



Using an approximate length-conditional approach to estimate von Bertalanffy growth parameters of North Pacific albacore (*Thunnus alalunga*)

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ABSTRACT

Growth models in stock assessments can strongly influence the estimated biomass that affect the conclusion of stock status and exploitation level. Recent studies on North Pacific albacore (*Thunnus alalunga*) growth obtained age-length data from hard parts and fit the age-length data to a von Bertalanffy growth model, assuming each observation of length is a random sample for a given age. However, these previous studies may have resulted in biased growth parameter estimates because these samples were not chosen at random and hence violated the assumptions of the method. In this study, we instead use an “approximate length-conditional” approach, which assumes that each fish is a random sample from that length bin based on an equilibrium population age structure, to fit age-length data from three previous studies. Results of the length-conditional approach resulted in a sex-combined growth curve that is similar to the previous estimates over the young and mid ages (age 2–6) but with different asymptotic lengths. Estimated growth parameters were not highly sensitive to assumed mortality rates but changing the data-weighting scheme can result in differences in estimated growth parameters. Although the length-conditional approach likely result in less biased estimated length-at-ages, especially for the youngest and oldest ages, the estimated growth curves from this study may not be representative of the stock due to potential regional differences in growth, and age and sex-specific movements. In order to successfully unravel the complexities of albacore growth observed in this and previous studies, given the complex life history, ocean-basin scale movements and multiple international fisheries, a well-coordinated and designed international sampling effort will be required.

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1. Introduction

Modeling the growth of fish, or how fish get bigger with age, is a key component of most fish stock assessment models (Francis, 2015). It is especially critical for stocks without large-scale production aging of hard parts because observed size compositions are converted to age compositions using a growth model. In addition to directly informing model processes like selectivity and recruitment, the age compositions can also strongly influence, albeit indirectly, key derived quantities like fishing mortality and relative population scale (Maunder and Piner, 2014). Therefore, the growth model used in an assessment can have major influences

on the estimated stock status and exploitation level (Wang et al., 2014).

The stock assessment of North Pacific albacore (*Thunnus alalunga*) in 2011 (ISC, 2011) and 2014 (ISC, 2014) found that growth was a key uncertainty in the assessments and strongly influenced model estimates of population scale. The growth estimates used in the stock assessment were based on 3 recent studies (Chen et al., 2012; Wells et al., 2013 and Renck et al., 2014), which were conducted to update studies from the 1950s and 60s (Otsu and Uchida, 1959; Clemens, 1961; Yabuta and Yukinawa, 1963). These three studies obtained matched pairs of data on fish age and length (age-length data) by aging hard parts (primarily otoliths) from fish with lengths measured during sampling. These age-length data were then fit to a von Bertalanffy growth model (VBGM). Wells et al. (2013) and Renck et al. (2014) primarily used albacore samples from the eastern and central North Pacific, although smaller numbers of samples were from the western North Pacific. In con-

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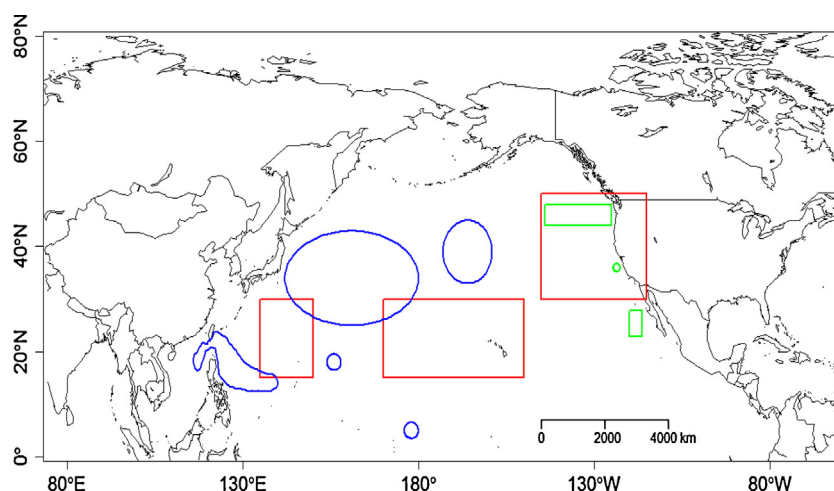


Fig. 1. Approximate regions where North Pacific albacore tuna otolith samples were collected by [Chen et al., 2012](#) (blue), [Wells et al., 2013](#) (red), and [Renck et al., 2014](#) (green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Sample sizes of age-length data from three recent studies on age and growth of North Pacific albacore used in this study.

Study	Female	Male	Unspecified sex	Total
Chen et al. 2012	125	148		273
Wells et al. 2013	34	92	360	486
Renck et al. 2014			125	125
Total	159	240	485	884

trast, [Chen et al. \(2012\)](#) primarily used samples from the western and central North Pacific ([Fig. 1](#)).

Similar to the vast majority of studies on fish growth utilizing age-length data from hard parts, [Chen et al. \(2012\)](#) and [Wells et al. \(2013\)](#) fit the age-length data to a VBG, assuming that each observation of length is a random sample for a given age (random at age; [Francis, 2015](#)). Because the age of a sample can only be determined after the sample has been taken, this assumption can be met by randomly sampling from the population. However, most age and growth studies, including those on North Pacific albacore do not perform random sampling and instead sample individuals according to predefined length bins that are spread across the size range of the species. For example, [Wells et al. \(2013\)](#) appeared to have oversampled the largest albacore from the Hawaii longline fishery ([Appendix, Fig. A1](#)) relative to the size range available. In addition, collected samples were predominantly male, and could therefore not account for the sex-specificity of growth for these samples.

