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**Integrated growth models from otolith and tagging data for yellowfin and bigeye tuna in the  
western and central Pacific Ocean**

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# 1 Abstract

Although growth estimates can have a large impact on stock assessment results and estimated stock status, growth information on yellowfin (*Thunnus albacores*) and bigeye (*T. obesus*) tuna in the western and central Pacific Ocean has, until recently, been limited. However, otolith growth studies conducted over the past few years have provided comprehensive age and length data for both species, plus tag-recapture data from a number of tagging studies in the region has accumulated. Integrated growth models were fit to the most recent otolith age and length and tag-recapture data for both species. The results show discrepancies between the two datasets for both species, with the tag-recapture data suggesting slower initial growth followed by a faster “second phase”, and a larger asymptotic length. The reason for these discrepancies is not yet understood and needs to be further investigated.

# 2 Introduction

Growth information for bigeye and yellowfin tuna in the western and central Pacific Ocean (WCPO) has, until recently, been limited. However, otolith studies conducted over the last few years have provided comprehensive age and length data for both species, plus tag-recapture data are available from a number of tagging studies conducted in the region over the past few decades. Estimates of growth used in stock assessments can be highly influential; this was seen for bigeye in the WCPO, for which the new otolith growth data suggested fish are considerably smaller-at-age than assumed in previous stock assessments (Farley et al. 2017) and inclusion of these data in the 2017 WCPO bigeye tuna stock assessment contributed to a much more optimistic view of stock status (McKechnie et al. 2017).

When fitting growth models, integrating multiple data sources can be beneficial since different data sources will often be most informative about different portions of the life cycle and different aspects of growth. For example, tag-recapture data are the only data that provide more than one observation per fish and, thus, valuable information about how individuals grow. While tagging data provides useful information about the growth rate of an animal, the animal’s age is unknown. Otolith direct aging data provide a direct estimate of the age of individuals, and often provide the only (or at least the majority of) information on older individuals. The use of an integrated approach allows for the different data sources to complement each other and provide a more robust and comprehensive basis for modelling growth.

Tagging datasets that are intended to estimate growth of fish should have a number of characteristics in order to provide useful information to the model. First, the time at liberty of each tag must be accurate. The release date of tags is typically well known and often recorded to the hour. Thus, uncertainty in the time at liberty is generally due to the recovery information. The second necessary feature of a high confidence tagging dataset is that the measurement of the fish at both release and recapture must be precise. Measurement error in either the length at release or recapture increases the uncertainty in the growth increment for a returned fish. Ideally, the measurement method (i.e., upper jaw to fork in tail length, UF) and measurement tool used would be consistent between release and recapture in order to reduce bias in growth increment measurements.

In this paper, we present results from fitting an integrated growth model to the most recent otolith and tagging datasets for both yellowfin and bigeye tuna in the WCPO. The integrated model used here was first developed for application to southern bluefin tuna (Eveson et al. 2004), and has since been applied to yellowfin and bigeye tuna in the Indian Ocean (Eveson et al. 2015).

## 3 Data

### 3.1 Tag-recapture data

Three tagging databases were investigated to develop a dataset to be used in the integrated growth models: the Regional Tuna Tagging Program (RTTP), the Pacific Tuna Tagging Program (PTTP), and the Japanese Tagging Program (JTP). The PTTP database has the most tag recoveries and the most information available for each tag release and return. Therefore, the PTTP database was initially investigated to develop a high confidence tagging dataset. This database consists of 80,800 tag returns of which 18,355 are yellowfin tuna and 13,123 are bigeye tuna.

#### ***High confidence tagging dataset***

The PTTP data were filtered sequentially according to various criteria in order to create a “high confidence” tagging dataset, for which the time at liberty and length at release and recapture were considered reliable. First, tagged fish were removed from the dataset where the species recorded at release did not match the species recorded at recapture. Similarly, tagged fish were removed from the analysis if the species or length at release had not been recorded properly and had been assigned a value based on the majority or mean of the school from which it was tagged. We also removed any tags that were part of a tag seeding experiment, were found at a cannery, or were not returned to a tagging agency. We also only retained tagged fish that were released and recaptured within the WCPO. Originally, we restricted our selection of tags to those that we believed would have accurate measurements of length at recapture; therefore, we started by using tag returns that had been measured by an observer, a tag return officer, or a port sampler with a measuring instrument. We then filtered these tags based on the uncertainty in the recapture date and the length at recapture. Specifically, the age at recapture was calculated using the growth curve in the most recent assessment for each species. The uncertainty in the tag return date was added to the calculated age and this new age was inserted back into the growth curve to give a predicted length. The difference between this predicted length and the observed length gave the amount of growth that could be expected given the uncertainty in the recapture date. Most tag return measurements are rounded to the nearest 1 cm and this was deemed to be an acceptable amount of measurement error. Therefore, tags were removed from the dataset if the expected growth given the uncertainty in the recapture date was greater than 1 cm. This allowed for the retention of larger fish with more uncertain dates of recapture, where growth is expected to be minimal, but removed fish that were relatively small and thus more likely to have larger growth increments in shorter periods of time.

This left only about 100 tag returns for each species with which to estimate growth; thus, we expanded our criteria to include any tags that had been returned in Japan. It was believed that tag returns from Japan were generally measured by port samplers, and although the forms used may not have information regarding the measurer, we decided these data should be included in the high confidence dataset. Similarly, a few recaptured fish that were measured by eye were removed, but we retained many for which the measurement method was unknown because it was thought that fish were generally accurately measured using a tool. The same filtering techniques described above were applied to these tag returns, which once again left approximately 100 fish for each species. These tags did not include many tag returns of large fish, so the rejection criteria were relaxed to include any tags that had been recaptured by a longline vessel and had been measured with a tool, regardless of the person measuring the fish. After the same filtering steps as above, only about 10 additional tags for each species were included in the high confidence tagging dataset. In total the high confidence tagging dataset consisted of 161 bigeye and 416 yellowfin tag returns (Figure 1).

There were insufficient recaptures in the PTTP high confidence dataset to substantially inform growth estimation for each species; in particular, there were very few large fish to inform the average maximum size of fish ( $L_{\infty}$ ). Furthermore, we investigated the difference between the release length and recapture length after 5 days at liberty to inform the measurement error in the growth increments (Figure 2). Given

the short period at liberty, we would expect any difference between lengths at release and recapture to be due to measurement error because it is unlikely for fish to grow significantly in such a short time period. Despite the rigorous filtering applied to the PTPP database there was still quite large measurement error in the data. Therefore, we concluded that there may be significant measurement error at release that could be related to the difficulty of measuring a live fish. The measurement error observed in the PTPP for bigeye and yellowfin was similar to the measurement error observed for skipjack from the skipjack stock assessment program (Lawson et al. 1984). Thus, we determined that a high confidence tagging dataset was not feasible and created a “moderate confidence” tagging dataset that included tags from the RTPP and JPTP, as well as additional tags from the PTPP where the quality of measurements at recapture were less certain.

### ***Moderate confidence tagging dataset***

To form a moderate confidence tagging dataset, tag returns from the PTPP were included for which recapture length was measured by an unknown person or a crew member as long as it was measured using a measuring tool. These tags were further filtered by the methods described above. We attempted to replicate the same methods for the RTPP and JPTP databases, but the necessary information was not recorded for these tagging programs. Tags returns from the RTPP were removed if any of the following conditions were true: 1. They were tagged outside of the WCPO or recaptured outside of the WCPO; 2. The species recorded at release did not match the species recorded at recapture; 3. The tag was found at a cannery; 4. The quality of measurement at release was thought to be inaccurate; 5. There was no vessel name of recovery; and 6. The uncertainty in the recapture date could result in greater than 1 cm of growth given the recapture length. For the JPTP, tag returns were removed that did not have known recapture location, release location, recapture date or measured length at release or recapture. Combining these data sources left a total of 2915 bigeye and 4336 yellowfin tag returns (Figure 3).

Throughout the process of filtering the data, the proportion of tags that had a length at recapture less than release was used as an indicator of the measurement error in the tag return data. It is generally accepted that fish length cannot decrease and thus a negative change in size would be due to measurement error either at release or recapture. Despite the numerous filtering steps described above, the proportion of tag returns with a negative change in size remained at approximately 25%. In addition, a large number of fish had a positive growth increment, but their rate of growth was considered unrealistic based on the time at liberty (see Figure 4 and Figure 5).

Thus, we concluded that additional filtering external to the information available within the tagging databases would be required. First, we omitted fish at liberty for less than 30 days, which not only eliminated a large percent of fish with negative growth, but also allowed for an initial effect of tagging on growth (assumed to be negligible after 30 days). This removed 51% of the bigeye records, and 43% of the yellowfin records. Second, a filtering process was applied that omitted records for which the growth rate (i.e., change in length between release and recapture divided by time at liberty) was outside a specified range of the data. Since the expected growth rate depends on both the release size of a fish and the time it was at liberty, we grouped fish into release size and time at liberty categories. Then, for each group, we omitted fish with a growth rate more than  $x$  times the interquartile range below the first quartile or above the third quartile of all growth rates in that group. Note that this is the criteria used in the boxplot function in R to determine outliers, where  $x$  is set using the range argument of the function. The categories used to group fish and the value of  $x$  were different for bigeye and yellowfin: for bigeye, fish were grouped into release lengths of <60 cm, 60-80 cm and >80 cm and days at liberty of 30-180, 180-365, 365-730 and >730 days, and a value of  $x=1$  was used; for yellowfin, fish were grouped into release lengths of <40 cm, 40-60 cm and >60 cm and days at liberty of 30-180, 180-365 and >365 days, and a value of  $x=0.5$  was used. This removed an additional 13% of bigeye records and 24% of yellowfin records, leaving 1256 bigeye and 1881 yellowfin tag returns for input to the integrated growth models.

Figure 4 and Figure 5 show which data were excluded from the integrated models for bigeye and yellowfin, respectively. While most of the excluded points are obvious outliers, some are less clear; unfortunately, we could not find an automated and impartial procedure that excluded all of the “obvious” outliers but did not also exclude some potentially legitimate records. Excluding these points should not bias the mean growth

curve since filtering was done in an unbiased/symmetric manner; however, it could reduce the estimated variability in length at age (i.e., result in smaller measurement error and/or process error estimates).

## 3.2 Otolith data

Farley et al. (2020) describes the otolith age and length data available for yellowfin and bigeye tuna in the WCPO, and presents results from fitting growth models to the otolith data alone, using all samples and only those for which the age readings had high readability scores ( $\geq 3$ ). In this paper, we use the same otolith datasets used in the otolith-only growth models to fit the integrated growth models, and we also fit the models using all of the otolith data and only the data with high readability scores.

# 4 Methods

Before fitting a growth model to the data, we needed to choose which growth function to use to describe mean length at age. A number of different functions exist, with the von Bertalanffy (VB) being the most common in fisheries. Here we considered both a VB function (eq 1) and a Richards function (eq 2), sometimes referred to as a generalized logistic, which allows for an S-shaped curve.

$$(1) \text{ VB growth function: } L_t = L_\infty(1 - e^{-k(t-t_0)})$$

$$(2) \text{ Richards growth function: } L_t = L_\infty(1 - \frac{1}{\beta}e^{-k(t-t_0)})^\beta$$

For both functions,  $L_t$  is upper jaw fork length (cm) at age  $t$  (years),  $L_\infty$  is the mean asymptotic length, and  $k$  is a relative growth rate parameter ( $\text{yr}^{-1}$ ). For the VB function,  $t_0$  is the age at which individuals have a theoretical length of zero (i.e. the curve crosses the x-axis). For the Richards function,  $t_0$  determines the point of inflection and  $\beta$  governs the shape of the curve.

