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Review and new analyses of skipjack growth in the Western and Central Pacific Ocean

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Executive summary

Growth is a key uncertainty in the skipjack stock assessment for the Western and Central Pacific Fisheries Commission (WCPFC) convention area. Three new growth curves were produced as possible alternatives for use in the 2022 WCPFC skipjack assessment. For the 2022 diagnostic case, growth is estimated internally within MULTIFAN-CL, largely informed by the information contained in the modal progression of length composition data. However, such internal estimates of growth can sometimes be influenced by maximising the likelihood associated with other data sources which are not closely associated with growth, such as proportions of tags returned at each time step. The three alternative externally estimated growth curves do not incorporate length composition data, and instead use data sources not available for the internal estimation of growth in the integrated assessment.

The first alternative growth curve ‘*WCPO meta’* was obtained from a meta-analysis of published growth studies in the western and central Pacific Ocean (WCPO). The second alternative is derived from the ‘*VBoto*’ model. This model incorporates daily otolith age data from young skipjack captured in Papua New Guinea and length-at-age data from ‘high confidence’ tag recaptures sourced from Pacific Tuna Tagging Programme (PTTP) and Japanese Tagging Programme (JPTP) records, with assumptions made allowing an age-at-release to be assigned to each tagged fish based on a von Bertalanffy curve fitted to daily otolith readings. The third alternative is derived from the ‘*VBtag.oto*’ model which incorporates the same daily otolith age data, the length-at-age data for both tag recaptures and tag releases, includes measurement error in the release and recapture lengths, and estimates the age-at-release (i.e. it does not fix the age-at-release based on external estimates of length-at-age from the otolith data).

Of these three alternatives, we recommend *VBtag.oto* as the preferred alternative growth option for the 2022 WCPFC skipjack assessment. Growth for *VBtag.oto* follows a von Bertalanffy curve with parameters: L_∞ = 73.4 cm fork length, K = 0.811 and t_0 = -0.607. This analysis is the first to develop and make use of a high-confidence tag-recapture dataset for the purposes of estimating growth in a WCPFC skipjack assessment, and is also the first to combine tag-recapture growth data with daily age estimates from otoliths for this purpose. We note however, that given absence of both very young and older fish in our datasets, care should be taken in extrapolating growth predictions outside the range of data used in our modelling.

There is a clear need for ongoing and improved data collection on age and growth in skipjack. We suggest that progress might lie in the pursuit of a range of techniques, including advances in epigenetic ageing approaches, further application of age validation experiments involving chemical marking of otoliths during tagging campaigns, and continued refinement of integrated modelling approaches appropriate for the new data that comes to hand. On this last point, focussing efforts on acquiring additional high quality tagging data across a broader spatial and temporal range, and for larger tagged fish with longer times-at-liberty, would also improve growth estimates for older age classes for which data are currently lacking.

1. Introduction

1.1 Background

Estimation of fish growth forms a core component of modern fishery stock assessments (Francis 2016; Kolody et al. 2016; Maunder et al. 2016). An individual's lifetime growth trajectory can be viewed as the net outcome of interactions among intrinsic (i.e. within-individual) and extrinsic (e.g. environmental, anthropogenic) factors; the nature of these trajectories and their variability among conspecifics in space and time providing us valuable insights into the demographics and productivity of harvested populations. Within age-structured stock assessment models, decisions around how to represent growth can impact the estimation of key management quantities - the growth equation typically being used to infer catch-at-age from catch-at-size, to calculate biomass from the age structure, and to estimate fishing mortality for fisheries with size-based selectivities, among other functions (see Francis 2016; Kolody et al. 2016). Indeed, the choice of growth parameters has been shown to impart substantial influence on estimates of stock status in recent assessments of skipjack tuna (*Katsuwonus pelamis*) and other tuna species in the Pacific Ocean (Harley et al. 2014; Aires-da-Silva et al. 2015; McKechnie et al. 2015, 2016; Vincent et al. 2019).

As in other oceans, obtaining accurate estimates of growth for skipjack tuna in the western and central Pacific Ocean (WCPO) has proved challenging. We have some evidence that growth rates are highest in the Pacific, where skipjack also attain the largest sizes (Murua et al. 2017). Growth rates may also vary within the Pacific (Bayliff 1988; Maunder 2001; Hoyle et al. 2010; Ashida et al. 2018), evidenced in part by the large variation in published growth curves derived from different studies across the region (Figure 1). That said, longstanding uncertainties in direct age estimates from otoliths and other hard parts continue for this species (Wild and Foreman 1980; Uchiyama and Struhsaker 1981; Adam et al. 1996; Sardenne et al. 2015; Luque et al. 2021), and difficulties in tracking modal progression using length frequency data have often necessitated the inclusion of tag-recapture information to derive biologically-plausible growth curves, for which a variety of elegant modelling approaches have evolved (e.g. Fabens 1965; Baker et al. 1991; Francis 1988, 1995; Wang et al. 1995; Maunder 2001; Laslett et al. 2002; Eveson et al. 2004, 2011, 2015, 2020; Aires-da-Silva et al. 2015; Dortel et al. 2015; Maunder et al. 2018). In their current incarnations, these approaches allow us to draw on the best information available about growth through the appropriate treatment of the tag-recapture data and its many uncertainties, the integration of multiple data types if available, and the flexibility to handle different functional forms for the growth curve (see Francis et al. 2016 for a succinct review).

The challenge in estimating skipjack growth has extended to the models used to assess stock status in the WCPO. The lack of clear modes in the length composition data has often hampered the estimation of all growth parameters within an integrated assessment. Moreover, perceived limitations in the available otolith and tag-recapture data have meant that these information sources, and the above-mentioned modelling approaches designed for them, have not been thoroughly explored for external growth estimation. Recent Western and Central Pacific Fisheries Commission (WCPFC) skipjack assessments using MULTIFAN-CL (Fournier et al. 1998) (i.e. Hoyle et al. 2011; Rice et al. 2014; McKechnie et al. 2016) have fixed growth, for their respective diagnostic cases, using the growth estimated internally from the 2010 assessment (Hoyle et al. 2010), while using sensitivities which consider alternative growth options, including using data from previous empirical studies (Leroy 2000; Tanabe et al. 2003a).

In the most recent assessment conducted in 2019, Vincent et al. (2019) used a multi-step approach to estimate growth curves that were fixed for the range of models used in the structural uncertainty grid. After determining that the length frequency scalars influenced the estimated von Bertalanffy growth curve parameters, three assessment models were explored that used different scalars for weighting the length frequency data (i.e. 1, 20, 40). These values were chosen to incorporate the full range of scalars where growth parameter estimates were not hitting lower bounds. The growth curve from the model with a length scalar of 20 was chosen as the diagnostic case *DiagCase 2019*. The two remaining growth curves *GrowthLow* (scalar = 1) and *GrowthHigh* (scalar = 40) were used as alternatives in the structural uncertainty grid for the axis of growth.

These growth curves are shown in Figure 1. We see that the estimated mean fork length of the first age class (i.e. age ¼ of one year old) for the 2019 diagnostic case was 23 cm, with relatively rapid growth estimated up until age eight quarters (~72 cm). Growth then slowed, with the oldest age class in the model (i.e. age 16 quarters) having mean fork length of ~84 cm (Vincent et al. 2019). The standard deviation of length-at-age was constant across the ages (Figure 1). The *GrowthLow* and *GrowthHigh* curves had moderately lower and higher mean fork lengths in the oldest age class, i.e. 78 cm and 85 cm, respectively, with the standard deviation of length-at-age again constant across ages for both curves.

The growth curve for the diagnostic case in the 2022 skipjack assessment *DiagCase 2022* (Castillo-Jordán et al. 2022) is estimated internally within MULTIFAN-CL (Figure 1, bold red line) and is largely informed by the length frequency data. However, in an integrated assessment framework with multiple data sources and multiple likelihood components, other data components can also potentially inform the estimation of growth parameters. Rather than apply arbitrary length scalars to weight the length frequency data, as was used in the previous assessment (Vincent et al. 2019), the Dirichlet multinomial likelihood is used in 2022 to scale the sample sizes of length frequency data for each fleet and time period used in the assessment, following the approach of Thorson et al. (2017). Using the Dirichlet multinomial scaling of length compositional data, growth is estimated internally within the assessment. The estimated growth from the 2022 diagnostic case (Figure 1, bold red line) is similar to the growth curve used in the 2019 assessment (Figure 1, dashed blue line), but the variance around that growth curve (Figure 1, red shading) now increases with age in 2022, in contrast to the 2019 growth curve (Figure 1, blue shading). The growth curves estimated internally in WCPFC assessments refer to the mean length by (quarterly) age class, not by absolute age, so these curves could potentially be translated horizontally depending on the absolute age class of an individual considered to be age class one in the assessment model.

Much has been written on the pros and cons of internal versus external estimation of the growth curve for use in stock assessments, and we point readers to papers by Kolody et al. (2016), Piner et al. (2011, 2016), and Zhu et al. (2016) for detailed appraisals and examples. If practicable, and if adequate data are available, it seems prudent to pursue both avenues to gain the best possible estimation of growth and representation of uncertainty in this growth (Kolody et al. 2016). This point was raised at the pre-assessment workshop (PAW), held in hybrid format in March 2022, where discussions highlighted a need to explore alternative growth options for inclusion as sensitivities in the 2022 skipjack assessment. The outcomes of an exploration of the available data and estimation models form the basis of this Information Paper to SC18.