Length-based sampling can lead to bias in the estimated growth parameters ([Piner et al., 2015](#); [Taylor et al., 2005](#); [Schueller et al., 2014](#)). It is unclear if the estimated growth parameters from previous studies on North Pacific albacore were biased but the sampling approaches used did not meet the assumptions of the method used for fitting age-length data. One possible way of improving the growth estimates from these age-length data is to treat them as an observed distribution of ages conditioned on a length interval (random at length; [Francis, 2015](#)). Estimating growth parameters from random at length data does not assume random sampling of the population but instead assumes each fish (its accompanying observed age) is a random sample from that measured length or length bin. The need to model the expected population age-structure from which the sample was taken has typically restricted the use of this length-conditional approach to within a stock assessment model (e.g., [Maunder, 2002](#); [Taylor and Methot, 2013](#); [Methot and Wetzel, 2013](#)). However, [Piner et al. \(2015\)](#) proposed and evaluated an “approximate length-conditional” approach to fitting

age-length data that is independent of a stock assessment model but is instead based on an equilibrium population age structure. It should be noted that the terms “approximate length-conditional” and “length-conditional” are used interchangeably in this paper to mean the equilibrium age-structure approach proposed by [Piner et al. \(2015\)](#), unless otherwise stated. [Piner et al. \(2015\)](#) used a series of simulations to evaluate the length-conditional approach. This study complements that study by using the length-conditional approach on real age-length data, with all its concomitant complications.

The objectives of this study are to: (1) use the length-conditional approach to fit age-length data from previous albacore growth studies and compare the growth estimates to those derived from a traditional approach, (2) study the sensitivity of the length-conditional approach to the assumed total mortality rate and data-weighting approaches, and (3) update the sex-specific and sex-combined growth model parameters from the three most recent otolith-based studies, due to a recent switch from a sex-combined to sex-specific growth models in the 2014 stock assessment.

2. Data and methods

2.1. Data

Paired age-length data ($n = 884$) from three recent North Pacific albacore age and growth studies ([Chen et al. \(2012\)](#), [Wells et al. \(2013\)](#) and [Renck et al. \(2014\)](#)) were used in this study ([Table 1](#)). These data included estimated ages of fish from otolith samples, measured fork lengths (cm), sampling dates, sampling regions and the sex of the fish for a portion of the samples. All data collected by [Chen et al. \(2012\)](#) included the sex of sampled fish (Female: $n = 125$, Male: $n = 148$). Only a quarter of data from [Wells et al. \(2013\)](#) specified the sex of the sampled fish, while the rest of the samples were not sex-specific (Female: $n = 34$, Male: $n = 92$, Unknown sex: $n = 360$). All samples from [Renck et al. \(2014\)](#) were juvenile alba-

core and no sex information was recorded. These studies sampled albacore from different regions in the North Pacific (Fig. 1). Chen et al. (2012) collected albacore samples from the western and central Pacific Ocean during 2001–2008. Wells et al. (2013) collected samples from across the western, central and eastern Pacific Ocean during 1990–2012. Renck et al. (2014) only collected samples from the eastern Pacific during 2010–2011.

Chen et al. (2012) and Wells et al. (2013) primarily concentrated on aging albacore using annual rings in order to estimate a von Bertalanffy growth curve for North Pacific albacore. However, Renck et al. (2014) used daily growth rings to determine differences in average growth between juvenile albacore (age=1–3) from two regions (northern: >40°N and southern: <40°N) in the eastern North Pacific. Details about the otolith-based age estimation procedures can be found in Chen et al. (2012), Wells et al. (2013), and Renck et al. (2014).

2.2. Growth model

As with the abovementioned previous studies, we assume that the growth of North Pacific albacore follows the VBGM (Von Bertalanffy, 1938),

$$L_a = L_\infty [1 - e^{-K(a-a_0)}] + \epsilon \quad (1)$$

where L_a is body fork length (cm) at age a , L_∞ (cm) is the mean asymptotic fork length, K (year^{-1}) is the Brody growth coefficient, a_0 (year) is the theoretical age at length equals 0, and ϵ is the error. To improve our ability to estimate the growth parameters, we used the Schnute reparameterization (Schnute, 1981) of the VBGM,

$$L_a = L_1 + (L_2 - L_1) \frac{1 - e^{-K(a-a_1)}}{1 - e^{-K(a_2-a_1)}} \quad (2)$$

where L_1 is the length at a younger age a_1 and L_2 is the length at an older age a_2 . The Schnute parameterization is more stable when conducting non-linear optimization, and the estimated parameters are less correlated (Galucci and Quinn, 1979, Section 3.2). In addition, the estimated L_1 , L_2 can be easily transformed back to L_∞ and a_0 .