The method used to fit these growth functions to the tagging and otolith data is a maximum likelihood approach, with an independent likelihood component for each of the datasets. The likelihoods are described in detail in Eveson et al. (2004, 2015); thus, only an overview will be given here. The method works for any growth function of the form:

$$L_t = L_\infty f(t - t_0; \theta)$$

where  $f$  is a monotone increasing function with parameter set  $\{t_0, \theta\}$  that approaches 1 as  $t \rightarrow \infty$ . For the VB function  $\theta = \{k\}$ , and for the Richards function  $\theta = \{k, \beta\}$

The likelihood for the tag-recapture data was developed by Laslett et al. (2002). The key feature of this method is that it models the release and recapture lengths ( $l_1$  and  $l_2$  respectively) as functions of age by treating age at tagging,  $A$ , as a random variable<sup>1</sup>.  $A$  is assumed to follow a specified distribution, and the parameters of this distribution are estimated within the model. If we condition on  $A$ , then the joint distribution of  $l_1$  and  $l_2$  is bivariate normal (see Laslett et al. 2002 for the explicit formula), and their unconditional joint density can be obtained by integrating over  $A$ . Here, a lognormal distribution with parameters  $\mu_{\log A}$  and  $\sigma_{\log A}$  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.

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<sup>1</sup> Note that  $A$  actually represents the age at tagging relative to  $t_0$ . The parameter  $t_0$  cannot be estimated from tagging data alone, but it can be with the inclusion of otolith data.

Another feature of this method is that it allows for individual variability in growth by modelling the asymptotic length parameter as a random effect. Here,  $L_\infty$  was assumed to follow a normal distribution with mean  $\mu_{L_\infty}$  and standard deviation  $\sigma_{L_\infty}$ .

The model also allows for any extra variability in length at age through an additive Gaussian error component with mean 0 and standard deviation  $\sigma_{tag}$ , which represents measurement error and/or additional process error. We allow for the recapture lengths of fish that were included in the high confidence dataset to have smaller measurement error than those of fish found only in the moderate confidence dataset by modelling  $\sigma_{tag}$  as follows:

$$\sigma_{tag}^2 = \begin{cases} \sigma_s^2 & \text{if from high confidence dataset} \\ \sigma_s^2 + \sigma_f^2 & \text{if from moderate confidence dataset only} \end{cases}$$

For the otolith likelihood, we assumed a Gaussian error distribution for length ( $l$ ) at age ( $t$ ) with mean

$$E(l) = \mu_{L_\infty} f(t - t_0; \theta)$$

and variance

$$V(l) = (\sigma_{L_\infty} f(t - t_0; \theta))^2 + \sigma_{oto}^2$$

where the first component of variance is due to individual variability in  $L_\infty$  and the second component is additional measurement/process error component. Note that, unlike the tag-recapture likelihood, the parameters that can be estimated from optimizing the otolith likelihood include  $t_0$ .

Residual plots were used to evaluate the model fits to both datasets. Note that to calculate residuals for the tagging data requires us to calculate fitted release and recapture lengths; to do so, we need to have a realized value of  $A$  for each fish. A natural approach is to use the mean of the posterior distribution for  $A$  conditional on the fish's release and recapture lengths. However, as explained in Laslett et al. (2004), this approach yields biased estimates, so we used the approximately conditionally unbiased estimator for  $A$  proposed in Laslett et al. (2004) instead.

## 5 Results

### 5.1 Bigeye

Figure 6 shows a map of the sampling locations for the otolith data and the tag-recapture data. Although there are areas of overlap, the otolith data are more concentrated to a central region than the tagging data (particularly the recaptures).

Figure 7 shows histograms of the release lengths, recapture lengths and times at liberty for tagged and recaptured bigeye included in the growth models. There are two modes in the release lengths at ~50-55 cm and 75-80 cm, which likely correspond to different age classes. The mean and median times at liberty are 422 and 203 days respectively, and the maximum is 5065 days.

Parameter estimates from fitting VB and Richards models to the otolith and tag-recapture data for bigeye are given in Table 1, using all otoliths and only those with high readability. In both cases, the mean VB and Richards growth curves are very similar (see Figure 8), but the Richards model provides a slightly better fit based on AIC (Table 1).

Figure 9 provides a series of diagnostic plots for the integrated Richards model for bigeye; only results using the high readability otolith data are shown since the results using all data are almost identical. Figure 9 (a) shows the estimated release ages for all fish, overlaid with the estimated lognormal distribution (note that

the age and log normal distribution estimates obtained directly represent age relative to  $t_0$ , but the age axis has been shifted by the estimated value of  $t_0$  so that it represents absolute age). Even though a unimodal distribution is being assumed, the individual age estimates are still able to capture the bimodal nature of the release ages suggested by the release lengths. Figure 9 (b) shows the mean fitted growth curve, overlaying the data – recall that age is not known for the tagging data, so the data are plotted using the estimated ages (see Methods). Figure 9 (c) shows the release and recapture length residuals (fitted minus true) plotted against length; there is a clear upward trend in the residuals, particularly for the recapture lengths, that indicates the model does not fit the tagging data well. Finally, Figure 9 (d) shows the residuals for the otolith data; there is an obvious lack of fit for fish <3 years.

## 5.2 Yellowfin

Figure 10 shows a map of the tag-recapture and otolith sampling locations for yellowfin, which are very similar to those for bigeye. Again, there are some areas of overlap between the two datasets, but the otolith data are more concentrated to a central region than the tagging data (particularly the recaptures).

Figure 11 shows histograms of the release lengths, recapture lengths and times at liberty for tagged and recaptured yellowfin included in the growth models. There is only one mode in the release lengths for yellowfin, centred at ~40 cm, with only a small number of fish tagged at sizes >70 cm. The mean and median times at liberty are 208 and 141 days respectively, and the maximum is 2380 days, which are substantially shorter than for bigeye.

Parameter estimates from fitting a VB model to the otolith and tag-recapture data for yellowfin are given in Table 2, using all otoliths and only ones with high readability. We could not get the Richards model to converge (the issue seeming to stem with estimating the release age distribution), so only the VB results are presented. Based on fitting VB and Richards models to the yellowfin otolith data alone (see Farley et al. 2020), the two models gave very similar results; thus, the VB model should be sufficient for evaluating how well an integrated model fits the data.

Figure 12 provides a series of diagnostic plots for the integrated VB model for yellowfin; only results using the high readability otolith data are shown since the results using all data are almost identical. Figure 12 (a) shows the estimated release ages for all fish, overlaid with the estimated lognormal distribution (again noting that the age axis has been shifted by the estimated value of  $t_0$  so that it represents absolute age). Figure 12 (b) shows the mean fitted growth curve, overlaying the data – recall that age is not known for the tagging data, so the data are plotted using the estimated ages (see Methods). Figure 12 (c) shows the release and recapture length residuals (fitted minus true) plotted against length; there is a clear pattern in the recapture residuals that suggest lengths of younger fish are being overestimated, and those of older fish are being underestimated. Finally, Figure 12 (d) shows the residuals for the otolith data; a smoothed curve through the data shows a lack of fit similar to that seen for the bigeye otolith data.

## 6 Discussion

The results of the integrated growth models show a lack of fit to both the otolith data and the tag-recapture data for bigeye and yellowfin in the WCPO. Farley et al. (2020) presents results from fitting VB and Richards growth models to the otolith data alone for both stocks. For bigeye, a Richards model fit the otolith data very well, with the residuals showing no trends or patterns. For yellowfin, the VB and Richards models gave very similar fits to the otolith data alone, and the residuals did not show the same strong pattern seen with the integrated model. Thus, the lack of fit observed for the integrated models appears to be due to inconsistencies between the tagging data and the otolith data, with the tagging data suggesting slower initial growth followed by a faster “second phase” of growth and a higher asymptotic length for both stocks (note that the indication of two-phase growth is strongest for yellowfin).

We investigated possible reasons for the discrepancies, including whether spatial differences in sampling locations or differences in gear types used to catch the fish could account for differences in growth between the otolith data and tagging datasets. To do so, we refit the models, first, limiting both datasets to a central spatial area where they overlapped the most, and second, limiting both datasets to longline captures only. Unfortunately, nothing that we considered resolved the discrepancies, so this remains an issue for discussion.

To reduce the uncertainty in measurement error of future tagging experiments, some changes could be implemented. Current tag return posters describe the measurement of fish as "fork length (from upper jaw to the tail fork) - flat, not body curve length". However, given the large uncertainty in the measurements of fish returned, it may be better to include an option of the measurement tool used on the tag return form, (e.g., callipers, measuring board, measuring tap over fish, measuring tape on ground). These different criteria would make it possible to further filter the data to determine which measurement methods are the most uncertain for the recapture length of fish. Additionally, a detailed description of the expected measurement technique on the tag return website should be displayed. The website should also make it clear that information should not be made up – it is preferable to leave a field blank than to fabricate any data, including the tag recapture date if it is unknown. In general, increasing the knowledge about the tagging program within the fishing community, advertisement of the tagging program, and resources toward collecting recaptured tags is warranted. Minimization of the measurement error at release of fish is also needed. One potential solution is to conduct electronic monitoring during tagging to provide an accurate measurement and species identification of the fish that can be referred to after tagging is completed. This may make it easier for the taggers to focus solely on tagging the fish quickly without the need to identify the species, condition of the fish, quality of tag placement, measure the length of the fish, et cetera. Alternatively, fish in poor condition or with badly placed tags could be retained and measured after they have perished to get a distribution of the measurement error at release directly. Incorporation of these recommendations within the tagging program could potentially allow for analyses of future tagging databases to produce a high confidence tagging dataset.

## 7 Acknowledgments

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## 9 Tables and Figures

**Table 1. Parameter estimates from fitting integrated VB and Richards growth models to the tag-recapture and otolith data for bigeye tuna. HR = high readability.**

Model	Otoliths	N_oto	N_tag	mu_Linf	sig_Linf	k	beta	mu_logA	sig_logA	sig_sci	sig_fish	t0	sig.oto	AIC
VB	All	1264	1256	157.99	10.74	0.348	--	0.376	0.292	2.440	2.194	-0.455	3.666	27057.3
Richards	All	1264	1256	155.26	10.44	0.400	1.342	0.013	0.424	2.446	2.020	-0.030	4.013	27024.8
VB	HR	1010	1256	159.78	12.05	0.339	--	0.391	0.288	2.378	1.954	-0.466	3.597	25290.7
Richards	HR	1010	1256	156.65	11.66	0.393	1.359	0.006	0.427	2.411	1.774	-0.013	3.998	25259.3

N\_oto and N\_tag give the number of otolith and tag-recapture data points used in the models

mu\_Linf and sig\_Linf are the parameters of the normal distribution for Linf;

mu\_logA and sig\_logA are the parameters of the lognormal distribution for the release age (A);

sig\_sci and sig\_fish are the SDs of the release and recapture measurement error distributions for scientists and fishers respectively;

sig\_oto is the SD of the measurement error distribution for the otolith data

**Table 2. Parameter estimates from fitting an integrated VB growth model to the tag-recapture and otolith data for yellowfin tuna. HR = high readability.**

Model	Otoliths	N_oto	N_tag	mu_Linf	sig_Linf	k	mu_logA	sig_logA	sig_s	sig_f	t0	sig_oto	AIC
VB	All	1567	1881	158.71	15.05	0.351	-0.024	0.249	1.695	3.697	-0.405	4.340	37743.0
VB	HR	1471	1881	158.88	15.40	0.349	-0.019	0.248	1.679	3.639	-0.409	4.316	37016.5

See footnote to Table 1 for parameter definitions

Figure 1. Proposed high confidence tagging dataset measured by port samplers, observers and tag return officers.

