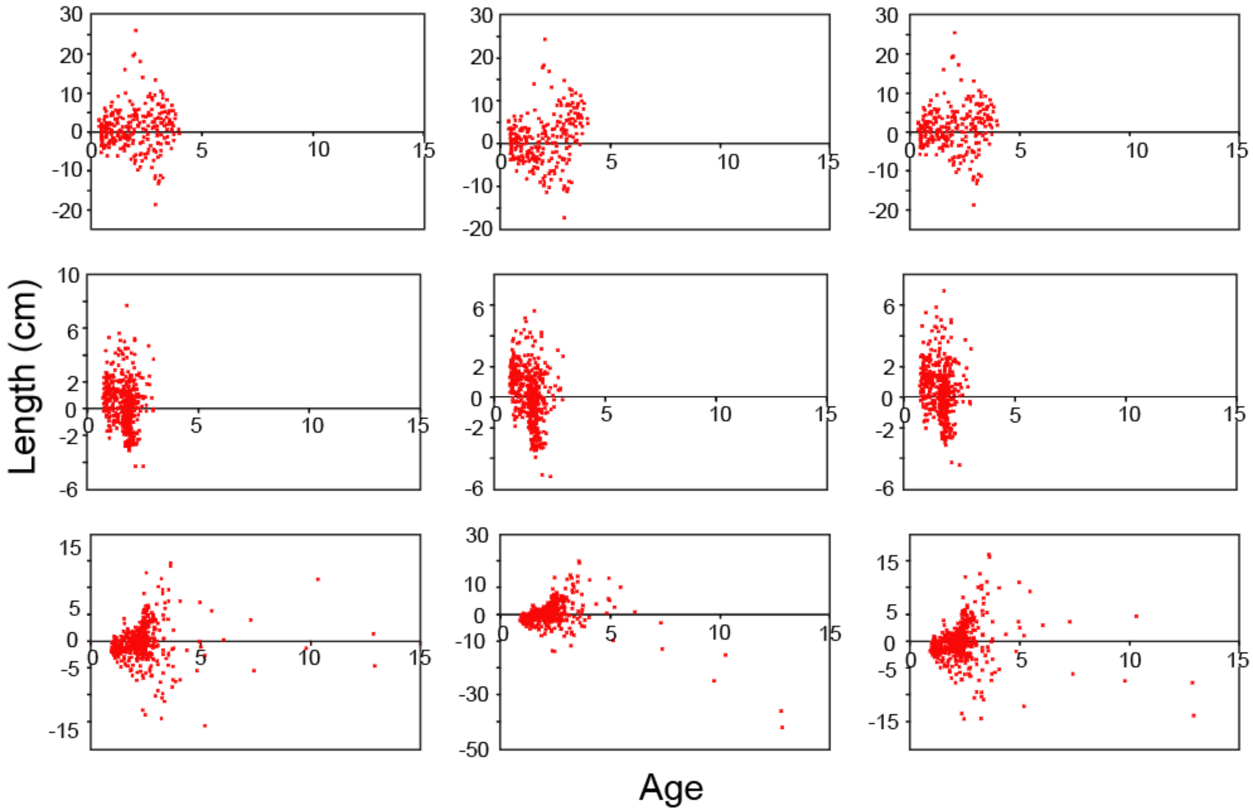

FIGURE 2. Residuals of the fit of the growth-cessation model (left panels) to the otolith age-length data (top), tagging length at release (middle), and tagging length at recapture (bottom) for bigeye tuna in the eastern Pacific Ocean compared to the von Bertalanffy (middle panels) and Richards (right panels) models.

