ESTIMATION OF GROWTH PARAMETERS FOR YELLOWFIN, BIGEYE AND SKIPJACK TUNA USING TAG-RECAPTURE DATA

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Abstract

One of the goals of the IOTC Working Party on Tagging Data Analysis (30 June – 4 July 2008, Seychelles International Conference Centre) is to estimate growth parameters for three tuna species (yellowfin, bigeye and skipjack) using tag-recapture data obtained from the large-scale Regional Tuna Tagging Project - Indian Ocean (RTTP-IO) (details of the tagging programme can be found at www.rttp-io.org). In this report, results are presented from fitting growth models to the tagging data for each species using both Fabens method and the method of Laslett, Eveson and Polacheck (Laslett et al. 2002). The results suggest that the two-stage 'VB log k' growth function developed in Laslett et al. (2002), which accommodates a change in the underlying growth curve at a given age, is appropriate for the yellowfin and bigeye data. For the skipjack data, a standard VB model appears to be adequate. It is important to note that the tagging data, at present, contain very limited information about growth of older fish. This should improve in future as tags are returned from fish that have been at liberty for longer periods, or if larger fish are tagged.

Introduction

Growth information for yellowfin, bigeye and skipjack tuna is limited. One of the goals of the Regional Tuna Tagging Project - Indian Ocean (RTTP-IO) is to provide estimates of growth parameters for these three species. As part of this project, large numbers of yellowfin, bigeye and skipjack tuna of different sizes and ages have been tagged since May 2005. Length measurements of all fish are taken upon release. When a tagged fish is recaptured, the fisherman is asked to record the tag number, species name, date and location of catch, and fork length of the fish (i.e., length from the nose to the middle of the tail), and to return the tag along with this information to the RTTP-IO headquarters in the Seychelles.

The change in length of a tagged fish between the time it was released and the time it was recaptured provides useful information for modelling growth. Because the age of a fish at release is unknown, the traditional approach has been to model the incremental change in length of the fish over the time it was at liberty (Fabens 1965; Francis 1988; James 1991). More recently, maximum likelihood approaches have been developed that model the joint density of the release and recapture lengths as opposed to modelling the length increment (Palmer et al. 1991; Wang et al. 1995; Laslett et al. 2002). In these cases, the age at release is modelled as a random variable.

In this report, both Fabens method and the method of Laslett et al. (2002), which will be referred to as the LEP method, were applied to the tag-recapture data for yellowfin, bigeye and skipjack.

Data

Tag-recapture data obtained as part of the RTTP-IO are used in this report. At the time of analysis, recapture data were available up to 14 May 2008. Not all of the data are appropriate for growth analysis since some of the necessary information may be missing or unreliable. Thus, a screening process was applied to the data prior to analysis. Specifically, recaptures were only included if:

- the recapture occurred at sea (since these are considered most reliable in terms of recapture date and recapture length measurement)
- the date of tagging and recapture were both recorded, and suggest a positive time at liberty (for a handful of records, the recorded recapture date is earlier than the recorded tagging date)
- the length of the fish at tagging and recapture were both recorded and considered reliable
- the type of length measurement at recapture was fork length (to correspond with the measurement at release)
- the state of the fish at release was considered good
- the species identification at tagging was considered accurate
- the species identification at recapture matched the species identification at tagging

The number of recaptures considered appropriate for analysis after screening were: 1654 for yellowfin; 1015 for bigeye and 1915 for skipjack.

Methods

Before fitting growth models to the data, an exploratory analysis was undertaken. This included producing simple data summaries and plots, and also calculating an average growth rate (cm/day) for each fish by dividing the difference between its recapture length and release length by the number of days it was at liberty. The purpose was to look for broad patterns in the data and to help determine an appropriate functional form for the growth curve used for each species.

Next, a range of growth functions were fitted to the data for each species using Fabens method (Fabens 1965). Although this method can lead to biased parameter estimates when individual variability in the growth parameters exists (Sainsbury 1980; Maller and deBoer 1988; Eveson et al. 2007), it was a simple and fast way to investigate which growth functions were reasonable for further consideration. Although Fabens method is traditionally used for fitting a von Bertanlanffy (VB) growth function, it can be extended to fit most growth functions. Essentially, Fabens method assumes that the release length of each fish falls exactly on the growth curve. It then finds the parameters of the growth curve which provide the best fit to the recapture data (i.e., that maximize the likelihood of the recapture data, assuming a normal distribution for the residuals).

The growth functions considered were: i) VB; ii) Richards; iii) 2-stage VB (Hearn and Polacheck 2003); and iv) VB with a logistic growth rate parameter, or ‘VB log k’ (Laslett et al. 2002). All of these functions can be expressed as

$$l(a) = L_\infty f(a - a_0; \theta)$$

where L_∞ is asymptotic length and *f* is a monotone increasing function with parameter set $\{a_0, \theta\}$ that equals 0 when $a = a_0$. The parameter a_0 can be thought of as the theoretical age at which a fish would have had length 0 if we were to project its growth curve backwards. This parameter cannot be estimated from tag-recapture data alone, so in order to fully define the growth curve, it must be determined from other sources.

For the four candidate growth functions, θ and *f* can be defined as follows:

i) VB: $\theta = \{k\}$ and $f(a - a_0; \theta) = 1 - \exp(-k(a - a_0))$

ii) Richards: $\theta = \{k, \alpha, \beta\}$ and
$$f(a - a_0; \theta) = (1 + \beta \exp(-k(a - a_0 - \alpha)))^{-1/\beta} - (1 + \beta \exp(k\alpha))^{-1/\beta}$$

iii) 2-stage VB: $\theta = \{k_1, k_2, \alpha, \omega\}$ and
$$f(a - a_0; \theta) = \begin{cases} \gamma(1 - \exp(-k_1(a - a_0))) & \text{for } a \le \alpha \\ 1 - \exp(-k_2(a - a_0 - \tau)) & \text{for } a > \alpha \end{cases}$$
where $\tau = \alpha + \frac{1}{k_2} \log\left(1 - \gamma(1 - \exp(-k_1 \alpha))\right)$

iv) VB log k: $\theta = \{k_1, k_2, \alpha, \beta\}$ and
$$f(a - a_0; \theta) = 1 - \exp(-k_2(a - a_0)) \left\{ \frac{1 + \exp(-\beta(a - a_0 - \alpha))}{1 + \exp(\alpha\beta)} \right\}^{-(k_2 - k_1)/\beta}$$

Note that the last term in the Richards function is not standard, but is included so that the function equals 0 when $a = a_0$. The equation for the 2-stage VB function looks complex, but simply represents a VB curve with growth rate parameter k_1 and asymptotic length γL_∞ up to age α, then a VB curve with growth rate parameter k_2 and asymptotic length L_∞ after age α. The term τ is necessary to ensure a smooth transition between the two curves at the change-point α. Similarly, the equation for the VB log k function represents a change in growth from a VB curve with growth rate parameter k_1 to a VB curve with growth rate parameter k_2, but in this case the transition is smooth rather than instantaneous and it occurs according to a logistic function. The parameter α governs the age at which the midpoint of the transition occurs, and β governs the rate of the transition (being sharper for larger values).

Once candidate growth curves were identified for each species, they were fitted to the data using the LEP method. Details of the method can be found in Laslett et al. (2002). The key feature of this method is that it models the release and recapture lengths as functions of age by treating age at tagging, *A*, as a random variable[1]. *A* is assumed to follow a specified distribution, and the parameters of this distribution are estimated within the model. In applying the LEP method to the three tuna data sets, a lognormal distribution was chosen for *A*; Laslett et al. (2002) showed that the results were fairly robust to the distribution used for *A* so long as it provided a reasonable approximation. Another feature of the LEP method is that it allows for individual variability in growth by modelling the asymptotic length parameter as a random effect. For all species, L_∞ was assumed to follow a normal distribution.

Both Fabens method and the LEP method are based on maximum likelihood, so Akaike's information criteria (AIC) could be used to compare model fits. Residual plots were also used to evaluate the fits. Note that to calculate the fitted recapture values (and thus the residuals) for the LEP method requires a realized value of *A* and L_∞ for each fish. These were estimated using the procedures described in Laslett et al. (2002). Briefly, for each fish, the mean of the posterior distribution for *A* and for L_∞ was calculated given the fish's release length and recapture length.

Results

All figures and results include only data that were considered appropriate for growth analysis after screening (see Data section).

Yellowfin

Figure Y1 shows histograms of the release lengths, recapture lengths and times at liberty for recaptured yellowfin tuna. There are two modes in the release lengths at ~ 48cm and 60cm that possibly correspond to age classes. Most tagged fish (~85%) were caught within a year of release, with the mean being 203 days and the maximum 977 days. Figure Y2 shows the length increment (recapture – release length) plotted against the number of days at liberty. Two bands can be distinguished in this figure. These correspond to fish from the two release modes. Specifically, the lower band, which represents slower growth, corresponds to fish from the smaller mode. This figure also reveals that a number of length increments are negative (4%), indicating that measurement error can be significant since fish are unlikely to have shrunk. A few outliers are also evident. Figure Y3 shows the average growth rate, calculated as centimetres growth per day, plotted against release length. Looking at the bottom panel, which excludes fish with extreme growth rates, there is a clear change in growth rates at a length of about 55cm, with smaller fish growing more slowly than larger fish. This lends strong support for a 2-stage growth model.

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[1] Note that *A* actually represents the age at tagging, a_1, relative to a_0 (i.e., $A = a_1 - a_0$). As noted previously, it is not possible to estimate a_0 from tagging data. Thus, it is important to keep in mind when looking at the results that the estimated distribution of *A* must be shifted by a_0 to represent true ages.

Figure Y4 shows the residual plots from using Fabens method to fit the four candidate growth functions to the yellowfin data. As expected from the exploratory analysis, the 2-stage VB and VB log k functions provide much better fits than the VB or Richards functions (note, however, that a smooth through the residuals reveals that there is still a small ‘wiggle’, indicating lack of fit, around the transition length.) The AIC values suggest that the VB log k provides the best fit (Table 1).

Following on from the above results, the LEP method was used to fit both the 2-stage VB and VB log k functions to the yellowfin data. Convergence was difficult to achieve for both models and parameter estimates were sensitive to the starting values; thus, the following results should be considered preliminary until further investigation. According to the AIC values, the VB log k model provided a significantly better fit, so only the results for the VB log k model are presented. Diagnostic plots are shown in Figure Y5. Plot (a) shows the values of *A* estimated for each fish, overlaid with the estimated lognormal distribution. Even though a uni-modal distribution is being assumed, the conditional estimates of *A* are still able to portray the bi-modal nature of the release ages suggested by the release lengths. Recall that *A* is the release age relative to a_0, so if the first mode was known to correspond to, say, age 1 fish, this would suggest that a_0 is equal to about -1.6. Plot (b) shows the recapture length residuals (fitted – true). A smooth through the points shows the same small lack of fit that was seen using Fabens method. Finally, (c) shows the release and recapture lengths plotted against estimated age relative to a_0 (i.e., *A* for the release lengths, *A* plus time at liberty for the recapture lengths), along with the mean fitted growth curve.

Bigeye

Figures B1-B3 for bigeye are analogous to Figures Y1-Y3 for yellowfin, and they show very similar features. In particular, there appear to be two modes in the release lengths at ~ 48cm and 62cm (Figure B1), although the second mode is much smaller in this case. The times at liberty are very similar to yellowfin, with a mean of 204 days, a maximum of 958 days, and ~85% of fish caught within a year of release. Despite having similar release lengths and times at liberty, the recapture lengths are much smaller for bigeye than yellowfin, which indicates they have slower growth. As with yellowfin, two bands can be distinguished in the plot of length increments versus days at liberty (Figure B2), with the lower slower-growing band corresponding to fish from the smaller release length mode. There are also some extreme outliers, and a number of fish with negative growth increments (3%). Figure B3, showing the average growth rate versus release length, strongly supports a 2-stage growth model for bigeye as well, with the change from slower to faster growth occurring at a very similar length as yellowfin (~55cm).

The results from using Fabens method to fit the four candidate growth functions to the bigeye data are given in Table 1 and Figure B4. The results confirm that a two-stanza growth function is appropriate for bigeye. In this case, the 2-stage VB function provides a slightly better fit according to AIC than the VB log k.

The LEP method was then used to fit both the 2-stage VB and VB log k functions to the bigeye data. In contrast to Fabens method, the AIC values suggest that the VB log k model provided a better fit. Also, the fitting routine reported convergence for the VB log k model but not for the 2-stage VB model. Thus, only the results for the VB log k model are presented (noting that the 2-stage VB results are very similar). Diagnostic plots are given in Figure B5. Again, plot (a) shows that even though a lognormal distribution is being assumed, the conditional estimates of *A* capture the bi-modal nature of the release ages suggested by the release lengths. In this case, if the first mode was assumed to correspond to, say, age 1 fish, this would suggest that the parameter a_0 is approximately equal to -3.1. Plot (b) shows the recapture length residuals (fitted – true). A couple of large outliers are evident; otherwise the fit looks reasonable (with perhaps a small trend revealed by the smooth). Finally, (c) shows the release and recapture lengths plotted against estimated age relative to a_0, along with the mean fitted growth curve.

Skipjack

Figures S1-S3 for skipjack have somewhat different features than the analogous plots for yellowfin and bigeye. Firstly, there is only one clear mode in the release lengths at ~50cm. The times at liberty are very similar (mean 200 days, max 958 days, and ~85% less than 1 year); however, the recapture lengths are not much larger than the release lengths and indicate considerably slower growth rates than for yellowfin or bigeye. This is confirmed in Figure S2, which shows much smaller changes in length over the same times at liberty. The percent of fish with negative growth increments is highest for skipjack (5%). Unlike the other two species, the growth rate plot for skipjack (Figure S3) does not show strong support for a 2-stage growth model.