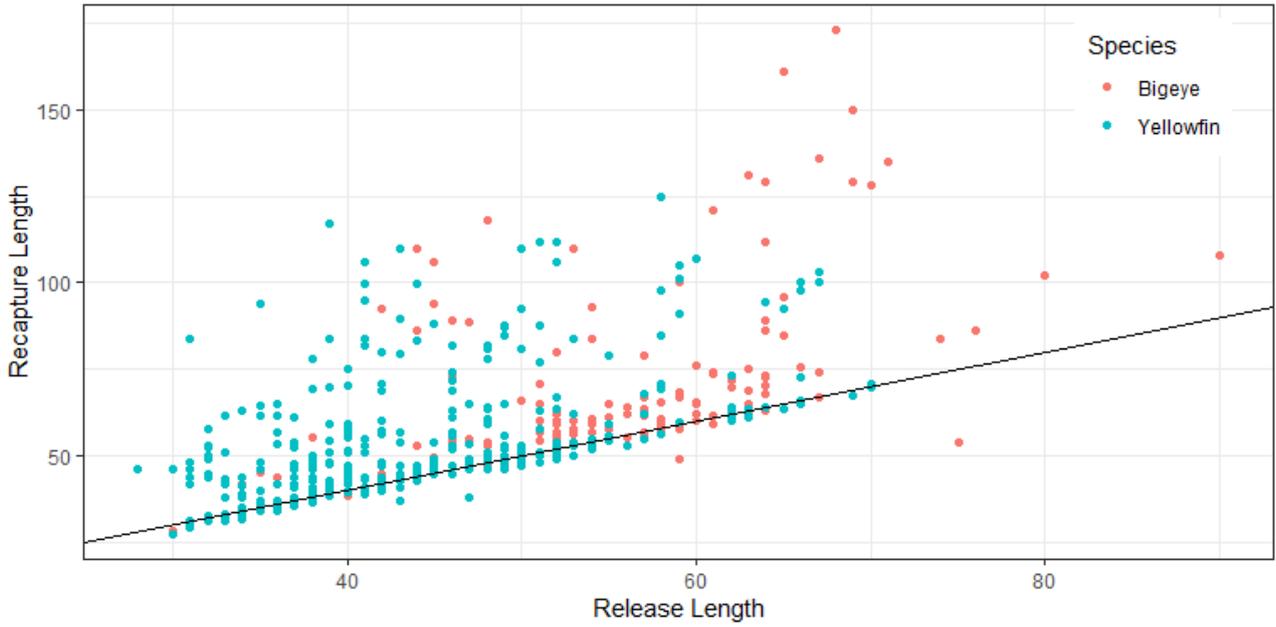


Figure 2. Difference in release and recapture length after 5 days at liberty for bigeye and yellowfin tuna from the proposed high confidence tag set.

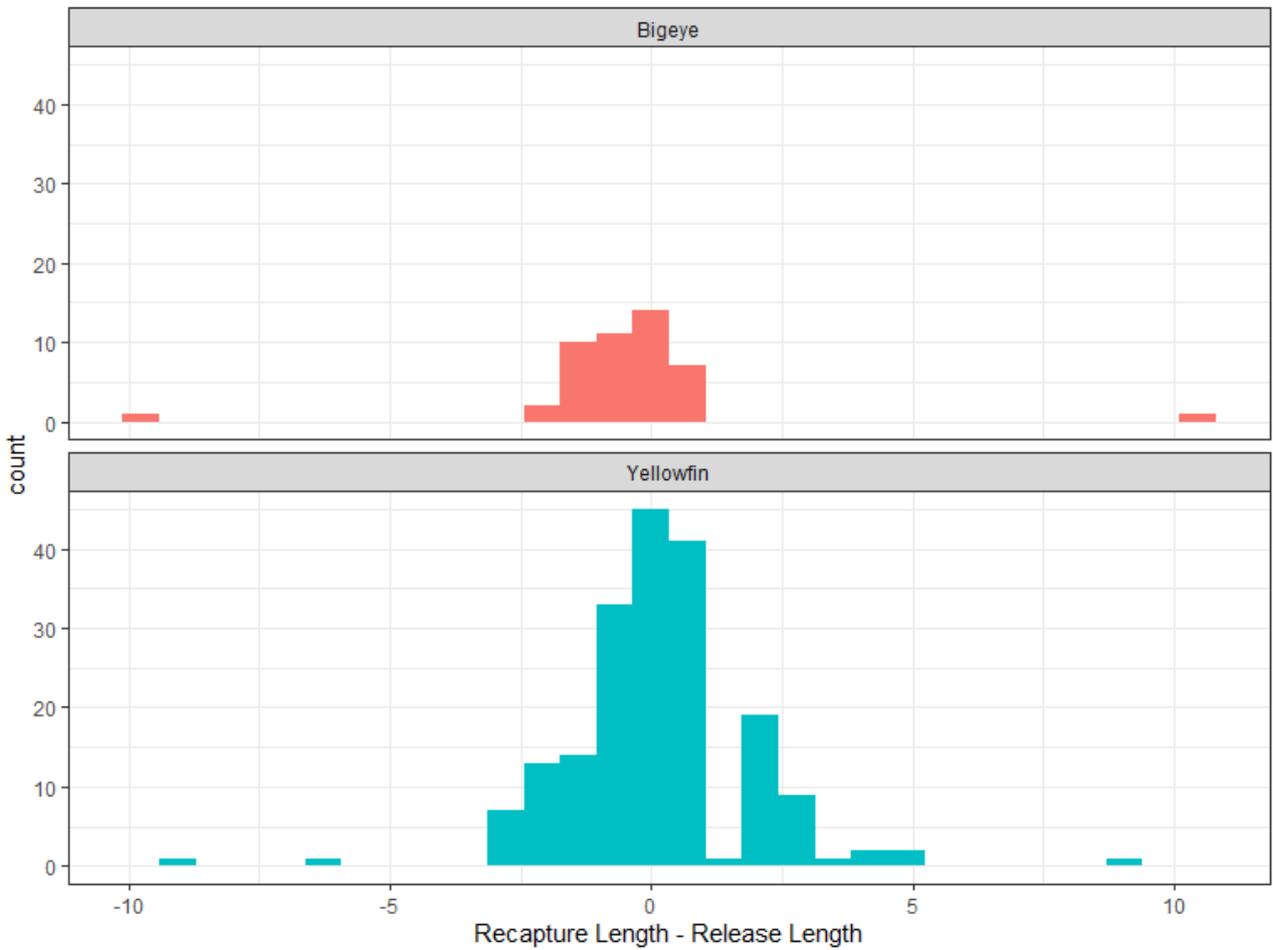


Figure 3. Release and recapture length of yellowfin and bigeye tuna from the PTPP, RTPP and JPTP proposed as the moderate confidence tagging set.

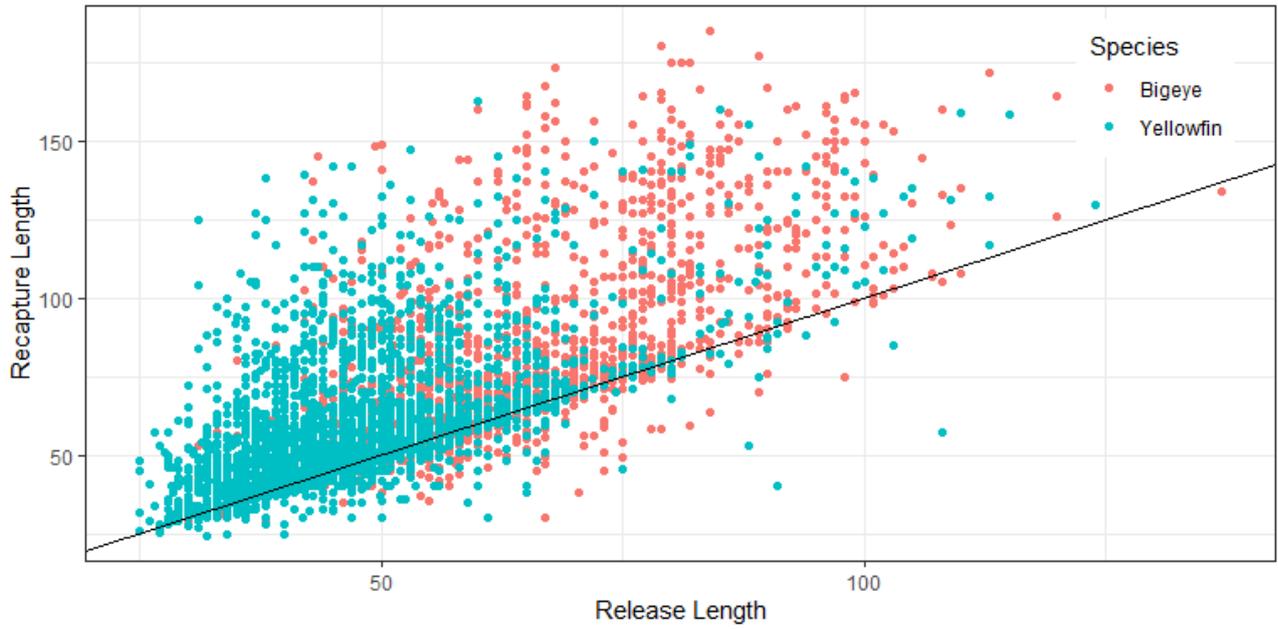


Figure 4. Growth rates by release length category calculated from the tag-recapture data for bigeye, showing points that were omitted from integrated growth models.

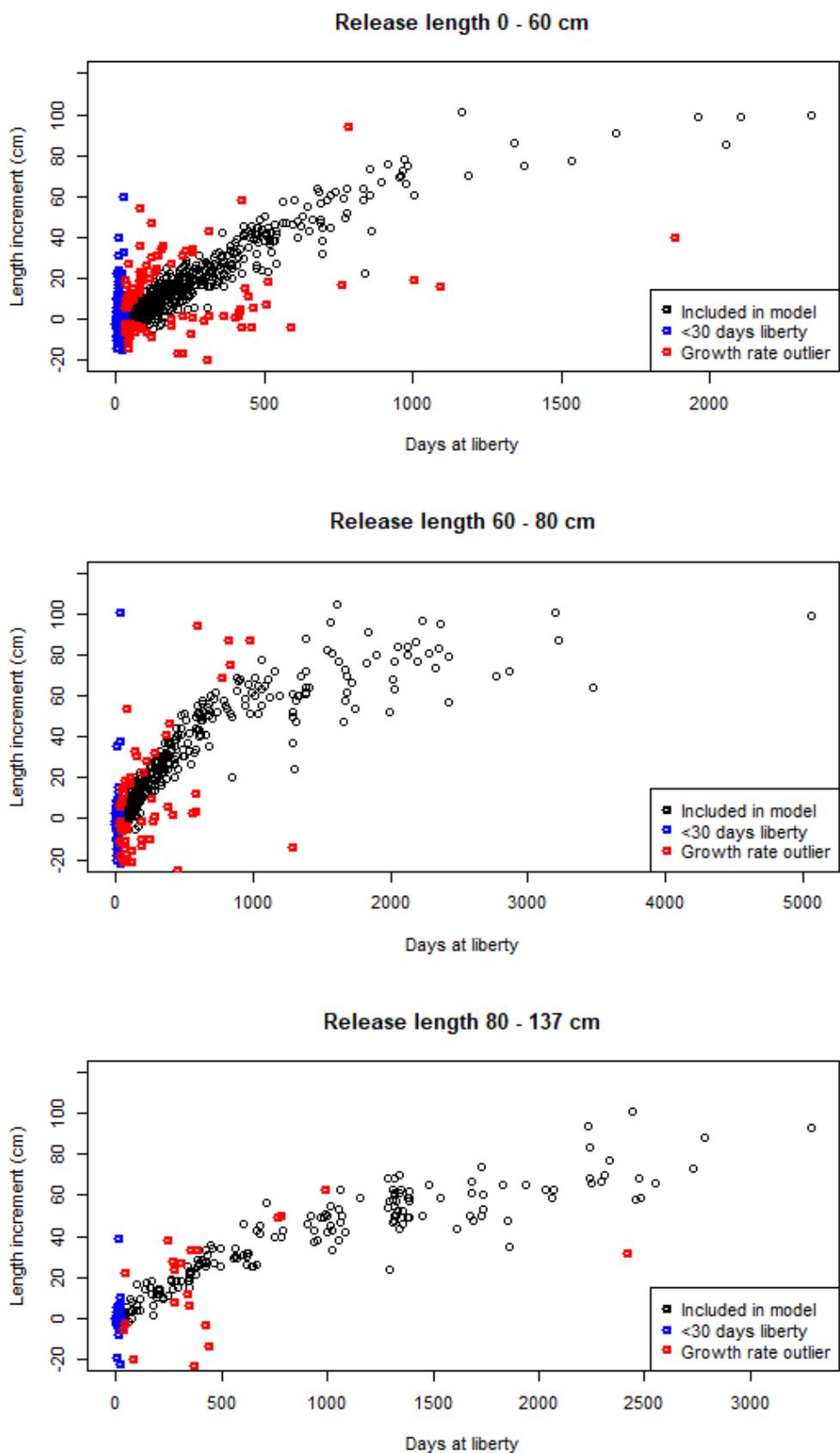


Figure 5. Growth rates by release length category calculated from the tag-recapture data for yellowfin, showing points that were omitted from the integrated growth models.