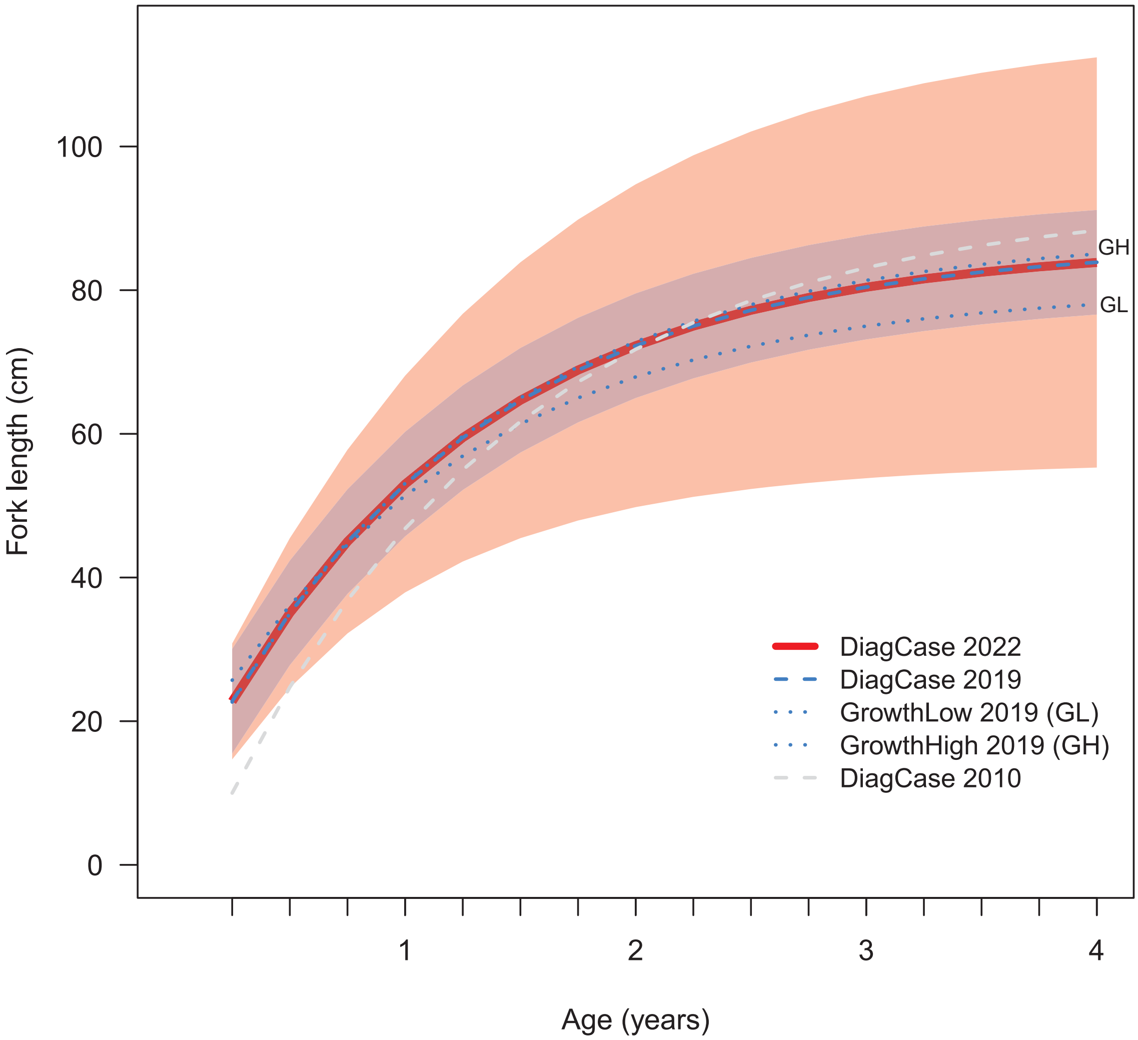


Figure 1: Growth curves used in the diagnostic case for WCPFC skipjack stock assessments from: 2010 (dashed grey line); 2019 (dashed blue line); 2022 (bold red line); with high and low growth options used in the 2019 uncertainty grid (dotted blue lines); and with shading indicating the 95% confidence intervals for estimates of the distribution of length-at age for the diagnostic case for assessments from 2019 (blue shading) and 2022 (red shading).

1.2 This study

Our investigation evolved through six stages that ultimately led to the *VBtag.oto* growth curve that we recommend to SC18 as our preferred alternative for growth in the 2022 skipjack stock assessment. We outline these stages here and provide further detail in the Methods and Results sections.

1. Meta-analysis: All available growth models for skipjack across the WCPO (Figure 2, red lines) and Eastern Pacific Ocean (EPO) (Figure 2, black lines) were collated and reviewed. The results led to the *WCPO meta* growth curve (see Figure 3).

2. Data sourcing and filtering: Making use of tag-recapture growth increment data was identified as 'the main opportunity for additional data on [SKJ] growth' by Vincent et al. (2019). Following this advice, we sought out a high-quality tag-recapture growth increment dataset from the Japanese Tagging Programme (JPTP), Pacific Tuna Tagging Programme (PTTP) and Regional Tuna Tagging Program (RTTP) databases for use in later modelling exercises. Drawing on expert advice and previous protocols used to filter tuna tag-recapture datasets across different oceans, we applied a series of filtering steps to these data (detailed in the Methods section), arriving at a 'high-confidence' tag-recapture dataset sourced from JPTP and PTTP records that covers a large portion of the WCPO assessment region. We also made use of an otolith dataset comprising daily age estimates for skipjack tuna ranging in size (fork length) between 30 and 69 cm, captured from Papua New Guinean waters (see Leroy 2000 for full details).

3. Exploratory data analysis: We used a series of exploratory plots to identify outliers in the otolith and tag-recapture datasets and to choose the appropriate functional form for the growth curve to be used to model growth.

4. *VBoto* model: In this initial modelling exercise, we integrated the high-confidence JPTP and PTTP tag-recapture dataset and otolith daily age estimates taken from Leroy (2000) using a two-step analytical approach. First, an initial von Bertalanffy growth curve is estimated from the otolith data to back-calculate the release age of tagged fish. Then, a final von Bertalanffy growth curve is estimated from the combined otolith and tagging data containing the age and length of individual fish. This model is hereafter referred to as *VBoto*. While useful as an interim modelling step, *VBoto* has some limitations. When back-calculating the age at release, it makes the strong assumption that there is no measurement error in release lengths, and when fitting the final growth curve, it assumes that all ages are known and exact. In reality, the main source of uncertainty is indeed the age of the fish, especially in the tagging data. The main strength of the analytical approach of the *GCM.oto* and *VBtag.oto* models, described below, is that they incorporate better this uncertainty, by explicitly estimating the unknown age of tagged fish using maximum likelihood.

5. *GCM.oto* model: A growth cessation model (GCM) had been developed by IATTC for analysing EPO skipjack tuna growth (Maunder et al. 2018, 2022a). The source code was shared by the authors and adapted to the current study of WCPO skipjack tuna. The source code for the shared GCM model was developed further for this study, adding the ability to fit the model to otolith data and tagging data at the same time, dubbed *GCM.oto*. The results from this model indicated that for the WCPO skipjack data, daily growth did not seem to follow a straight line (constant daily growth) followed by a flat curve for the older fish, as dictated by the GCM model theory. Instead, the WCPO seemed to follow a von Bertalanffy pattern, which resulted in the development of a new model *VBtag.oto*, based on the framework from *GCM.oto* but using a traditional von Bertalanffy growth curve.

6. *VBtag.oto* model: The development of the recommended model from this study was inspired by the *GCM.oto* model (see above) and drawing on the original ideas in Palmer et al. (1991), Wang et al. (1995), Laslett et al. (2002) for modelling the joint density of tag and recapture lengths conditional on the age-at-release. Following the approach of Maunder et al. (2018) the model estimates the age-at-release of each individual as a fixed, rather than a random effect. Further details are provided in the Methods and Results section below.

2 Methods and Results

2.1 Meta-analysis

The first step in our investigation was to review the available growth studies on skipjack conducted across the WCPO and EPO, and to compile the growth parameters produced by each of these studies. Most parameters were drawn from comprehensive reviews by Gartner et al. (2008) and Murua et al. (2017) which summarised information on 22 different curves (see Table S15 in Murua et al. 2017 for the full suite of parameter estimates). We added information from three studies (Leroy 2000, Ku et al. 2015 and Maunder et al. 2022a) that were not included in those reviews (Table 1). Our primary interest was to compare the growth parameters from these 25 studies with those for the proposed diagnostic case from the 2022 WCPFC skipjack assessment (*DiagCase 2022*) and those used in previous WCPFC skipjack assessments. In three of the past five assessments – Hoyle et al. (2011), Rice et al. (2014) and McKechnie et al. (2016) – the growth parameters used in the diagnostic cases were fixed at the values estimated internally by Hoyle et al. (2010). Hence, we focus only on the growth curve from Hoyle et al. (2010): *DiagCase 2010*, and the three growth curves from Vincent et al. (2019): *DiagCase 2019*, and the *GrowthLow 2019* and *GrowthHigh 2019* alternatives applied in the 2019 uncertainty grid.

The majority of the studies reviewed used some formulation of the VB growth function to model skipjack growth (see Murua et al. 2017), and thus, L_∞, K and t_0 were the growth parameters most commonly available to us. To compare the various growth trajectories, we used the reported VB parameters to plot estimated mean growth curves for each study using the VB growth curve (Beverton and Holt 1957):

$$L_t = L_\infty(1 - \exp(-K(t - t_0))) \qquad (1)$$

where L_t is the upper jaw fork length (cm) at time t (years), L_∞ is the asymptotic mean maximum fork length, K is the annual growth rate parameter and t_0 is the theoretical age at length zero. MULTIFAN-CL uses a re-parameterisation of the VB function:

$$L_t = L_1 + (L_n - L_1)\left(\frac{1 - \exp(-K^q(t - 1))}{1 - \exp(-K^q(n - 1))}\right) \qquad (2)$$

where t is now a quarterly time step, L_1 and L_n are fork lengths (in cm) at the first and oldest age-class, respectively (n = 16 quarters of age for skipjack), and K^q is the quarterly growth rate parameter. Estimates for these parameters for the recent skipjack assessment growth curves are provided in Table 1, with the curves themselves overlaid in Figures 1 and 2.

To facilitate comparison of the reviewed growth curves with past and current MULTIFAN-CL growth curves, we plotted all growth curves across the full age range used in MULTIFAN-CL skipjack assessments i.e. from age one quarter (i.e. ¼ of one year old) to age 16 quarters and older (i.e. four years and older) (see Figure 2). We note that this sometimes led to the extrapolation of growth curves outside the size and/or age range of the data encompassed by the original studies. There were also several instances where the t_0 parameter was not reported and none of the underlying data were available to fit the curve. In these cases, we set $t_0 = 0$ following the approach of Eveson et al. (2015) and Murua et al. (2017).

Finally, we calculated the mean length-at-age and 2.5% and 97.5% quantiles at quarterly time steps for a selection of these WCPO growth curves. We excluded the growth curves used in WCPFC stock assessments (i.e. *DiagCase 2010*, *DiagCase 2019*, *GrowthLow 2019*, *GrowthHigh 2019*, *DiagCase 2022*) and the growth curve from Ku et al. (2015) from these calculations, with the curve from Ku et al. (2015) considered to be unrepresentative. The resulting mean length-at-age curve produced by this meta-analysis represents alternative growth curve 1: '*WCPO meta*' for the 2022 WCPFC skipjack assessment. This curve is plotted in yellow along with the *DiagCase 2022* (red) in Figure 3.