The results from using Fabens method to fit the four candidate growth functions to the skipjack data are somewhat less clear (Table 1 and Figure S4). The AIC values suggest the 2-stage VB and VB log k provide equally good, and better, fits than the VB or Richards functions. From the residual plots, it would be difficult to distinguish between the different growth functions; although a smooth through the points reveals a very slight lack of fit with the VB and Richards curves at the smallest release lengths.

Based on the above, the LEP method was used to fit the VB and VB log k functions to the skipjack data. The VB log k model essentially converged to the VB model, with the transition age estimated to be almost zero (so that all the data was above it). Furthermore, the AIC values were almost the same. Thus, we only present results from the VB model. Figure S5 shows the diagnostic plots. For skipjack, the estimated *A* values have a uni-modal distribution, as suggested by the distribution of release lengths. The recapture residuals suggest a good fit. Plot (c) shows the release and recapture lengths plotted against estimated age relative to a_0, along with the mean fitted growth curve. This plot would suggest a greater lack of fit at young ages than shown in the residuals. Laslett et al. (2004) explain that this is an artefact of the estimates of *A* being conditionally biased. They suggest an alternative estimator of *A* for graphical purposes, but time did not permit us calculating it for this report. Note that this is an issue for all species, but is just most apparent for skipjack.

Discussion

The results from all analyses suggest that a two-stanza growth model capable of accommodating a change in the underlying growth function at a given age is necessary for yellowfin and bigeye. The 'VB log k' growth function developed in Laslett et al. (2002) appears to be a reasonable choice. For the skipjack data, the results are not quite as clear, but a standard VB model appears to be adequate.

Limitations in the data must be recognized. Although a large number of tags have been released as part of the RTTP-IO project, the times at liberty for fish that have been recaptured to date are relatively short. As more recapture data with longer times at liberty become available, estimates of growth should be improved. Furthermore, there is large variability in the data, with a few obvious outliers as well as many fish recorded as having negative growth. For future analyses, it would be beneficial to establish an unbiased set of criteria that can be used for 'weeding out' the outliers. This is not as simple as just removing the records with negative growth, because just as many recapture lengths will likely have been overestimated as underestimated; only removing those that were underestimated would create a bias towards faster growth.

The LEP method has several theoretical advantages over Fabens method—the most important being that it provides unbiased parameter estimates when individual variability in growth exists. Nevertheless, it requires more parameters to be estimated and is much more computationally intensive. Moreover, without sufficient data spanning a wide range of the growth curve, it can be difficult to achieve convergence. This was an issue in applying the LEP method to the data from all three species. The fits should become more stable as more data with longer times at liberty become available.

Lastly, a small amount of validated otolith data are available for yellowfin. Figure Y6 shows these data along with the mean VB log k curve estimated from the tag-recapture data (using the LEP method). In plotting the VB log k curve, a value of -1.1 was used for the a_0 parameter to make the mean length of an age 2 fish consistent with the otolith data. However, this resulted in the otolith data for younger fish (< age 1) falling well below the growth curve. These initial results suggest that the tag-recapture and otolith data are not entirely consistent; however, more otolith data and further investigation are needed before any conclusions can be drawn.

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Table 1. Negative log likelihood and AIC values obtained using Fabens method to fit four candidate growth functions to the yellowfin, bigeye and skipjack tagging data.

		Yellowfin		Bigeye		Skipjack	
	No. par	Neg LL	AIC	Neg LL	AIC	Neg LL	AIC
VB	3	6113.8	12233.6	3230.6	6467.2	4267.6	8541.2
Richards	4	5707.3	11422.6	3148.8	6305.6	4270.1	8548.2
2-Stage VB	6	5428.6	10869.2	3080.3	6172.6	4253.5	8519.0
VB log k	6	5358.1	10728.2	3095.7	6203.4	4253.5	8519.0

Figure Y1. Histograms of release lengths, recapture lengths and days at liberty for recaptured yellowfin tuna.

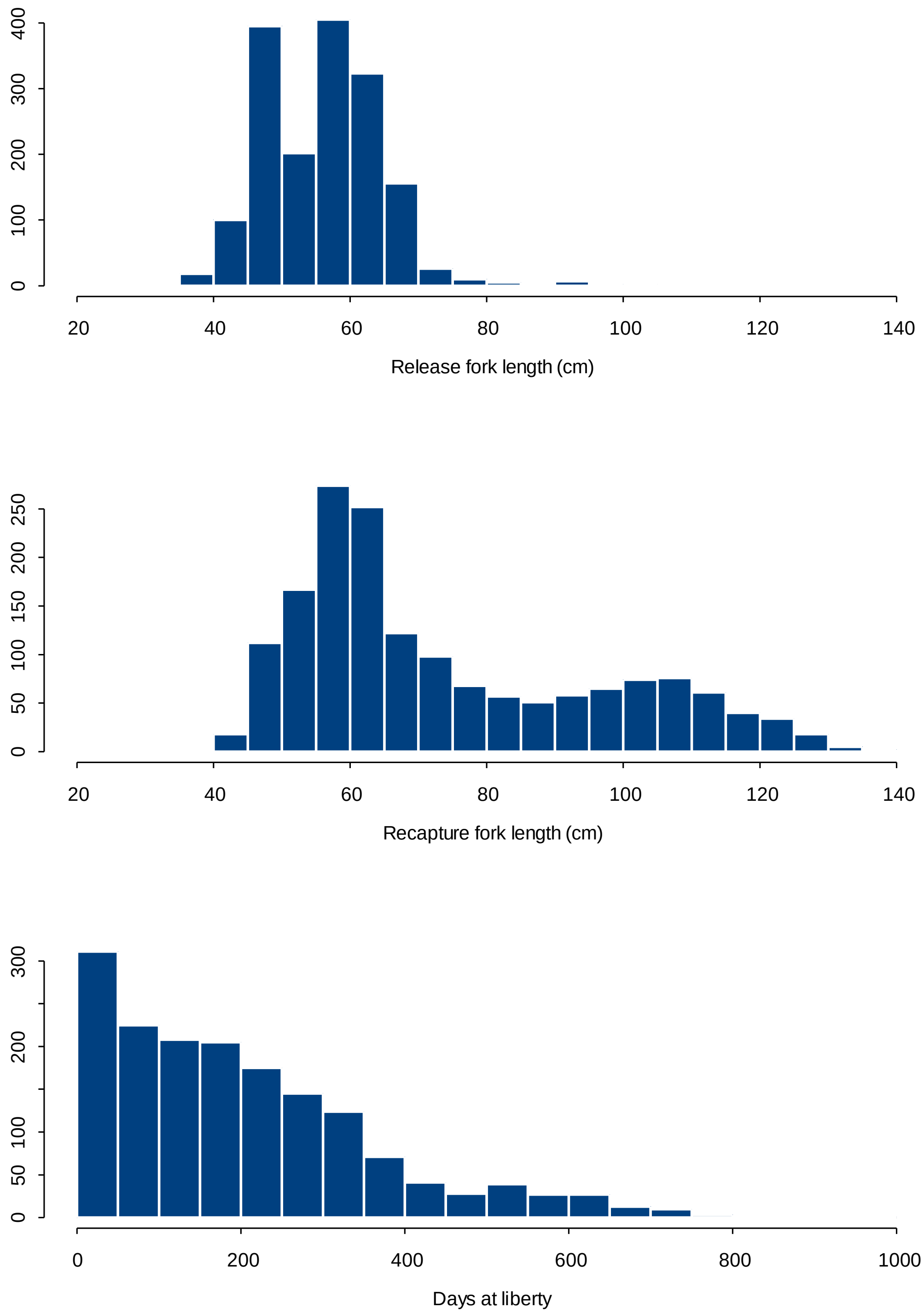


Figure Y2. Growth increment (i.e. recapture length – release length) versus time at liberty in days for recaptured yellowfin tuna.

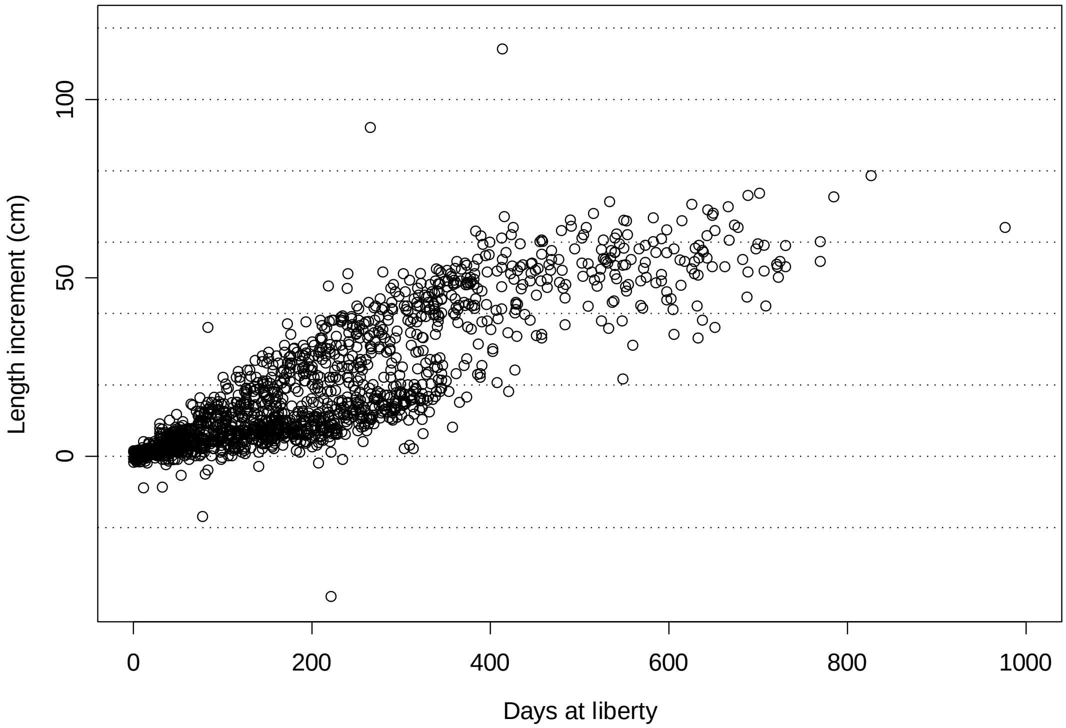
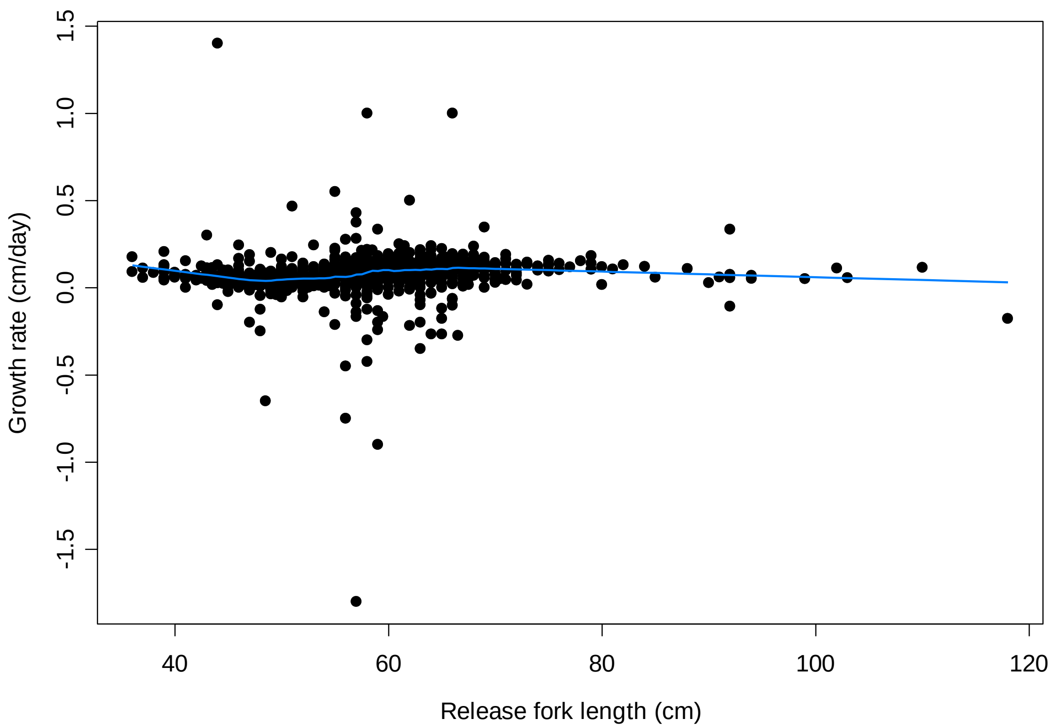


Figure Y3. Empirical growth rate of recaptured yellowfin tuna (calculated as centimetres growth per day) versus release length. The top plot shows all data; the bottom plot includes only growth rates within the 5th and 95th quantiles. A non-parametric smooth (solid line) has been added to help visualize trends in the data.