The age-length data were fit to VBGMs using both the traditional and length-conditional approaches (Piner et al., 2015). In the traditional approach of fitting data to the VBGM, the difference between the predicted (\hat{L}_a) and observed (L_a) lengths was minimized using least squares, with the error (ϵ) assumed to have a normal distribution $N(0, CV \times \hat{L}_a)$ that includes both process and observation errors. With the length-conditional approach, we aggregated the paired age-length samples into an observed matrix with elements of $n_{a,L}$, where n is the number of observations in age bin a and length bin L . The age distribution for a given length bin is assumed to be random and therefore follows a multinomial distribution. The log-likelihood for each element in the matrix, given the growth parameters ($\hat{\theta}$), is the product of the number of samples at that length, n_L , the observed proportion of age given the length, $P(a|L)$, and the log of the expected proportion of age conditioned on the observed length, $\ln(\hat{P}(a|L))$. The total log-likelihood was then obtained by summing across all lengths and ages. The expected matrix of $\ln(\hat{P}(a|L))$ was calculated from a simple population model that assumed an equilibrium approximation of the age structure, and required an assumed total mortality rate (Z , year^{-1}). Use of the length-conditional approach decomposes the error in Eq. (1) into the process error, assumed to be normally distributed with a mean of zero and an estimated CV ($N(0, CV)$), and is the same as the traditional approach except that the observation error has been separated and assumed to have a multinomial distribution. Addi-

tional details on the length-conditional approach can be found in Piner et al. (2015).

Although the basic underpinnings of this study and Piner et al. (2015) were the same, there were three main differences in the model fitting due to this study using real age-length data. First, we used the Schnute parameterization of the VBGM due to improved model optimization (see above). Second, we used quarterly age bins and 1 cm length bins. Based on the age-length observations and preliminary model runs, using annual age bins were too coarse and introduced substantial bias, especially at young ages (age=0 and 1). Third, we applied a tail compression scheme because it stabilized model optimization and did not affect results. The tail compression function aggregated any data less than 2.5% quantile or more than 97.5% quantile to the edge of the age bins for all length bins.

2.3. Model settings

Based on the recently completed assessment of North Pacific albacore (ISC, 2014), we assumed that the stock experienced a constant instantaneous mortality rate of 0.5, which was approximately the sum of the assumed natural mortality and estimated fishing mortality of the stock in the assessment. We initialized the population model with 10,000 fish at age=0 and let the population reach a maximum age of 15. The initial values for the growth parameters were set to: $L_1 = 55$ cm (age=1), $L_2 = 110$ cm (age=12), $K = 0.264$ year^{-1} and a constant CV of 0.1. L_∞ and a_0 were then calculated from estimated L_1 and L_2 . The parameters L_∞ , K , a_0 and CV were used to describe the mean growth and process error in the following subsequent length-conditional model runs. All analyses were performed using R v3.1.0 software (R Development Core Team, 2014) and the traditional model fitting method was performed using the “FSA” and “nlstools” packages.

2.4. Baseline model diagnostics and sensitivity analyses

We applied the length-conditional method to age-length data from Wells et al. (2013), using this as the baseline sex-combined growth model for model comparisons and diagnostics. The estimated growth parameters L_∞ , K , a_0 and CV, with associated 95% confidence intervals, were compared to the same parameters estimated using the traditional approach. Pearson’s residuals were used to examine model fit of the length-conditional model. Changes in likelihood by length bin with respect to a range of fixed L_∞ (i.e., a likelihood profile) were examined to understand the contribution of each length bin on the change in total likelihood for the model.

The key assumed parameter in the length-conditional approach is total mortality, which can be highly uncertain. While the total mortality rate used in the baseline model ($Z=0.5$) was based on a recent stock assessment and thought to be reasonable, we conducted a sensitivity analysis of the model to fixed mortality rates ranging from 0.1 to 1. With the length-conditional approach, we can also use the number of samples at length L , n_L , as a data-weighting parameter for each length bin. In this study, we examine the use of data weighting in the model in an attempt to correct for issues in the sampling effort. We run the baseline model with three different data weightings (observed sample sizes, equal sample sizes in each length bin, and weighting by population age structure at equilibrium) and examined how parameter estimates were affected.

2.5. Alternative growth models

After finalizing the baseline model, the length-conditional method was applied to age-length data from all three previous studies. Both sex-combined and sex-specific growth models were fit to study potential sexual dimorphism in albacore growth (Chen et al., 2012). Similar to the baseline model, we performed a sensi-

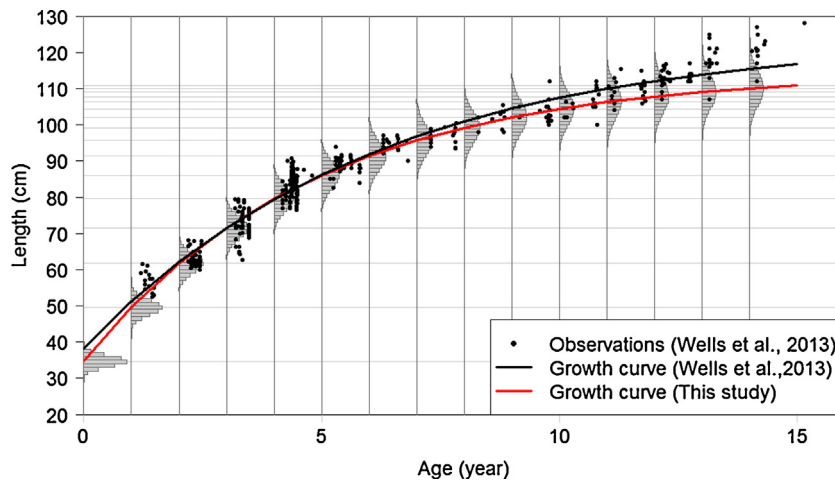


Fig. 2. Estimated sex-combined growth curves of North Pacific albacore based on data from Wells et al. (2013) (black dots) using the traditional model fitting method (black line) and the approximate length-conditional method (red line). Gray bars indicate expected length-at-age at each whole age. Conditional age-at-length observations are in fractional ages. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Von Bertalanffy growth parameters from two recent studies, and this study. Numbers in parentheses are 95% confidence intervals.

