Estimating individual growth variability in albacore (*Thunnus alalunga*) from the North Atlantic stock; aging for assessment purposes.

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Keywords

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ABSTRACT

Length-frequency data and derived catch at age matrices are used in north Atlantic albacore (*Thunnus alalunga*) stock assessment conducted within the International Commission for the Conservation of Atlantic Tunas (ICCAT). Growth is assumed to follow the von Bertalanffy model with the assumption that growth parameters are constant over time and the same for all fish. However individual growth variability is an important factor not considered and affecting the input into the modelling of the population. This study describes a Bayesian hierarchical model applied to model the individual variability in the parameters asymptotic length (L_∞) and growth rate (K) of the von Bertalanffy growth model for North Atlantic albacore. The method assumes that the L_∞ and K values for each individual fish are drawn from a random distribution centered on the population mean values, with estimated variances. Multiple observations of spine diameter at age for individual fish were obtained by direct reading of spine sections collected in 2011 and 2012. A suite of back calculation methods were then applied to the measurements of annuli diameters in the aged individuals observed to back-calculate lengths at each age. The von Bertalanffy model was fitted to the measured and back-calculated lengths. Models with and without individual growth variability were compared using the deviance information criterion (DIC) to find the best model. Normal and log-normal error distribution models were used to analyse the data. Additionally, subsamples of the data were used to evaluate whether an unbalanced age-distribution in the data affects estimates of growth parameters. It was found that North Atlantic albacore asymptotic length (L_∞) varies significantly between individual fish but not individual rate growth (K), for all back-calculation methods. Furthermore, negatively correlated relationships between von Bertalanffy growth parameters of asymptotic mean (L_∞) and growth rate (K) were estimated for North Atlantic albacore with the array of models

explored. The overall estimated values of K and population mean L_∞ parameters were similar to values estimates in previous north Atlantic albacore growth studies.

Introduction

Atlantic albacore tuna (*Thunnus alalunga*) is large pelagic fish that inhabits the temperate and subtropical waters of the Atlantic Ocean. It is an economically important species that is managed under the International Commission for the Conservation of the Atlantic tunas (ICCAT). In the Atlantic three stocks are identified for assessment purposes: North and South Atlantic separated at 5º N in the Atlantic and a third Mediterranean stock (ICCAT, 2006-2013). Commercial fisheries in the Northern Atlantic have targeted the albacore stock by surface fisheries since the 1930s and longline fleets beginning in the 1950s (ICCAT, 2013a). The surface fishery represents roughly 80% of the total catch and the longliners account for 20 % in the last two decades (ICCAT, 2014). The surface fishery includes three different type of vessels according to the gears: mid-water pair pelagic trawls, trollers and baitboats. Spanish baitboats and troll landings represent an approximate participation in the fishery between 55 to 65% of the total annual surface fishery landings from the North Atlantic stock.

The last assessment of North Atlantic albacore stock, performed in 2013, reported substantial uncertainty on the current stock status considering the set of models applied, but it was concluded that the status of the spawning stock biomass was overfished (ICCAT, 2014).

North Atlantic albacore are assessed with a variety of models, including a length based model (Multifan-CL) that requires a growth curve as input, and two other models: VPA and Stock Synthesis (SS) that are fitted to catch-at-age data calculated from catch-at-length data using a von Bertalanffy (von Bertalanffy, 1938) growth curve (ICCAT, 2013a). Moreover, the growth function is used to derive reference points for sustainable management (Beverton and Holt, 1957; ICCAT, 2013a).

Direct aging data have been used to study growth. A number of studies have been conducted to describe the growth of northern albacore (Bard and Compeán–Jimenez, 1980; Bard, 1981; Gonzalez-Garcés and Fariña-Perez, 1983) based on reading of the first fin ray of the first dorsal fin to determine age and fit a von Bertalanffy (von Bertalanffy, 1938) growth model, considering constant parameters for the population. The most recent study, assumed constant parameters and used the first dorsal fin ray section readings along with updated release and recapture tag data in an integrated model to fit the von Bertalanffy function (Santiago and Arrizabalaga, 2005). The analysis of the North Atlantic albacore population (ICCAT, 2014) has incorporated knowledge on the growth biology based on Bard´s (1981) growth model and Santiago and Arrizabalaga´s (2005) growth estimates to characterize the population dynamics of the north Atlantic albacore stock. The catch- at-size data for northern stock is analyzed to derive an annual age-length key (ALK) by applying the Kimura and Chikuni iterative method (1987) and using Bard´s (1981) growth parameters (ICCAT, 2014; Ortiz, 2014).

Generally, when growth models are fitted to length-at-age data, only one observation is available for each individual animal. Therefore, it is not possible to determine what fraction of the variation in measured length is due to measurement error, and what fraction is due to variation in growth between individual fish. Thus, the residual error in a fitted growth model includes both individual variation and measurement error. When multiple observations are available for each individual, for example from tag-and-recapture data, it is possible to evaluate how much individual variation exists in the growth model parameters, and to estimate the correlation between growth parameters across individual fish (Zhang et al. 2009).

None of the growth models use in the assessment of the North stock albacore incorporate individual variability in the von Bertalanffy growth function parameters. However individual variation in growth is expected depending on physiological and environmental conditions. The first model incorporating individual variation in the K and L_∞ von Bertalanffy growth parameters was described by Sainsbury (1980); later Kirkwood and Sommers (1984) continued investigating variation in maximum length between individuals. Moreover, Hampton (1991) modified those approaches incorporating a model error component and estimates of a release length measurement error term fitted by maximum likelihood. The available North Atlantic albacore tag-release data were analysed to estimate von Bertalanffy growth parameters based on Hampton´s model that incorporates individual variation in growth, release length measurement error and model error terms (Ortiz de Zárate and Restrepo, 2001).

Back calculation methods are employed to estimate length of a fish at previous age based on reading of calcified structures such as: otoliths, scales and fin rays (spines), among other skeleton structures. This technique re-creates the life history of individual fish. This method assumes that there is a relationship between the length of the fish and the skeleton structure, either linear or allometric (Bagenal, 1978; Campana, 1990; Francis, 1990; Folkvord and Mosegaard, 2002; Ricker, 1992).

One albacore spine aging study used a linear relationship recommended by Campana (1990) to back-calculate lengths (Santiago and Arrizabalaga, 2005); meanwhile other spine studies incorporated proportional methods to back-calculate lengths (Cheng *et al*., 2012; Duarte-Neto *et al*., 2012; Kopf *et al*., 2011; Sardenne *et al*., 2014). Methods for back-calculation of length-at-age generally assume that the relationship between fish length and hard part diameter is a family of lines radiating from a common point near the origin, with different slopes for each fish (Francis, 1995). This assumption allows individual fish lengths to vary more when they are larger than when they are smaller, which is biologically reasonable and performs well in simulation studies (Schirripa, 2002). However, which back calculation method is best suited to be applied may depend on the functional form of relationship between length and annulus diameter, and other growth characteristics that may vary between stocks (Schirripa, 2002). In the thorough review of types of back-calculation methods by Francis (1990), he recommended that both regression of body length-scale to scale radius (BPH) and scale radius- to body length (SPH) be used for each fish population because neither is clearly preferable. Later, Ricker (1992) proposed the geometric mean regression using both relationships named by Francis (1990) to estimate the y-intercept for the back-calculation of length from hard structures annuli, in the absence of any biological intercept estimate. This method was applied by Pilling *et al*. (2002) to back-calculate lengths

from otolith radius counts over the life span of a number of individuals of tropical emperor (*Lethrinus mahsena*) and the lengths were used to fit models that incorporated individual variation in growth.