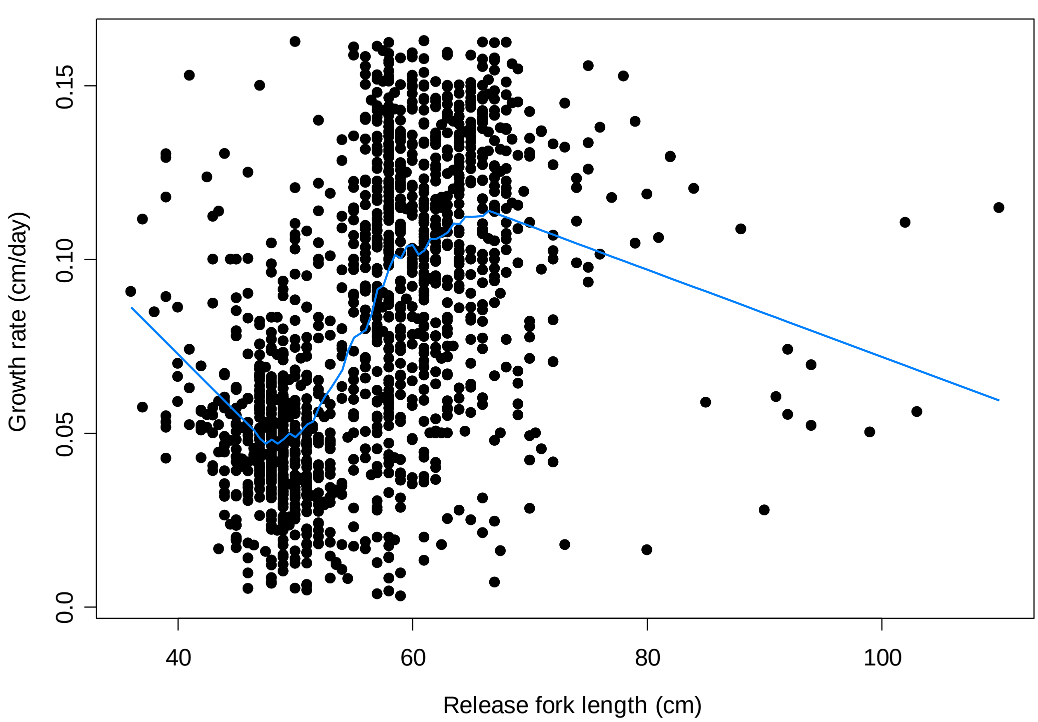
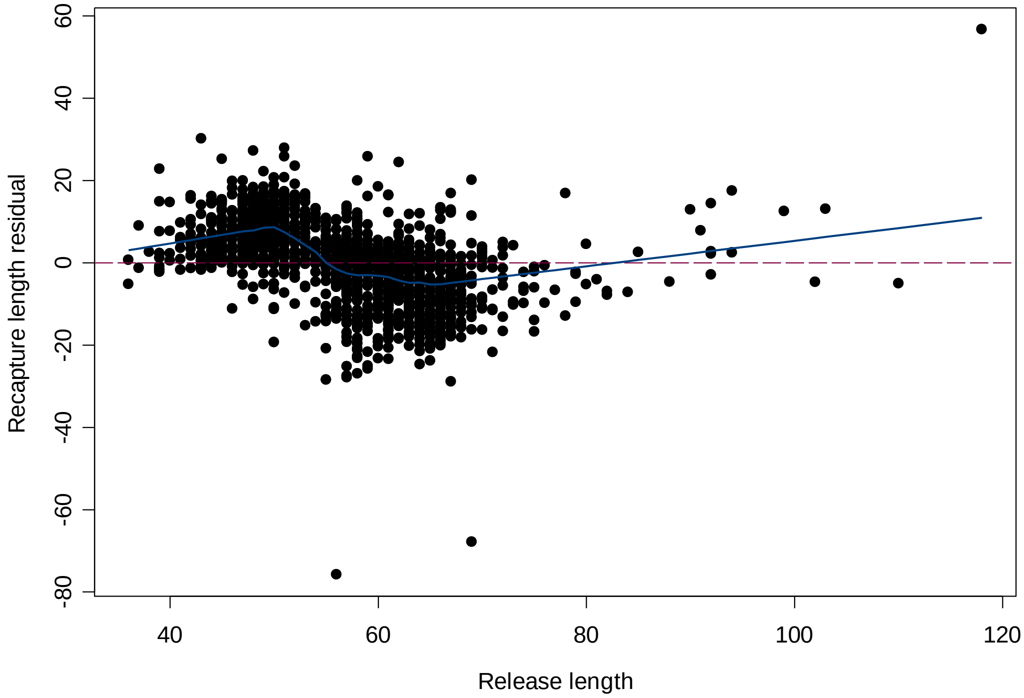
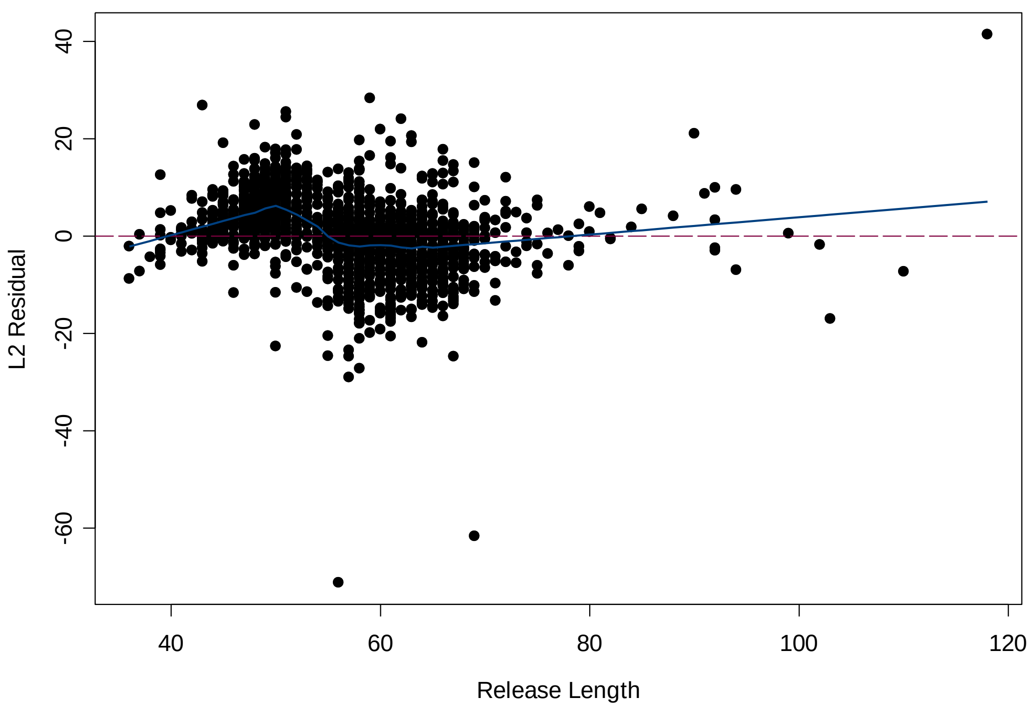


Figure Y4. Residuals from fitting the four candidate growth functions to the yellowfin tag-recapture data using Fabens method. A non-parametric smooth of the data (solid line) has been added to help visualize any trends. (In the y-axis label, L2 denotes recapture length.)

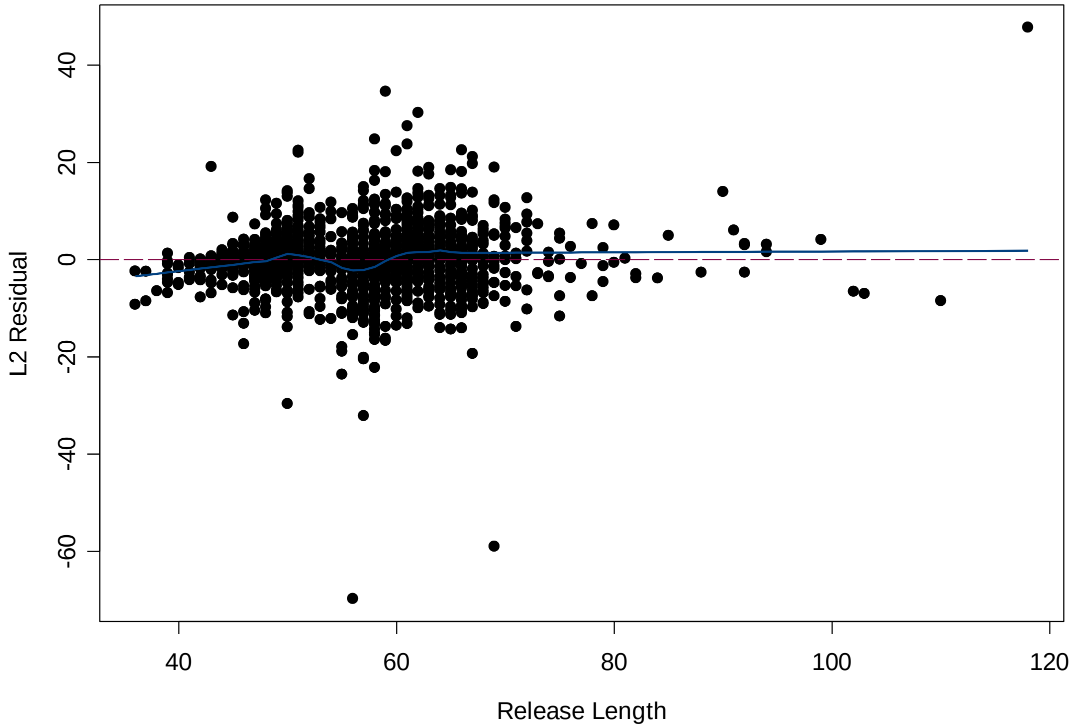
i) VB



ii) Richards



iii) 2-Stage VB



iv) VB log k

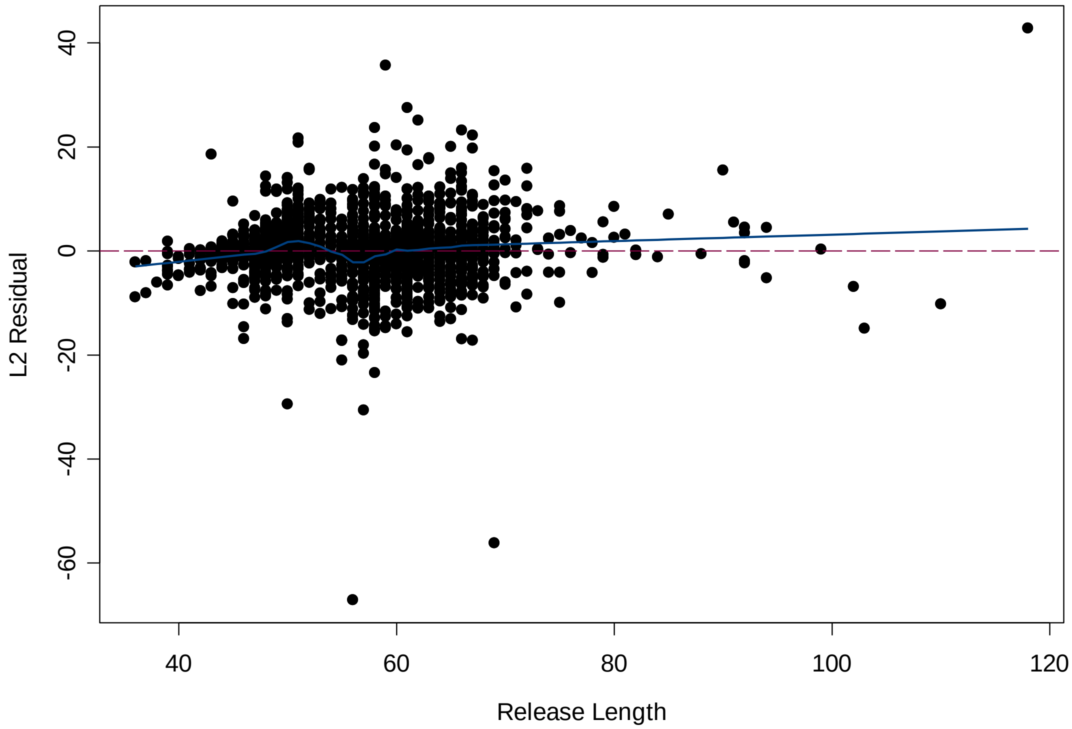
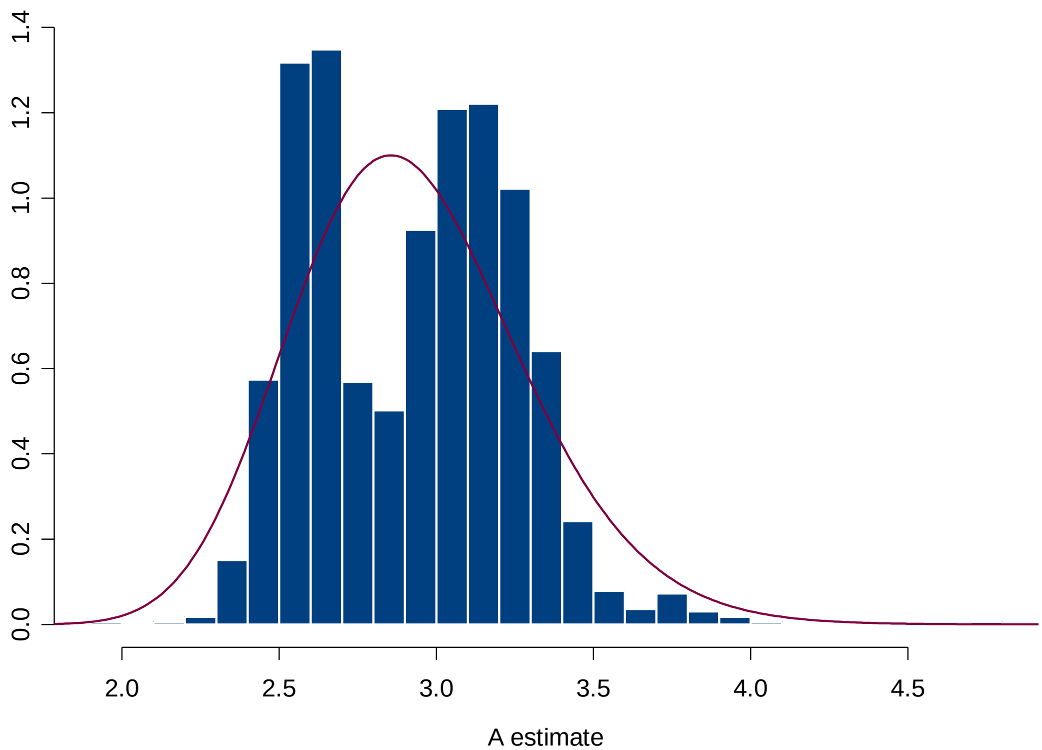
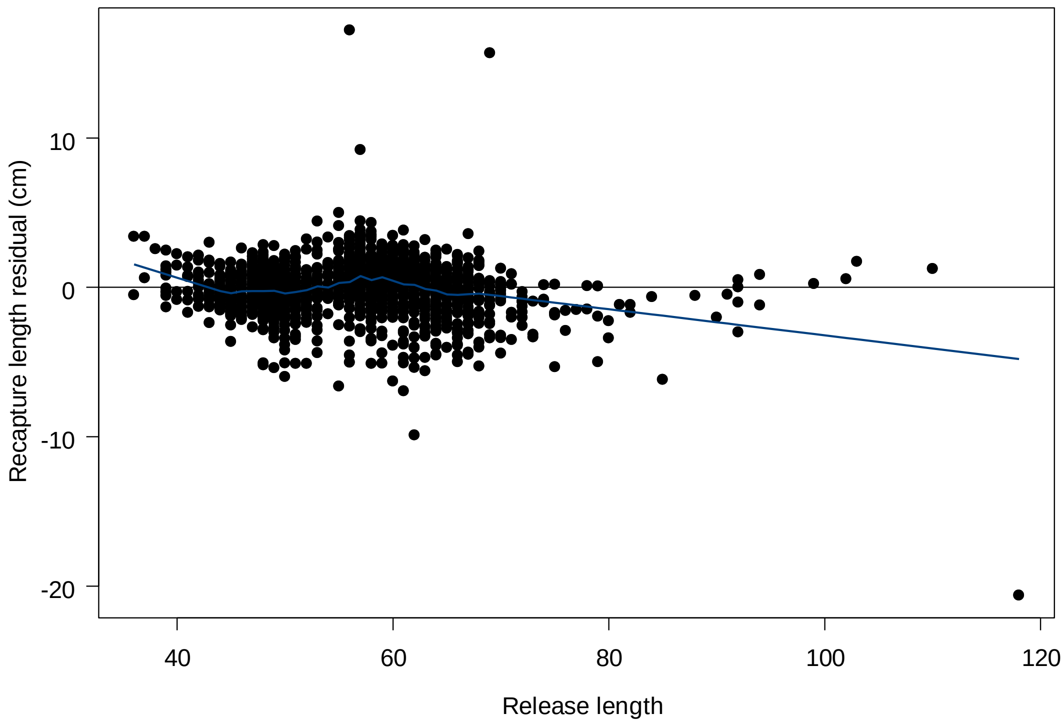