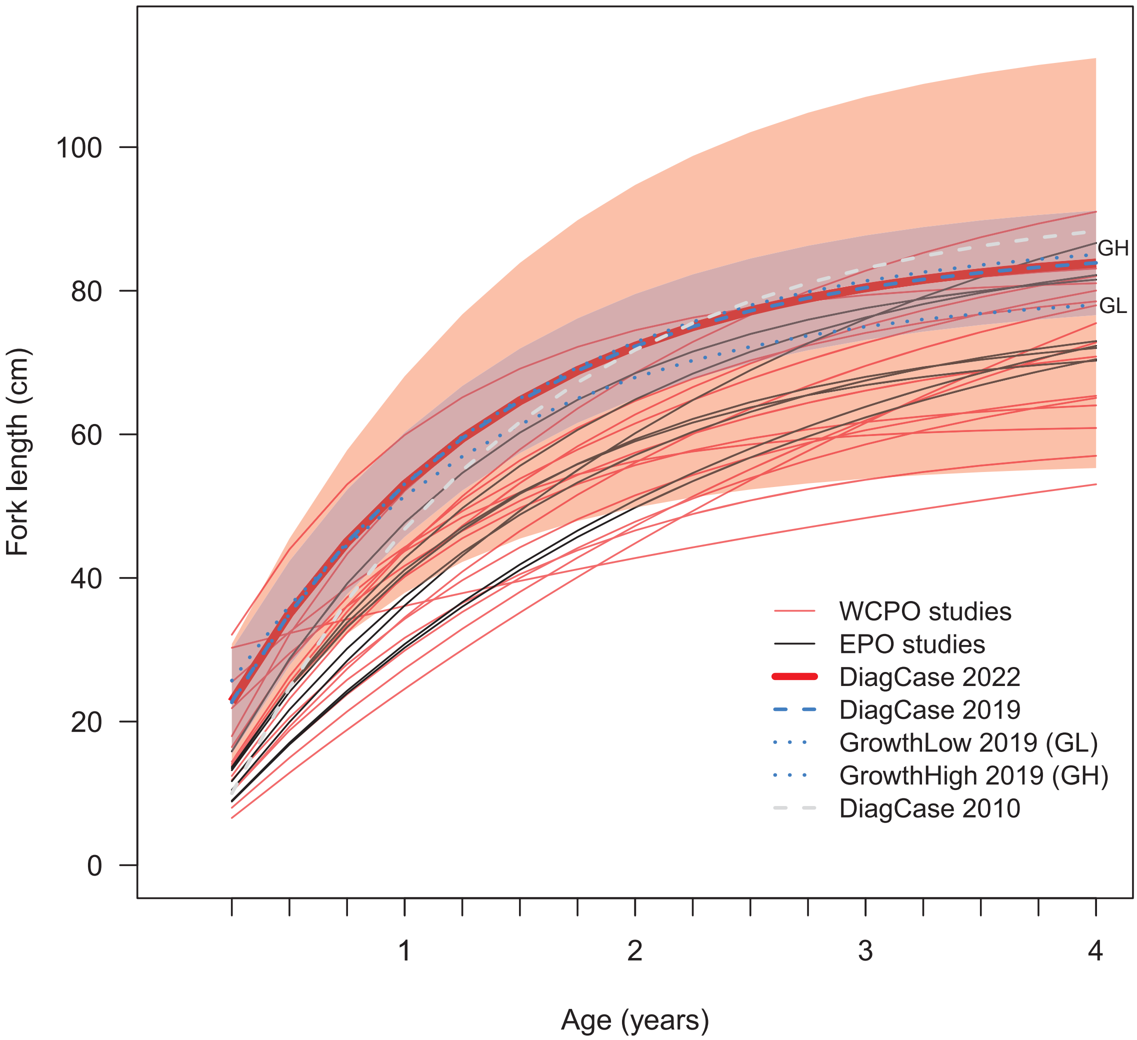


Figure 2: Growth curves used in the diagnostic cases for WCPFC skipjack stock assessments from: 2022 (*DiagCase 2022*, bold red line); 2019 (*DiagCase 2019*, dashed blue line); with low growth (*GrowthLow 2019*) and high growth (*GrowthHigh 2019*) options used in the 2019 uncertainty grid (dotted blue lines); 2010 (*DiagCase 2010*, dashed grey line). Shading indicates the 95% confidence intervals for the diagnostic case for assessments from 2022 (red shading) and 2019 (blue shading). Also shown are growth curves obtained from the review of growth studies on skipjack conducted across the WCPO (red lines) and EPO (black lines) (see Table 1 for author details, and Table 1 and Table S15 from Murua et al. (2017) for parameter estimates for each curve).

This analysis was conducted using the ‘FSA’ package (Ogle et al. 2022) in R (R Core Team 2022), and we point readers to this GitHub repository: https://github.com/PacificCommunity/ofp-sam-skj-tag-growth-public for full R code.

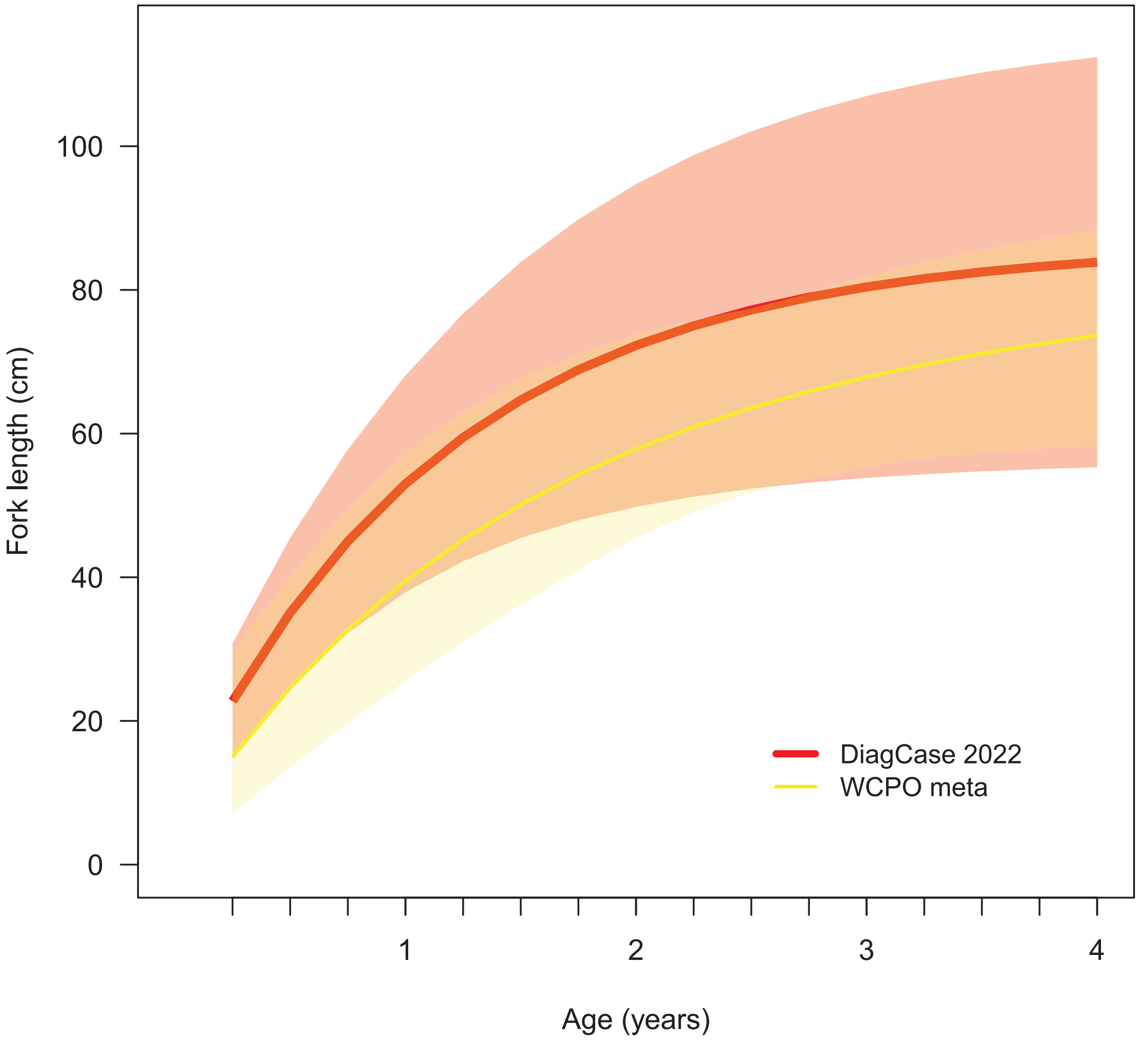


Figure 3: Alternative growth curve 1: Estimated growth curve for the 2022 diagnostic case (*DiagCase 2022*, bold red line); and mean length-at-age growth curve from our meta-analysis of published WCPO growth studies (*WCPO meta*, yellow line). Red shading indicates the 95% confidence intervals for *DiagCase 2022*; yellow shading indicates the 2.5% and 97.5% quantiles of mean length-at-age from the selected WCPO studies reviewed in the meta-analysis.

Table 1. Parameter estimates for growth curves used in recent WCPO skipjack assessments, and three externally estimated growth curves that used direct age estimates from otoliths or tag-recapture growth increment data in the WCPO or EPO. The resulting mean length-at-age curves given by these parameters are overlaid in Figure 2, together with 22 other curves from studies of skipjack growth across the Pacific Ocean[1]. LFMP = length frequency modal progression; MFCL = MULTIFAN-CL; internal = the growth curve was estimated within the integrated assessment framework, with other model parameters estimated at the same time; external = the growth curve was estimated outside of an integrated assessment framework; VB = von Bertalanffy; GCM = growth cessation model.

Source	Curve	Region	Data	How estimated	Growth function	Parameters[4]
Castillo-Jordán et al. (2022)	*DiagCase 2022*	WCPO	LFMP	MFCL, internal	VB	L_1=22.761, L_n= 83.865, K^q=0.215
Vincent et al. (2019)	*DiagCase 2019*	WCPO	LFMP	MFCL, internal	VB	L_1=22.783, L_n=83.883, K^q=0.215
Vincent et al. (2019)	*GrowthLow 2019*	WCPO	LFMP	MFCL, internal	VB	L_1=25.705, L_n=78.031, K^q=0.212
Vincent et al. (2019)	*GrowthHigh 2019*	WCPO	LFMP	MFCL, internal	VB	L_1=22.667, L_n=85.047, K^q=0.210
Hoyle et al. (2010)	*DiagCase 2010*	WCPO	LFMP	MFCL, internal	VB	L_1=10.000, L_n=88.317, K^q=0.197
Leroy (2000)[2]	Leroy (2000)	WCPO	Daily otolith age estimates	external	VB	L_∞=81.874, K=1.091, t_0=-0.206
Ku et al. (2015)	Ku et al. (2015)	WCPO	Annual otolith age estimates	external	VB	L_∞=77.4, K=0.176, t_0=-2.569
Maunder et al. (2022a)[3]	Maunder et al. (2022a)	EPO	Tag-recapture data	external	GCM	L_∞=78, K^q =1.43, $r_{\max}$=6.64, A_{fix}=2 qtrs, L_{fix}=37

[1] We refer readers to Table S15 from Murua et al. (2017) for parameter estimates for these 22 curves. WCPO studies included were: Brock (1954) in Joseph and Calkins (1969); Kawasaki (1963) in Joseph and Calkins (1969); Rothschild (1966) corrected and uncorrected, in Joseph and Calkins (1969); Chi and Yang (1973) in Wild and Hampton (1994); Josse et al. (1979); Skilman (1981); Uchiyama and Struhsaker (1981); Wankowski (1981); Yao (1981) in Wild and Hampton (1994); Sibert et al. (1983); Brouard et al. (1984); Tanabe et al. (2003a); Leroy (2000); Wang et al. (2010) and Ku et al. (2015). EPO studies included were: Schaefer (1961) in Joseph and Calkins (1969); Joseph and Calkins (1969); Josse et al. (1979); Sibert et al. (1983); Bayliff (1988) grouped and ungrouped.
[2] We note that the VB parameter estimates listed here for Leroy (2000) differ markedly from those originally reported by Leroy (2000) (i.e. L_∞ = 62.17, K = 2.37, t_0 = -0.04). Leroy's original VB model was based on 57 out of the 61 otolith age estimates – excluding age estimates from the four largest fish, and the model also included some additional tag-recapture growth increment data. The VB parameters presented here in Table 1 relate to a model estimated using only the otolith data from Leroy (2000) (n = 61), including the four largest fish, with fork lengths ranging between 61 and 69 cm for these larger fish.
[3] Refer to Maunder et al. (2022a,b) for definitions of the growth cessation model parameters.
[4] Units for all length parameters are in cm.