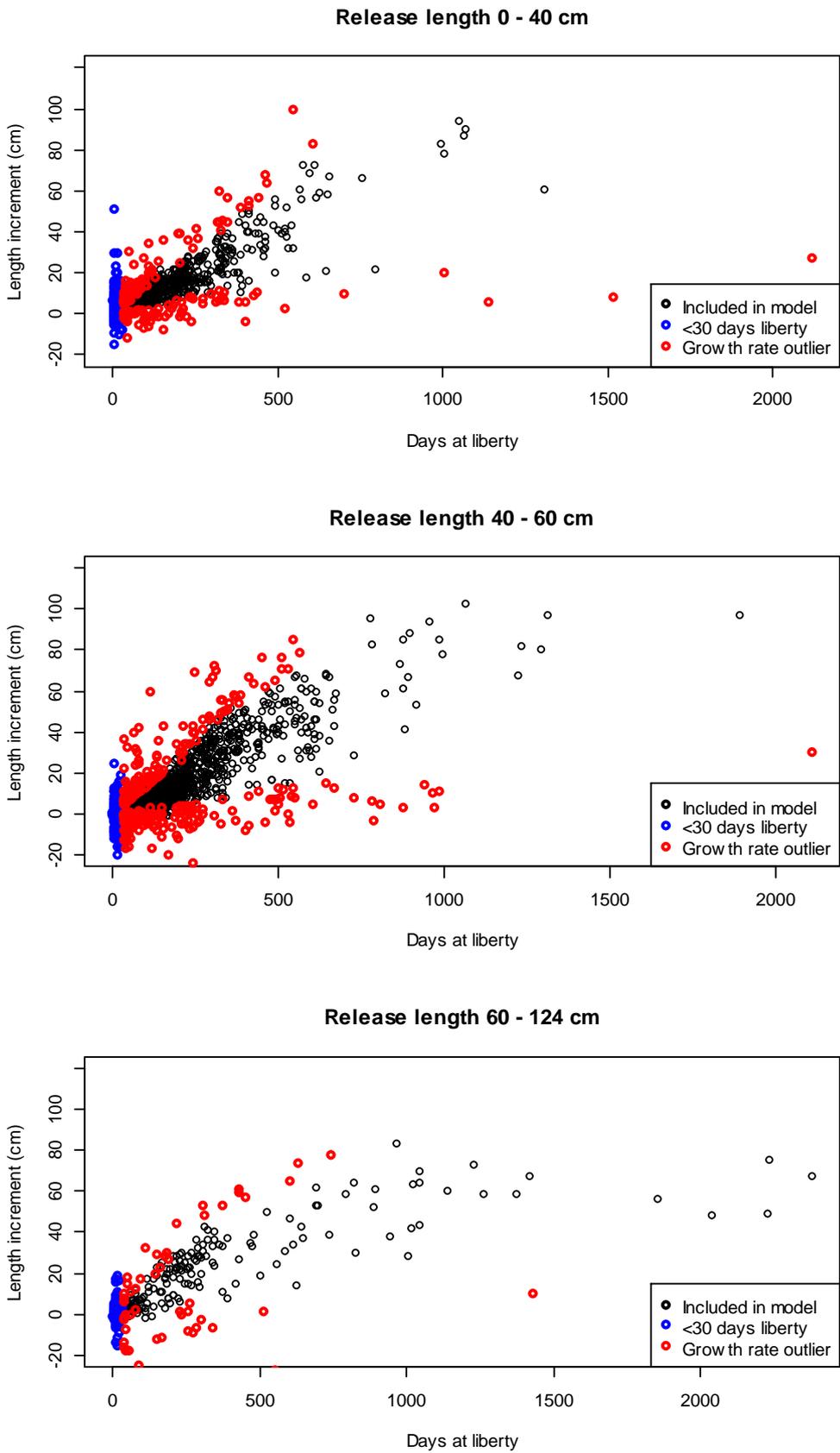


Figure 6. Map showing locations of otolith samples and tag releases and recaptures for bigeye data used in the integrated models.

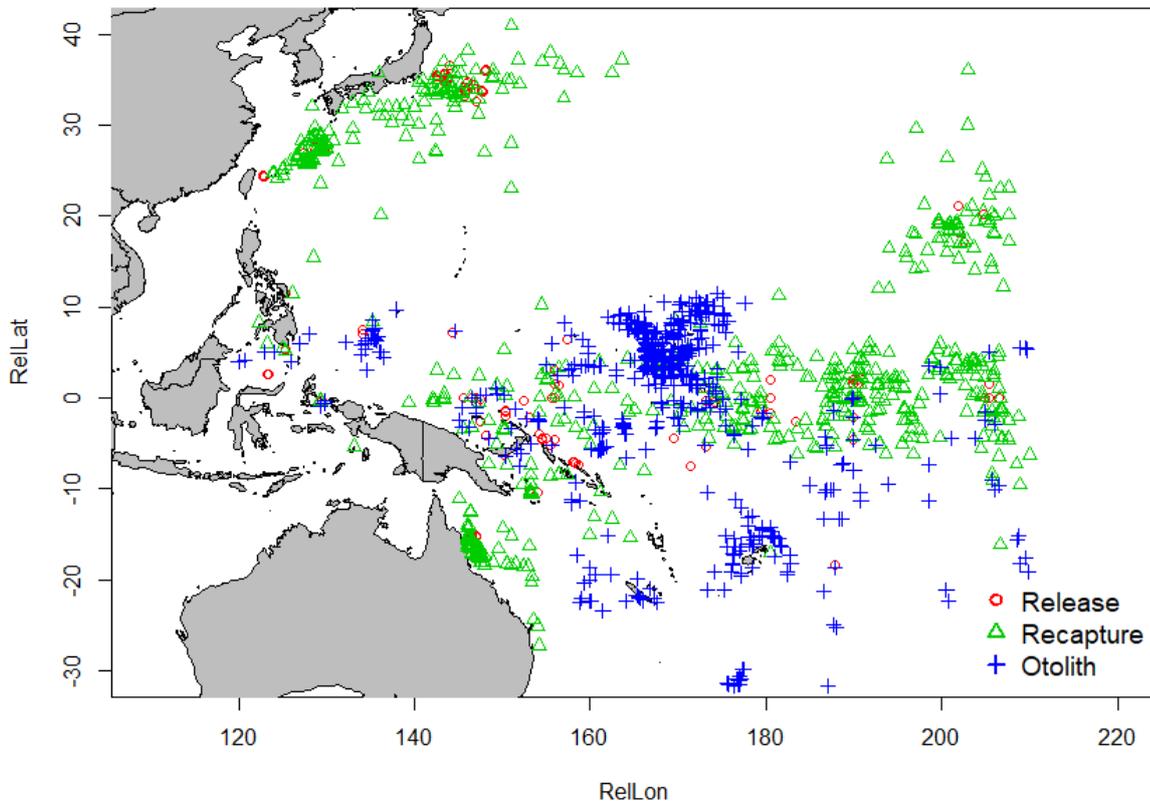


Figure 7. Histograms of (top to bottom) release length, recapture length and days at liberty for bigeye.

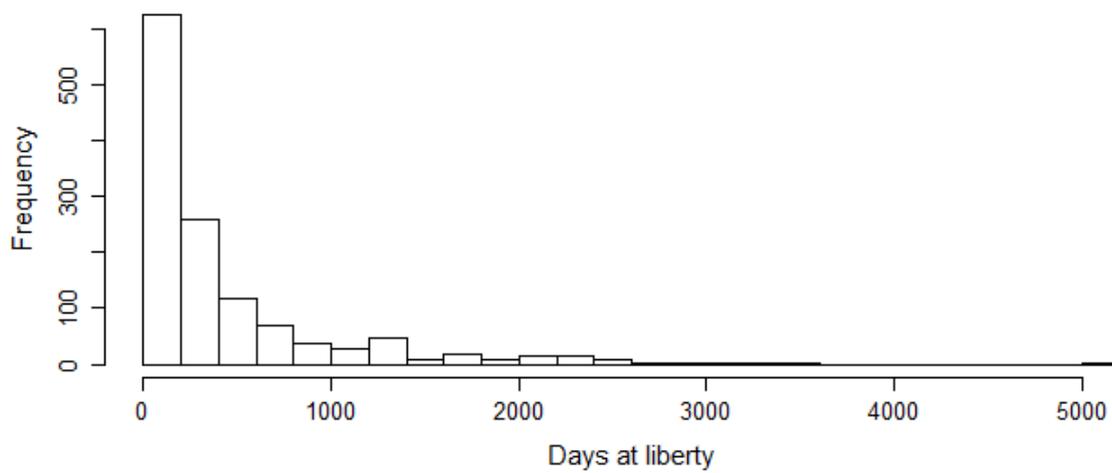
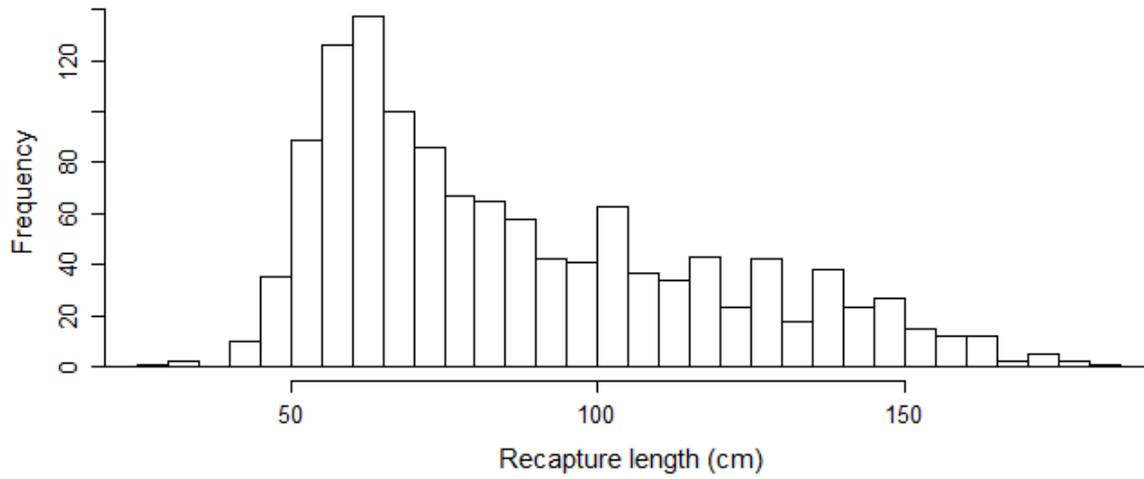
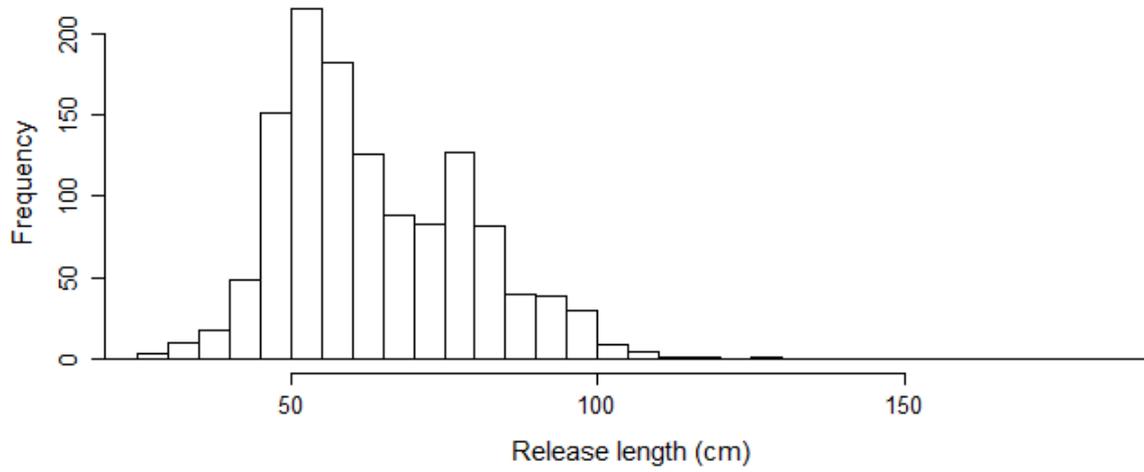