Figure Y5. Diagnostic plots from fitting a VB log k growth function to the yellowfin tag-recapture data using the LEP method, assuming a lognormal distribution for *A*. (a) Histogram of the estimates of *A* for each fish overlaid with the estimated lognormal distribution. (b) Residuals in recapture lengths with a non-parametric smooth (solid line) to help visualize any trends. (c) Release and recapture lengths plotted against estimated age (relative to a0), along with the mean fitted growth curve.

a)



b)


Recapture length residual (cm)
10
0
-10
-20
40
60
80
100
120
Release length

c)

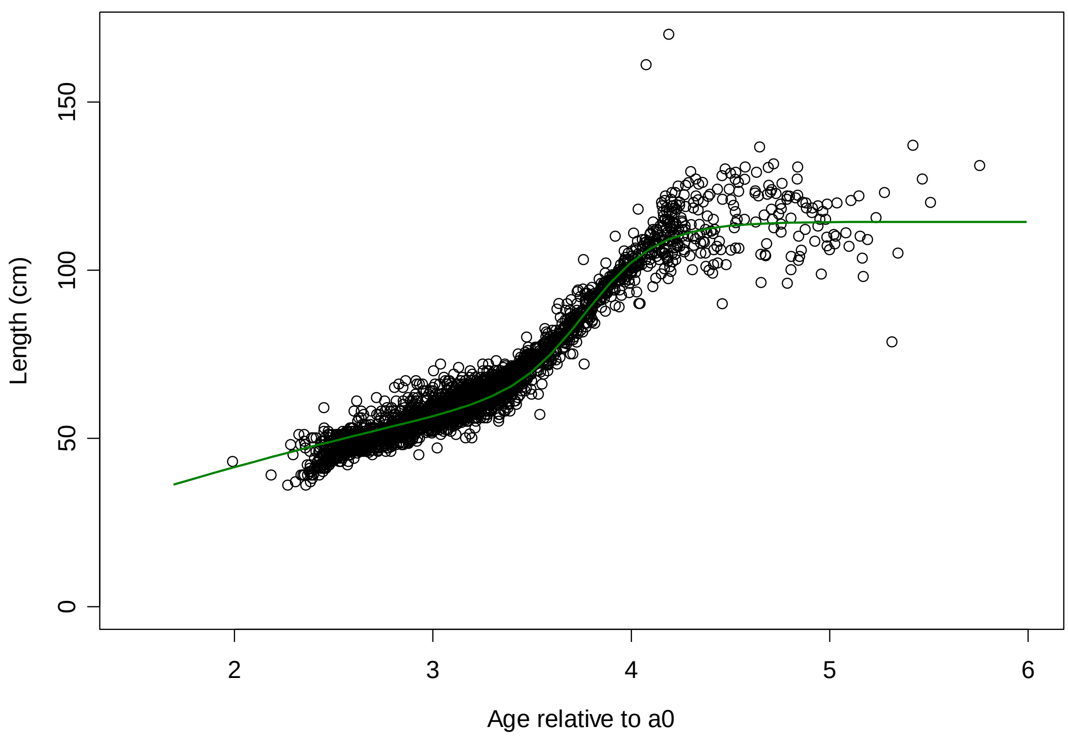

Length (cm)
150
100
50
0
2
3
4
5
6
Age relative to a0

Figure Y6. Plot showing the validated otolith data for yellowfin tuna, overlaid with the estimated mean VB log k growth curve from Figure Y5 (c). Note that an a0 value of -1.1 was used in plotting the VB log k curve so that the length of an age 2 fish was consistent with the otolith data.

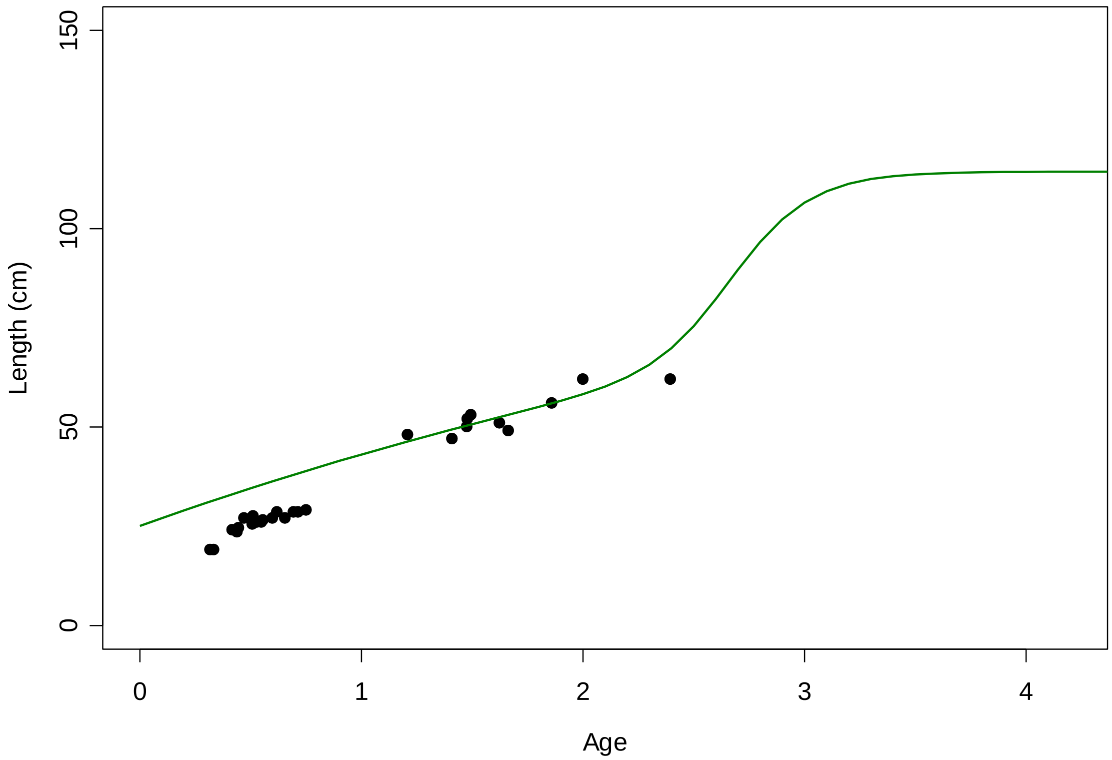


Figure B1. Histograms of release lengths, recapture lengths and days at liberty for recaptured bigeye tuna.

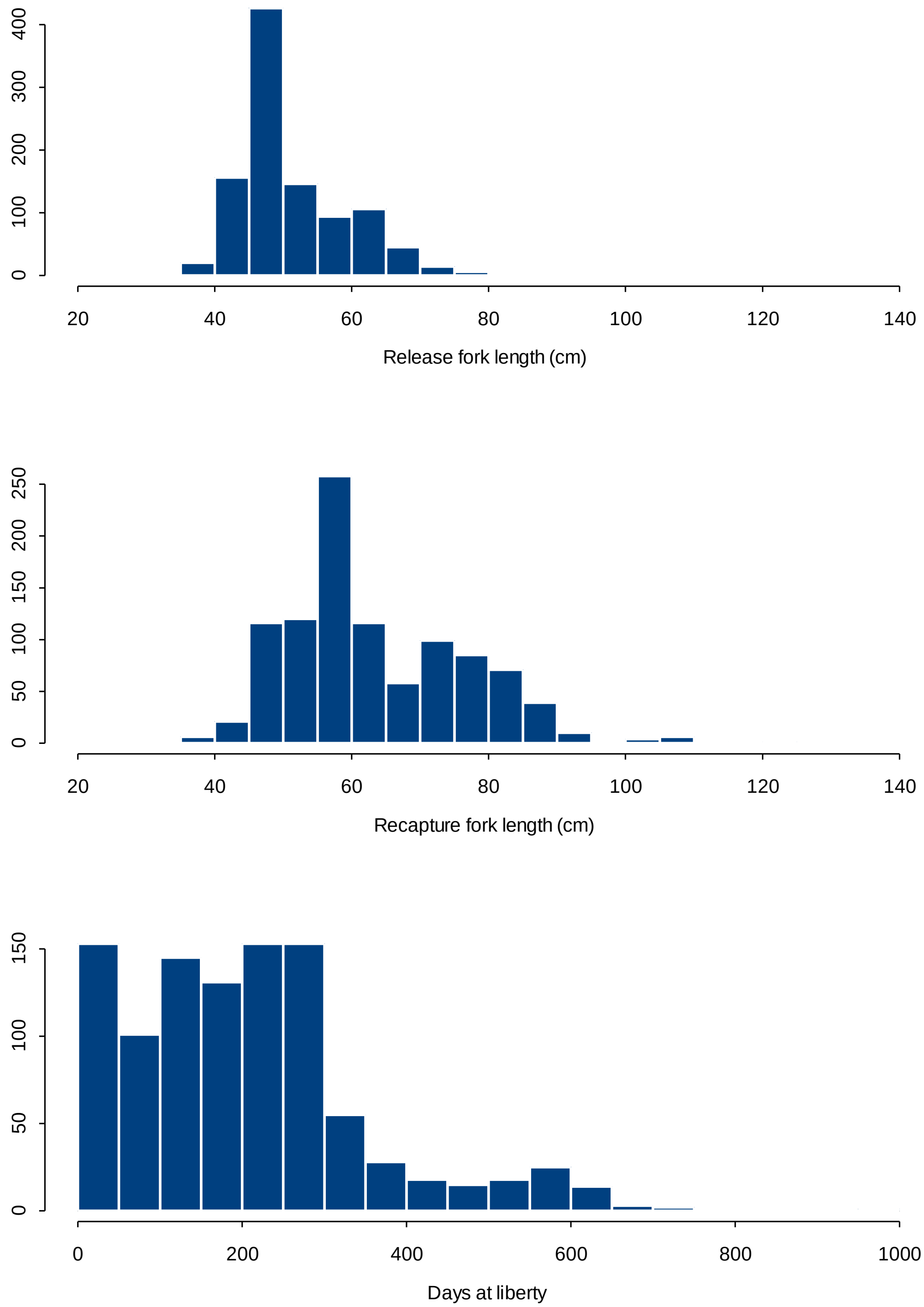


Figure B2. Growth increment (i.e., recapture length – release length) versus time at liberty in days for recaptured bigeye tuna.