2.2 Data screening to obtain a 'high confidence' growth increment tagging dataset

To obtain a high confidence tagging dataset, we used selected data from both the JPTP and PTTP. Neither of these tagging programmes were specifically designed to collect high quality length data for tagged fish at release and recapture, so we screened both datasets based on protocols established by the Secretariat of the Indian Ocean Tuna Commission (IOTC) (Eveson et al. 2015) and adopted some of the procedures applied in integrated growth models for yellowfin and bigeye in the WCPO (Eveson et al. 2020). For this study, and following the requirement within MULTIFAN-CL of using a single growth curve, we made the simplifying assumption that growth rates do not vary by region in the WCPO.

The data screening steps were selected in an attempt to remove records with missing or unreliable data. Any record that failed on any of the following criteria was excluded from the dataset.

i. Species is identified to be skipjack
ii. Recapture length (for PTTP recaptures) is measured at the Shimizu Lab in Japan
iii. Recapture length (for JPTP recaptures) is identified as measured fork length (Aoki et al. 2022), and is neither estimated nor deduced nor recorded as N/A
iv. Days at liberty are greater than one month (≥ 30 days)
v. Daily growth rate is neither negative (≥ 0 cm/day) nor too high (≤ 0.2 cm/day)
vi. Recapture date is reliable (reliability field ≤ 3 for PTTP records and equal to 1 for JPTP records, see Aoki et al. (2022) for specifications of reliability fields for JPTP records)
vii. Recapture length measurement (for JPTP recaptures) is reliable (reliability field ≥ 1, see Aoki et al. (2022) for specifications of reliability fields)
viii. Release length measurement (for PTTP recaptures) is reliable (reliability field = 1)

We applied these screening steps to both the JPTP data (resulting in a screened dataset with n = 241 coupled tag-recapture records) and the PTTP-ShimizuLab data (screened dataset n = 247 coupled tag-recapture records). These two datasets are complementary, as they span different geographic regions of the Pacific covered by the 2022 WCPFC skipjack stock assessment (Figure 4). A key limitation of these datasets is the scarcity of records from small and large individuals – size classes which do appear in the catch, but which are not often tagged. That said, while the bulk of our records are from fish < 60 cm fork length at recapture, the screened JPTP dataset contains some data on larger individuals, and includes several useful records with longer times-at-liberty (i.e. approaching 800 days) (Figure 5), thus providing at least some information about growth in larger size classes. Acknowledging this limitation, given the screening steps employed, we consider the combined JPTP and PTTP-ShimizuLab datasets as a 'high confidence' tag-recapture dataset for growth analysis in the WCPO region.

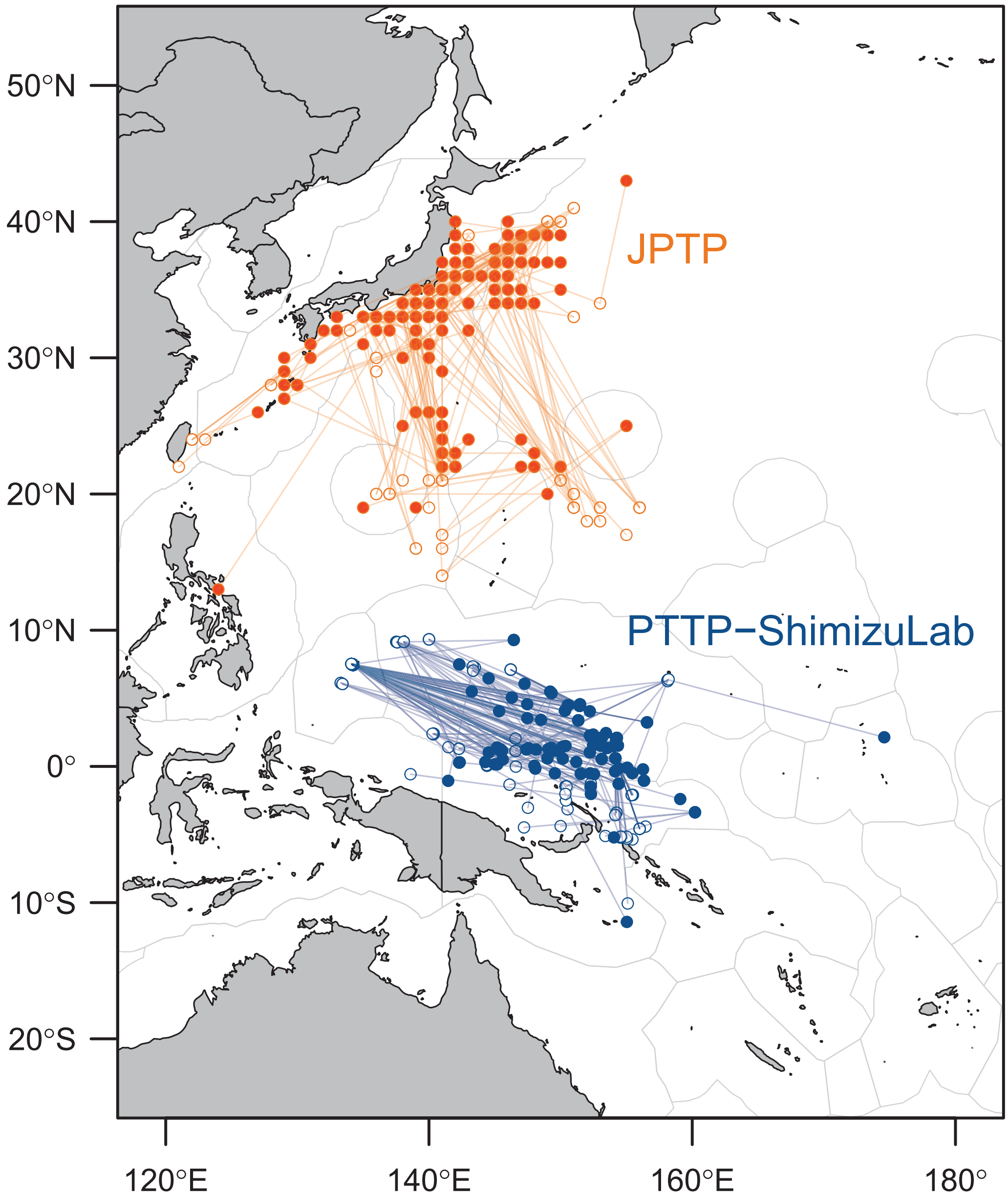


Figure 4: Map showing locations of the screened tag recaptures from the JPTP (orange, more northern) and PTTP-ShimizuLab (blue, largely equatorial) datasets. Open circles are tag release locations, and filled circles are tag recapture locations.

2.3 Exploratory data analysis

Finding appropriate functional forms for the growth curves

Selecting the most biologically plausible functional form for a growth curve is an important step in any growth modelling exercise. When suitable tag-recapture data are available, plotting the growth rate against the mean size of individual fish at tagging and recovery can help reveal the presence and location of transition points between distinct growth stanzas. This approach has been used to help select the most appropriate functional form for growth, given the available data (Eveson et al. 2015, Maunder et al. 2022a,b). While von Bertalanffy growth functions are still widely applied in modelling tuna growth (see Murua et al. 2017), more flexible curves that incorporate multiple growth stanzas (e.g. Hearn and Polacheck 2003; Laslett et al. 2002; Maunder et al. 2018, 2022a) have recently shown improved fits for several species, including skipjack in the Indian Ocean (e.g. Hillary et al. 2008; Eveson et al. 2015) and more recently in the EPO (Maunder et al. 2022a,b).

We plotted individual growth rates (cm/day) from the tag-recapture data against the mean of the individual fish lengths measured at release and at recapture. This plot can be used to seek evidence for multi-stanza growth, indicated by a distinct change in growth rate at a particular size. A growth rate plot can also be used to distinguish between a linear decreasing trend (suggesting a VB growth model may be appropriate) or a flat trend, indicating size-independent (constant) growth (suggesting a growth cessation model may be appropriate).

Growth rate plots for the JPTP data, the PTTP-ShimizuLab data and both datasets combined (Figure 5), show evidence of growth rates decreasing with size, especially for the PTTP-ShimizuLab data, suggesting a VB curve is an appropriate functional form to model the growth of skipjack in the WCPO.

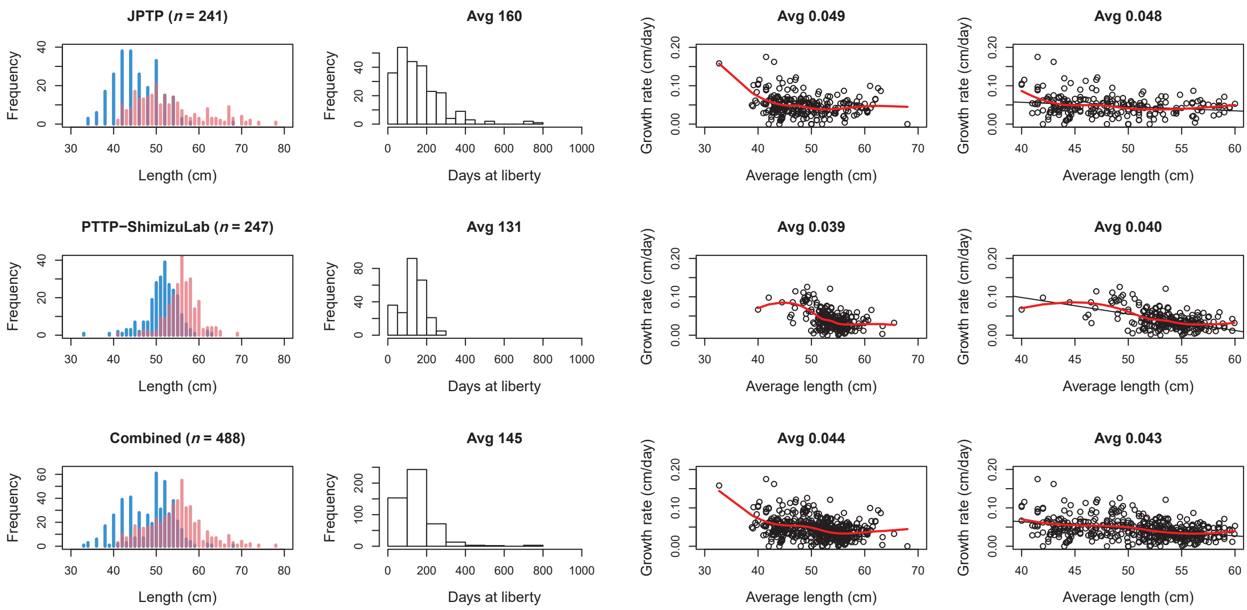


Figure 5: Summaries of screened tag-recapture data from the JPTP dataset (top row) and PTTP-ShimizuLab dataset (bottom row), and both datasets combined (third row). The first column shows the distribution of release (blue) and recapture (red) lengths, and the second column shows the distribution of days at liberty. The third and fourth columns show the growth rate (cm/day) of individual tagged fish as a function of the mean length (mean of release and recapture lengths) for different ranges of mean lengths, with a range of 30-70 cm for column 3 and a range of 40-60 cm for column 4, The red line in columns 3 and 4 is a loess smoother to indicate trends and the black line in column 4 is a linear regression line.

Information on sex was not available for our data so growth was assumed to follow the same growth curve for each sex. Previous work on skipjack growth in the region has found no evidence for strong sex-specific growth differences (e.g. Ku et al. 2015).