Study	Data source	Sex	Fitting method	L_{∞} (cm)	K (year ⁻¹)	t0	CV
Wells et al. 2013	Wells et al. 2013	Sex-combined	Traditional	124.1	0.164	-2.239	-
Chen et al. 2012	Chen et al. 2012	Male	Traditional	114.0	0.253	-1.01	-
Chen et al. 2012	Chen et al. 2012	Female	Traditional	103.5	0.340	-0.53	-
This study	Wells et al. 2013	Sex-combined	Length-conditional	114.5 (113.7,115.4)	0.207 (0.197,0.215)	-1.75 (-1.89,-1.61)	0.042 (0.040,0.043)
This study	Wells et al. 2013 & Chen et al. 2012	Male	Length-conditional	107.5 (106.5,108.5)	0.278 (0.265,0.292)	-0.95 (-1.06,-0.84)	0.050 (0.049,0.051)
This study	Wells et al. 2013 & Chen et al. 2012	Female	Length-conditional	107.3 (106.1,108.6)	0.266 (0.249,0.283)	-1.01 (-1.15,-0.87)	0.049 (0.047,0.052)
This study	All	Sex-combined	Length-conditional	111.6 (111.0,112.3)	0.241 (0.233,0.249)	-1.32 (-1.41,-1.23)	0.047 (0.046,0.048)

tivity analysis on the effects of sampling weight on the estimated growth parameters of both male and female albacore.

3. Results

3.1. Baseline model

Applying the length-conditional approach to fit a VBGM to data from Wells et al. (2013) resulted in a sex-combined growth curve that is generally comparable to the traditional method from juvenile through the early adult ages (Fig. 2). However, the asymptotic length L_{∞} estimated with the length-conditional approach was 9.6 cm less than that estimated using the traditional method (Table 2). The length-conditional approach did not treat the unusually large fish from Hawaii (Wells et al., 2013) as representative of the average size at age, unlike the traditional method.

3.2. Model diagnostics

Pearson’s residuals of the baseline model fit ranged from -3 to +16 SD, with positive residuals being larger than negative residuals (Fig. 3). Interestingly, for a given length bin, there is often a pattern of “positive-negative-positive” residuals across ages, which may be indicative of errors in the otolith aging process. The likelihood profile of L_{∞} of the baseline model (Fig. 4) suggested a

reasonable relative likelihood range, with age-length data in the 81–90 cm length bins having the largest changes in likelihood. However, the maximum likelihood estimate of L_{∞} was 114.5 cm (95% CI: 113.7–115.4 cm), which was relatively consistent with the maximum likelihood estimates from the 91–110 cm length bins but smaller than the estimates from the 81–90 cm.

3.3. Sensitivity analyses

The estimated parameters from the baseline model were not highly sensitive to assumed mortality rates. When we fixed the mortality rates at values ranging from 0.1 to 1, the estimated L_{∞} was reduced from 121.1 to 109.8 cm, K was increased from 0.186 to 0.218 year⁻¹, and the estimated CV decreased from 4.3% to 3.9% (Table 3).

The effect of using three different data-weighting schemes (observed sample sizes, equal weighting for all length bins, and weighting based on expected population numbers at length) on the estimated growth model can be seen in Fig. 5. Using observed sample sizes and equal weighting for all length bins resulted in relatively similar growth models. However, using a weighting based on the expected population numbers at length resulted in the largest estimated L_{∞} , even larger than with the traditional method.

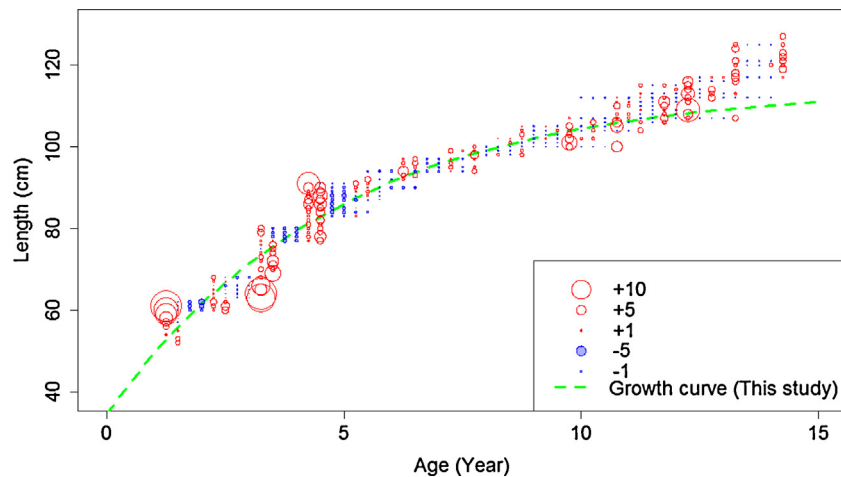


Fig. 3. Pearson's residuals plot of the estimated sex-combined growth curve of North Pacific albacore based on data from Wells et al. (2013) (green dash line). Positive residuals (observed-expected; units in SD) are indicated in red, while negative residuals are in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