The objective of this paper is to use multiple length and age reading estimates for individual albacore tuna, where lengths were back-calculated from the measured diameters of the annuli readings of cross-sections of first dorsal fin ray (spine), to evaluate how much the growth parameters vary between individual fish in the North Atlantic albacore population. Growth models were fitted and evaluated using Bayesian hierarchical models. Several alternative back-calculation models were used to determine whether the choice of back-calculation method influences the estimated growth curve parameters or the conclusions about individual variation. Finally, alternative sub-sets of the data were used to evaluate whether differences in sample sizes across ages influenced the results, and whether using back-calculated lengths gave different average results from using lengths at capture only. This study is the first attempt to use an array of back-calculated lengths from spine measured annulus to estimate growth parameters for North Atlantic albacore incorporating individual variability in the von Bertalanffy function model.

Material and Methods

Sampling of spines (first fin ray)

As part of the monitoring of the activity of the Spanish albacore (*Thunnus alalunga*) fisheries, biological samples are collected from the landings at the main fishing ports (Ortiz de Zárate *et al*. 2013; Ortiz de Zárate *et al*. 2015, *in press*). A number of trips were sampled to obtain the length frequency of the catch by applying random sampling stratified according to commercial categories of catches landed at the main fishing markets. Random samples of the first fin ray (spine) from the first dorsal fin were removed during the albacore length sampling procedure. For each fish, the total fork length (FL) to the nearest centimeter, date, and catch area were noted. Spines were collected based on a length-stratified sampling protocol by 1 cm class length, covering the whole length range of albacore landings. Sampling design of spines was stratified by spatial and temporal strata. Collection of spines was done once a week at selected fishing ports, covering different geographical areas (1ºx1º degrees), during the fishing season, from June to November in the Northeast Atlantic (Figure 1). The samples in this study were collected during the 2011 and 2012 albacore fishing seasons and no sex information was recorded. The length composition of all albacore sampled is displayed in Figure 2.

Ageing from spine readings

The criteria used to interpret the pattern of observed translucent or hyaline bands (annuli) formed on the spine cross sections of albacore, was based on the hypothesis of Bard and Compeán (1980), which assumes that the formation of two annuli per year throughout the life span of North Atlantic albacore corresponding to its migratory behaviour between feeding (spring-summer/

autumn-winter) and spawning grounds (Bard, 1981). Albacore birth date was assumed to be the first of June, in agreement with a protracted spawning period from March to October, with a peak in June-July (ICCAT, 2006-2013) in the North Atlantic Ocean. For age determination, the first visible annulus was identified as formed during the first migration of juvenile albacore from the spawning area to the wintering area at an approximate age of six months (Bard, 1981). The appearance of the first annuli has been validated with daily increments reading on otoliths from the North Atlantic albacore (Lu *et al*., 2007) and daily increments readings on otoliths of Pacific albacore (Bigelow *et al.*, 1993, 1995).Then the successive annual mark formed by double annuli (spring-summer and autumn) and a dark growth band was assigned to age group 1 and, by counting successive annual marks formed, the age of each fish was determined. If an autumn annulus was already formed, age was determined as belonging to the same year class (i.e. 1 year class). Some spine sections had formed a single translucent annulus and dark growth zone, as an annual mark, however, in the majority of spines the double spring-summer annuli and dark growth zone annual pattern was visible. For north Atlantic albacore, oxytetracycline injections of tagged albacore released and recaptured, being at liberty one and two years, although samples size was small (n=21), seemed to verify that one annulus is formed on spring-summer and another in autumn, likewise, an alternative observed pattern in adult albacore (> 5 years), was defined by forming one annulus per year, consequently a single annulus and dark zone was associated with a given age in some older individuals (Ortiz de Zárate *et al*., 1996). Recently a north Atlantic albacore growth study using spine readings, suggested that one of the annual rings is formed mainly between July and September (Santiago and Arrizabalaga, 2005). Occasionally, vascularization obscured the first double annuli, the spring one for age 1 and occasionally even for age 2, or either spring or autumn annuli or both, in older fish. Estimated mean annulus diameter (mm) and standard deviation (s.d.) for age group 1, 2 and 3 by month were applied to identify the corresponding first visible annulus and the following visible annuli were counted from this value (Ortiz de Zárate *et al*., 2005). In our study, the identified first annuli represented 16% (autumn annulus age 1) and 2.6% (spring-summer or autumn annulus age 2) of the two combined year sample.

The aging method used in our study was tested previously to estimate the precision and relative bias by applying the procedure described by Eltink (2000) among three readers. The overall coefficient of variation (CV) was 8.5% and an overall agreement of 82% between readers was observed (Ortiz de Zárate *et al*. 2005), which implied a good level of precision (Campana, 2001; Campana *et al*., 1995). For this study, only one reader was generally involved in readings. In 2011, a sub-sample of 75 fish and in 2012, a subsample of 175 fish, including many of the older fish where ages might be more ambiguous, were read by two readers independently. Age readings were compared with two different tests of symmetry using χ^2 statistics (Bowker,1948; Evans and Hoenig,1998). Precision between readers was estimated with a new approach developed by McBride (2015) and implemented on template by S. Sutherland (NOAA). The results of the two independent readers showed no evidence of asymmetry in 2011, for the Bowker´s test of symmetry (Chi.sq= 13.33; d.f.=10, p= 0.21) and Evans and Hoenig´s test (Chi.sq= 1.84; d.f.=3, p= 0.61). In 2011, the estimated CV was 9.7 %, considered an acceptable value (Campana, 2001). Comparison of the two independent readings in 2012 shows evidence of asymmetry for the Bowker´s test (Chi.sq= 18.9; d.f.=8, p= 0.015), but for the Evans-Hoenig´s test (Chi.sq= 7.79; d.f.=3, p= 0.051) the null hypothesis of symmetry could not be rejected. The

estimated CV among two readers was 8.6 %. The number of samples that disagreed were 24 and 50 in 2011 and in 2012 respectively. Those samples were read again jointly by the two readers and agreement was reached to a final age. Only 2 and 3 spines from the last joint reading were discarded in the two consecutive years 2011 and 2012. The final sample used for the analysis included all the single-reader ages, and the agreed ages from the double-reader subsample.

Finally, based on the annuli pattern formation having either the spring-summer or the autumn annulus close to the edge of the section read and the date of capture, only one single annulus measured diameter, either spring or autumn, in all the annual double annuli read was used in the back-calculation of length to obtain the growth trajectory of each individual fish.

Statistical analysis

Growth increment analysis

Data were available for fish that were captured in both 2011 and 2012. To evaluate whether there was any annual variation or variation between cohorts in growth increments, we calculated annual growth increments for each measured spine diameter. The annual increment was the change in spine diameter from one spine annulus to the next, divided by the difference in age between the two spine annulus (usually one year, sometimes 0.75 or 1.25 year depending on when the fish was captured, and whether the spring-summer or autumn annulus was used; see *growth model* section below for an explanation of how ages were calculated). A linear model was used to evaluate the effect of age (as a numerical variable) and cohort (as a factor) on the size of the annual increment. The interaction between age and cohort was included to evaluate whether there was an effect of year. To ensure an adequate sample size at each age and cohort, only cohorts from 2009 and later, for fish of age four or less at the time of the increment formation, were included.

Length back-calculation

The geometric mean regression (GMR) allows estimation of the *y*-intercept to apply as a biological correction factor to mitigate Lee´s phenomenon (Lee, 1912) when back calculating length from spines (Ricker, 1992). The observed data in 2011 and 2012 were combined and fitted to GMR and simple linear regression models following three methods:

Method 1. The geometric mean regression method (Ricker, 1992; Pilling *et al.* 2002) was used to calculate the following regression using all the measured fish fork lengths and spine section diameters at capture from the 2011 and 2012 data sets combined:

(1) $S_i = a_S + b_S L_i + \varepsilon_{S,i}$

(2) $L_i = a_L + b_L S_i + \varepsilon_{L,i}$

Where S_i is the spine diameter at capture for fish i, L_i is the length at capture for fish i, a_S, b_S, a_L, b_L are the regression coefficients, and $\varepsilon_{S,i}$and $\varepsilon_{L,i}$ are normally distributed error terms with means of zero, and estimated variances. The parameters of the geometric mean regression, a and b, were calculated as:

(3) $$b = \sqrt{b_L / b_S}$$

and

(4) $$a = mean(L_i) - b \cdot mean(S_i)$$

Then the Fraser-Lee (Fraser, 1916, Lee, 1920) proportional model was applied to back-calculate lengths $(L_{i,j})$ for the all the measured annuli for each individual fish using the following equation:

(5) $$L_{i,j} = \frac{(L_i - a)S_{i,j}}{S_i} + a$$

Where L_i is the length of fish i at capture, S_i is the spine diameter at capture, $L_{i,j}$ is the back-calculated length age j, $S_{i,j}$ is the spine diameter at age j and a is the y-intercept from the GMR regression. The standard error $e_{i,j}$ of $L_{i,j}$ is assumed to equal the standard error calculated from the regression of L on S.