2.4 *VBoto* model

Based on the plots of growth rate against mean length for the otolith and high-confidence tag-recapture datasets (Figure 5), we chose to use a VB growth curve as the basis for subsequent model development. The *VBoto* model draws on information from two separately fitted VB growth curves: the first curve is fitted only to the Leroy (2000) daily otolith age readings and the second curve is fitted to a combination of the high-confidence JPTP and PTTP-ShimizuLab tag-recapture dataset and the otolith data.

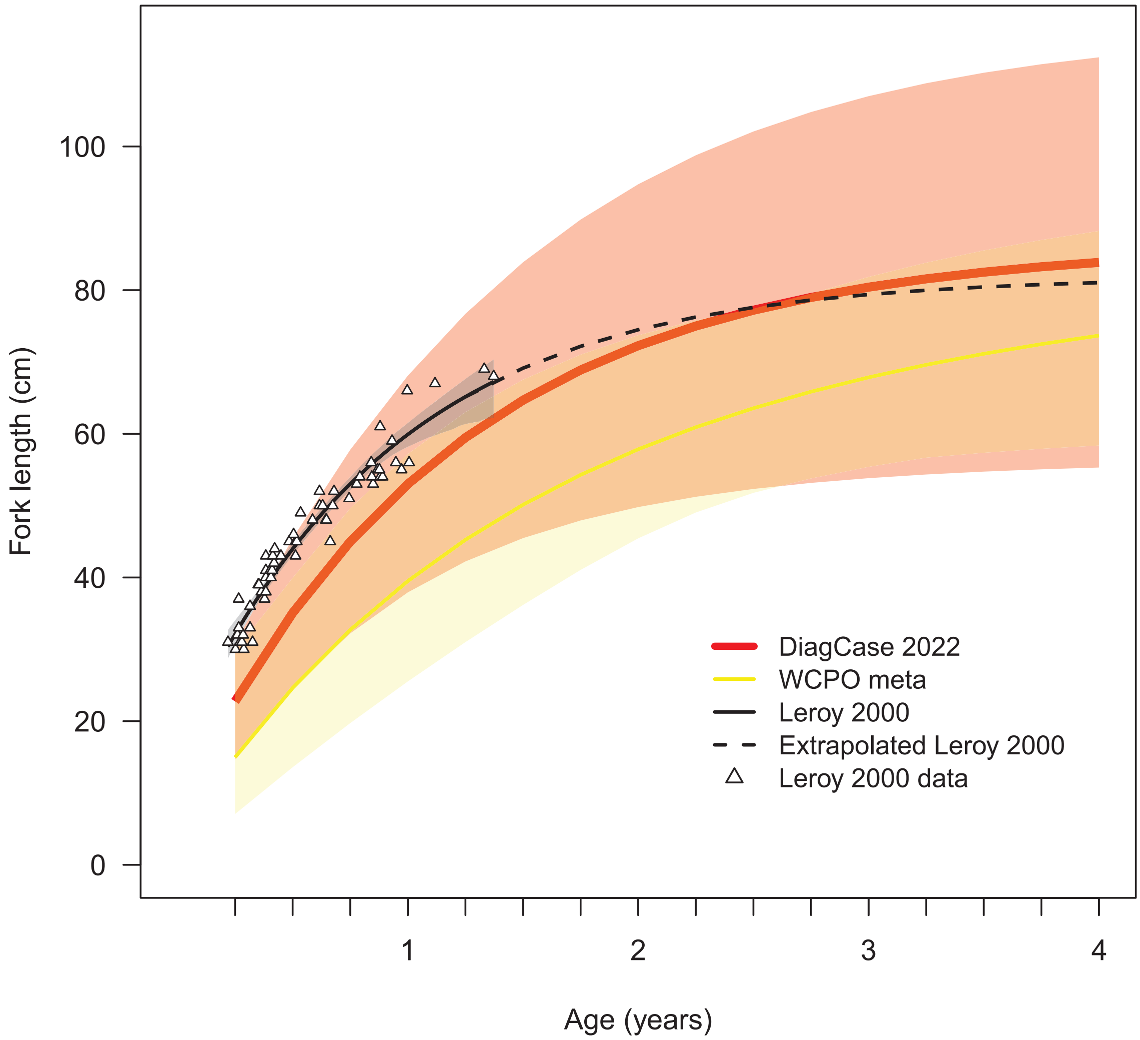


Figure 6: Estimated growth curve WCPFC skipjack diagnostic case from 2022 (*DiagCase 2022*, bold red line); meta-analysis of published WCPO growth studies (*WCPO meta*, yellow line); and fitting to otolith length-at-age data (Leroy 2000). As in Figure 3, red shading indicates the 95% confidence intervals for the *DiagCase 2022*, and yellow shading indicates the 2.5% and 97.5% quantiles of mean length-at-age from the selected WCPO studies reviewed in the meta-analysis. The white triangles are the daily age estimates from otoliths read by Leroy (2000). The black line is a VB curve fitted only to the Leroy (2000) otolith data, with shading to indicate bootstrapped 95% confidence intervals around the mean length-at-age, and with the black line dashed for ages beyond the range of the Leroy (2000) data.

Our modelling procedures for the *VBoto* model were as follows:

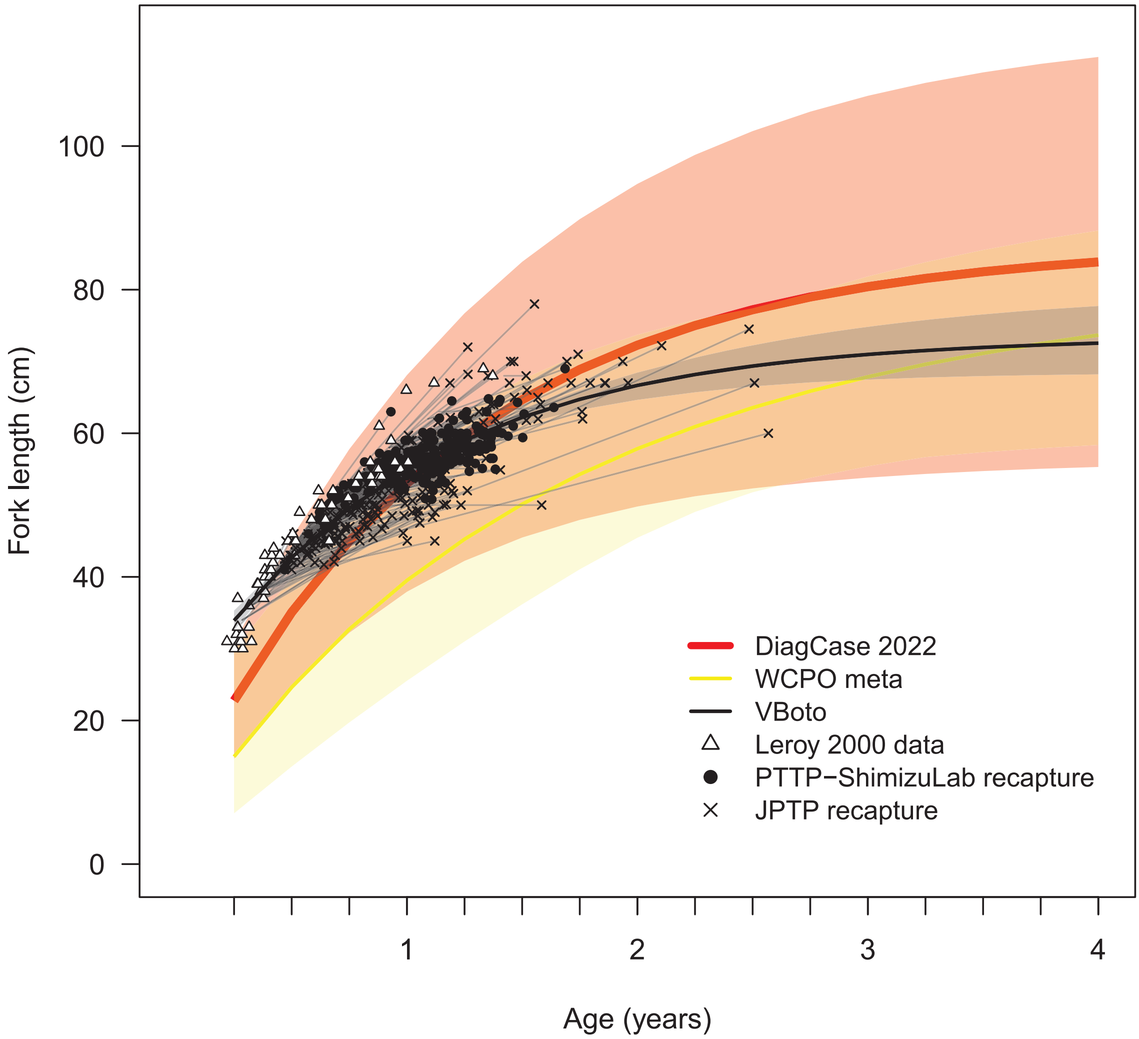
i. First fit a VB curve to the Leroy (2000) otolith based daily age estimates (n = 61). This VB model assumes normally distributed errors N(0, σ^2) from the mean length-at-age. Parameter estimates for this initial VB curve are shown in Table 1 and Figure 6.
ii. We rearranged the VB equation to solve for age at a specified length, following Ogle and Isermann (2017).
iii. Using the mean growth curve fitted in step i, the age-at-release was calculated for each tagged individual as a function of the recorded length at release.
iv. The known time-at-liberty was added to the age-at-release to obtain the calculated recapture age for each tag return. Note, that this analysis excluded individuals with release lengths that fell outside the 30-69 cm fork length range, from the Leroy (2000) analysis, to ensure that age-at-release was not extrapolated outside the range of the length data used to estimate the initial VB curve. This resulted in the exclusion of only one individual from the tag-recapture dataset.
v. Using these ages assigned to the recapture length records, we fitted a second VB curve, this time using both the otolith data (n = 61) and adding the recapture length-at-age data (n = 487), producing a combined dataset with n = 548 datapoints. This results in a model referred to as the *VBoto* model, which also assumes normally distributed errors N(0, σ^2) (Figure 7, black line). Note that we chose to exclude the length and estimated age-at-release in this model, as these age-at-release estimates come directly from the growth curve fitted to the Leroy (2000) otolith data in step i. Further, one of our data screening steps involved retaining only individuals with times-at-liberty of > 30 days partly to minimise the impact of the otolith growth curve used to estimate age-at-release on the *VBoto* model outputs.

Model fitting, checking and plotting

Starting values for the VB growth parameters were derived from initial model fits or by using the ‘vbStarts’ function in the FSA package. With these values set, we fit the models to the otolith data alone (in step i), and to the combined otolith and recapture data (in step v) using the ‘nls’ function in the ‘stats’ package. Standard visual checks were used to assess model adequacy, including plots of residuals versus estimated age. We obtained parameter estimates for L_∞, K and t_0 and predicted the mean length-at-age for the *VBoto* model across the 16 quarterly age classes specified in the MULTIFAN-CL skipjack assessment. Finally, we computed bootstrapped 95% confidence intervals around the mean length-at-age using the ‘Boot’ function in the ‘car’ package, and plotted out the results, overlaying the tag-recapture vectors for all recaptured individuals (Figure 7).