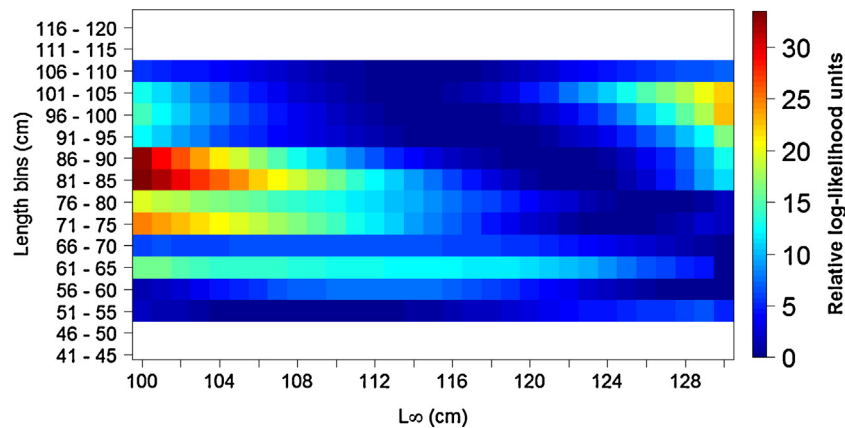


Fig. 4. Likelihood profile on L_{∞} : relative changes in negative log-likelihood of the model fit of each observation length bin, when the L_{∞} parameter is fixed at different lengths ranging from 100 to 130 cm. Observation length bins are aggregated at every 5 cm for visualization purposes. A sex-combined growth curve fit to data from Wells et al., 2013 was used. The total negative log-likelihood reached minimum when L_{∞} was 114.5 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Sensitivity of estimated growth parameters to the assumed instantaneous total mortality rate (Z). A sex-combined growth model was fit only to data from Wells et al. (2013) using the approximate length-conditional approach. A Z of 0.5 was assumed for all other analyses.

Z	L_{∞}	K	t_0	cv	Total likelihood
0.1	121.1	0.186	-1.82	0.043	1151.07
0.2	119.4	0.192	-1.80	0.043	1152.40
0.3	117.7	0.197	-1.78	0.042	1154.13
0.4	116.3	0.199	-1.83	0.042	1156.62
0.5	114.5	0.207	-1.75	0.042	1159.01
0.6	113.6	0.209	-1.75	0.041	1162.18
0.7	112.4	0.212	-1.75	0.041	1165.93
0.8	111.4	0.215	-1.76	0.040	1170.24
0.9	110.6	0.216	-1.77	0.040	1175.10
1.0	109.8	0.218	-1.79	0.039	1180.50

3.4. Alternative growth models

The estimated sex-combined growth curve using all three data sources was similar to the growth model using only data from Wells et al. (2013), albeit with a slightly smaller L_{∞} of 111.6 cm, and a larger CV of 4.7% (Fig. 6, Table 2). Using only age-length data with sex information ($N=240$ males and 159 females) from Wells et al. (2013) and Chen et al. (2012), resulted in male and female growth

curves that were relatively similar. For example, the estimated male growth curve had L_{∞} of 107.5 cm and the female growth curve had L_{∞} of 107.3 cm (Table 2). A sensitivity analysis using equal data weighting for all length bins also resulted in similar growth curves for both male and female albacore (Fig. 7A and 7B).

4. Discussion

Length-based sample selection of large North Pacific albacore biases growth parameter estimation, leading to a higher estimate of the asymptotic length of North Pacific albacore than that estimated by length-conditional approach. Otolith samples were taken from fisheries in different regions of the Pacific Ocean with different selectivity patterns in order to incorporate fish from the entire size range into the age-length dataset. However, the selection bias was most notable for samples taken from the Hawaii longline fishery (Appendix, Fig. A1). Our use of the length-conditional estimation procedure accounted for this size-based selection by treating samples as random at length (Francis, 2015).

Piner et al. (2015) concluded that the length-conditional approach was more robust to length-based sampling processes than the traditional method if the assumptions behind the method are met. During preliminary debugging of our length conditional