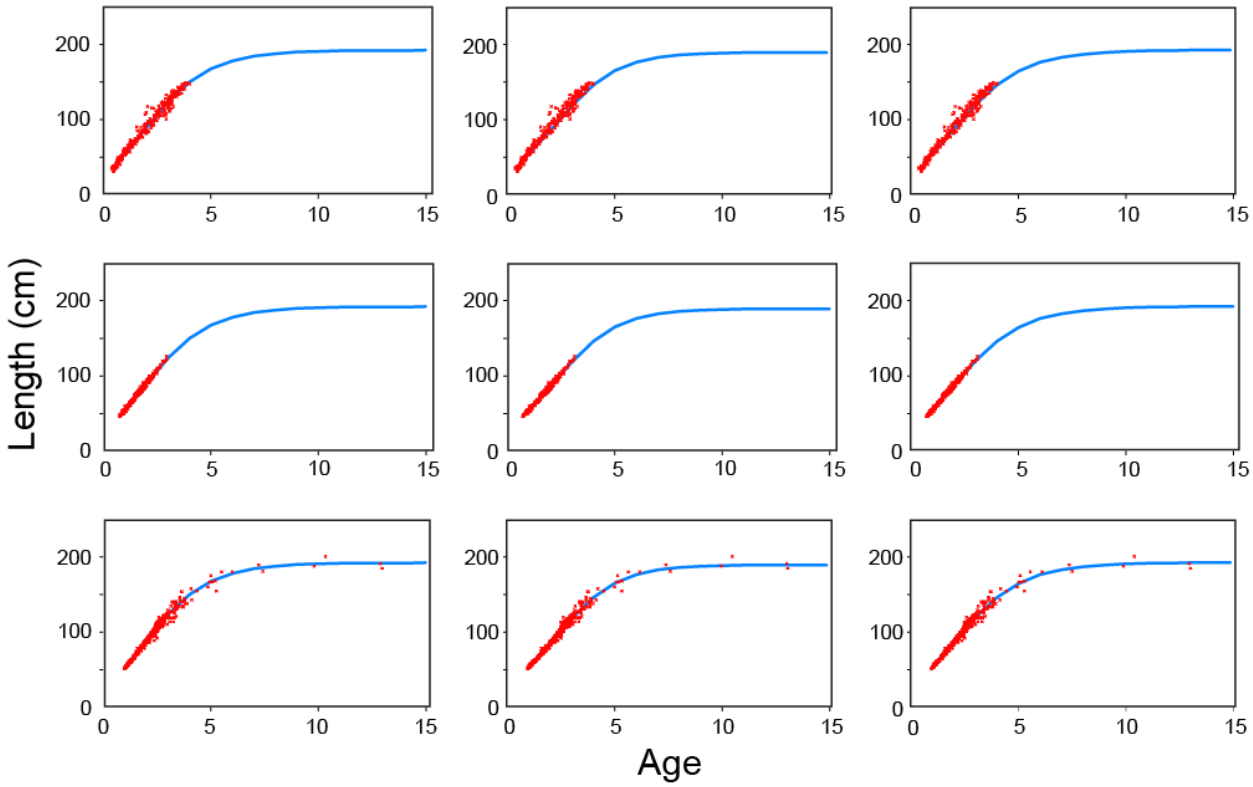

FIGURE 3. Fit of the Richards growth model to the otolith age-length data (top), tagging length at release (middle), and tagging length at recapture (bottom) for bigeye tuna in the eastern Pacific Ocean for different weightings of the data: 1) up-weighting tag recaptures ≥180 cm by 100 (left panels), 2) down-weighting age-length data by 0.01 (middle panels), 3) down-weighting age-length data by 0.1 (right panels).