Figure 8. Comparison of the VB and Richards growth curves estimated from the integrated model fit to the bigeye tag-recapture and high-readability otolith data. Note that the figure looks almost identical for the models fit to all otolith data.

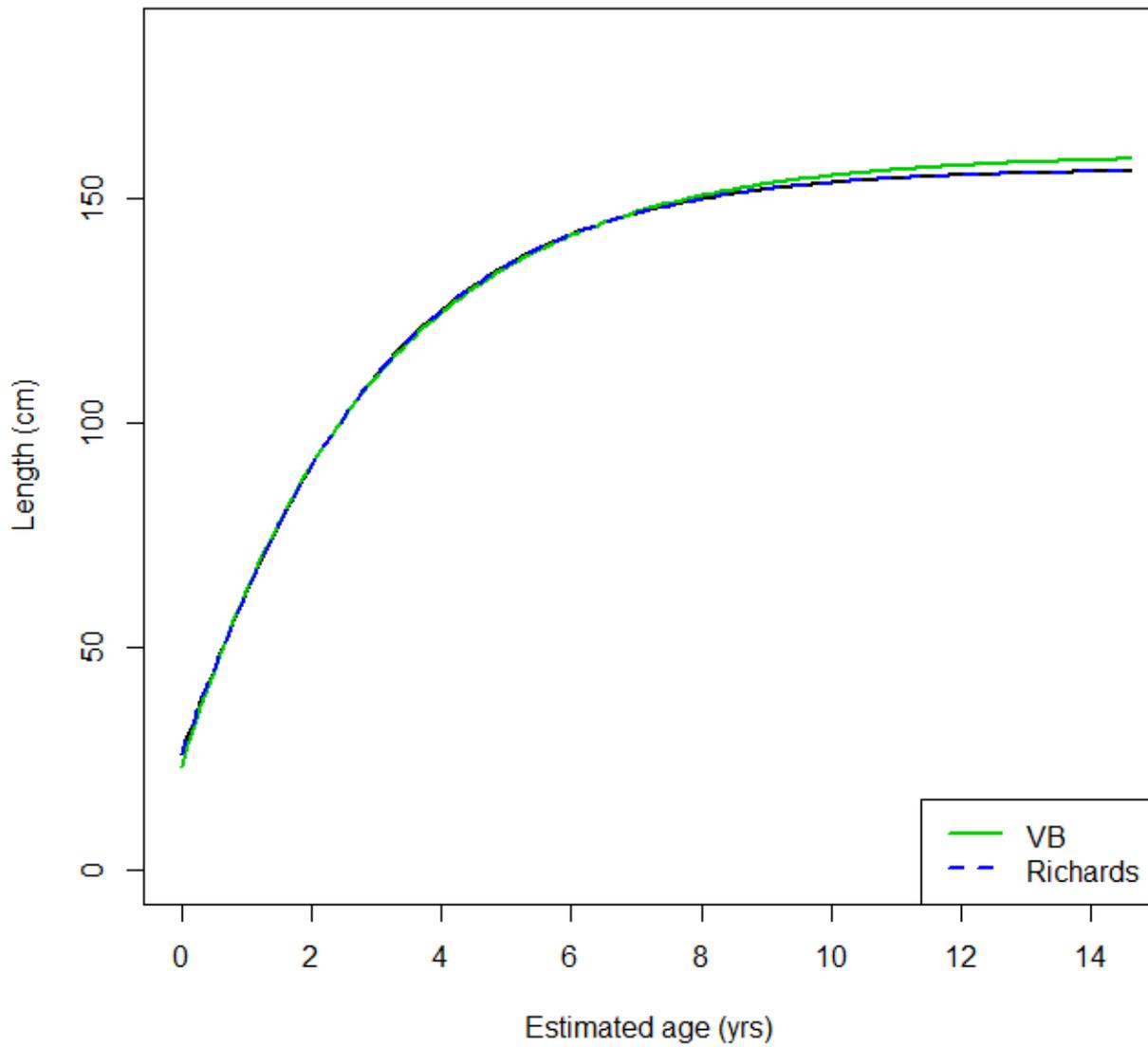
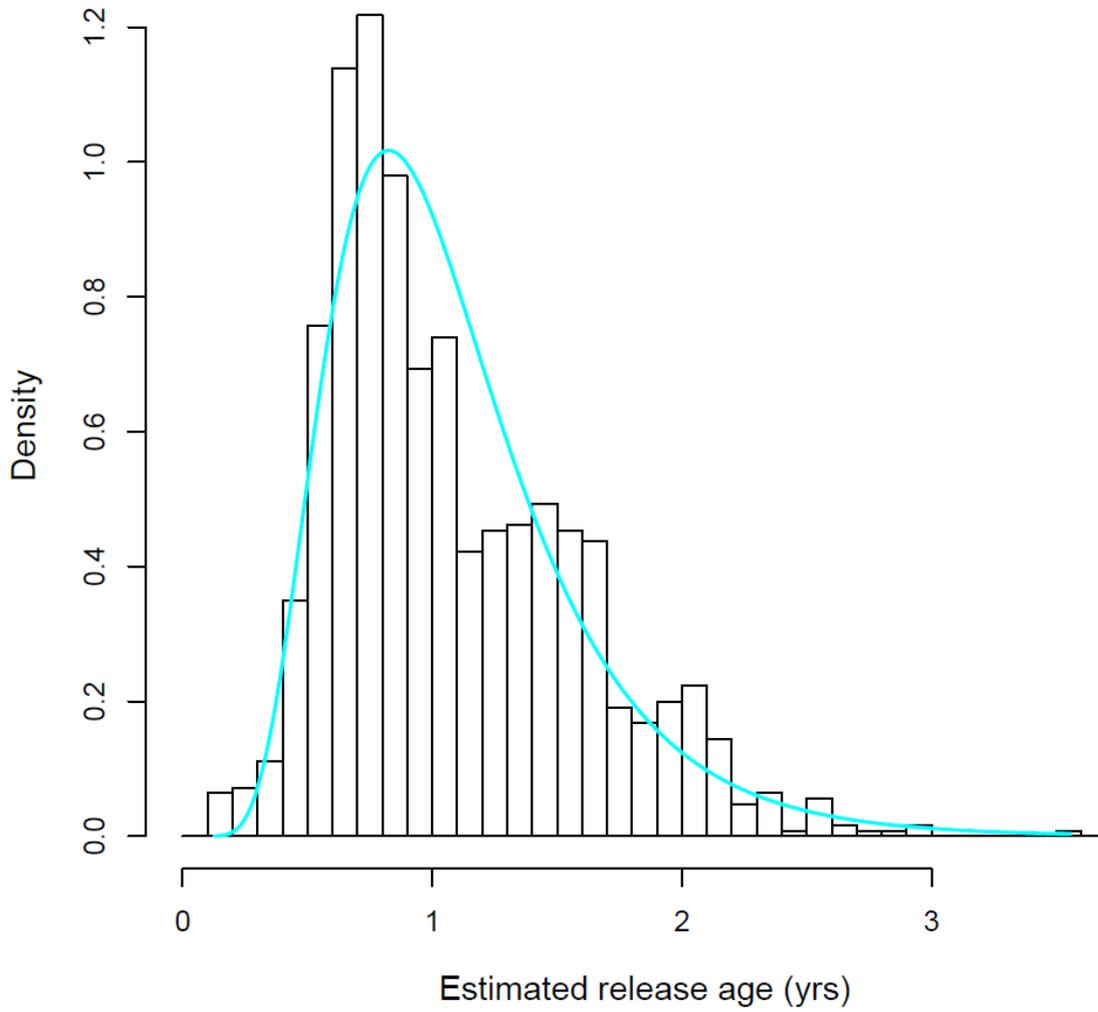
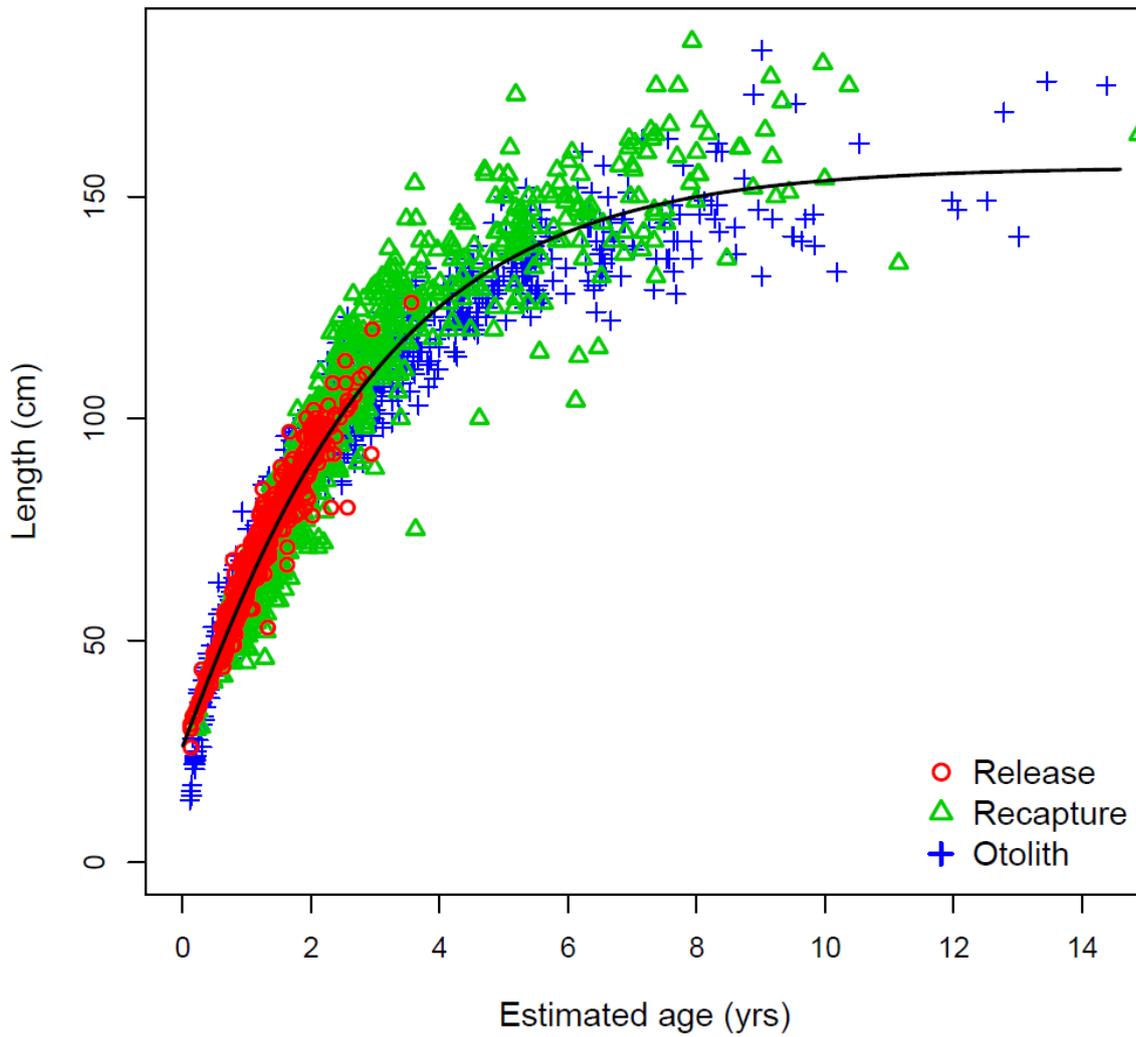