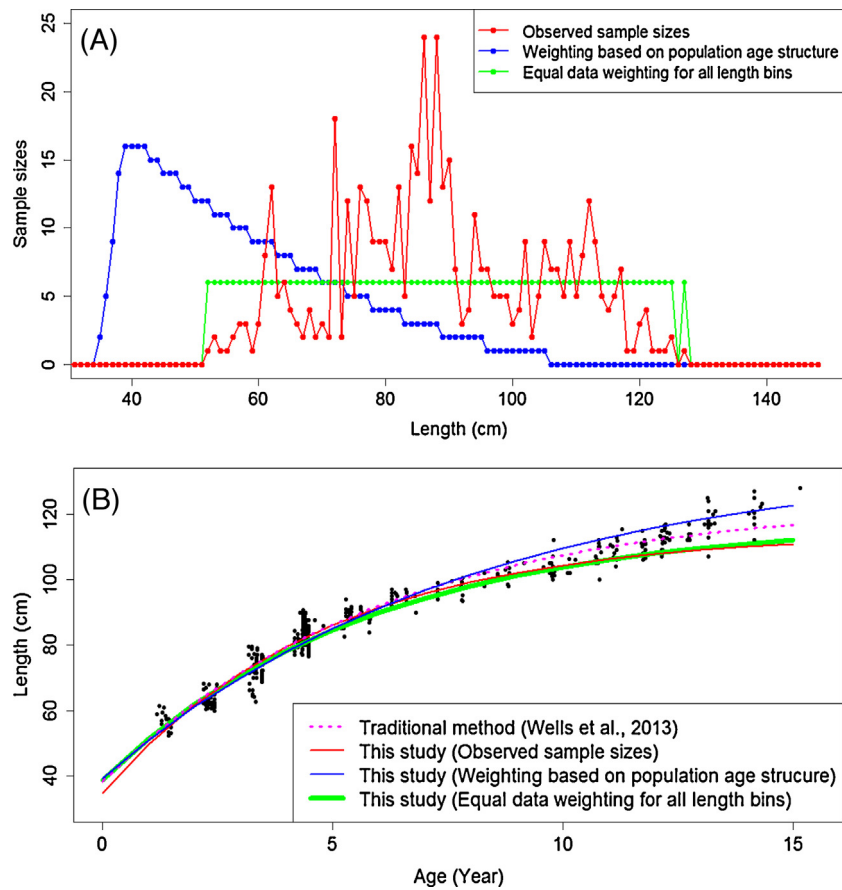


Fig. 5. Effect of (A) different data weighting schemes on (B) estimated growth curves: observed data sample sizes (red), data weighting based on expected population age structure at equilibrium (blue), and equal data weighting for all length bins (green). The estimated growth curve using the traditional methods is shown as a dotted magenta line. All growth curves are sex-combined growth curves using data from Wells et al., 2013. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

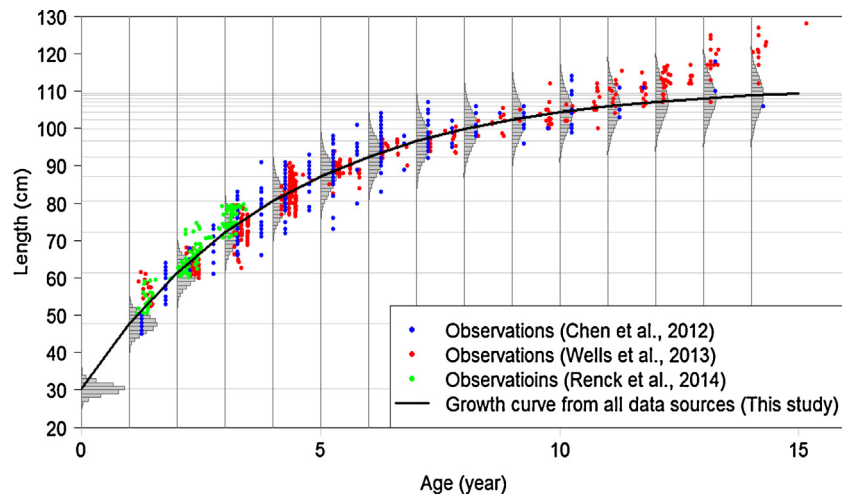


Fig. 6. Estimated sex-combined growth curve (black line) of North Pacific albacore based on data from all three previous studies: Chen et al. (2012) (blue dots), Wells et al. (2013) (black dots), and Renck et al. (2014) (green dots) using the approximate length-conditional method. Gray bars indicate expected length-at-age distribution at each whole age (vertical lines). Horizontal lines indicate expected mean length-at-age at each whole age. Conditional age-at-length observations are in fractional ages. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

algorithm, we also conducted a series of simulations to compare estimated growth curves from the traditional and length conditional methods to a 'true' growth curve (Appendix, Fig. A2). These simulations also indicated that the length conditional approach resulted in less biased estimated length at ages, especially for the youngest and oldest ages. Large errors in the total mortality used in

the approximate length-conditional method to generate the equilibrium age structure can introduce bias in parameter estimation (Piner et al., 2015). In this albacore case study, the mortality rate was based on a stock assessment estimate and growth estimates were not highly sensitive to changes in that mortality rate. We also note that the assumption of equilibrium population structure is an