Method 2. The geometric mean regression (GMR) on log-transformed data (Ricker 1992, Folkvord and Mosegaard, 2002) was fit to the combined data set to estimate the constant of allometry (ν).

(6) $$\log(S_i) = \alpha_S + \beta_S \log(L_i) + \varepsilon_{S,i}$$

(7) $$\log(L_i) = \alpha_L + \beta_L \log(S_i) + \varepsilon_{L,i}$$

(8) $$\nu = \sqrt{\beta_L / \beta_S}$$

Then the method proposed by Monastyrsky (1930) was used to back-calculate lengths $(L_{i,j})$ for all the measured annuli for each individual fish using the following equation:

(9) $$L_{i,j} = \left(\frac{S_{i,j}}{S_i}\right)^{\beta} L_i$$

The standard error $e_{i,j}$ of $L_{i,j}$ is assumed to equal the standard error calculated from the regression of log(L) on log(S), converted from normal to lognormal.

Method 3. When back-calculated lengths are used to fit a growth curve, the choice of back-calculation model may constrict the amount of individual variation the growth model can estimate in each of the growth parameters (Francis, R.I.C.C., personal communication, Francis 1995). To test whether the use of a proportional back-calculation method influenced the degree of individual variation in the growth parameters, a back calculation method was applied that did not make this assumption. The simple linear regression of log of spine diameter at capture against log of length at capture (equation 7) was applied. The same equation was used to infer the back calculated lengths at previous ages from the measured annuli at previous ages. Linear regression implies that the same slope between L (length) and S (diameter spine) can be applied to all fish. This simplified approach is not recommended for back-calculation because the proportional methods have been found to be more accurate (Guteuter, 1987; Francis, 1990; Folkvord and Mosegaard, 2002; Schirripa, 2002). However, the method is useful for testing the hypothesis, proposed by Francis (1995), that the individual variation found in the growth curve is a consequence of the assumed back-calculation method.

All regressions and back-calculations were conducted in R version 3.1.2 (R Core Development Team 2015). The means and standard errors of the predicted lengths from each back-calculation method were used as inputs to the growth models (see next section).

Graphical tools were used to examine for homogeneity and normality of the data being regressed (Zuur *et al*., 2010). The predicted mean length at age estimated by the three methods were examined for comparison across methods and against measured lengths.

Growth models

A quarterly cycle was determined to describe annual variability in growth with relation to birth date. Thus for each individual fish, the decimal age at capture was estimated based on the quarter in which the fish was captured. Fish captured in June were age x.0, fish captured in July, August or September were age x.25, and fish captured October, November or December were age x.5, where x is the age in years inferred from the spine reading. For every fish, the measured length and age at capture were used in the model fitting. For fish aged 2 or more, back-calculated ages and lengths were used for all the ages prior to capture for which an annulus was visible. The back-calculated lengths were assumed to apply to ages that were either x.0 or x.25 years of age, depending on whether the spring-summer or the autumn band was measured.

The multiple observations from 2011 and 2012 of measured and back-calculated lengths and ages were used to fit the parameters of the von Bertalanffy growth model with possible individual variation in the growth parameters (Helser and Lai 2004, Zhang et al. 2009):

(10) $$L_{t,i} = L_{\infty,i}\left(1 - \exp\left(-K_i(t - t_0)\right)\right) + \varepsilon_{t,i}$$

Where $L_{t,i}$ is length at age t for individual fish i, $L_{\infty,i}$ is asymptotic mean length for fish i, K_i is the growth rate for fish i, and t_0 is the age at zero length, assumed to be the same for all fish, and ε_i is

a normally distributed error term with an estimated variance. In the most complex model, both K_i and $L_{\infty,i}$ were estimated as normally distributed random effects with estimated means and variances (Table 1). Alternative models treated L_∞, or K as constant across the population.

The variance σ of the error term $\varepsilon_{t,i}$ was either assumed to be constant across all the data points or it was informed by the standard errors of the predicted lengths from the back calculation model. For measured lengths, the residual standard deviation was always assumed to be constant. For the back calculated lengths, the residual standard deviation was either the same as the residual standard deviation of the measured lengths, or it was assumed to be proportional to the estimated standard error $e_{t,i}$ of the length prediction:

$$\sigma_{t,i} = \sigma_{measured} \quad \text{if length is measured}$$

(11) $$\sigma_{t,i} = e_{t,i}\sigma_{back} \quad \text{if length is back-calculated}$$

where σ_{measured} and σ_{back} are estimated parameters.

The majority of the fish in the back-calculated dataset were only one or two years old. Thus, the sample size of young fish was much higher than the sample size of older fish. When fitting growth curves, a very different sample size in each age category can lead to bias in estimates of growth parameters (Thorson and Simpfendorfer, 2009). Therefore, we ran the models with the fish subsampled to give a more even sample size among the younger ages. All fish that were captured at age 5 or higher were included, but fish captured at age 1 to 4 were sub-sampled so that there were roughly 80 fish in each age, including both back-calculated and measured lengths. To further evaluate the implications of having an unbalanced sample across ages, we also fit the model with only fish age 5 or less.

As an additional model test, the growth model was fitted to the observed lengths only. With only measured lengths, there was only one sample per individual fish, so individual variation in growth could not be estimated. To evaluate whether sample size in each age category caused bias in the results, the model was fitted to all the observed lengths, and also to a dataset in which the younger ages were sub-sampled to a sample size of 30 per age category, and to only fish age 5 or under five.

In addition to the assumed normal error distribution, we fit the growth models with the log-normal distribution error and compared the fit of the model.

(12) $$L_{t,i} = L_{\infty,i}\left(1 - \exp\left(-K_i(t - t_0)\right)\right)e^{\varepsilon_{t,i}}$$

The models were fitted in a Bayesian framework, with uninformative priors on all the parameters (Table 1). All analyses were conducted in JAGS, which uses the Gibbs sampler form of the Markov Chain Monte Carlo (MCMC) algorithm; JAGS was run using the R2Jags package for the R statistical software (R Development Core Team 2015, Su and Yajima 2014). Two MCMC

chains were run with a burn in of 50,000 and an additional run of 200,000 with a thin of 20. The Gelman-Rubin diagnostic was used to ensure convergence of the MCMC chains on the posterior distribution (Gelman, 2007). Models that had not converged according to this diagnostic were run for an additional 200,000 iterations. To compare models that included individual variation on different growth parameters, the deviance information criterion (DIC) was used (Lunn *et al.* 2013). The DIC weights the trade-off between model fit and the number of parameters estimated, and the model with the lowest DIC is best supported by the data. Only models fitted to the same back-calculated length data-set can be compared with the DIC.

Results

In 2011, a sample of 583 spines collected from June to October was examined, for fish ranging from 41 to 120 cm (FL) size, likewise in 2012, spines examined amounted to 902 in total with a length range 40 to 112 cm (FL), samples were collected from June to November respectively and no sex information was available to be incorporated in the analysis.