Figure 9 (a-d). Results from fitting an integrated Richards growth model to the bigeye tag-recapture and high-readability otolith data.

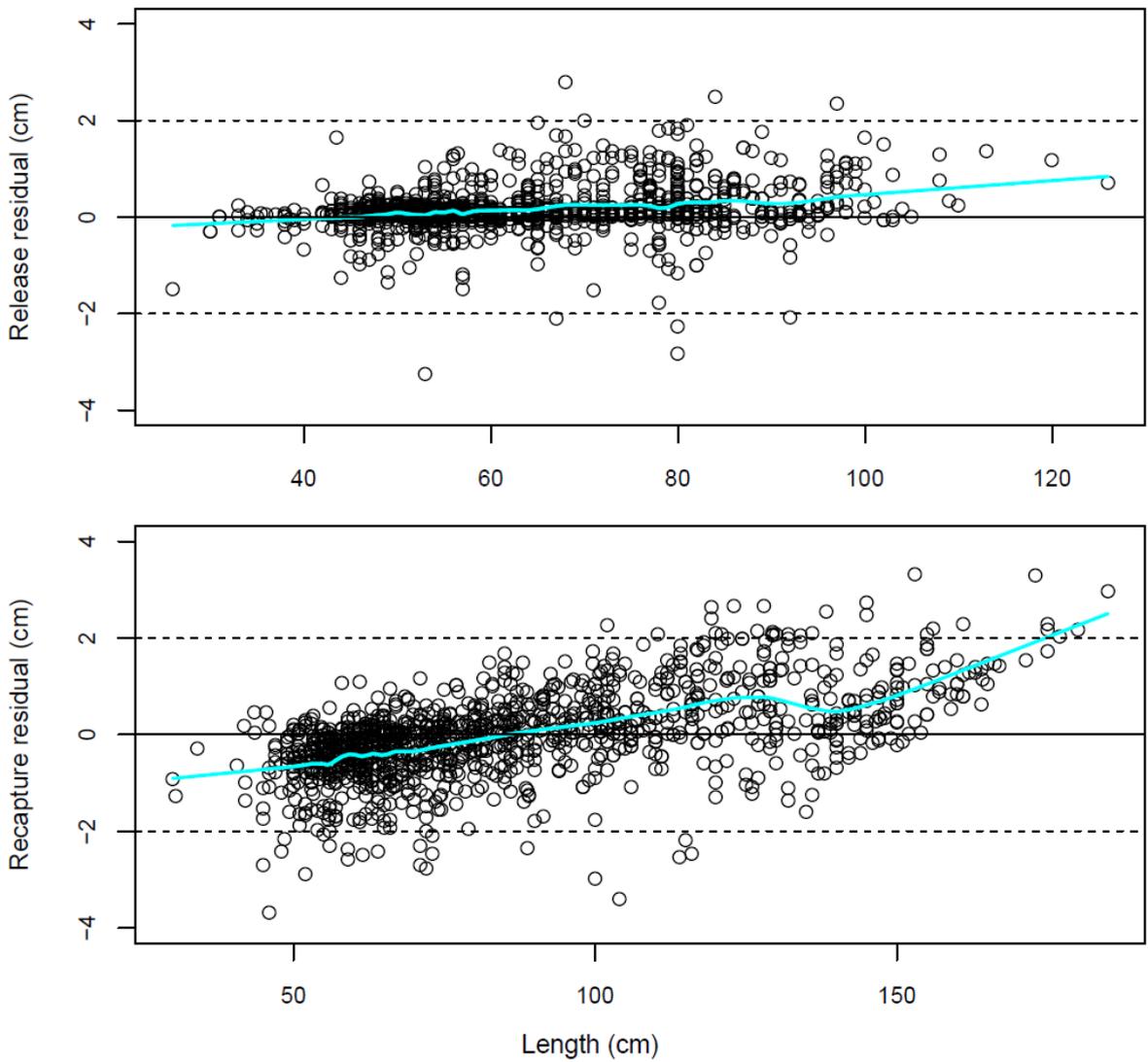
(a) Estimated release age distribution (blue line) overlaying conditionally unbiased estimates of individual release ages.



(b) Estimated mean growth curve (black line) and data, Red circles = release points; green triangles=recapture points; blue crosses=otolith data. Note that release ages are estimated as in (a), and recapture ages equal estimated release age plus time at liberty.



(c) Standardised residuals for the tag-recapture data, with a smooth through the points to help visualize patterns (blue lines).



(d) Standardised residuals for the otolith data, with a smooth through the points to help visualize any patterns (blue line).

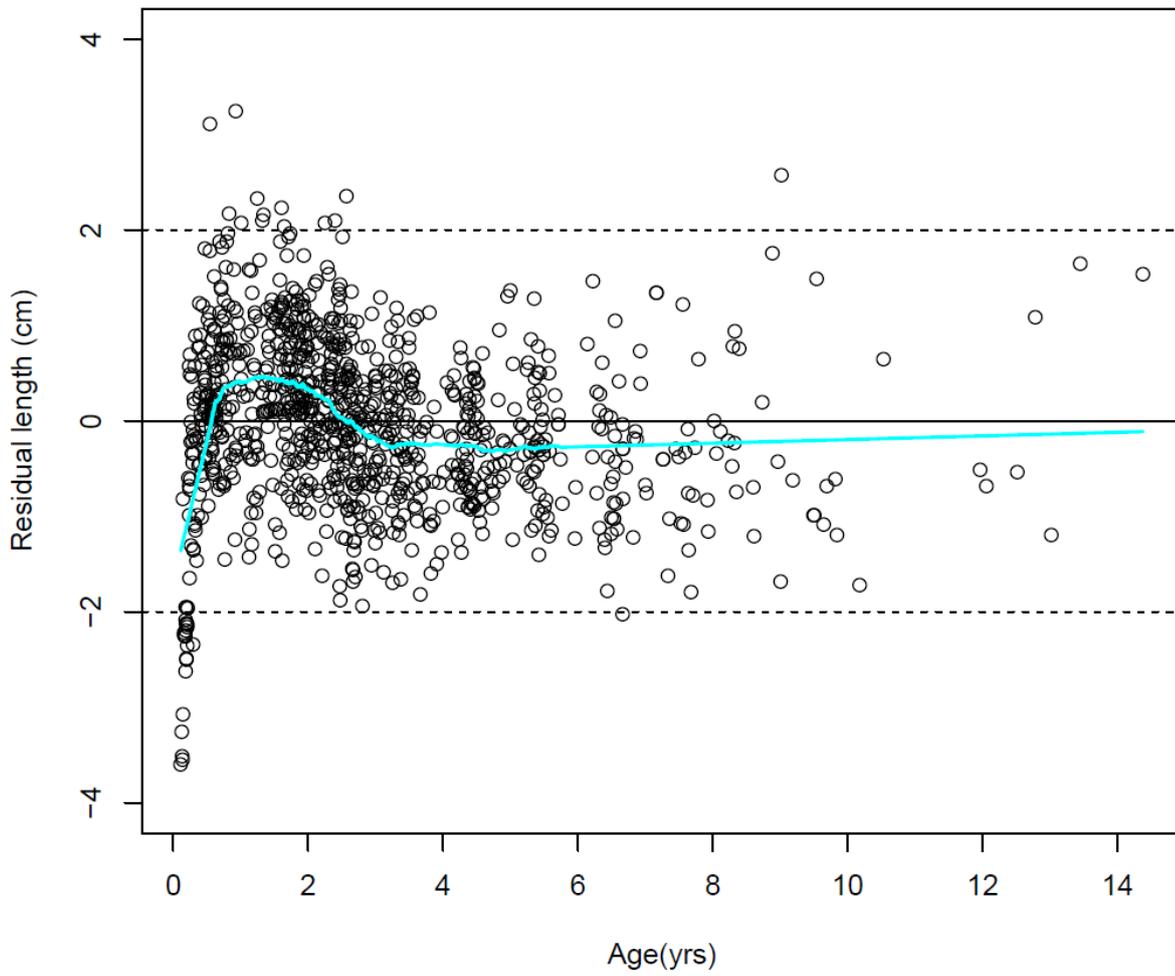


Figure 10. Map showing locations of otolith samples and tag releases and recaptures for yellowfin data used in the integrated models.

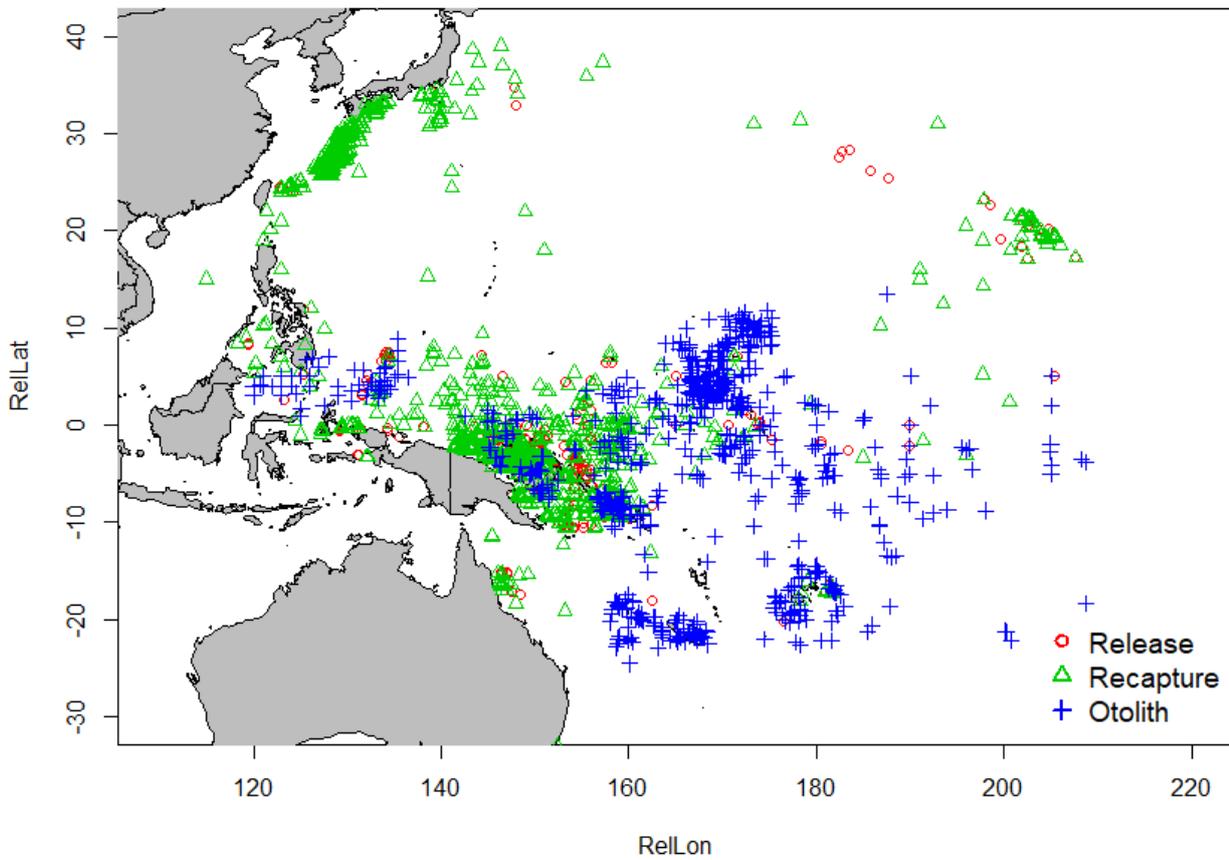


Figure 11. Histograms of (top to bottom) release length, recapture length, and days at liberty for yellowfin.