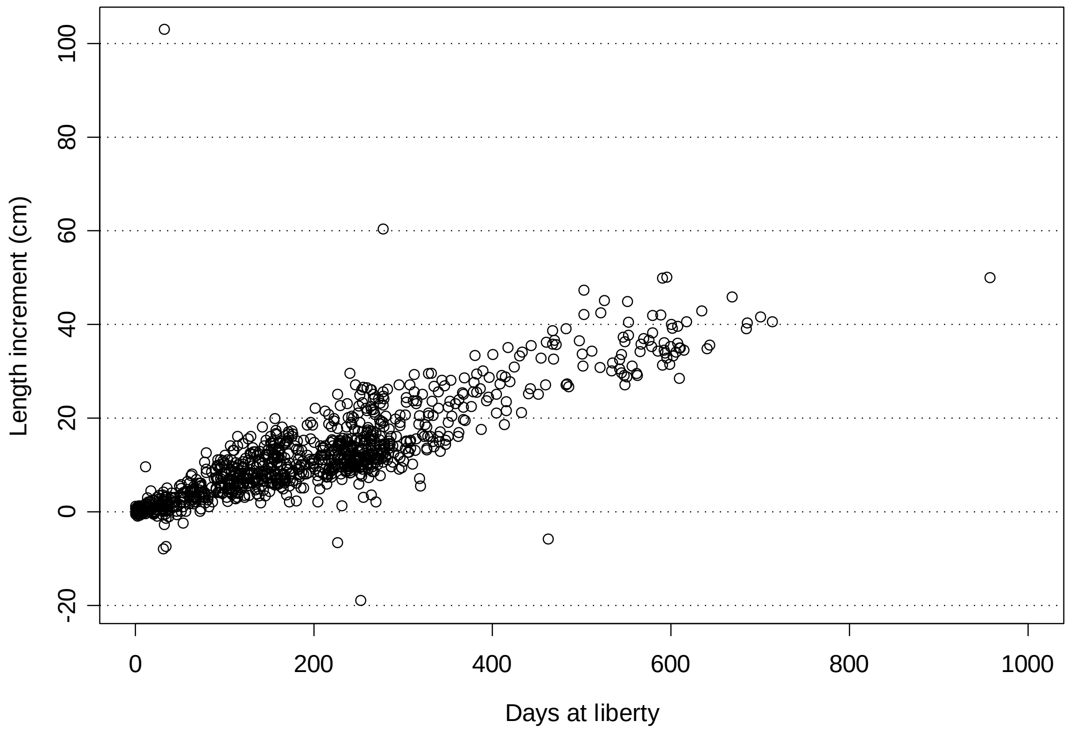


Figure B3. Empirical growth rate of recaptured bigeye tuna (calculated as centimetres growth per day) versus release length. The top plot shows all data; the bottom plot includes only growth rates within the 5th and 95th quantiles. A non-parametric smooth (solid line) has been added to help visualize trends in the data.

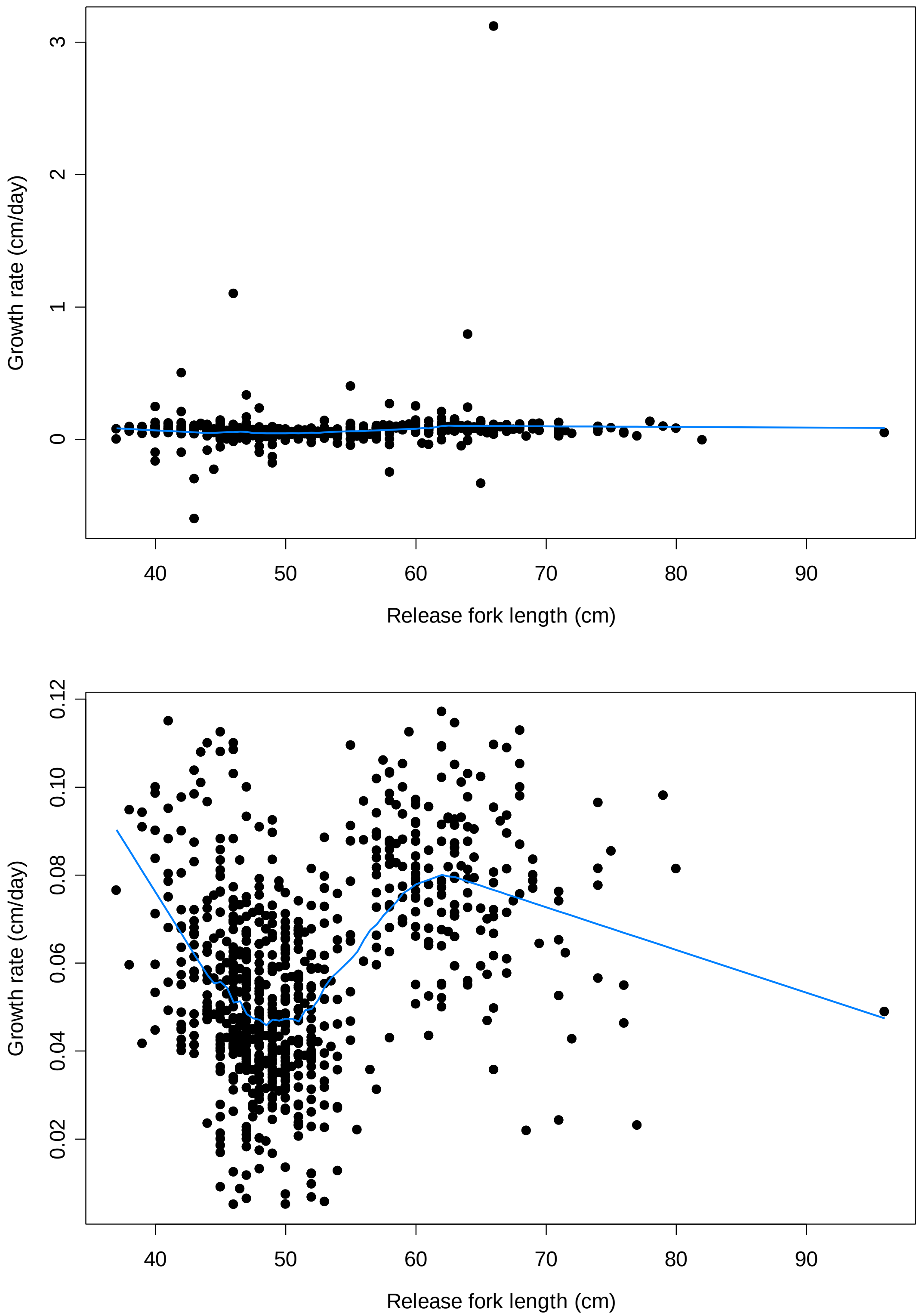
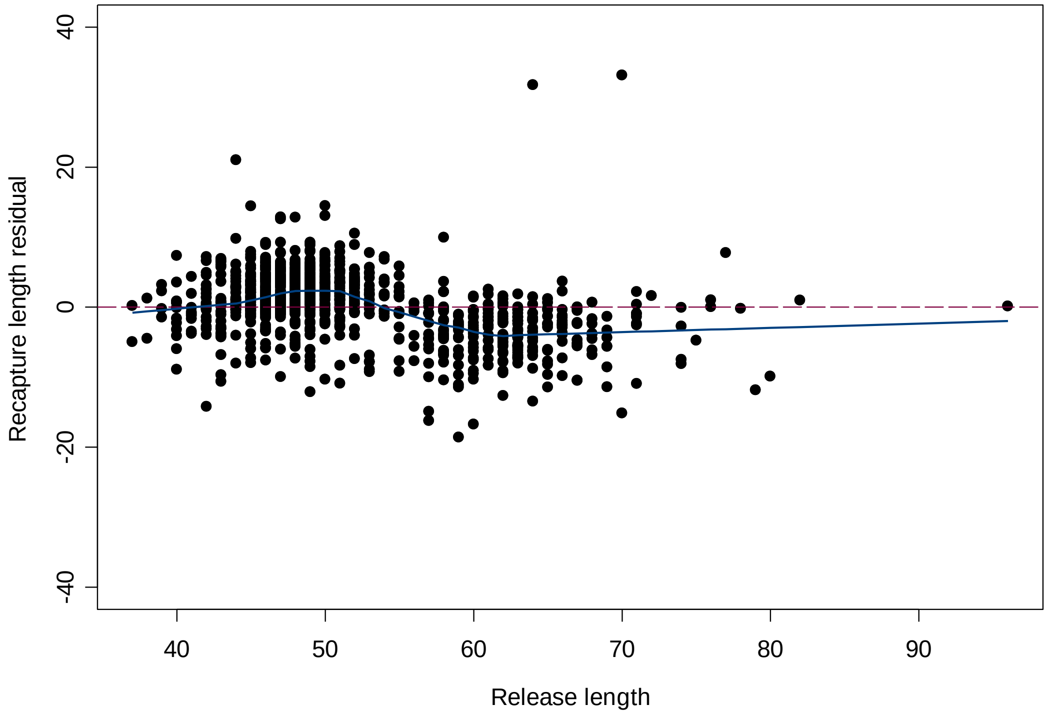
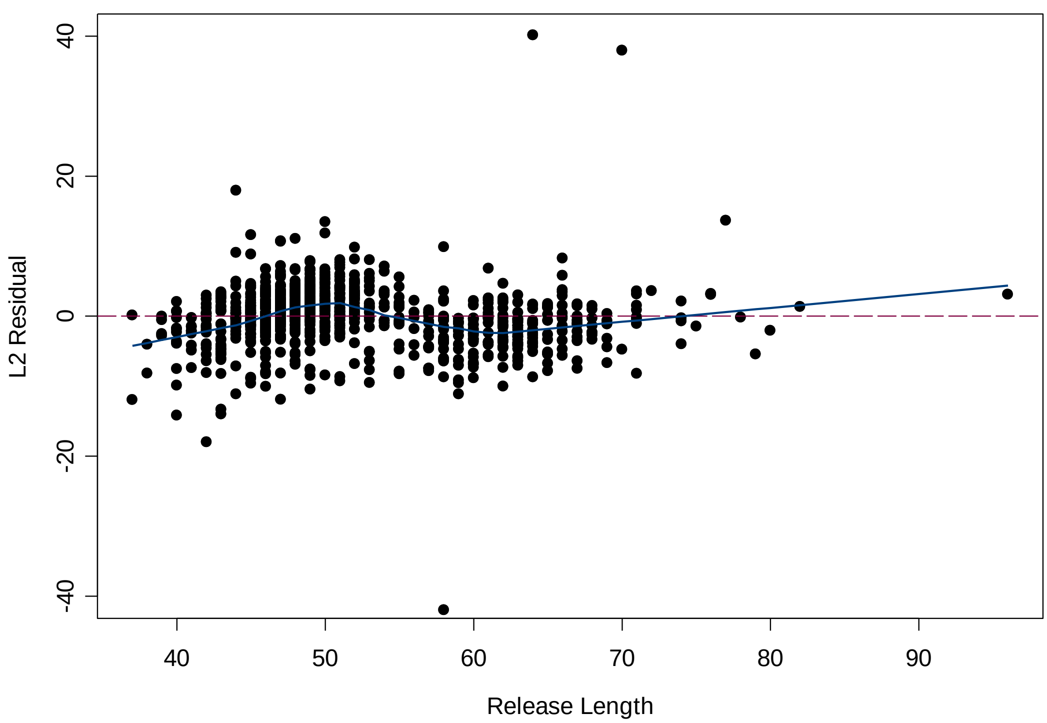


Figure B4. Residuals from fitting the four candidate growth functions to the yellowfin tag-recapture data using Fabens method. A non-parametric smooth (solid line) has been added to help visualize any trends. (In the y-axis label, L2 denotes recapture length.)