Growth increment analysis

Of the 1485 individual fish collected in 2011and 2012, 84% were three years old or younger. From these fish there were 1891 distinct spine increments (Table 2). The size of the growth increment declined linearly with the age at which the spine formed, but there was no significant influence of the cohort on this trend (Table 3). Therefore, for the remainder of the analyses, data from both years were combined.

Back-calculation models

A total number of 1891 annuli observations were used in the three models applied to back-calculate length.

The three regression models used for back-calculation of length found high correlation between the measured length at capture and the diameters of the spine section. Geometric mean regression (GMR) and simple log-linear regression (Method 1 and Method 3) explained 95% of the variance on the observed data (adjusted $R^2 = 0.951$, p-value< 0.05, a= 15.84, b= 14.86), likewise the log-geometric mean regression (log-GMR) model also showed a high correlation between the length at capture of fish and the diameter of the spine section, the variance explained was 95% (adjusted $R^2 = 0.953$, p-value< 0.05, a= 3.27, b= 0.76 in log scale).

The dispersion of the residuals against fitted values and the Quantile-quantile (QQ) plots for the GMR and log-GMR regression model fits are shown in Figures 3a,b,c,d. The residuals indicate that the regressions on log(L) and log(S) give the best fit from the point of the distribution of variance (Figure 3c,d). Therefore the log-GMR model was chosen as the best to back-calculate

length and used to fit the different models of growth. Some additional model runs were done using the GMR for comparison.

Mean length-at-age back calculated and their standard deviations from each of the three methods: GMR and Fraser-Lee (1), log-GMR and Monastyrsky (2), log-linear regression (3) and the observed mean length data are displayed in Table 2. Of the three back-calculation models, the two GMR methods gave similar mean predicted lengths, particularly for age groups 1 to 5 showing similar variation. For fish above age 5, the observed variation is larger, due to small sample size for larger fish. The back-calculation approach appears to underestimate the variability in lengths of younger fish. Overall, the CV of different mean length-at-age did not exceed 10% neither for the observed nor the three back-calculations methods. The highest CV was found for the observed mean length of age 1 albacore.

In the three models, the range of variation in lengths at age was comparable between the mean predicted lengths and the measured lengths for spines of a similar diameter (Figure 4a, b, c). The regression did not allow individual fish to have different mean predictions so that its mean predictions are a simple line (Figure 4d). Method 3 assumes that all variation in length at age between individual fish is residual error. On the other hand, the proportional back-calculation methods, are able to predict lengths for particular fish that vary from the mean prediction at a given spine diameter.

Growth models

When the fish were subsampled to give a roughly similar sample size in the well-sampled ages, the resulting sample contained 470 observations from 97 individual fish (Figure 5b). Because it was necessary to keep all the back-calculated lengths for each fish that was selected in the sub-sample, the younger ages are dominated by back-calculated lengths. Also, it was not possible to have completely balanced sample sizes in all the younger ages. Nevertheless, the subsample is more balanced than the complete dataset. The subsample for measured lengths only included 200 fish (Figure 5e).

For all three back calculation methods, for both the complete sample and a more balanced sub-sample, we ran models with: (1) individual variation in both L_∞ and K, (2) individual variation in L_∞ only, and (3) no individual variation. For the log-GMR back-calculation method 2, which we considered to be the best back-calculation method, models with different error structures were also considered. With all the combinations of the data sets, error structures, and mixed models , there were 27 candidate growth models. All had adequate convergence diagnostics (see Appendix) and appeared to fit the data well.

When a balanced sub-sample of the data was used, for all three back-calculation methods the DIC preferred the growth model that included individual variation in L_∞ but not K (Table 4). For the log-GMR and log-regression methods, this model was also preferred when the subsample was used; however, for the complete dataset using the log-regression method, the DIC preferred the model with no random effects. In addition, for the log-GMR subsample, the DIC preferred the

normal error structure to lognormal, and equal residual variances to SE-weighted residual variances. For the complete dataset of log-GMR data, the DIC preferred lognormal error to normal error, for the subsample, normal was preferred. Considering that the subsampled data is more balanced across ages, and that the log-GMR is the best back-calculation method, the best dataset is log-GMR subsample. For this dataset, the DIC prefers the model with constant residual error, normal residuals, and individual variation in L_∞ only.

Although the choice of back-calculation method (log-GMR method 2 versus log-regression method 3) did not influence which parameters had significant individual variation, it did influence the amount of individual variation between fish in L_∞ (Figure 6). Though the models with individual variation in L_∞ were generally preferred for all back-calculation models, there was a greater variation in L_∞ for the model fitted to log-GMR lengths than to the model fitted to lengths inferred by log-regression. Individual fish had L_∞ values that varied from 108 to 135 cm in the log-GMR model, but only from 116 to 134 in the regression model (Figure 6). The GMR model (method 1, not shown) was similar to the log-GMR.

The back-calculation methods influenced the values of the mean for L_∞ and K, but not as much as the sample size and distribution of fish ages in the sample (Figure 7, Table 5). Datasets dominated by younger fish tended to estimate larger values of L_∞ and smaller values of K, but this effect was less pronounced when random effects were included in the model. When only measured lengths were used, using the complete dataset, which was dominated by young fish gave values of L_∞ and K similar to those calculated using only young fish (left 3 points in Figure 7). Similarly, when back-calculated lengths were fitted with no random effects, the model estimated larger values of L_∞ for the complete dataset then for the subsample (right two points in Figure 7). The model with a random effect in L_∞ was less sensitive to sample sizes, with similar estimates of the mean of L_∞ for the complete dataset and the subsample (middle points in Figure 7).

The main difference between the models with and without random effects was the allocation of variance (Table 5). The random effects model estimated a smaller residual variance σ_ε than the fixed effects model, because some of the variability in length at age was interpreted as variation in growth between individuals. The random effects model also estimated a slightly lower correlation between the mean values of L_∞ and K. The model with random effects in L_∞ implies that most of the variation in length at age is individual variation (Figure 8). The mean growth curve is quite similar with or without random effects (Figure 8).

Discussion

We were unable to find any annual variability between cohorts or years in the growth increments, possibly because we only had two years of captures in the data set. With a longer time series, it might be possible to evaluate whether some years had larger growth increments than others within the random effects modeling framework (Shelton and Mangel, 2012).

512 The high correlation found between length and spine radius, gave support to the back-calculation
513 methods applied to derive information about growth for each individual albacore (Ricker, 1992).
514 The application of GMR methods allowed calculation of a *y*- intercept value to be used along
515 with a proportional method to back-calculate lengths; thus, results were biologically plausible
516 (Folkvord and Mosegaard, 2002; Ricker, 1992). In this context, the back-calculation proportional
517 method followed in our approach accommodated previous knowledge on statistical efficiency of
518 proportional model application (Guteuter, 1987 *in* Quinn and Deriso, 1999) also applied in other
519 tuna species (Cheng *et al,* 2012; Duarte-Neto *et al*., 2012) and billfishes (Kopf, *et al.*, 2011).
520
521 The deviance information criterion (DIC) preferred the models with individual variation in L_∞ but
522 not K for both the standard log-GMR back-calculation method, and when a simple regression was
523 used to back calculate lengths. Accordingly, the result that variation exists in L_∞ but not K seems
524 not to depend on the assumption of growth from a common intercept in the back-calculation
525 model. Thus, we can probably conclude that the result that there is more variation in L_∞ than K is
526 not an artifact of the functional form of GMR back-calculation, as suggested by Francis (1995), at
527 least for North Atlantic albacore.
528
529 Similar results about individual variation in L_∞ but not K were found from analyses on length
530 increment derived from the release-recapture information available from tagging experiments (
531 models 3, 4 and 7 and Tagging (equation3) in Table 6). In contrast, another albacore growth
532 study based on a model that integrated spines and tagging data did not find variability in L_∞ (last
533 model in Table 6, Santiago and Arrizabalaga, 2005). None of the analyses, neither those using
534 tagging data (Table 6) nor our study (Table 5), found individual variation on the growth rate
535 parameter (K). Thus individual variation on L_∞ only seems to be the most plausible model for
536 North Atlantic albacore. On the other hand, a simulation study by Eveson *et al.* (2007)
537 concluded that when variability exists in both growth parameters it is rare that both sources of
538 variability can be detected; therefore, they recommended using models that include individual
539 variation in both parameters even if only one was found to vary significantly.
540
541 The means of L_∞ and K are consistent with previous studies based on spine readings, or the spine
542 and tagging data integrated models (Table 6). However, estimates derived from tagging data
543 were affected by low reporting rates of fish at longer time at liberty and a paucity of return data
544 for larger fish from commercial fleets, consequently smaller asymptotic L_∞ were estimated (Table
545 6, Ortiz de Zárate and Restrepo, 2001; Santiago and Arrizabalaga, 2005). Our estimates, a mean
546 asymptotic L_∞ of 120 cm and growth rate (K) of 0.21, are nearly identical to the values (L_∞ =122
547 cm, K= 0.209) found by Santiago and Arrizabalaga (2005) based on both spines and tagging data,
548 and used in the current assessment (ICCAT, 2013b). The introduction of individual variation into
549 the growth model, which is biologically realistic, does not lead to a substantial change in
550 expected distribution of lengths at age for this species, given the similar length range covered in
551 both studies, compare Santiago and Arrizabalaga (2005, their Table 2) to our study (Figure 2).
552
553 Using either all the data or a more balanced subsample gives somewhat different estimates of the
554 mean L_∞ and K parameters (Figure 7). Datasets dominated by younger fish tended to estimate
555 higher values of L_∞ and lower values of K. The mean values of L_∞ were slightly higher when only