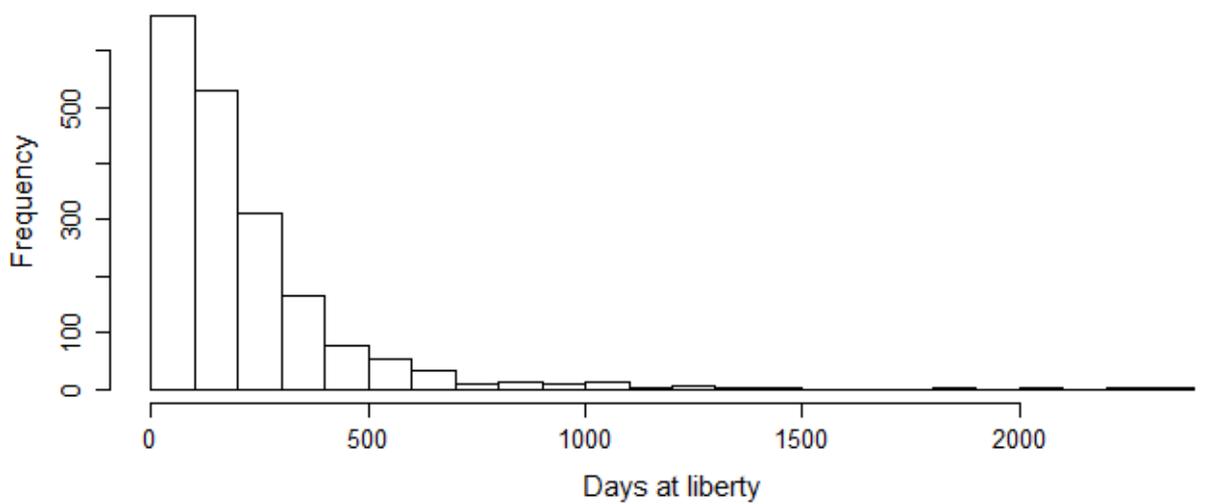
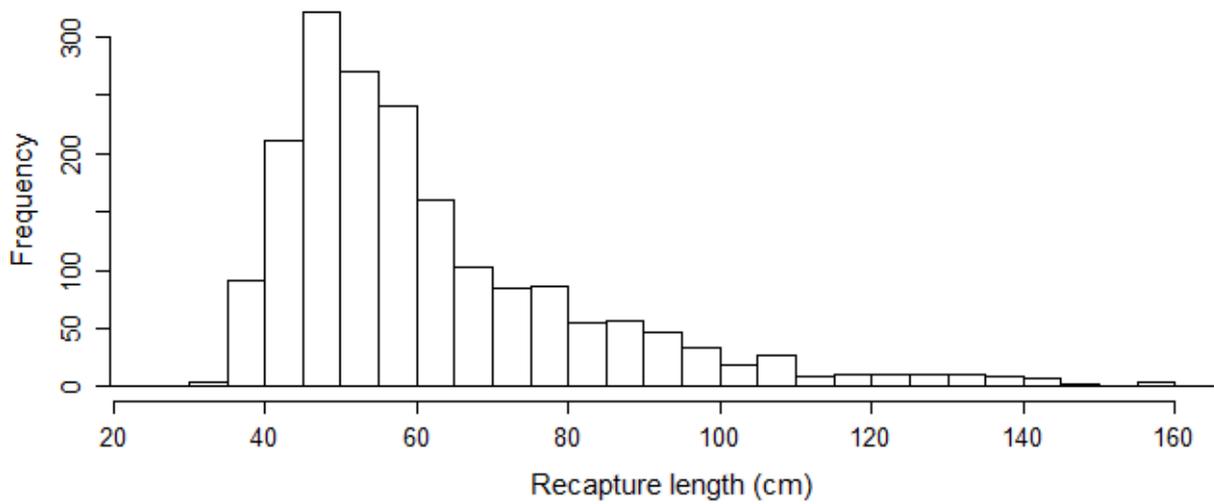
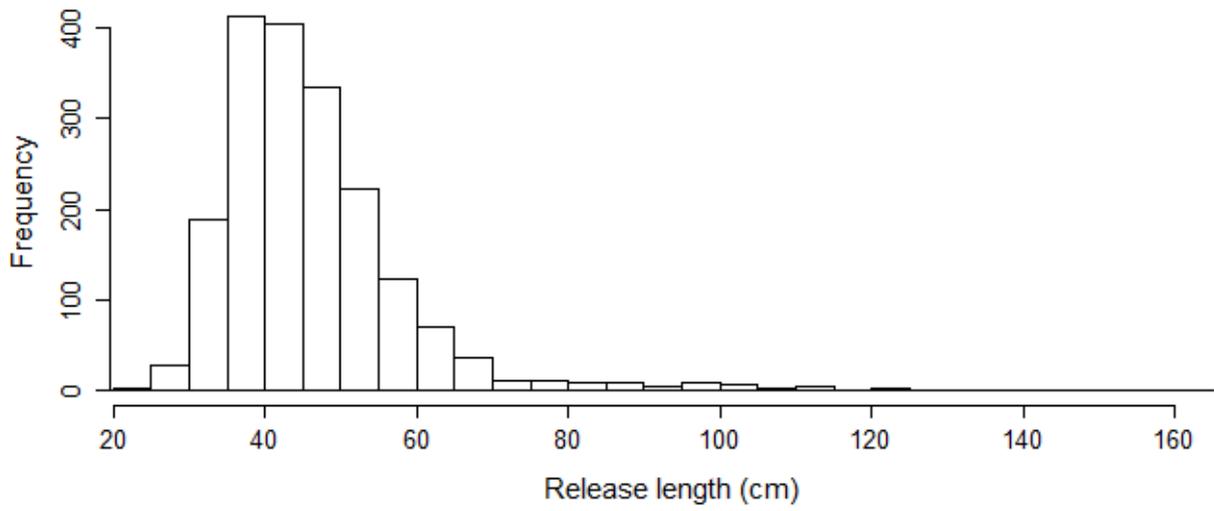
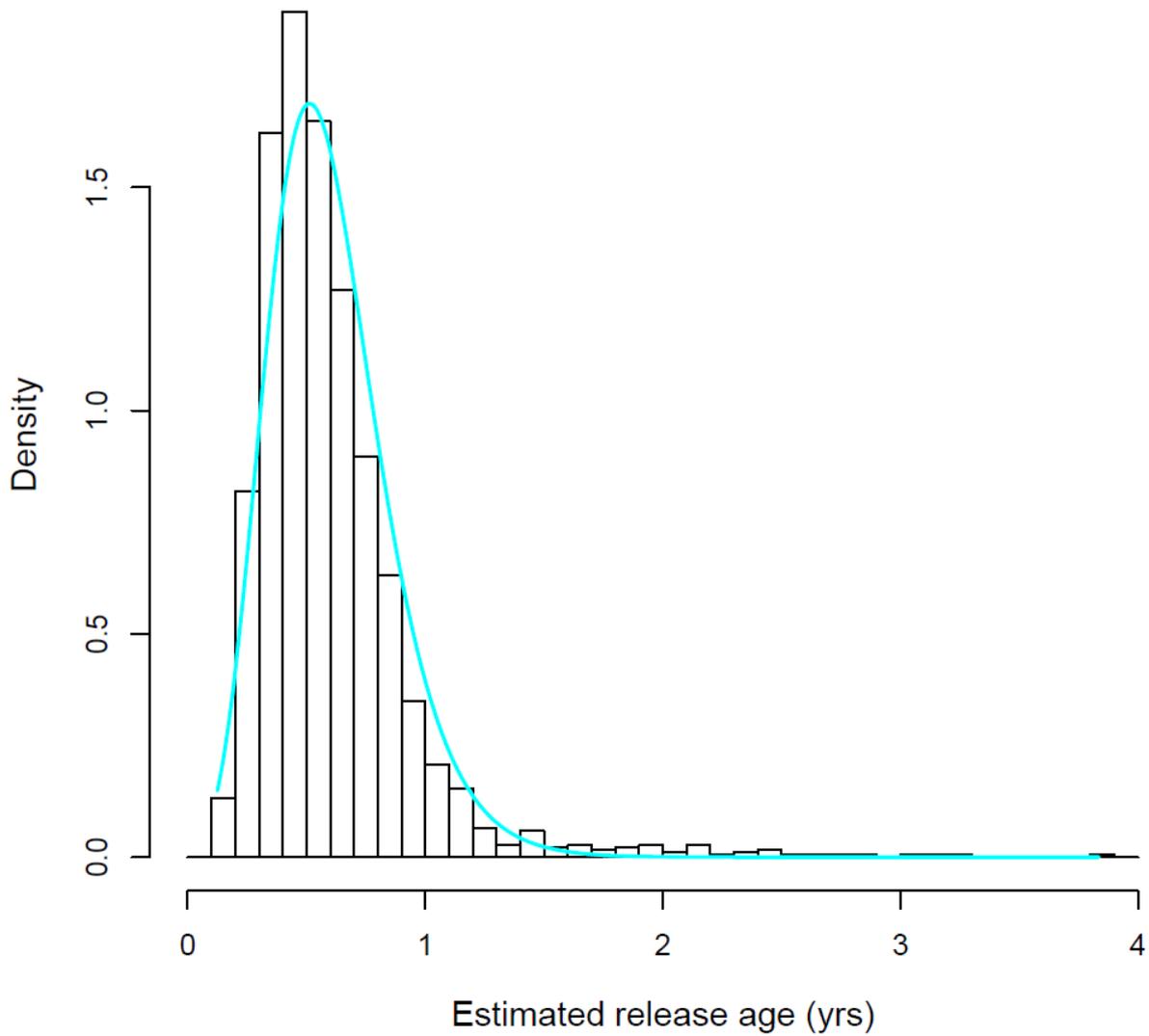
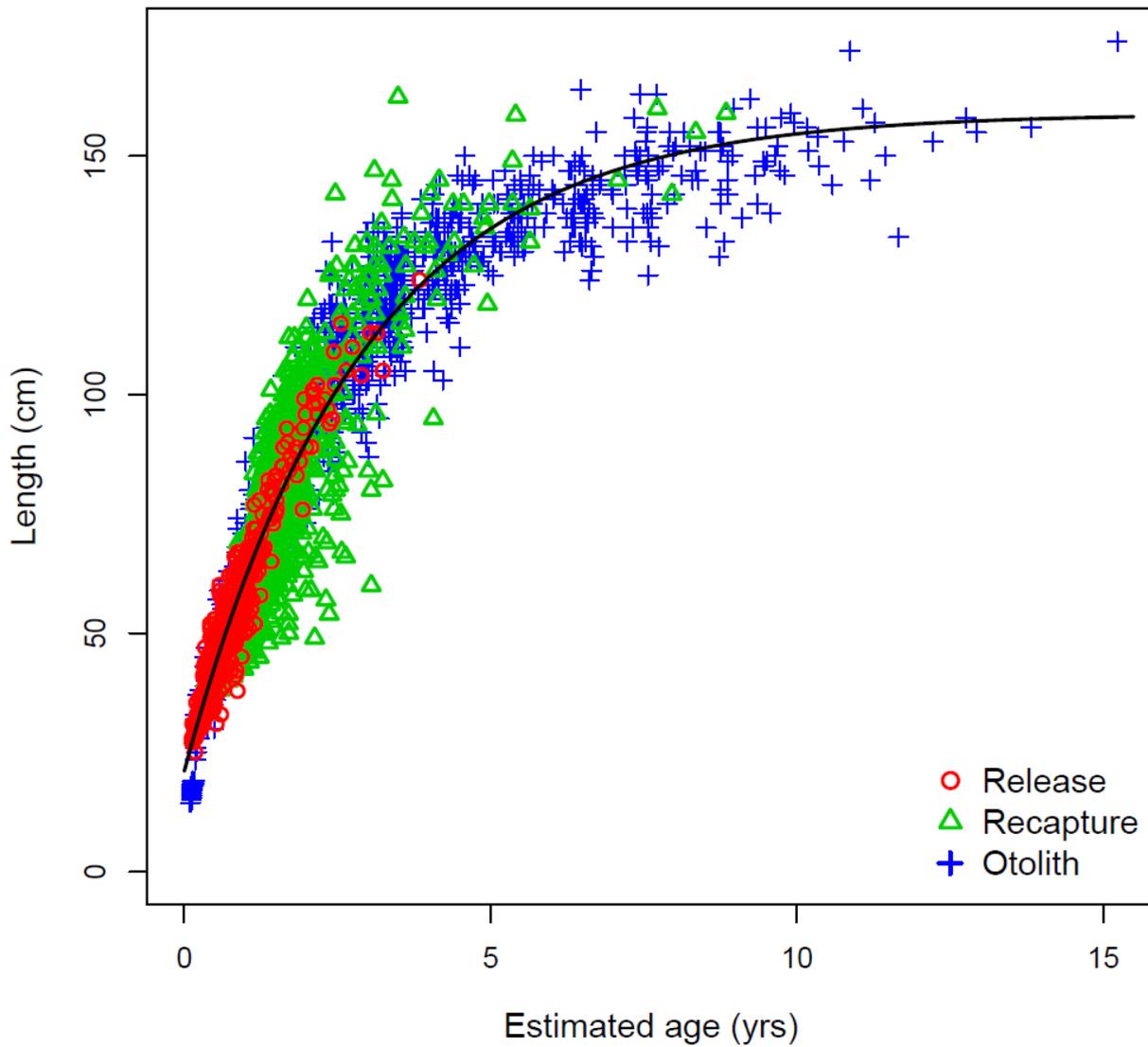