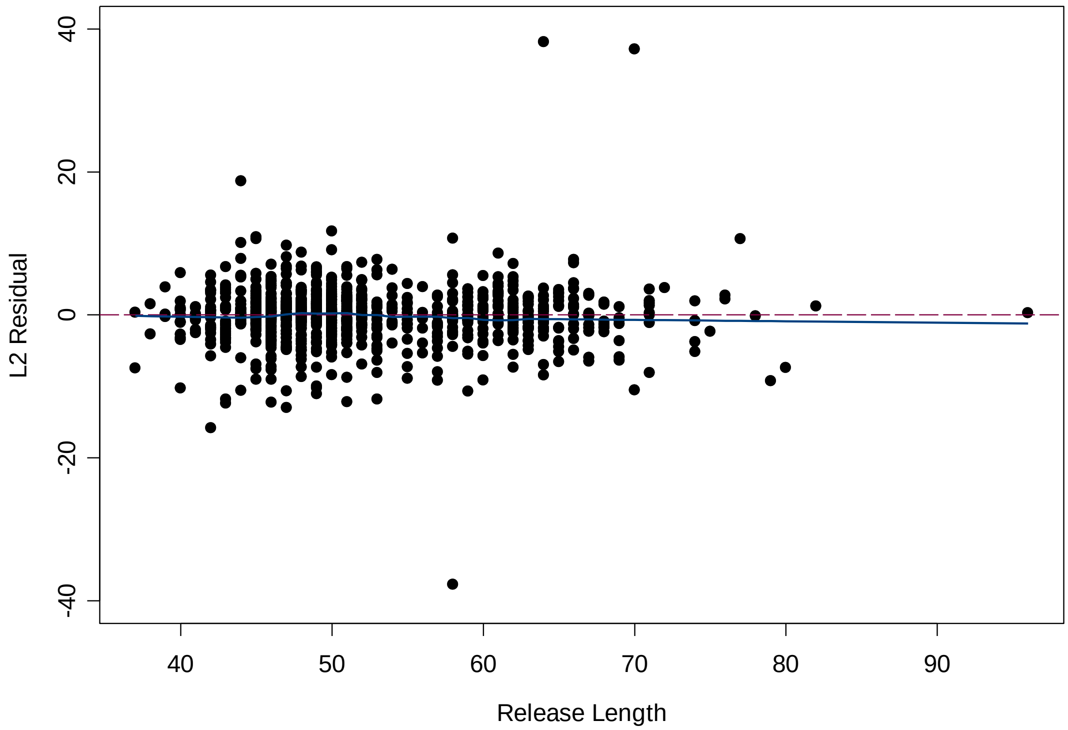
i) VB



ii) Richards



iii) 2-Stage VB



iv) VB log k

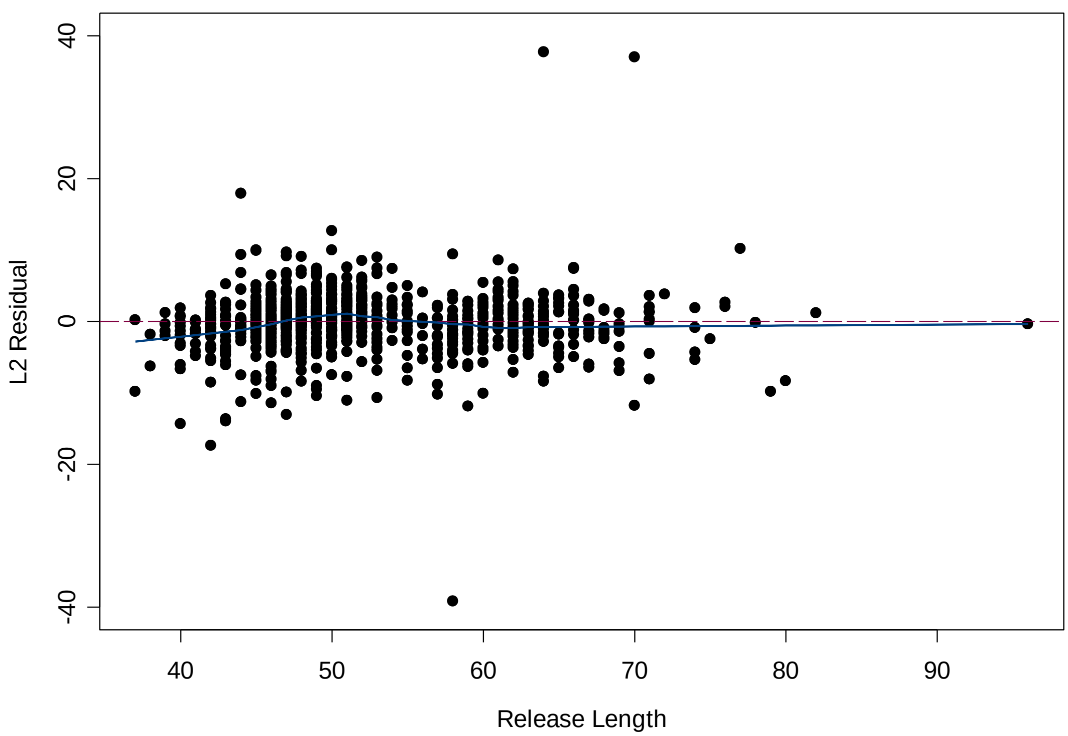
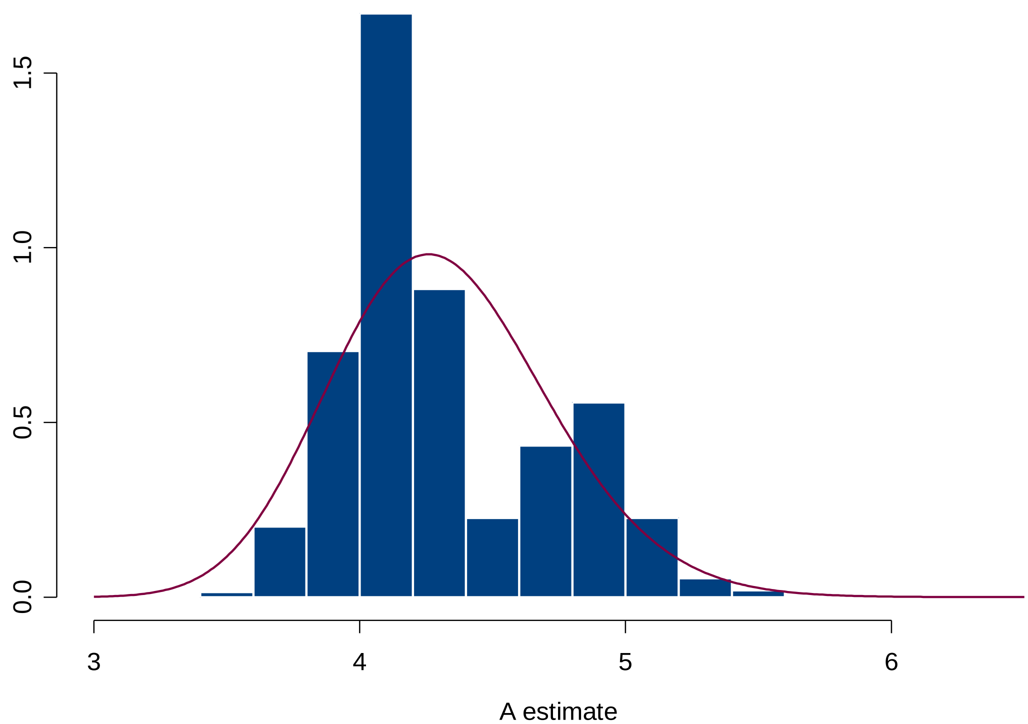
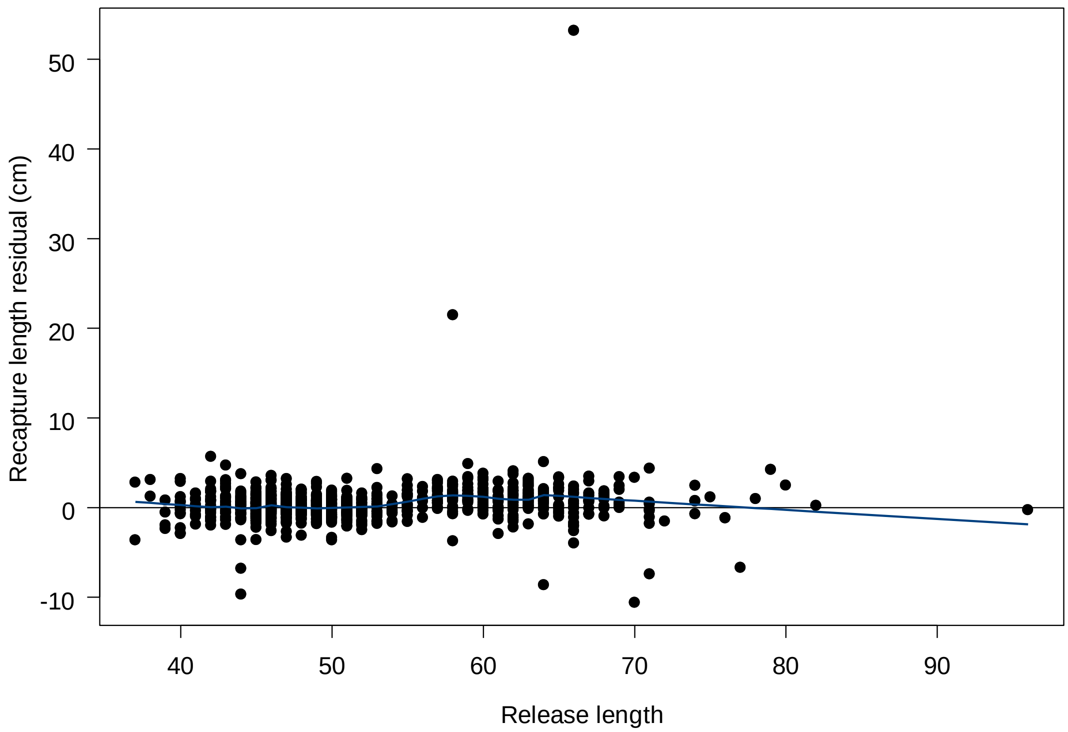


Figure B5. Diagnostic plots from fitting a VB log k growth function to the bigeye tag-recapture data using the LEP method, assuming a lognormal distribution for *A*. (a) Histogram of the estimates of *A* for each fish overlaid with the estimated lognormal distribution. (b) Residuals in recapture lengths with a non-parametric smooth (solid line) to help visualize any trends. (c) Release and recapture lengths plotted against estimated age (relative to a0), along with the mean fitted growth curve.

a)



b)


50
40
30
20
10
0
-10
Recapture length residual (cm)
40
50
60
70
80
90
Release length

c)

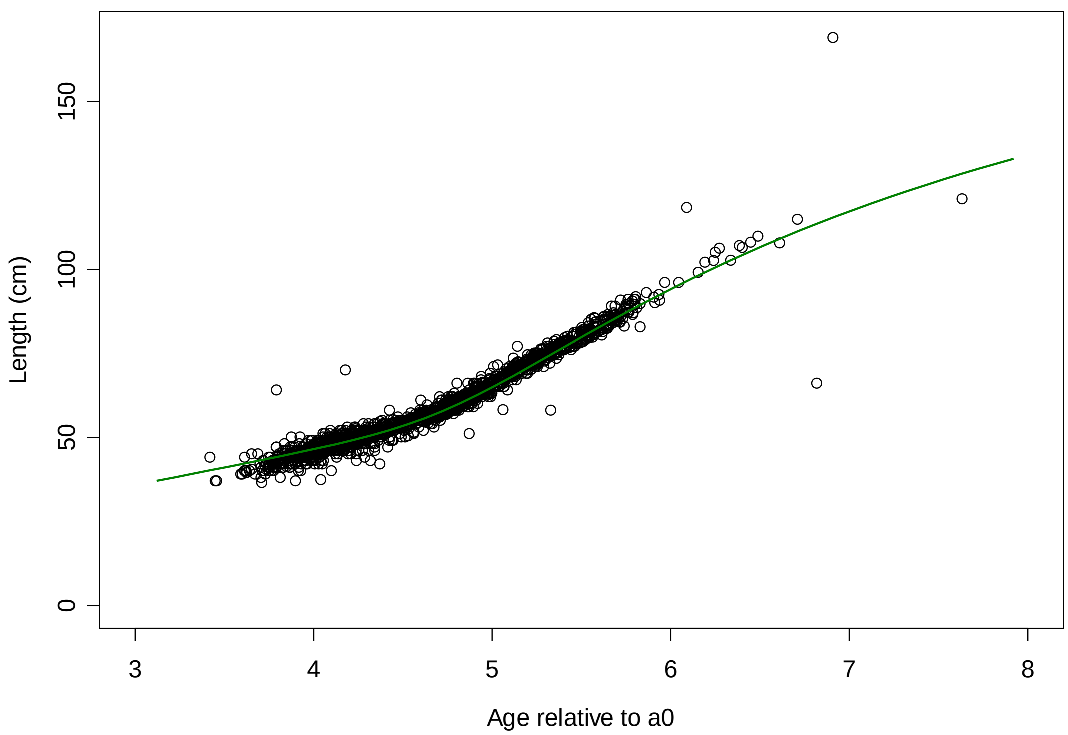

150
100
50
0
Length (cm)
3
4
5
6
7
8
Age relative to a0

Figure S1. Histograms of release lengths, recapture lengths and days at liberty for recaptured skipjack tuna.

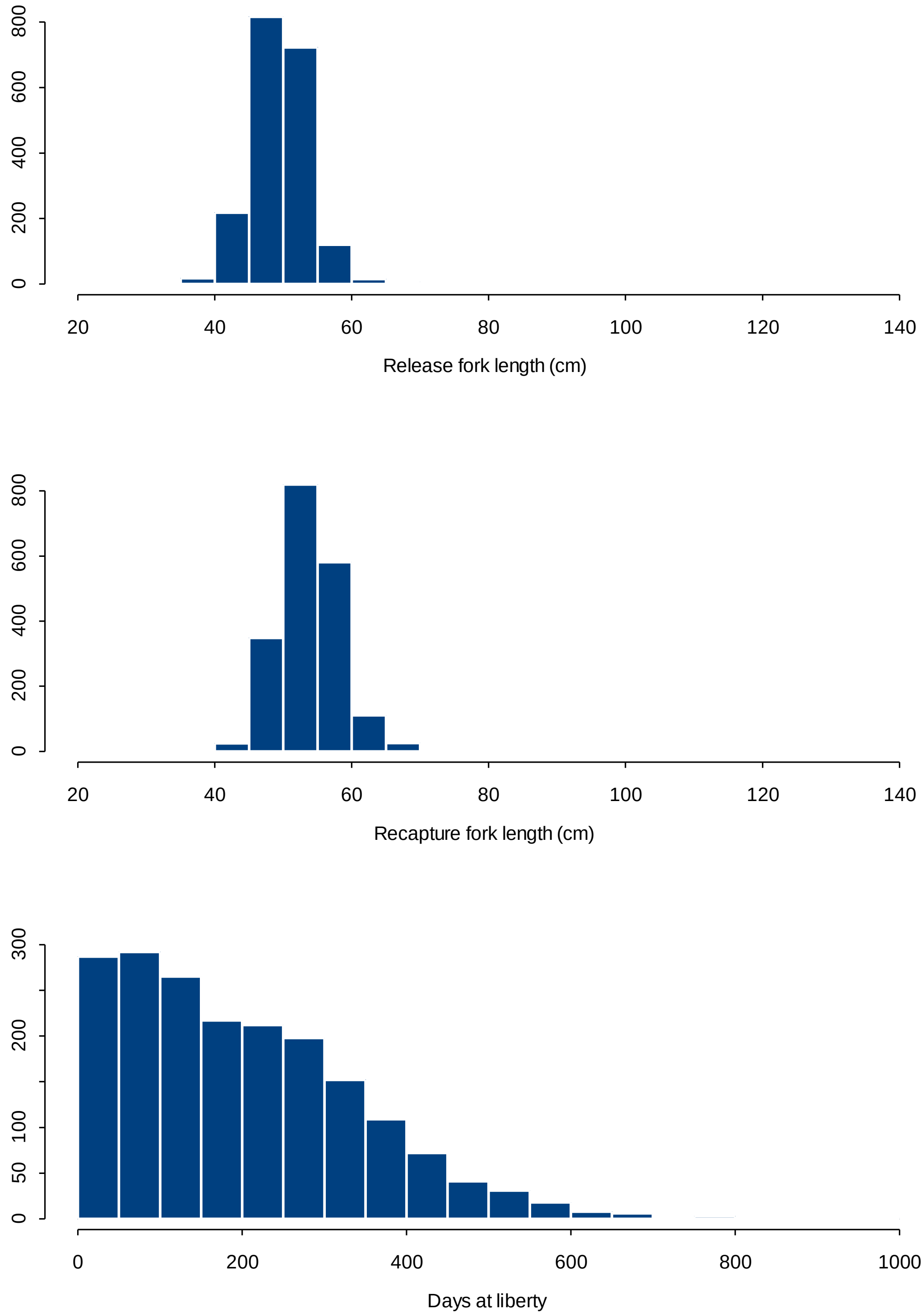


Figure S2. Growth increment (i.e., recapture length – release length) versus time at liberty in days for recaptured skipjack tuna.