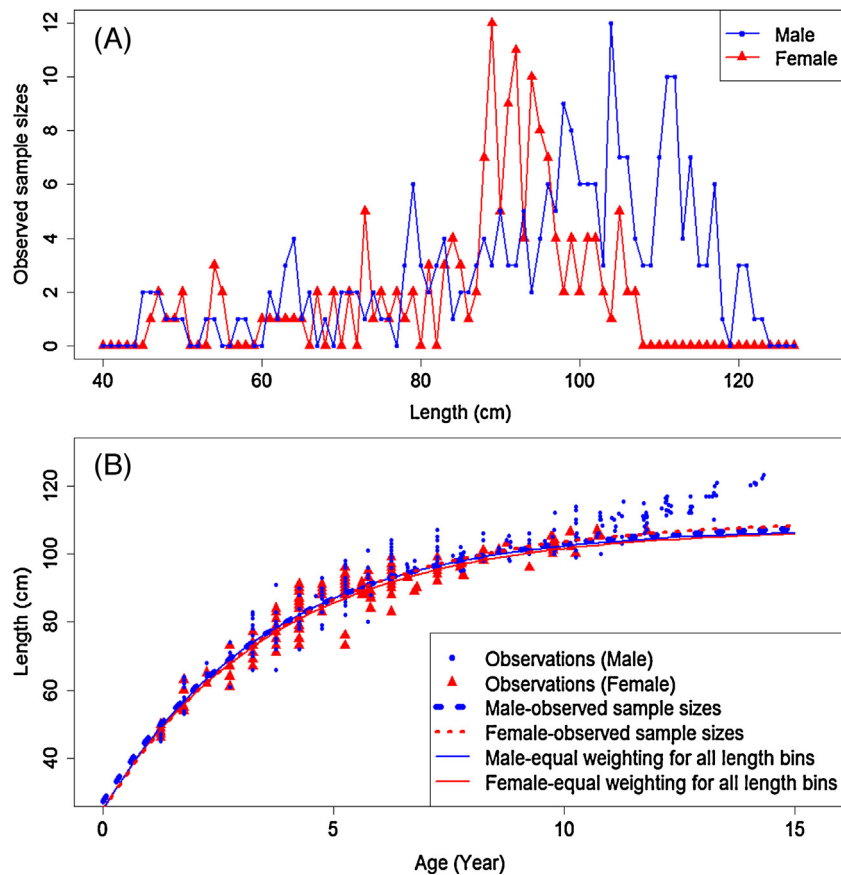


Fig. 7. Observed sample sizes (A) and estimated growth curves (B), for male (blue) and female (red) North Pacific albacore, using data from [Chen et al. \(2012\)](#) and [Wells et al. \(2013\)](#). Observed sample sizes (dashed lines) and equal weighting for all length bins (solid lines) were used to fit the data with the approximate length-conditional method. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

oversimplification but violations of this assumption were shown to affect precision and not bias ([Piner et al., 2015](#)). Therefore, our growth estimates of North Pacific albacore may be an improvement over previously published estimates.

The complex life history of North Pacific albacore, together with ocean-basin scale movements, leads us to believe that some additional important model processes governing growth estimation remain unmodeled. Some of these processes include regional differences in growth, and age and sex-specific movements. There are some indications of regional and possibly sex-specific growth for North Pacific albacore. Albacore appear to grow to a larger size in the central North Pacific compared to the western North Pacific ([Chen et al., 2012](#); [Wells et al., 2013](#)). However, a recent study on South Pacific albacore growth did find significant differences in length-at-age and growth parameters between sexes and across longitude, with fish approximately 6 cm larger on average in the eastern South Pacific than the western South Pacific ([Williams et al., 2012](#)). Although [Chen et al. \(2012\)](#) reported that albacore growth was sexually dimorphic in the Western and Central Pacific Ocean, we did not find sexual dimorphism in the growth of North Pacific albacore in this study. However, we cannot preclude the existence of sexual dimorphism in growth given the inadequacies in the sampling effort. Future sampling effort of North Pacific albacore must include sex as sampling strata in order to adequately examine this question.

North Pacific albacore may also exhibit age-specific movements, which would violate the assumptions of random at length used in this study. Juvenile albacore appear to feed along the North Pacific transition zone and are caught by several international fisheries (e.g., [Polovina et al., 2001](#); [Xu et al., 2015](#)). Limited work has been

done to elucidate the movements of large, adult albacore but size composition data from stock assessments of North Pacific albacore indicate that large, adult albacore tend to be caught in equatorial regions by longline fisheries targeting bigeye tuna ([ISC, 2014](#)). In addition, male and female adult albacore may have different habitat preferences. Large, adult albacore caught by the Hawaii longline fishery appear to be predominantly male but large, adult female albacore (up to 140 cm fork length) have been caught by Chinese and Japanese longline fisheries in other areas (Y. Chen – Shanghai Ocean University, China and K. Satoh – National Research Institute of Far Seas Fisheries, Japan, pers. comm.). If albacore exhibit both age- and sex-specific movements, samples from fisheries capturing these fish would exhibit sex-specific age-selectivity in addition to size-selectivity. If this is indeed the case, we would need to model both age- and length-based processes to reliably estimate growth. This level of model complexity would most easily be done inside an integrated assessment model.

Although not explicitly modelled in this study, ageing error also potentially contribute to growth estimate error. A complete age validation study for North Pacific albacore has not yet been completed. The daily growth increment analysis conducted by [Wells et al. \(2013\)](#) is not a validation technique, rather it serves to mitigate or reduce an important systematic bias in detecting annuli or interpreting otolith microstructure. Namely, it helps to confirm the location of the first and sometimes the second annuli, which are often difficult or impossible to determine on albacore tuna otoliths. Equally important is that ageing criteria differed among studies. [Wells et al. \(2013\)](#) counted growth increments within the otolith, defined as one translucent and one opaque zone, whereas [Chen et al. \(2012\)](#) counted indentations on the outer edge of the otolith