Results

The *VBoto* model had estimated parameters L_∞ = 73.5, K = 1.01 and t_0 = -0.365. The predicted mean length-at age at age ¼ year was 33.91 cm, and at age 4 years was 72.6 cm. The oldest estimated age at recovery was 2.57 years. Given the nature of the tag-recapture data, with the bulk of our recovered individuals falling within the 40 to 60 cm size class, the model had very little information for fish > 70 cm fork length, and tended to overpredict the length-at-age for the smallest fish in the otolith dataset (i.e. those from 30-32 cm fork length). There was no clear trend in the residuals for the recapture records across the range of estimated ages, with the recapture records spread evenly around the mean growth curve (Figure 7). There appears to be a residual pattern with the otolith records, with the fitted curve generally estimating larger sizes than the data for the smaller and younger otolith records and estimating smaller sizes than the data for the larger and older otolith records.



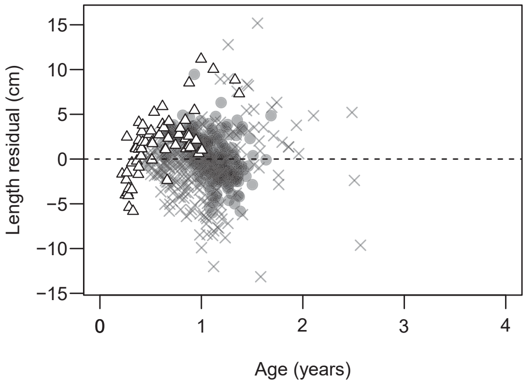


Figure 7: Alternative growth curve 2: Estimated growth curve WCPFC skipjack diagnostic case from 2022 (*DiagCase 2022*, bold red line); meta-analysis of published WCPO growth studies (*WCPO meta*, yellow line); and fitting to otolith and tag recapture length-at-age data (*VBoto*, black line). Shading in red and yellow is as for Figure 3. The white triangles are the daily age data from Leroy (2000). The black circles are the imputed length-at-age data for the tag recaptures from the PTTP-ShimizuLab data, and the black crosses are the imputed length-at-age data from the JPTP recaptures, where the age-at-recapture is calculated by adding the time-at-liberty to the assigned age-at-release. The straight grey lines link release and recapture data points for individual fish. The black line is the *VBoto* mean length-at-age curve fitted to the white triangles and the white circles, with bootstrapped 95% confidence intervals around the mean length-at-age shown by the black shading. The lower panel shows the length residuals plotted against estimated age for the otolith data (white triangles), the PTTP-ShimizuLab tag recapture data (black circles) and the JPTP recapture data (black crosses).

2.5 *GCM.oto* model

Despite evidence from our exploratory data analysis that supports the choice of VB as our preferred functional form for the growth curve (Figure 5), given the recent work in the EPO on skipjack using the growth cessation model (GCM) (Maunder et al. 2022a,b), we thought it prudent to explore fits to our data using this growth cessation functional form and later compare those fits to a similar model (*VBtag.oto* see details in Section 2.6) that uses a VB functional form. The GCM was run using similar settings to those chosen for skipjack in the EPO (Maunder et al. 2022a,b). A key difference is that our version of this GCM (*GCM.oto*) simultaneously fits to both otolith and tagging data.

Parameters were estimated using traditional maximum likelihood estimation in Template Model Builder (TMB, Kristensen et al. 2016), except for the sigma parameters: σ_a fixed at 10^{-7}; σ_{ME} fixed at 0.222; and σ_b estimated. Diagnostic plots of residuals versus estimated ages were used to assess model adequacy, and we used R^2 calculated as a criterion for selecting between the *GCM.oto* and *VBtag.oto* models. See Appendix 1 for full details on model structure and the GitHub repository https://github.com/PacificCommunity/ofp-sam-skj-tag-growth-public for C++ and R code to fit both models.

Results

The *GCM.oto* model had estimated parameters L_∞ = 63.9, K = 2.58 and r_{max} = 36.9. The predicted mean length-at age at age ¼ year was 33.2 cm, and at age 4 years was 63.9 cm. As with the previous models, this model has very little information for fish > 70 cm fork length, and tended to overpredict the length-at-age for the smallest fish in the otolith dataset (i.e. those from 30-35 cm fork length). There is no clear trend in the residuals for the both the release and the recapture records across the range of estimated ages, with these records spread evenly around the mean growth curve (Figure 8). As with *VBoto*, there continues to be a residual pattern with the otolith records, with the fitted curve generally estimating larger sizes than the data for the smaller (< 35 cm) and younger otolith records and estimating smaller sizes than the data for the larger (> 35 cm) and older otolith records. However, in this case the curve overpredicts the lengths for the majority of the otolith data points. The value of R^2 for *GCM.oto* was 0.857.

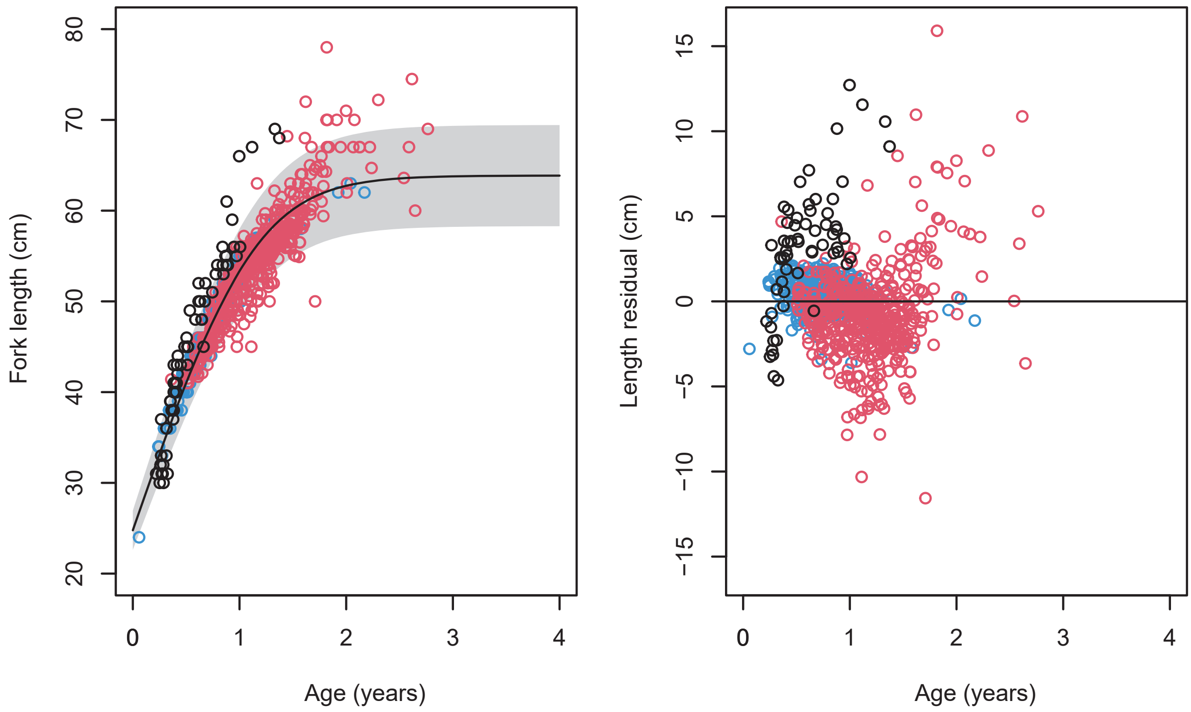


Figure 8: Fit of the *GCM.oto* model to the combined otolith and tag-recapture length-at-age data. Left panel shows the mean length-at-age curve (black line) with otolith length-at-age (black circles), and estimated release length-at-age (blue circles) and recapture length-at-age (red circles) overlaid. Right panel shows the length residuals plotted against estimated age. Grey shading represents the 95% prediction intervals from the *GCM.oto* fit.

2.6 *VBtag.oto* model

The *VBoto* model assumes that age-at-release is known precisely and is estimated without error from the otolith data – two strong assumptions that do not admit the very real uncertainty we have around otolith-based ageing in skipjack. Further, by excluding the release records in model fitting, *VBoto* does not take advantage of all the information available from the tag-recapture data.

We sought to improve upon *VBoto* by following the proposal of Palmer et al. (1991), Wang et al. (1995) and Laslett et al. (2002) of modelling the joint density of tag and recapture lengths and estimating the age-at-release from the tagging data. This method was extended by Eveson et al. (2004), who integrated length frequency data, otolith age estimates and tag-recapture data into the framework. Aries de Silva et al. (2015) simplified the Eveson et al. (2004) approach by relaxing some of the stronger assumptions and dropping the random effect specification for the asymptotic length parameter L_∞, while Francis (2016) made some further adjustments by allowing for correlation between length deviates at release and recapture. In developing the growth cessation model fit to otolith and tag-recapture data for EPO bigeye tuna (*Thunnus obesus*), Maunder et al. (2018) proposed a further modification to the Aries de Silva et al. (2015) approach by estimating the age-at-release of each individual as a fixed, rather than a random effect. We followed the Maunder et al. (2018) approach here.

Model structure, fitting, checking

The *VBtag.oto* growth model has three likelihood components based on the fits to the observations: lengths at tag release; lengths at tag recapture, and lengths from the otolith data. Each assumes underlying VB growth with normally distributed errors. Unlike the approaches of Laslett et al. (2002) and Aries de Silva et al. (2015), the unknown age-at-release is estimated as a fixed effect, following Maunder et al. (2018, 2022a), which helps with model convergence and relaxes the need for distributional assumptions for the age-at-release. The age-at-recapture is then the estimated age-at-release plus the known time-at-liberty. The variability in length-at-age was allowed to vary linearly with age for each of the likelihood components. See Appendix 1 for a full description of the model.

The *VBtag.oto* model directly incorporates measurement error in the release and recapture lengths, and does not rely on the otolith data to estimate age-at-release. Measurement error and process error (the latter driven by individual variation in length-at-age) are both assumed to follow normal distributions. For the purposes of this analysis, and given the attention paid to obtaining reliable recapture lengths in our data filtering steps, we considered it reasonable to assume the same variance for the measurement error in the release and recapture lengths. However, we acknowledge this may be a simplification for many tag-recapture datasets where uncertainties and/or differences exist in the quality of release and/or recapture lengths.

Like the *GCM.oto* model, parameters were estimated using traditional maximum likelihood estimation in TMB, except for the sigma parameters (see Appendix 1 for details) which were fixed: $\sigma_a = 2.0$; and $\sigma_b = 2.5$, based on empirical coverage. Again, diagnostic plots of residuals versus estimated ages were used to assess model adequacy, and we calculated R^2 for model comparison.

Results

The *VBtag.oto* model had estimated parameters $L_\infty = 73.4$, $K = 0.811$ and $t_0 = -0.607$. The predicted mean length-at age at age ¼ year was 36.75 cm, and at age 4 years was 71.7 cm. As with the *VBoto* model, this model has very little information for fish > 70 cm fork length, and tended to overpredict the length-at-age for the smallest fish in the otolith dataset. There is no clear trend in the residuals for the both the release and the recapture records across the range of estimated ages, with these records spread evenly around the mean growth curve (Figure 9). Like the *VBoto* and *GCM.oto* models, there appears to be a residual pattern with the otolith records, with the fitted curve generally estimating larger sizes than the data for the smaller (< 42 cm) and younger otolith records and estimating smaller sizes than the data for the larger (>42 cm) and older otolith records. The value of R^2 for *VBtag.oto* was 0.890 compared with the value of R^2 for *GCM.oto* which was 0.857. This indicates a better fit to our data using the *VBtag.oto* model.