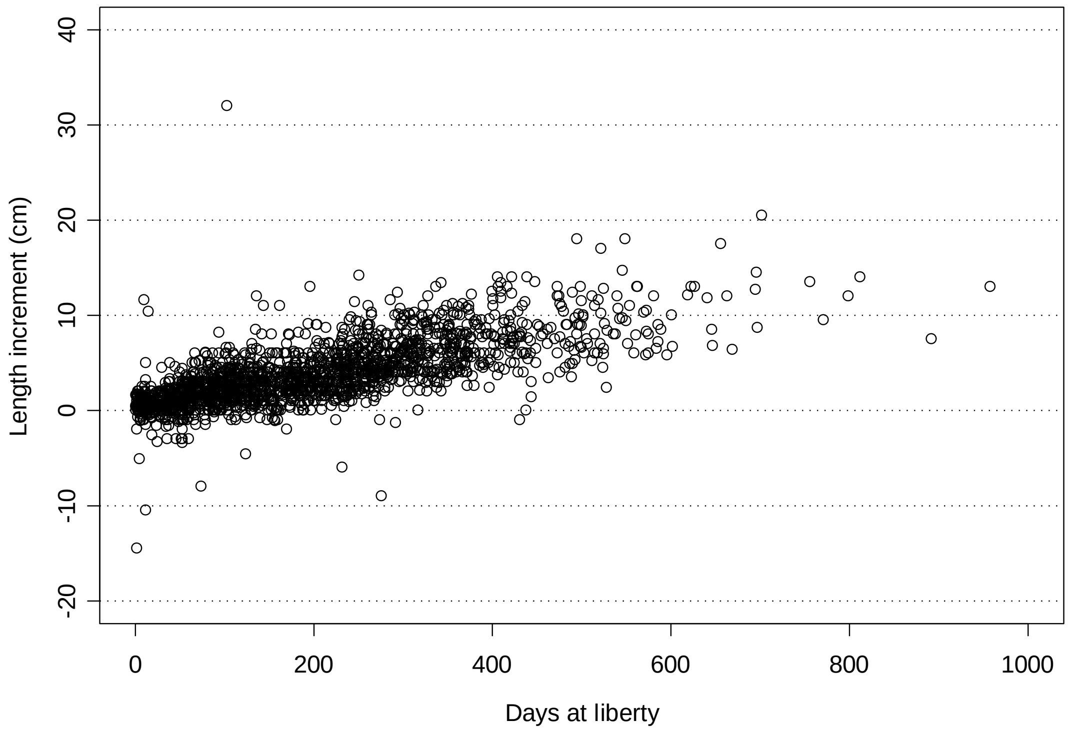
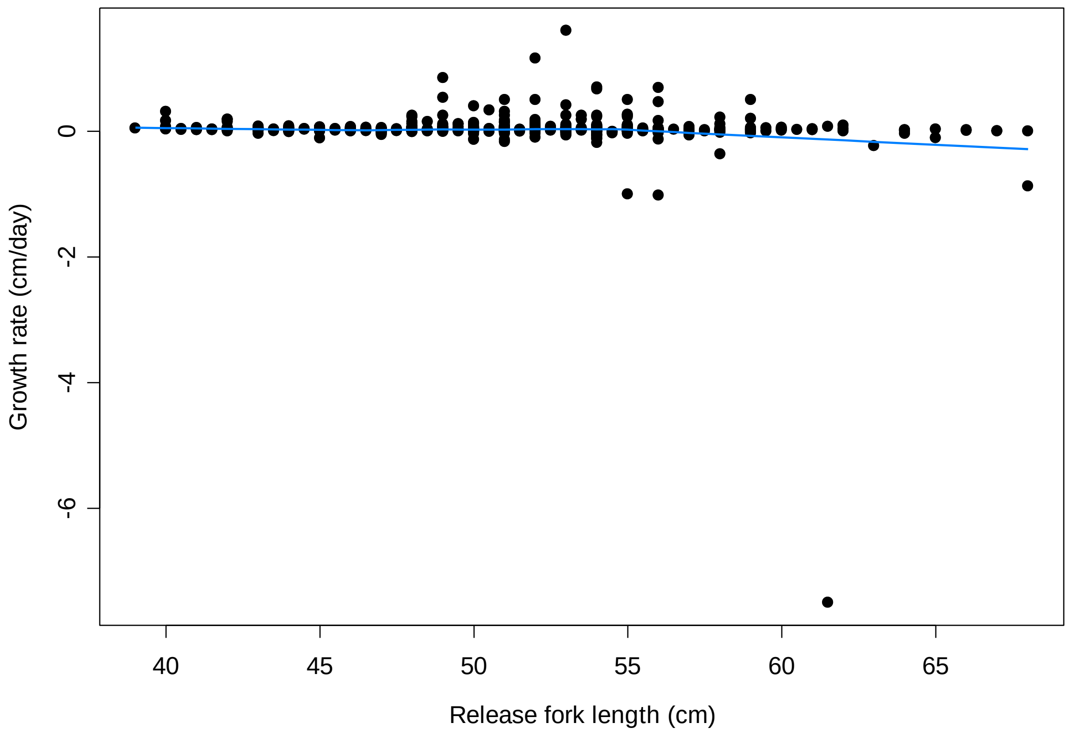


Figure S3. Empirical growth rate of recaptured skipjack tuna (calculated as centimetres growth per day) versus release length. The top plot shows all data; the bottom plot includes only growth rates within the 5th and 95th quantiles. A non-parametric smooth (solid line) has been added to help visualize trends in the data.



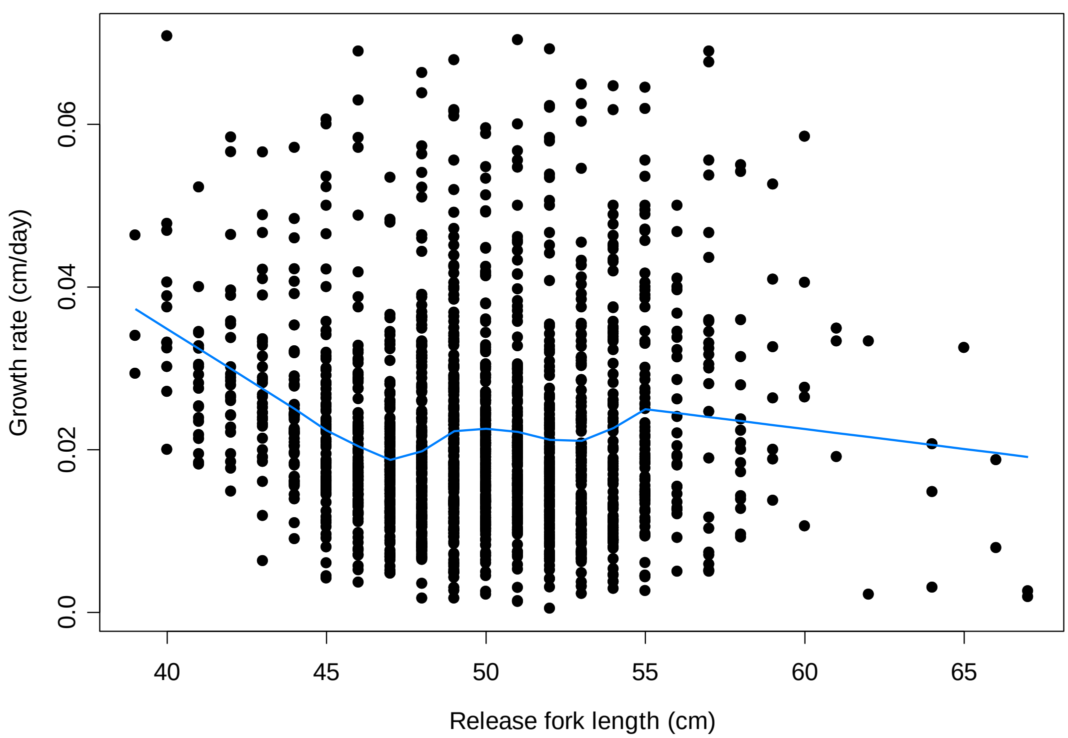
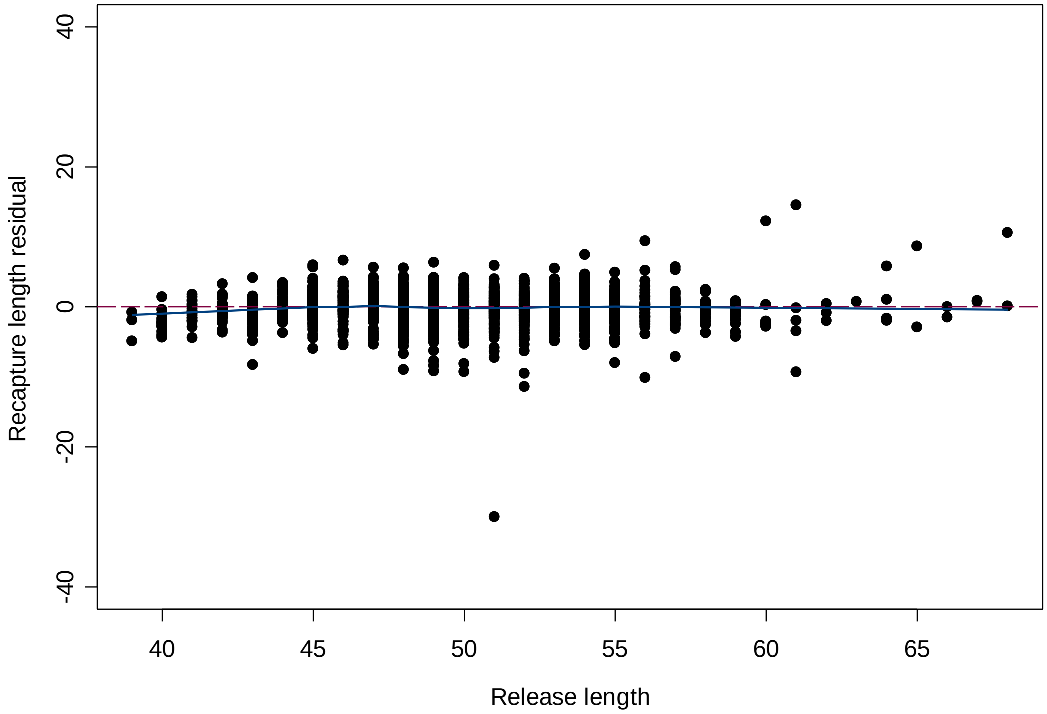
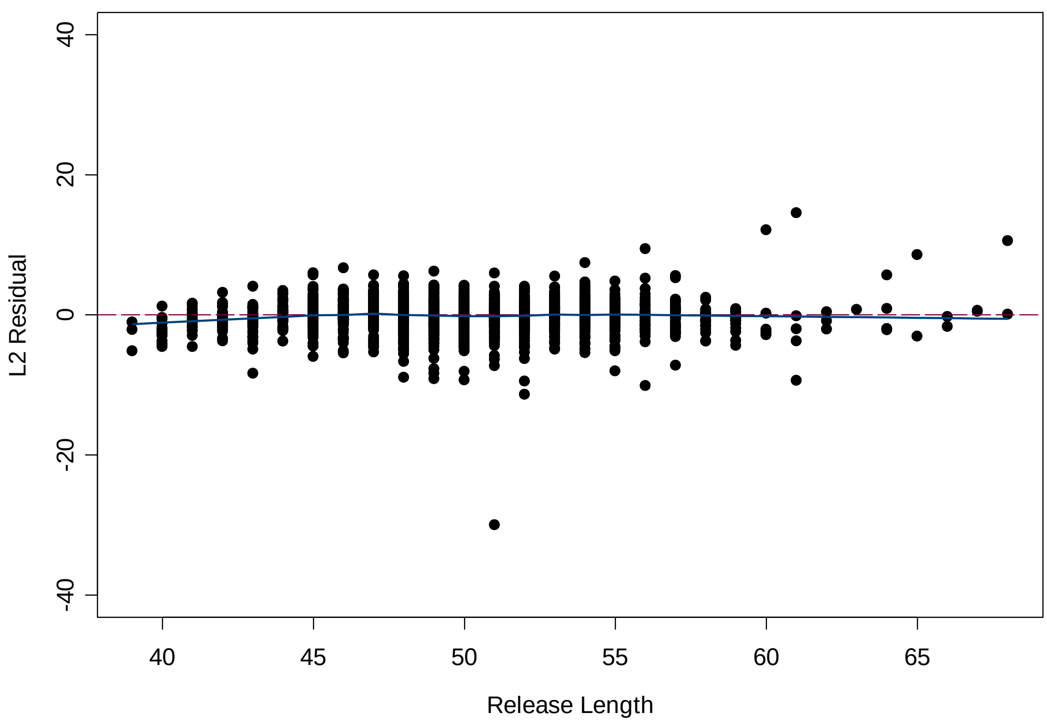


Figure S4. Residuals from fitting the four candidate growth functions to the skipjack tag-recapture data using Fabens method. A non-parametric smooth (solid line) has been added to help visualize any trends. (In the y-axis label, L2 denotes recapture length.)