556 measured lengths were used than when the back-calculated lengths were analyzed (Figure 7).
557 Few large fish were included in the dataset (>90 cm), which may be the reason that small changes
558 in the modeling assumptions gave different L_∞ results. A dataset that is more informative about
559 L_∞ might be more robust to the choice of estimation methodology. The length range of albacore
560 samples used in our study represents the selectivity of surface fleets that target albacore in North
561 Atlantic stock and represent nearly 80% of total catch (ICCAT,2013b; ICCAT, 2014).
562 Nevertheless, availability of a larger sample of the adult albacore fraction of the population
563 would improve precision on older albacore aging.
564
565 Our study corroborates the hypothesis of negatively correlated asymptotic mean length (L_∞) and
566 growth rate (K) for north Atlantic albacore, as has been found in other species (Helser and Lai,
567 2004; Pilling et al., 2002). The correlation between L_∞ and K obtained from the random effects
568 model (-0.85) is very close to the negative correlation of -0.8 assumed in simulation studies
569 (Hampton and Majkowski, 1987).
570
571 There are some caveats involved in the use of spines rather than repeated measurements of length
572 to estimate individual variability in estimate individual variation in growth. The method assumes
573 that there is a high correlation between spine length and fish length, that the functional
574 relationship between fish length and spine length is known, and that the relationship does not
575 change over time or between individuals (Schirripa 2002). We found a clear linear relationship
576 between log(spine diameter) and log(fork length), which supports this approach (Figure 4).
577 It is worth noting that estimates of the mean growth parameters based on spine readings at
578 capture (Measured only, Table 5), yielded similar growth parameters to those calculated with
579 back-calculated lengths (Table 5, best model, and fixed effects). This could be interpreted as a
580 verification that the backcalculation is not introducing bias.
581
582 Because of size-selectivity in the fisheries, lengths of fish captured at age one may be skewed
583 larger than the lengths at age 1 back-calculated from fish caught at older ages. In general, mean
584 length-at-age 1 estimates from observed length varies across studies (Table 2, Bard, 1981,
585 Santiago and Arrizabalaga, 2005). In our study, using Method 2 to reconstruct the individual
586 trajectory by back-calculation estimated the smallest mean length-at-age 1. Size-selectivity may
587 explain some of the differences between studies, and it is not clear which methods generate the
588 least biased distribution of lengths at age 1.
589
590
591 Our study advances understanding of growth of the north Atlantic albacore population by
592 including random effects in the von Bertalanffy growth parameters to model individual variation
593 on growth. The Bayesian hierarchical modeling approach performed well when incorporating
594 individual trajectories to model growth of north Atlantic albacore and the fitted model explained
595 the current growth of the North Atlantic population of albacore. This approach allows testing
596 hypotheses about the back-calculation method and about the impact of size of the sample and
597 length coverage for the albacore von Bertalanffy growth model of North Atlantic albacore.
598 Further research on the uncertainty on age of young albacore (i.e. age one) and the differential
599 growth rate for sexually mature males and females can be addressed in future analyses.
600 Moreover, the time effect of growth needs to be tested with longer time series to evaluate whether

there is year-to-year variability in growth. Future simulations studies to evaluate modeling growth would contribute to explore uncertainties about the growth of this stock.

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Author contribution

V. Ortiz de Zárate. Design of sampling scheme, aging and back-calculation methods. E. A. Babcock. Design of growth modeling and analysis conducted in JAGS using the R statistical software. Both authors wrote manuscript sections and contributed to discussion.

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857
858
859 Table 1. Estimated parameters in the full growth model and their priors. For models without
860 individual variation in a parameter, the values for each individual fish are equal to the population
861 mean.
862

Parameter	Description	Prior
$L_{\infty,i}$	Individual fish asymptotic length	Normal(μ_L,σ_L)
K_i	Individual fish growth rate	Normal(μ_K,σ_K)
μ_L	Population mean L_∞	Lognormal(0,1000)
σ_L	Standard deviation in L_∞ between fish	Uniform(0.0001,1000)
μ_K	Population mean growth rate	Lognormal(0,1000)
σ_K	Standard deviation in K between fish	Uniform(0.0001,10)
t_0	Population mean age at L=0	Normal(0,1000)
σ_ε	Standard deviation of the measurement error ε	Uniform(0.0001,100)
$\sigma_{measured}$	Standard deviation of the measurement error ε	Uniform(0.0001,100)
σ_{back}	Standard deviation multiplier for back calculated lengths	Uniform(0.0001,100)

863

Table 2. Albacore observed length (cm) and back-calculated length (cm) obtained by the three methods described in the study for the aggregated samples from 2011 and 2012.

	Observed Length						BCL Method 1-Fraser-Lee					BCL Method 2-Monastyrsky				BCL Method 3 Regression	
	Age	N	mean	st dev	CV%	SE	N	mean	st dev	CV%	SE	mean	st.dev	CV%	SE	mean	st.de
	1	538	53.3	6.49	12.2	0.28	898	52.2	3.7	7.2	0.12	51.8	4.1	7.9	0.14	52.1	
	2	348	64.4	3.97	6.2	0.21	594	63.9	3.9	6.0	0.16	64.2	4.1	6.4	0.17	64.1	
	3	364	74.7	4.42	5.9	0.23	234	74.1	4.4	5.9	0.29	74.8	4.6	6.1	0.30	74.6	
	4	155	83.4	4.53	5.4	0.36	81	84.0	5.2	6.1	0.57	84.9	5.3	6.3	0.59	84.2	
	5	41	90.8	4.09	4.5	0.64	39	93.3	6.3	6.7	1.01	94.1	6.3	6.7	1.00	91.6	
	6	11	99.1	5.45	5.5	1.64	26	100.2	7.8	7.8	1.53	100.7	7.5	7.5	1.48	97.4	
	7	13	106.6	7.87	7.4	2.18	13	100.7	5.3	5.3	1.48	101.1	5.2	5.2	1.45	98.5	
	8	9	102	4.33	4.2	1.44	3	107.8	5.0	4.7	2.90	108.0	5.1	4.7	2.92	103.8	
	9	4	110	4.32	3.9	2.16	1	100.4				101.4				106.3	
	10	1	105				1	103.2				104.0				109.0	
	11	1	108				1	106.9				107.4				112.5	
	Total	1485					1891										

Table 3. Analysis of variance for the model of the effect of numerical age and the factor cohort on annual growth increment.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
age	1	3.47	3.47	93.32	<0.0001
cohort	2	0.09	0.04	1.15	0.32
age:cohort	2	0.09	0.05	1.24	0.29
Residuals	1328	49.36	0.04		

Table 4. DIC comparison of growth models fitted to lengths back-calculated by the three methods. The best growth model for each dataset is the one with Δ_{DIC} =0. All models had normally distributed residuals and constant residual variance except where noted.