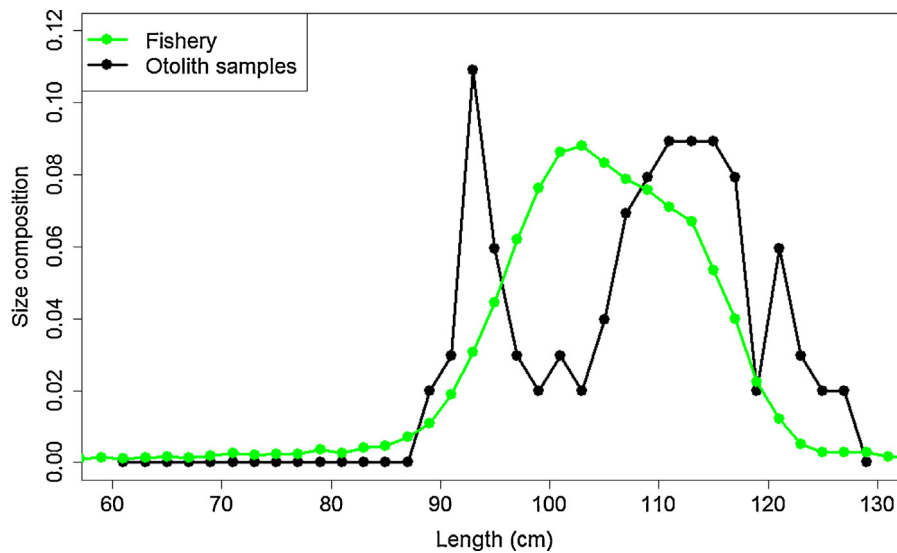


Fig. A1. Relative size composition of the sampled albacore from US longline vessels based in Hawaii used in the Wells et al. (2013) study (black) compared to the overall size composition of the albacore catch from the same fishery (green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

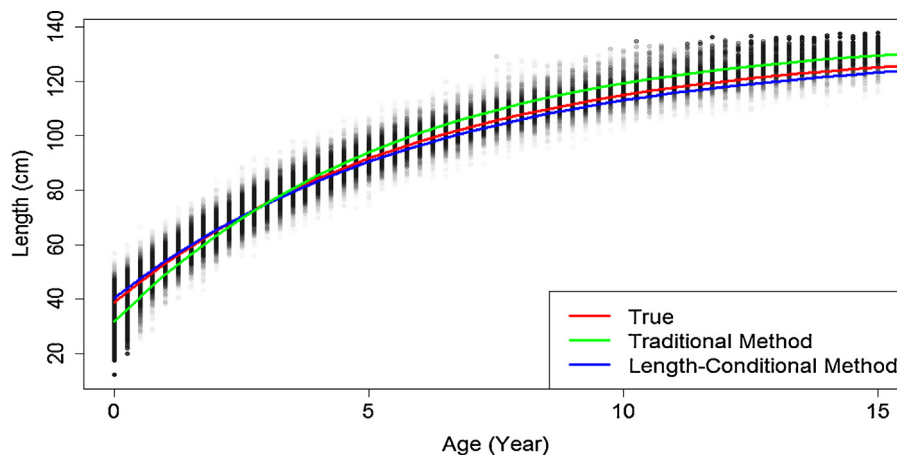


Fig. A2. Von Bertalanffy growth curves estimated from simulated data using the traditional (green) and approximate length-conditional (blue) model-fitting methods. Synthetic age-length data (grey circles) were obtained by simulating a population with a total mortality of 0.5 and a “true” growth curve (red). At each quarterly age, 10000 samples were randomly selected from mean and standard deviation for that quarterly age. The population age structure was generated by recruiting 106 fish at age-0, and subjecting that cohort to total mortality rate of 0.5. 1000 samples were then selected randomly from each 1 cm length bin from this population pool. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

on the assumption that they frequently accompanied the opaque zone of annuli as defined by Wells et al. (2013). In addition, Wells et al. (2013) assigned age based on a May 1 birth date, whereas Chen et al. (2012) subtracted 0.25 years from all age estimates to account for the time interval between birth and annulus formation.

One interesting observation from the baseline model diagnostics is the recurring pattern of “positive-negative-positive” residuals to the model fit. This may be indicative of consistent errors in the aging of otolith samples conducted by the previous studies. While a close examination of aging errors is beyond the scope of this study, we speculate that the recurring pattern of “positive-negative-positive” residuals may be due to the use of a fixed birth date to estimate the age of samples to a resolution of <1 year. For example, Wells et al. (2013) calculated the absolute decimal ages as the number of observed annual rings plus the percentage of the year passed from the assumed birth date of May 1, which was the peak of the spawning season, to the date of capture in order to avoid bias in growth estimates due to bias in sampling dates. An examination of the daily rings of juvenile albacore showed that

albacore hatch dates were protracted from February to September, with 73% of all fish hatched from April through July (Renck et al., 2014). Potential bias from this may be reduced by using daily rings to age juvenile fish, where this effect is likely largest, and transitioning to annual rings in older fish. In addition, the absolute residual values are smaller between age-7 and 10, which seems to correspond with smaller sample sizes within those ages.

The growth estimates in this study are likely an improvement over those in the previous studies because some length-based sampling biases have been accounted for in the estimation methods (Piner et al., 2015; Taylor et al., 2005; Schueller et al., 2014). However, in the case of North Pacific albacore, it is likely that the estimation of growth remain uncertain due to unknown model processes. Because of the difficulty in diagnosing these modeling misspecifications, further improvements in our understanding of North Pacific albacore growth will likely require a coordinated and well-designed sampling plan among multiple international fisheries. Refining the estimates of North Pacific albacore remain a high priority to improve the stock assessment.

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Appendix

Figs. A1 and A2

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