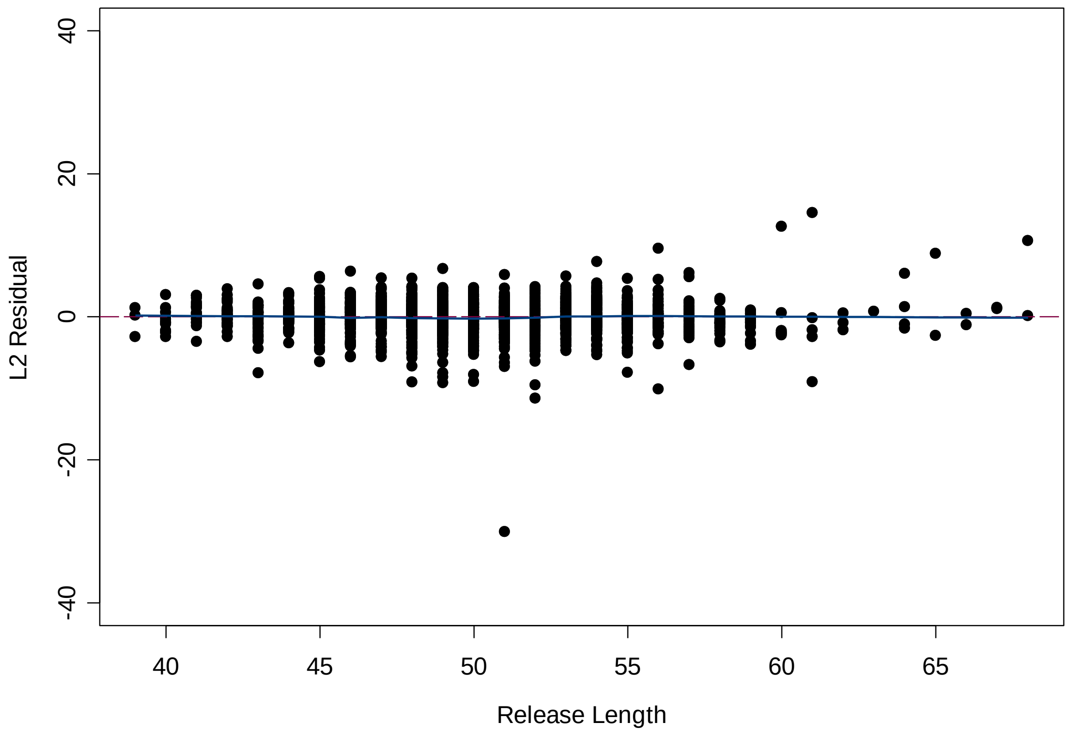
i) VB



ii) Richards



iii) 2-Stage VB



iv) VB log k

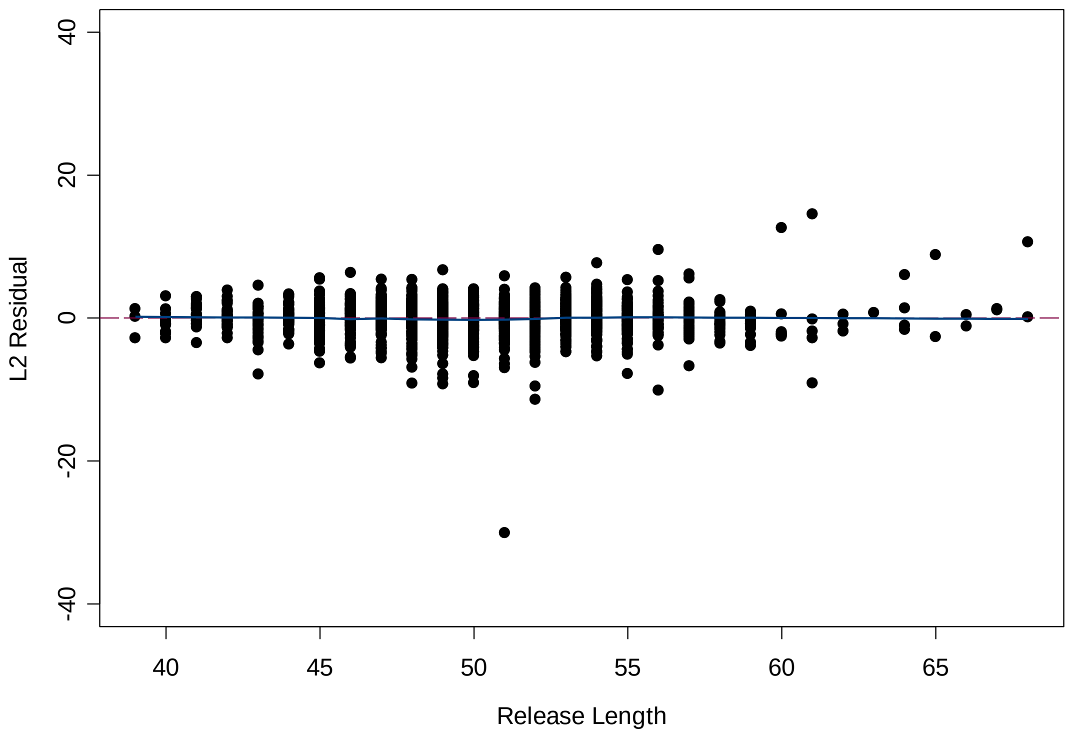
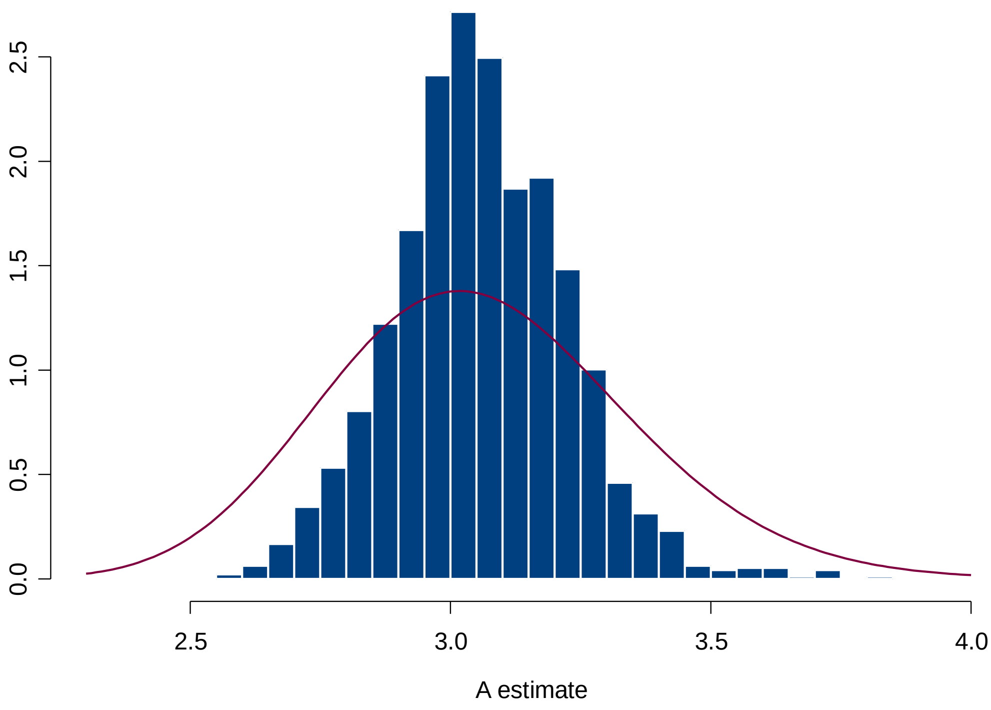
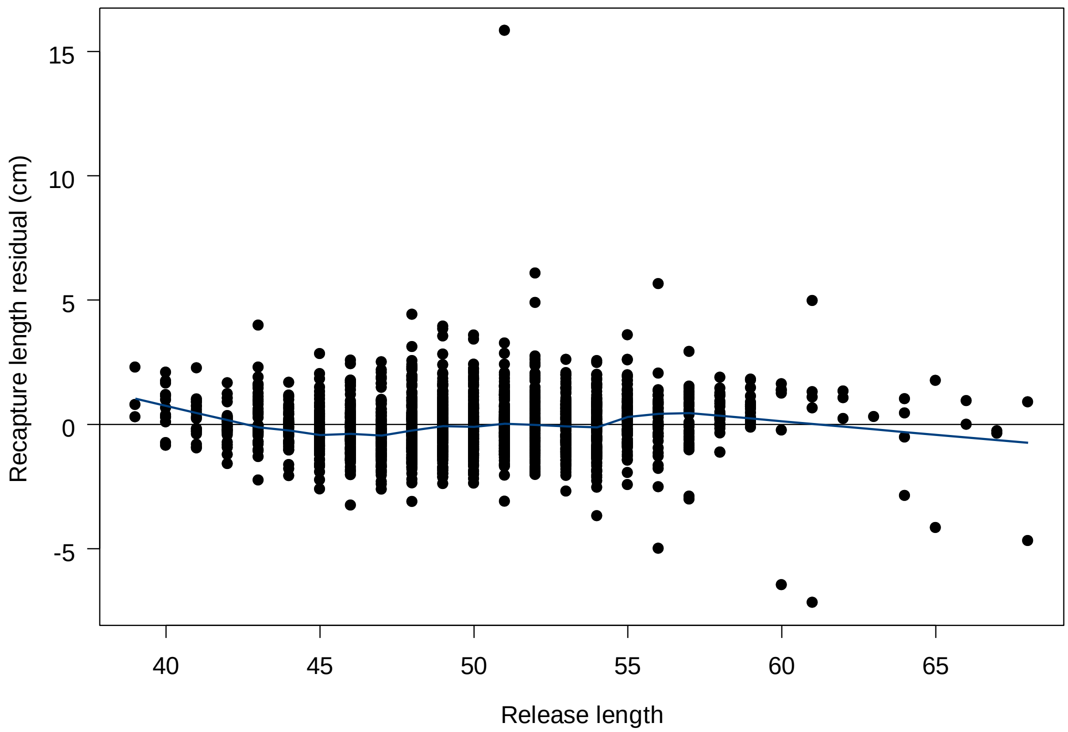


Figure S5. Diagnostic plots from fitting a VB growth function to the skipjack tag-recapture data using the LEP method, assuming a lognormal distribution for *A*. (a) Histogram of the estimates of *A* for each fish overlaid with the estimated lognormal distribution. (b) Residuals in recapture lengths with a non-parametric smooth (solid line) to help visualize any trends. (c) Release and recapture lengths plotted against estimated age (relative to a0), along with the mean fitted growth curve.

a)

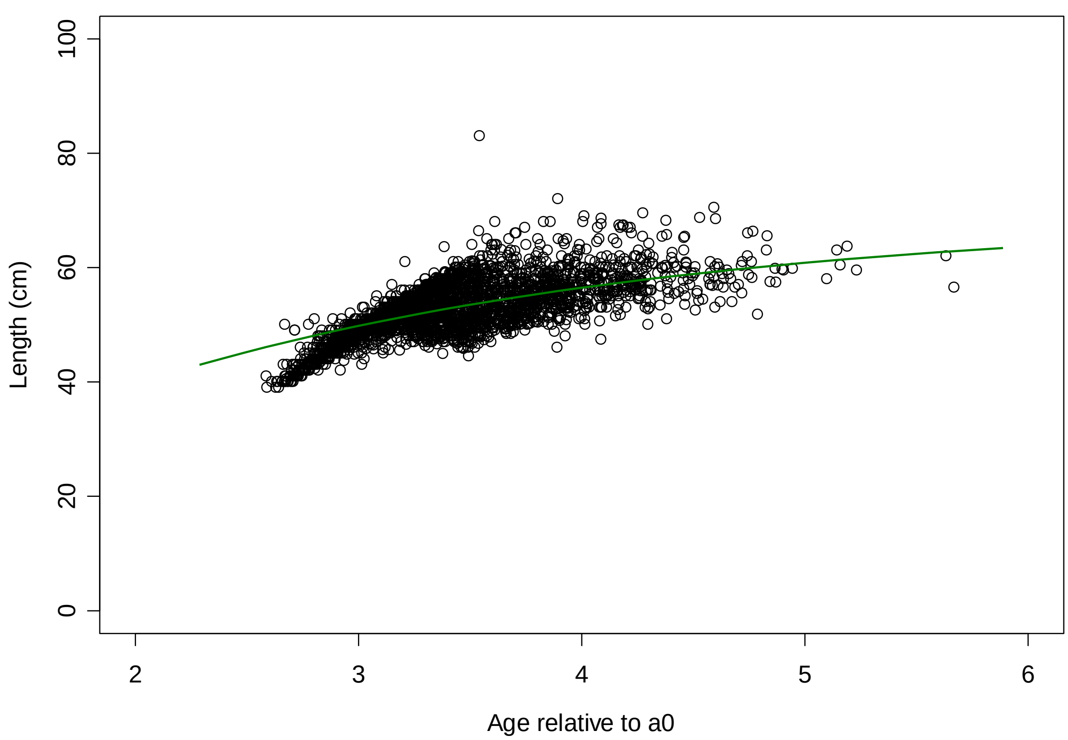


b)



Recapture length residual (cm)
15
10
5
0
-5
40
45
50
55
60
65
Release length

c)



Length (cm)
100
80
60
40
20
0
2
3
4
5
6
Age relative to a0