Figure 12 (a-d). Results from fitting an integrated VB growth model to the yellowfin tag-recapture and high-readability otolith data.

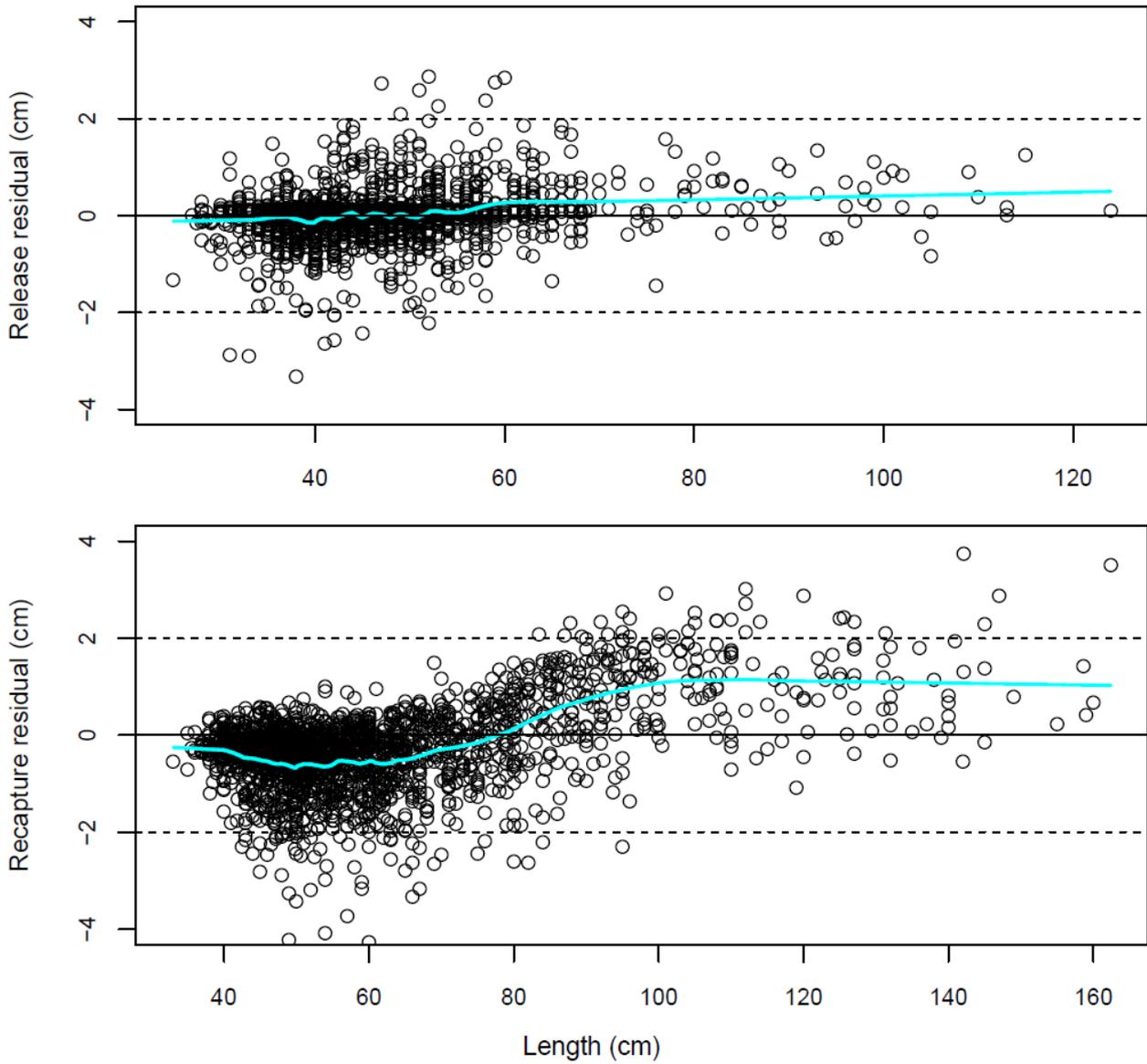
(a) Estimated release age distribution (blue line) overlaying conditionally unbiased estimates of individual release ages.



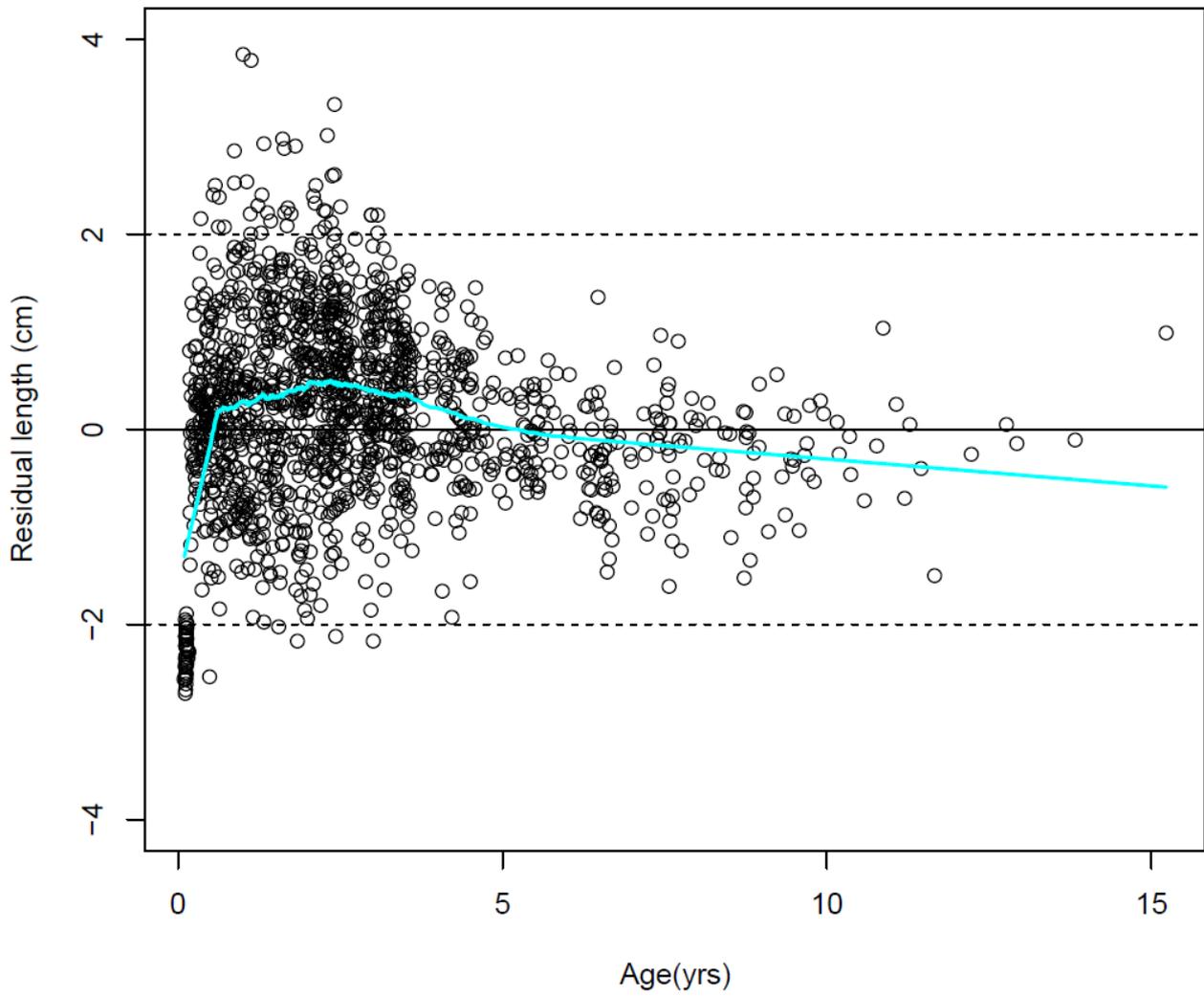
(b) Estimated mean growth curve (black line) and data, Red circles = release points; green triangles=recapture points; blue crosses=otolith data. Note that release ages are estimated as in (a), and recapture ages equal estimated release age plus time at liberty.



(c) Standardised residuals for the tag-recapture data, with a smooth through the points to help visualize patterns (blue lines).



(d) Standardised residuals for the otolith data, with a smooth through the points to help visualize any patterns (blue line).





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