Data	Subsample	Error model	Random effects	Δ_{DIC}
GMR	all data		L_∞, K	182.10
			L_∞	0.00
			none	135.57
GMR	subsample		L_∞, K	112.78
			L_∞	0.00
			none	70.35
log-GMR	all data		L_∞, K	614.92
			L_∞	497.31
			none	893.48
		se weighted	L_∞	19.99
		lognormal	L_∞	0.00
log-GMR	subsample		L_∞, K	129.49
			L_∞	0.00
			none	557.78
		se weighted	L_∞	47.53
		lognormal	L_∞	14.05
log-regression	all data		L_∞, K	2611.59
			L_∞	2536.50
			none	0.00
log-regression	subsample		L_∞, K	5.56
			L_∞	0.00
			none	144.66

Table 5. Medians and 95% credible intervals of estimated parameters from the DIC best model, which has individual variation in L_∞, with the model with no random effects and the model applied to measured fish only shown for comparison. Cor(LK) is the posterior correlation between the mean value of L_∞ and the mean value of K. Data are subsampled and the log-GMR back calculation method was used.

	Best: L_∞ random	Fixed effects	Measured only
cor(LK)	-0.85	-0.96	-0.96
σ_ε	2.38(2.21-2.56)	4.93(4.63-5.26)	4.68(4.26-5.18)
σ_L	6.6(5.6-7.9)		
μ_L	120.2(117.2-123.3)	123.4(118.7-129.1)	126.1(119.7-134.8)
μ_K	0.21(0.2-0.23)	0.20(0.18-0.23)	0.19(0.16-0.22)
t_0	-1.62(-1.76-1.49)	-1.62(-1.89-1.38)	-1.63(-2.01-1.32)

Table 6. Growth parameters estimated by different models applied to tagging data and spine readings from previous studies of North Atlantic albacore. The parameters $\sigma^2_{L\infty}$ or σ^2_K are the estimated standard deviation between individuals, with zero implying no variation found. If no value is given, the model did not include individual variation. The parameter σ^2_e is the normal variance of the residual error and σ^2_m is the release measurement error in the model. Normal variance error was estimated for tagging data set ($\sigma^2_{e\,T}$) and spine data set ($\sigma^2_{e\,S}$).

			Model estimates						
Model	Data	n	L_∞ (cm)	$\sigma^2_{L\infty}$	K(y^{-1})	σ^2_K	σ^2_e	σ^2_m	to (y)
von Bertalanffy model [1]	Spines	352	124.7		0.23				-0.989
Model 3 [2]	Tag data	298	105.6	59.1	0.33		12.4		
Model 4 [2]	Tag data	298	105.6	68.7	0.33		7.7	7.6	
Model 7 [2]	Tag data	298	105.6	68.7	0.33	0	7.7		
Tagging (Equation 3) [3a]	Tag data	309_a	110.5	55.04	0.29		12.9		
von Bertalanffy model [3b]	Spines	761_b	127.1		0.18		21.7		-1.616
von Bertalanffy model [3a+b]	Spines+Tag	a + b	122.2	0	0.21		21.56 $_T$		-1.338
							22.15 $_S$		

[1] Bard, 1981, von Bertalanffy model.

[2] Ortiz de Zárate and Restrepo, 2001, using von Bertalanffy models adapted by Hampton (1991).

[3a] Santiago and Arrizabalaga, 2005, using von Bertalanffy models adapted by Hampton (1991).

[3b] Santiago and Arrizabalaga, 2005, spines von Bertalanffy model.

[3a+b] Santiago and Arrizabalaga, 2005, spines + tag joint analysis von Bertalanffy model.

Figure captions

Figure 1. Map of the study area in the Northeast Atlantic Ocean. Albacore spine samples locations in 2011 and 2012.

Figure 2. Length frequency distribution of sampled albacore. Years 2011 and 2012 combined.

Figure 3. Residuals and QQ-normal plots of the residuals from (a-b) a linear regression of length against spine diameter, and (c-d) a linear regression of log(length) against log(spine diameter).

Figure 4. (a) Measured lengths and mean line for each kind of regression, and lengths predicted from each spine diameter using (b) GMR, (c) log-GMR and (d) log- linear regression, with measured lengths shown for comparison.

Figure 5. Sample sizes used in growth model fitting, for (a) all measured and back-calculated lengths, (b) fish subsampled so that sample sizes are more equal, (c) only young fish (1-5 age), (d) all measured lengths, and (e) measured lengths subsampled so samples sizes are more equal, and (f) only young measured fish with an equal sample size.

Figure 6. Histograms of the median values of L_∞ across individual fish, from the DIC best model by back-calculation method (a) log-GMR, and (b) log- linear regression. These models were calculated from a subsample of the data and had individual variation in L_∞ only.

Figure 7. Median and 95% credible intervals of the population mean values of (a) L_∞ and (b) K for models fitted to the log-GMR data, with varying sample sizes and with and without random effects in L_∞. The results from models with measured data only are shown for comparison.

Figure 8. The best model applied to the subsampled data from the log-GMR back-calculation. The solid line is the median growth curve, grey lines are individual growth curves, and points are length data. Growth model parameters fitted (mean L_∞ = 120.2; K=0.21; t_0 =-1.62). The growth curve fitted to the same data using fixed effects, and the curve fitted to a subsample of measured data only are shown for comparison (black dotted lines).

Figure A1. Priors and posteriors for the estimated parameters in the model fit to a subsample of measured data (a-d), a subsample of measured and log-GMR back-calculated data with fixed effects only (e-h), and the best model for the log-GMR data, with a random effect for L_∞(i-m).