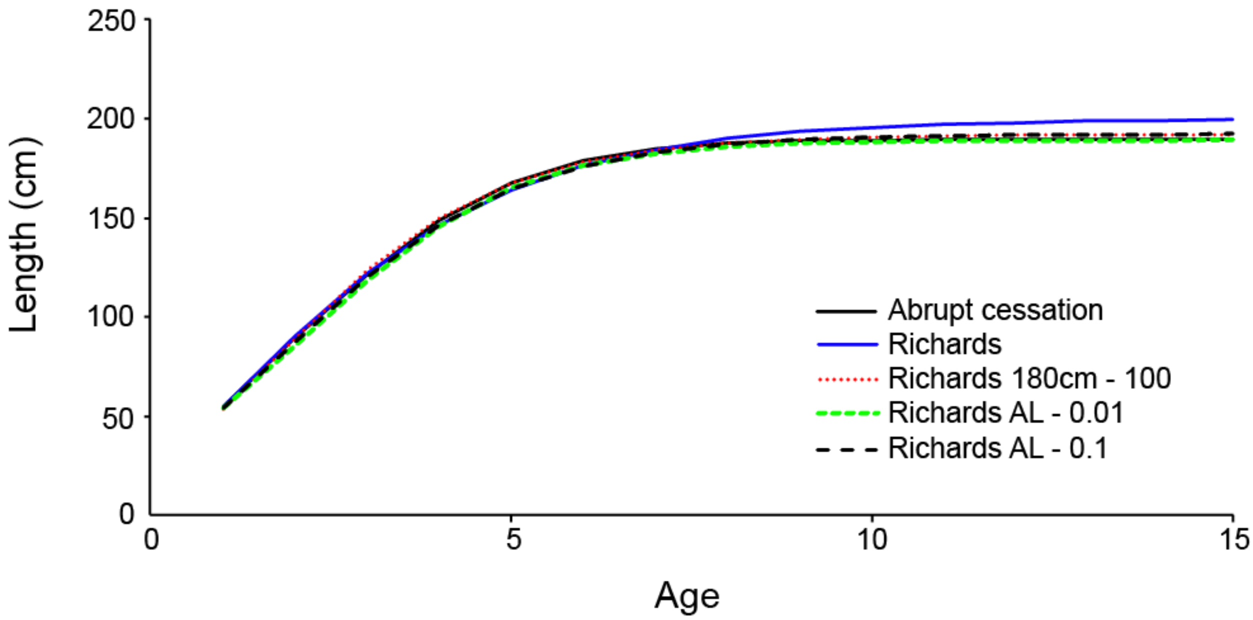

FIGURE 4. Growth-cessation model compared to the Richards growth model for different weightings of the data: 1) up-weighting tag recaptures ≥180 cm by 100 (Richards 180 cm - 100), 2) down-weighting age-length data by 0.01 (Richards AL – 0.01), 3) down-weighting age-length data by 0.1 (Richards AL – 0.1).

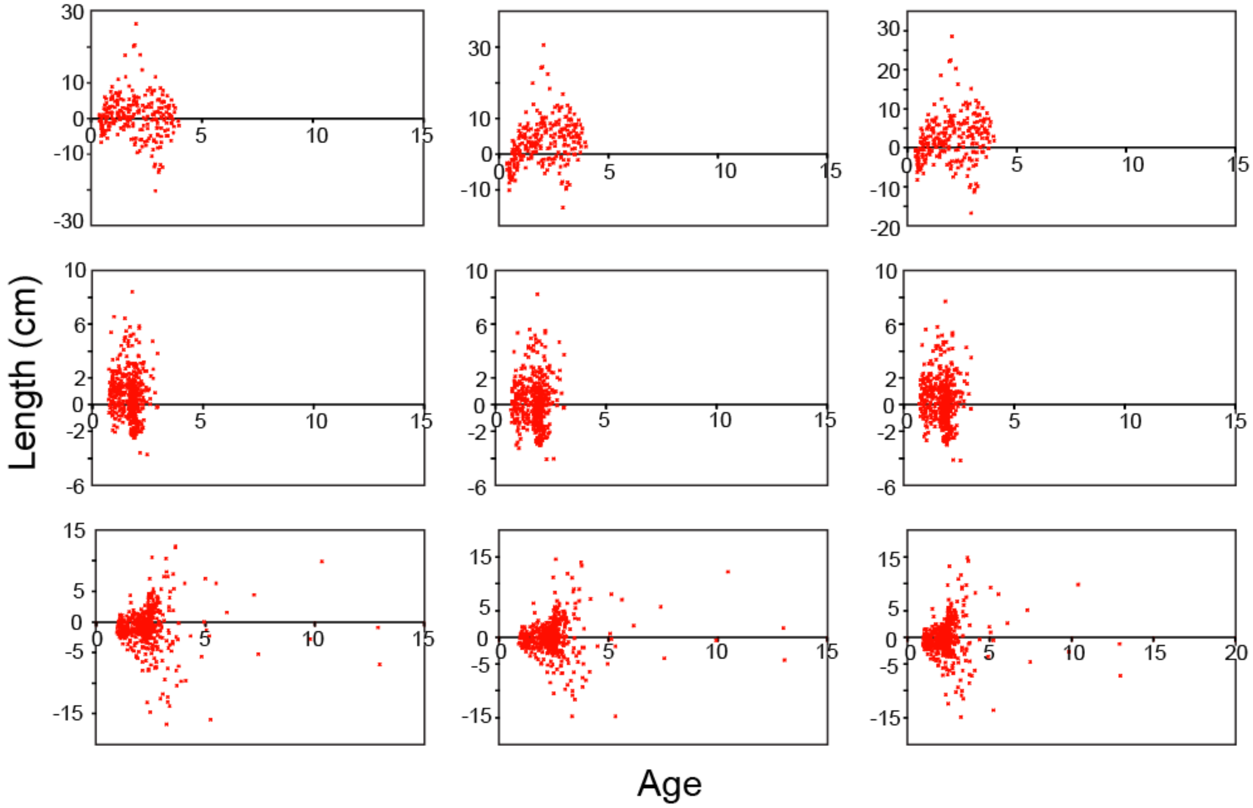

FIGURE 5. Residuals of the fit of the Richards growth model to the otolith age-length data (top), tagging length at release (middle), and tagging length at recapture (bottom) for bigeye tuna in the eastern Pacific Ocean for different weightings of the data: 1) up-weighting tag recaptures ≥180 cm by 100 (left panels), 2) down-weighting age-length data by 0.01 (middle panels), 3) down-weighting age-length data by 0.1 (right panels).