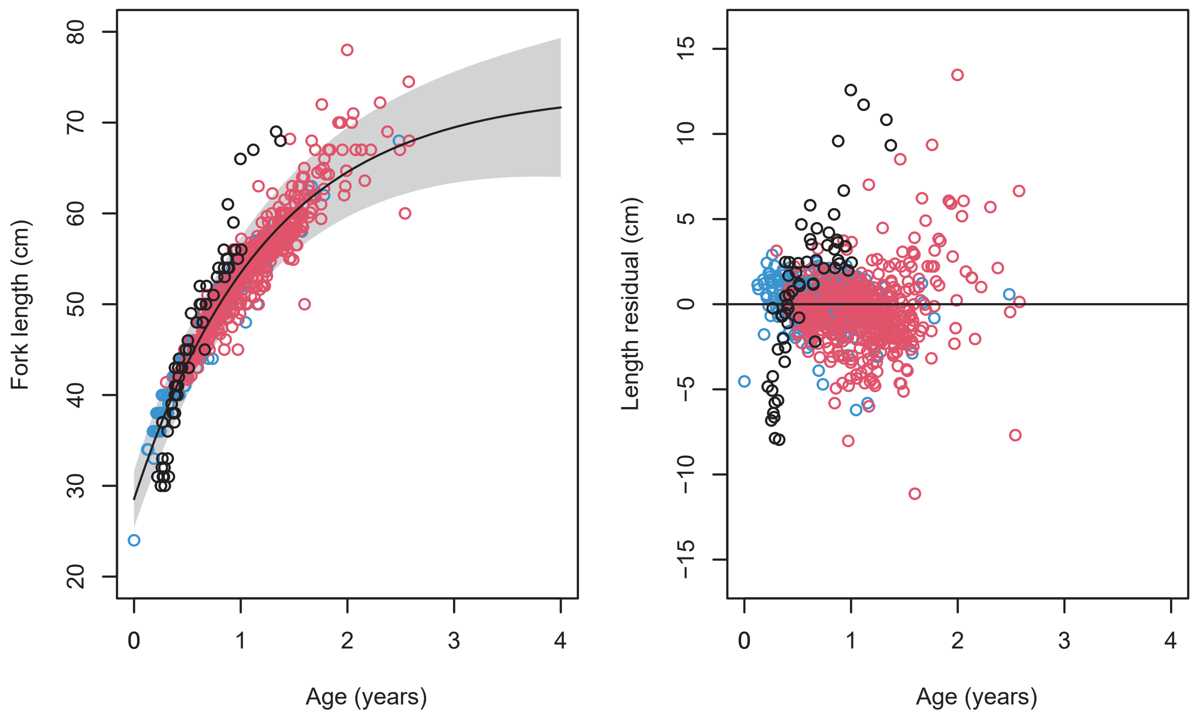


Figure 9: Fit of the *VBtag.oto* model to the combined otolith and tag-recapture length-at-age data. Left panel shows the mean length-at-age curve (black line) with otolith length-at-age (black circles), and estimated release length-at-age (blue circles) and recapture length-at-age (red circles) overlaid. Right panel shows the length residuals plotted against estimated age. Black shading represents the 95% prediction intervals from the *VBtag.oto* fit.

2.7 Summary plot of main modelling results

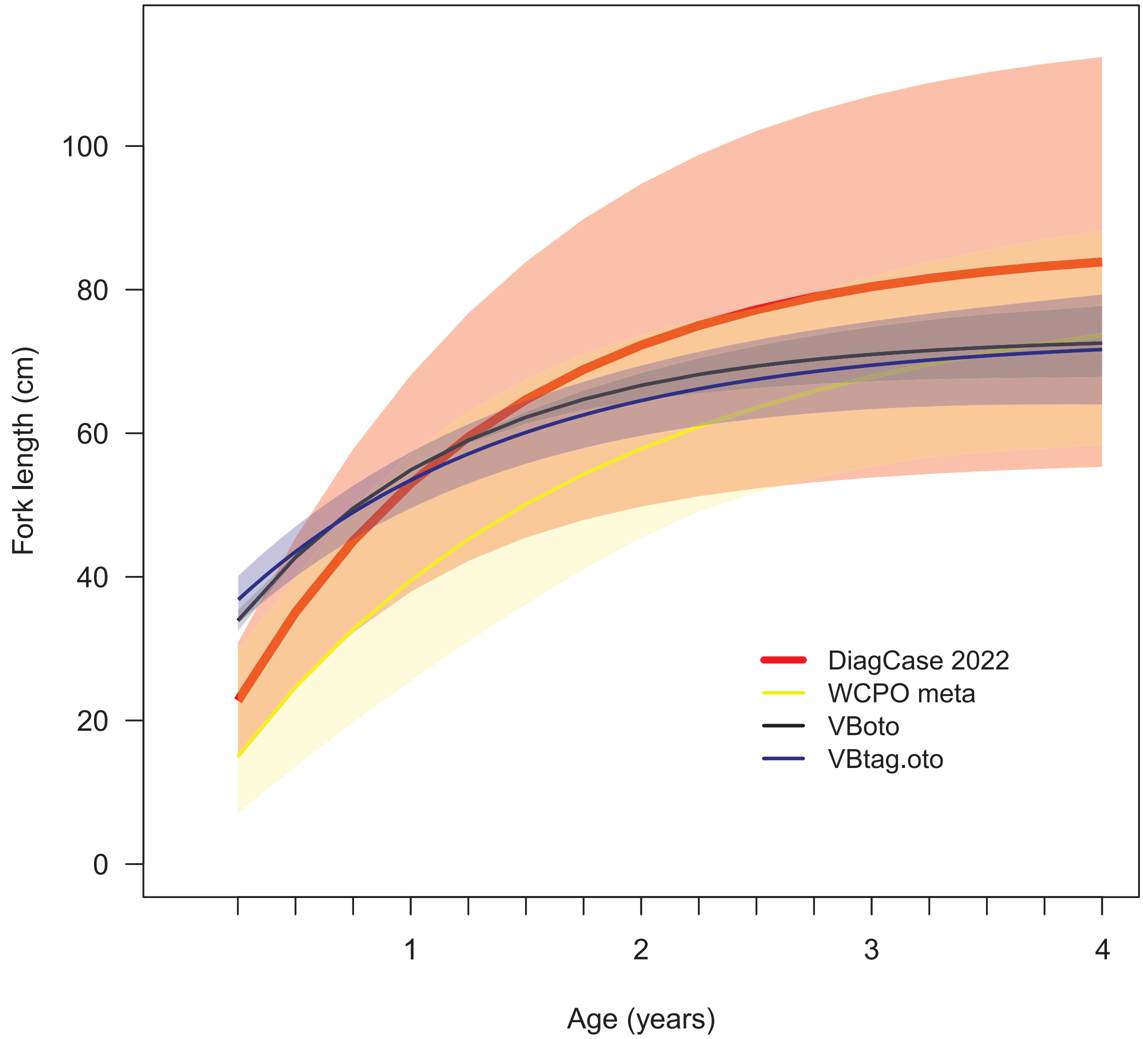


Figure 10*:* All three alternative growth curves: Estimated growth curve from WCPFC skipjack diagnostic case from 2022 (*DiagCase 2022*, bold red line); meta-analysis of published WCPO growth studies (*WCPO meta*, yellow line); fitting to otolith and tag recapture length-at-age data (*VBoto*, black line); and fitting to otolith, tag recapture length-at-age data and tag release length-at-age data (*VBtag.oto*, blue line). Shading in red, yellow and black are as for Figure 7. Blue shading represents the 95% prediction intervals from the *VBtag.oto* fit.

3 Discussion and Conclusions

Three new growth curves were produced as possible alternatives for use in the uncertainty grid for the 2022 WCPFC skipjack assessment (Figure 10). The first alternative growth curve '*WCPO meta*' was obtained from a meta-analysis of published growth studies in the WCPO. The second alternative is derived from the '*VBoto*' model. This model incorporates daily otolith age data (Leroy 2000) from young skipjack captured in Papua New Guinea and length-at-age data from 'high confidence' tag recaptures sourced from PTTP-ShimizuLab and

JPTP records, with assumptions made allowing an age-at-release to be assigned to each tagged fish based on a von Bertalanffy curve fitted to daily otolith readings. The third alternative is derived from the '*VBtag.oto*' model which incorporates the same daily otolith age data (Leroy 2000), and the length-at-age data for both tag recaptures and tag releases, includes measurement error in the release and recapture lengths, and does not rely on the otolith data to estimate age-at-release.

Out of these three alternative growth forms, we recommend the use of the *VBtag.oto* as the preferred alternative growth option for the uncertainty grid in the 2022 WCPFC skipjack assessment. Growth for *VBtag.oto* follows a von Bertalanffy curve with parameters: $L_\infty = 73.4$ cm fork length, $K = 0.811$ and $t_0 = -0.607$. While we were able to provide estimates of prediction uncertainty for a range of our models, based on bootstrapping procedures, or looking at the uncertainty in the data used to fit our models, greater variability around the growth curve is likely to be required when these growth curves are used in an integrated stock assessment, especially when additional length frequency data is included. Care should also be taken using predictions from these alternative growth curves for sections of the parameter space that are not informed by the data used to estimate this growth beyond. For skipjack, this applies especially to predicted lengths for older fish, and indeed to estimated values for L_∞.

This analysis is the first to develop and make use of a high-confidence tag-recapture dataset for the purposes of estimating growth in a WCPFC skipjack assessment. We suspect that the difficulties we encountered in ensuring the accuracy of certain data fields (e.g. reliability of recapture length measurements, reliability of recapture date entries) for the vast amounts of tagging data available across the region have hampered previous efforts to estimate growth based on this data type. While not immune to these difficulties, our application of a series of rigorous screening steps, in conjunction with consulting tagging database and fisheries experts across the WCPFC membership resulted in a dataset we were confident to use in our modelling exercises.

This analysis is also the first to combine tag-recapture growth data with daily age estimates from otoliths to estimate growth in a WCPO skipjack assessment. The Leroy (2000) otolith dataset contains valuable information on growth in younger WCPO skipjack not provided by the tagging data; however, we caution that debate continues as to the accuracy of hard parts such as otoliths, fin spines and vertebrae for estimating age and growth for skipjack. This has stemmed in part from discrepancies in the number of daily increments detected and times-at-liberty for chemically marked and released individuals (e.g. Wild and Foreman 1980; Wild et al. 1995; Sardenne et al. 2015), and high variability in age estimates of the same samples among different teams of otolith readers. Moreover, although the deposition of daily increments on sagittal otoliths has been validated for larval, juvenile and adult stages (Radtke 1983; Tanabe 2003a,b,c; Kayama et al. 2007), difficulties in replicating such results on other samples, and the lack of validation of annual growth increment formation in the species continues to impact our ability and confidence to estimate ages in older specimens using otoliths.

Questions regarding the representativeness of otolith age estimates taken from one region of the ocean and applied to another are also relevant. Our otolith age records came from a small sample of young skipjack captured by purse seine vessels operating in the Papua New Guinea EEZ (Leroy 2000). While considered the most reliable otolith-based age estimates that we have access to from the WCPO, the sample size is small, the collection area is limited, and the accuracy of the increment counts for older individuals (i.e. with age estimates of > 1 year old) is less certain (B. Leroy, pers. comm.). However, given the relatively limited amount of empirical information available on the age and growth of young skipjack in this region, our priority was to extract the maximal information possible from the available data, and hence we decided to include all 61 otolith age readings in our analysis.