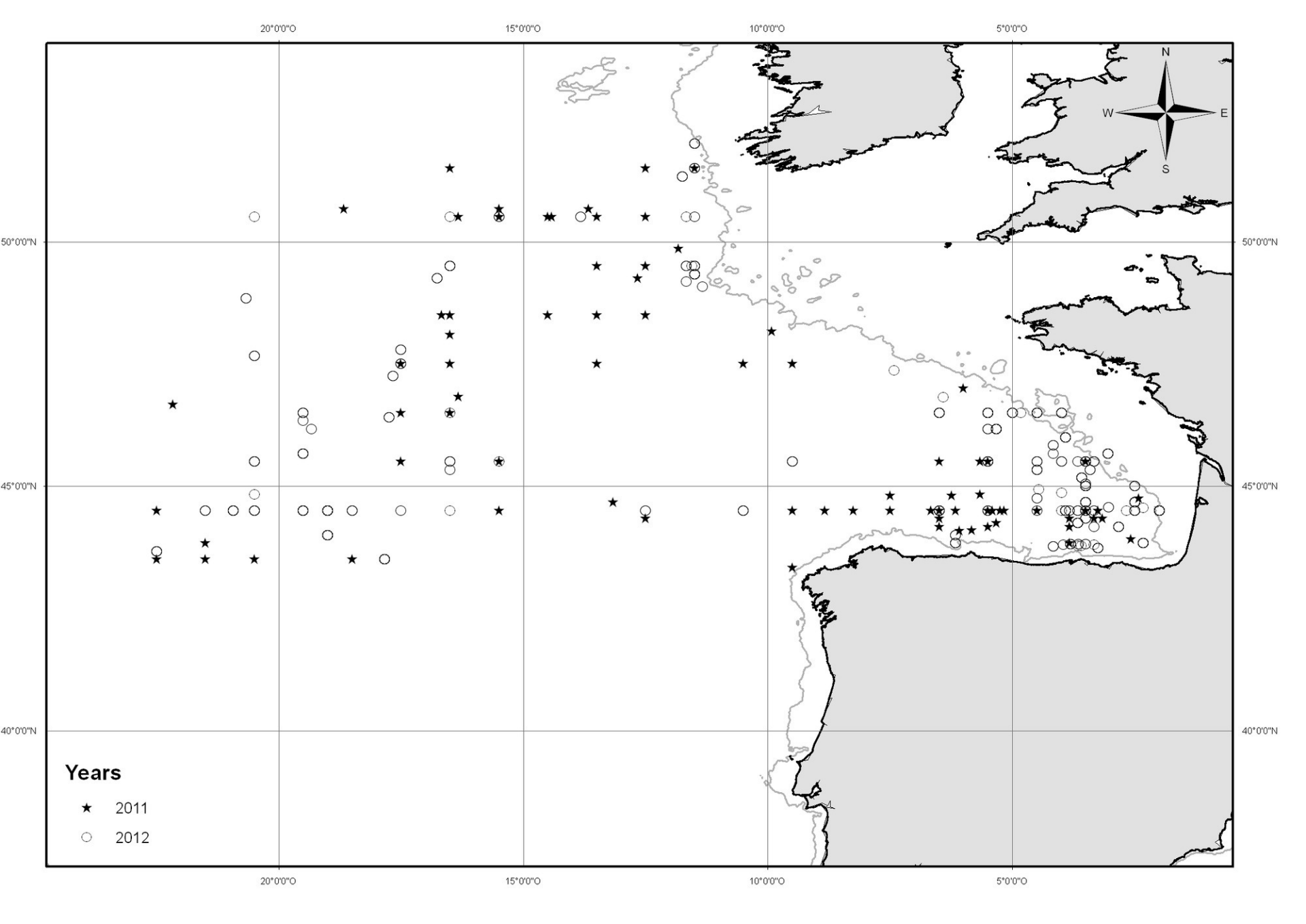
Appendix.

All of the models had Gelman-Rubin diagnostic values near one and an effective sample size greater than 100, which indicates that the MCMC has adequately converged on the posterior distribution (Lunn *et al.* 2013). Also the Bayesian P value, which is a diagnostic of model adequacy, was close to 0.50, as expected for good model fit (Table A1). For two representative models, the priors and postereriors of the estimated parameters are shown in Figure A1. The priros were all uninformative. The fact that the posteriors are well estimated and relatively narrow implies that the data were sufficiently informative to estimate these parameters.

947
948 **Table A1.** Diagnostics of model convergence and fit. The effective number of parameters should
949 be more than 100 and the GR diagnostic near 1.0 for MCMC convergence. The Bayesian P value
950 is a summary of the residuals, which should be near 0.5 for an adequate model fit.
951
952

Data	Subsample	Error model	Random effects	Effective n	GRD	P value
GMR	all data		L_∞, K	1200	1.01	0.50
			L_∞	100	1.02	0.50
			none	2800	1.00	0.49
GMR	subsample		L_∞, K	430	1.01	0.50
			L_∞	310	1.01	0.50
			none	480	1.00	0.49
log-GMR	all data		L_∞, K	490	1.01	0.50
			L_∞	100	1.02	0.50
			none	2400	1.00	0.50
		se weighted	L_∞	1200	1.00	0.49
		lognormal	L_∞	110	1.01	0.50
log-GMR	subsample		L_∞, K	870	1.00	0.49
			L_∞	2100	1.00	0.49
			none	1400	1.00	0.49
		se weighted	L_∞	4100	1.00	0.48
		lognormal	L_∞	360	1.01	0.48
log-GMR	young only		L_∞	630	1.00	0.50
log-regression	all data		L_∞, K	560	1.02	0.50
			L_∞	710	1.00	0.50
			none	1300	1.00	0.50
log-regression	subsample		L_∞, K	1000	1.02	0.49
			L_∞	520	1.00	0.49
			none	6900	1.00	0.50
log-regression	young only		L_∞	160	1.02	0.49
Captured	all data		none	340	1.01	0.49
Captured	subsample		none	2600	1.00	0.49
Captured	young only		none	1200	1.00	0.49