Despite this inclusion, a key limiting factor in our analysis was the absence of both very young and older fish in our datasets. The age structure chosen for the WCPO skipjack stock assessment includes 16 age classes, with the first age step at ¼ of one year old, up to the last age class which incorporates individuals 4 years (16 quarters) or older. The oldest individual estimated in our tag-recapture datasets is ~2.5 years old (see Figure 7 and Figure 9) and hence there is a considerable portion of the estimated growth curve for which we have no data to directly inform growth estimates, making it challenging to infer anything substantive about L_∞ from the data at hand. We know from the catch length frequencies that skipjack in the 20-30 cm range are caught by fisheries in certain regions (e.g. the Philippines' ringnet fishery) (Hare et al. 2022; Macdonald et al. 2022), yet the smallest skipjack in our otolith dataset was 30 cm fork length. We also know that skipjack up to ~90 cm are captured by the longline fishery (Hare et al. 2022). Yet the sizes encountered during recent tagging campaigns typically fall within the 40-70 cm fork length range (SPC-OFP 2020, 2021, 2022a) with recaptures by the fishery often occurring very soon after release (Figure 5). Ultimately, these factors make it difficult to obtain representative information about growth at both very young and older ages from the existing otolith and tag-recapture data, regardless of the screening steps employed.

When growth is estimated internally using length composition data only within an integrated stock assessment framework, the model is largely using modal progression in the length composition data to infer information on growth rates. This approach naturally incorporates the full size and age range of skipjack captured by the commercial fisheries across the region – data not used in our approach to estimating growth externally using existing otolith and tag-recapture data. The internal estimation of growth within a stock assessment also ensures the appropriate consideration of the effects on the size composition data resulting from the different selectivity patterns for each fishery. Growth estimates from integrated stock assessments which use length frequency data can be sensitive to the sample size weighting assigned to the length composition data, especially in the absence of otolith or tag recapture growth data. Using the Dirichlet multinomial approach to weighting length composition data (Thorson et al. 2017) can eliminate the need to make a subjective decision on sample weighting, or the need to explore sensitivities to the weighting of length composition data. This appears to be a defensible approach for internal growth estimation within future WCPFC skipjack assessments. That said, given the different growth trajectories we observe between the *DiagCase 2022* estimate this year and our externally estimated growth curve from *VBtag.oto*, it seems wise to follow the advice of Kolody et al. (2016) who stated that if possible and tractable, we should attempt to estimate growth both internally within an integrated assessment model, and externally to it, in order to get the best possible representation of growth and to understand how different sources of data, or certain data limitations, can give rise to different growth forms.

For external estimation of growth, there is a clear need for new and better data on age and growth in skipjack. SPC's port sampling collaboration with SOCSKSARGEN Federation of Fishing & Allied Industries (SFFAII) and the Bureau of Fisheries and Aquatic Resources ministry (BFAR) in General Santos, Philippines, continues to provide an important source of biological samples for young, ringnet-caught skipjack in the 20-30 cm fork length range. This work will continue over the coming year through WCPFC Projects 35b (SPC-OFP 2022b) and

90 (Macdonald et al. 2022), with a focus on boosting numbers of otoliths and muscle samples available for this size class. The upcoming 6th Western Pacific pole-and-line tagging cruise (WP6) in the Solomon Islands' EEZ presents another opportunity for new data collection. WP6 will run between September and October 2022 and will focus on conventional tagging of skipjack and yellowfin, biological sampling for the WCPFC Pacific Marine Specimen Bank and ongoing work on tuna genetics and genomics. In addition, SPC is planning to expand the strontium chloride ($SrCl_2$) marking experiment on skipjack first trialled during WP5 in 2019. Tag recovery rates will likely be much higher in the archipelagic waters of the Solomon Islands compared with the region traversed by WP5, and good numbers of recaptures from $SrCl_2$ marked individuals will contribute important data to the ongoing otolith-based ageing work underway in the Indian Ocean (J. Farley and P. Eveson pers. comm.). WP6 will also contribute data towards new research exploring DNA-based ageing approaches in skipjack. Termed epigenetic ageing, this technique is simple, non-lethal, and shows great promise from trials on zebrafish, salmon and southern bluefin tuna, among other species (see Mayne et al. 2019, 2020a,b, 2021a,b). During WP6, SPC will collect a muscle biopsy from all $SrCl_2$ marked fish at release, and through pushing the WCPO tag recovery network to ensure a muscle sample is also collected at recovery, this will provide much-needed samples for validation of the epigenetic ageing model currently in development for skipjack. This will be particularly useful if at least some of our tagged fish remain at liberty for more than six months. In an effort to get data from these fish with longer times-at-liberty, our idea is to focus on free schools for the $SrCl_2$ releases during WP6. This will hopefully reduce the chance of recaptures after short times-at-liberty as may occur with releases of tagged fish from anchored-FAD associated schools.

Our modelling approach could also benefit from some refinement. As additional data becomes available and novel methodologies (as outlined above) are developed for collecting data on age and growth, this could allow further exploration of a range of different model specifications that may help resolve some of the apparent inconsistencies seen in this study, such as the residual patterns observed for the fits to the otolith data (Figure 9).

In conclusion, in order to further improve and extend the growth modelling work for skipjack in WCPO, we invite SC18 to consider the need for:

1. **Better ageing data**, through continued sampling, use of emerging technologies, and collaboration among scientific and fisheries agencies to increase the number and quality of age measurements across a broader range of fish lengths (and ages), a larger spatial area and longer time series. This would ensure representative sampling throughout the ranges of the stocks being assessed.
2. **More tag-recapture data**, covering a broader area with high reliability in key data fields. In particular, attention should be paid to obtaining precise length measurements at release, due to potential problems in the accuracy of measuring live, active specimens by inexperienced taggers (see Eveson et al. 2020), precise length measurements at recapture, either on board fishing vessels or in port, and accurate records for recapture date.
3. **Further development of modelling approaches**, including the integration of catch length frequency data with the otolith and tag growth data used here (as done by Eveson et al. 2004), and advancements in the way we model tag-recapture information. These could involve further exploration of alternative growth functions such as the growth cessation, Richards or multi-stanza growth curves if supported by the data, and further investigation into the treatment of uncertainty, particularly the sigma structure of the *VBtag.oto and GCM.oto* models. Growth information obtained from recaptures with very short times-at-

liberty could also be used to inform the measurement error at release (Eveson et al. 2020). Finally, gauging the effects of shrinkage on growth estimates for recaptured fish (following Maunder et al. 2022b) stored under differing conditions post-capture is an area of interest for skipjack and other tunas.

Code and data availability

R and C++ code to run all analyses presented in this paper are publicly available in this GitHub repository: https://github.com/PacificCommunity/ofp-sam-skj-tag-growth-public.

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Appendix 1

Description of the VBtag model

Growth

Growth follows a traditional von Bertalanffy form,

$$\hat{L}_i \;=\; L_\infty\Big(1 - e^{-k(t_i - t_0)}\Big)$$

where $\hat{L}_i$ is the predicted length of individual i, t_i is the age of individual i, and L_∞, k, and t_0 are growth curve coefficients.

Likelihood

A traditional normal likelihood is used:

```
dnorm(y, mu, sigma)
```

The model has three likelihood components, baesd on the fit to observed lengths at tag release, lengths at tag recaptures, and lengths from the otolith data:

$$f \;=\; \log L_{\mathrm{rel}} \;+\; \log L_{\mathrm{rec}} \;+\; \log L_{\mathrm{oto}}$$

Unequal variances

The variability in length at age (σ) varies with age:

$$\log \sigma_i \;=\; \text{intercept} \;+\; \text{slope} \times t_i$$

Model parameters

L_∞, k, t_0	growth curve coefficients
σ_a, σ_b	sd(length) at ages a and b
age	vector of estimated age at release for all tagged fish

Parameters are estimating using traditional MLE, except the sigma parameters are fixed (estimated iteratively and externally).

Input data

```
DATA_VECTOR(Lrel);        // length at release (tags)
DATA_VECTOR(Lrec);        // length at recapture (tags)
DATA_VECTOR(liberty);     // time at liberty (tags)
DATA_VECTOR(Aoto);        // age (otoliths)
```

```
DATA_VECTOR(Loto);        // length (otoliths)
DATA_SCALAR(a);           // younger age where sd(length) is sigma_a
DATA_SCALAR(b);           // older age where sd(length) is sigma_b
```

Source code

Link to GitHub (requires GitHub login).

Background and model variations

GCM

SPC is exploring various methods to estimate growth parameters for the 2022 stock assessment of skipjack tuna. As part of this exploration, there was interest in fitting a growth cessation model (GCM), described in Maunder et al. (2018).

Mark Maunder shared the GCM model code with the SPC growth modelling team via email (2022-05-28). This model is written in Template Model Builder (TMB) and estimates ages from tagging data, based on the observed length increase between the date of release and date of recapture.

L_∞, k, $r_{\max}$	growth curve coefficients
A_{fix}, L_{fix}	additional growth curve coefficients
σ_a, σ_b, σ_{MEb}	sd(length) coefficients
age	vector of estimated age at release for all tagged fish

VBtag

The SPC data do not show clear signs of growth cessation, so the SPC team decided to write a similar model that uses a traditional von Bertalanffy model.

The VBtag model is simpler than the GCM model, describing the growth curve with 3 parameters (L_∞, k, t_0) instead of 5 parameters (L_∞, k, $r_{\max}$, A_{fix}, L_{fix}).

The main difference between VBtag and a 'plain vanilla' von Bertalanffy model is that VBtag estimates the release age of tagged fish, using the same approach as the GCM model. The parameter vector of estimated ages uses half of the degrees of freedom from the tagging data, where each tagged fish provides two observed values to be fitted by the model: length at release and length at recovery.

GCM_oto

The GCM_oto model is the same as the GCM model, with the addition of including the otolith data. This introduces no additional parameters.

VBtag_oto

The VBtag_oto model is the same as the VBtag model, with the addition of including the otolith data. This introduces no additional parameters.

Appendix 1 continued

Variance treatment in the GCM model

Likelihood

In the GCM model (Maunder et al. 2018), σ is used in the calculation of log-likelihoods in a traditional manner:

```
dnorm(y, mu, sigma, true)
```

Unequal variances

In the calculation of σ, it increases with the size of fish:

$$\sigma_i \;=\; \sigma_a \;+\; (\sigma_b + \sigma_{\mathrm{ME}}) \times \hat{L}_i$$

Model settings

In the default model settings, some σ coefficients are fixed and others estimated:

σ_a is fixed near zero (10^{-7})

σ_b is estimated

σ_{ME} is fixed at 0.0222

Source code

```
PARAMETER(ln_sd_a);
PARAMETER(ln_sd_b);
PARAMETER(ln_sd_MEb);

sd_a = exp(ln_sd_a);
sd_b = exp(ln_sd_b);
sd_MEb = exp(ln_sd_MEb);

Lrel_sd(i) = sd_a + sd_b * Lrel_pred(i);
Lrel_MEsd(i) = sd_MEb * Lrel_pred(i);

Lrel_nll(i) = -dnorm(Lrel_obs(i),
                     Lrel_pred(i),
                     Lrel_sd(i) + Lrel_MEsd(i),
                     true);
```