953
954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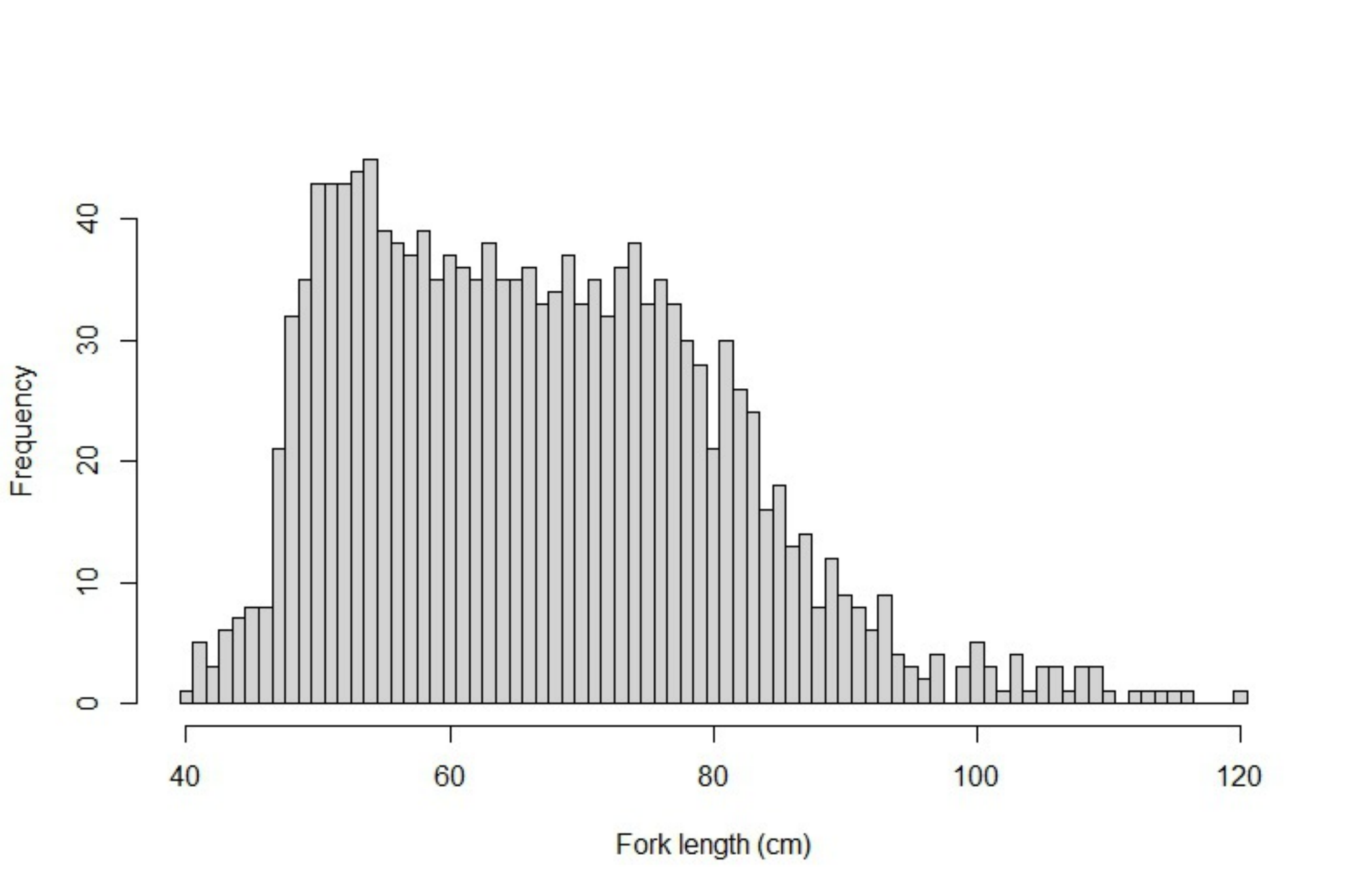
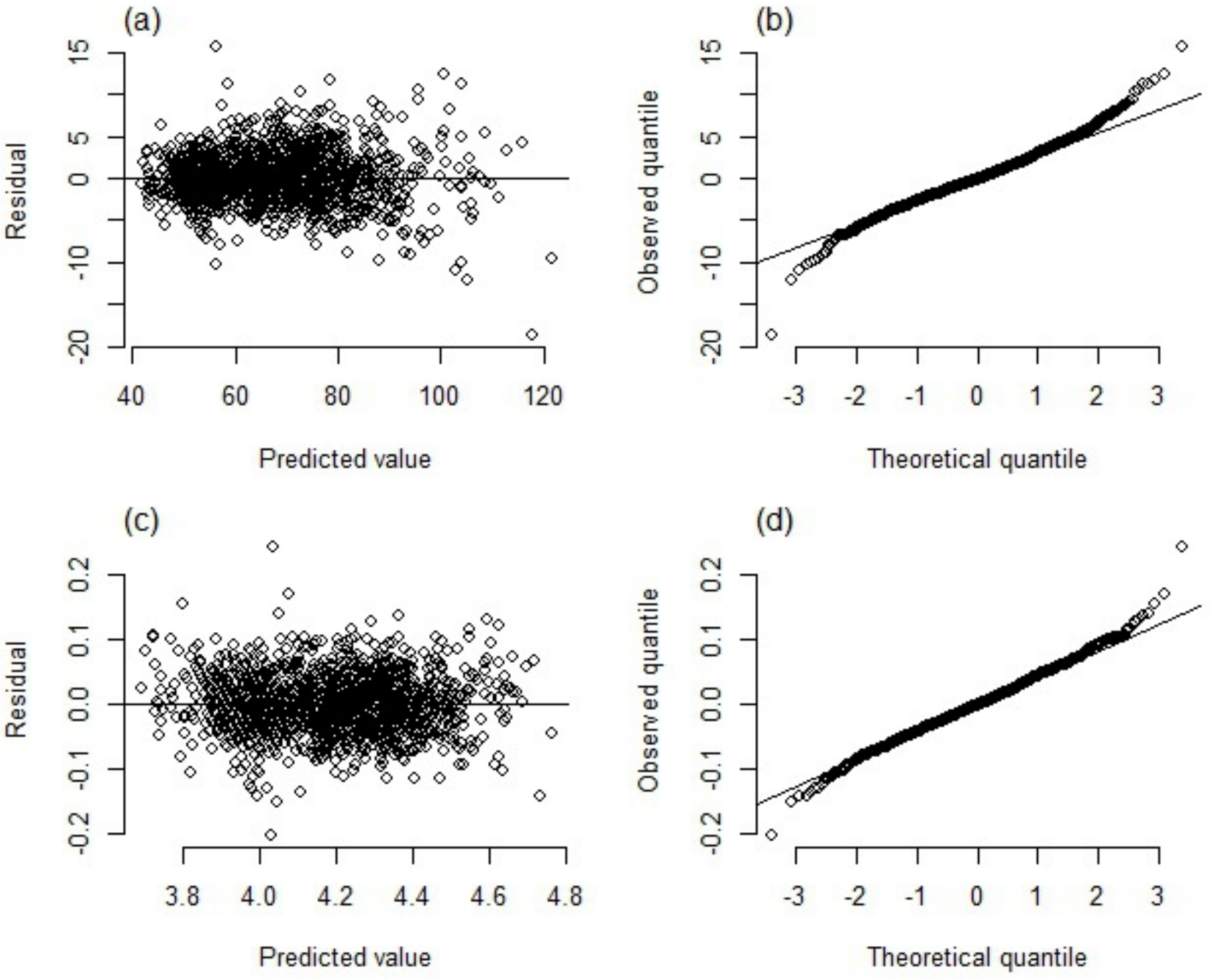
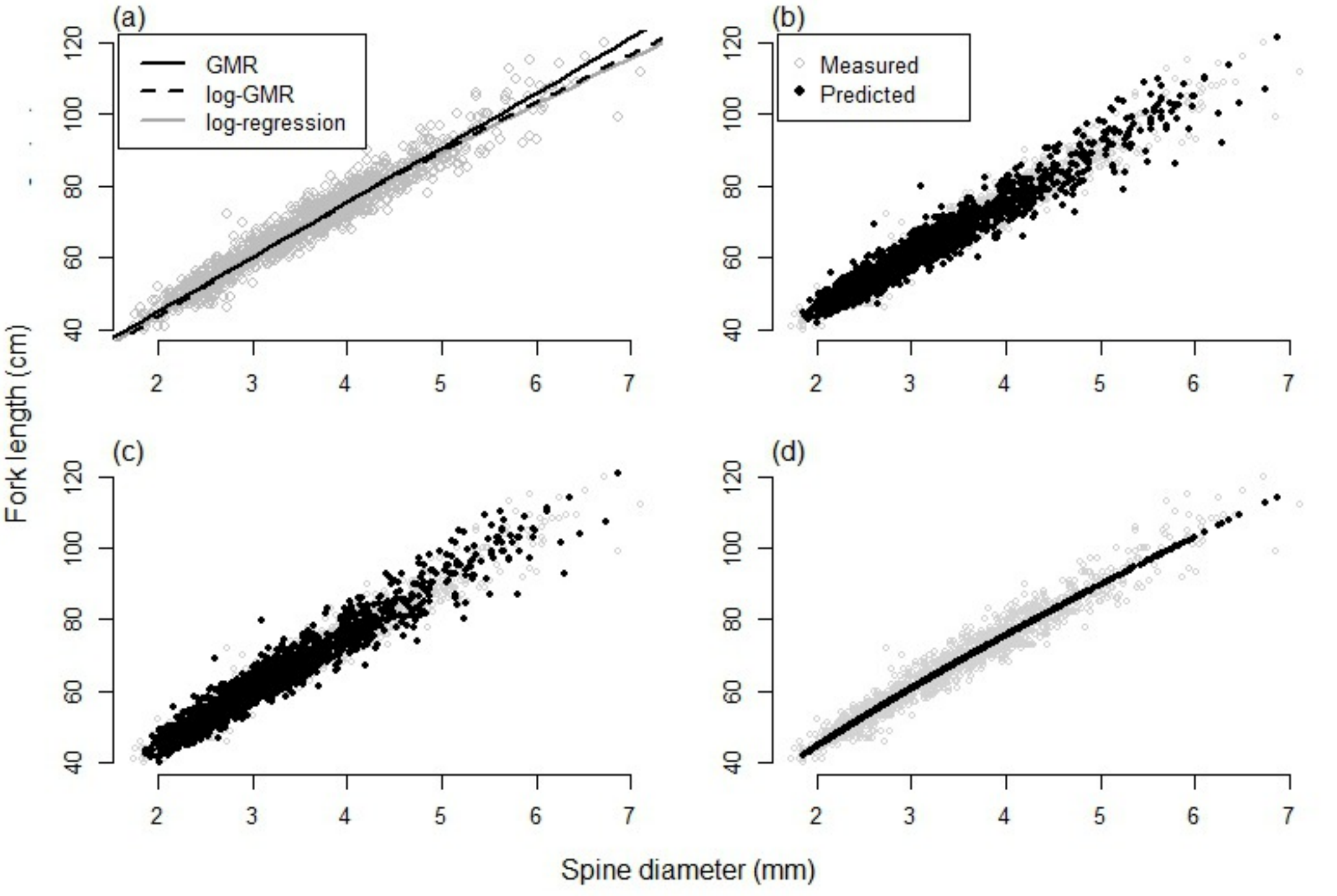
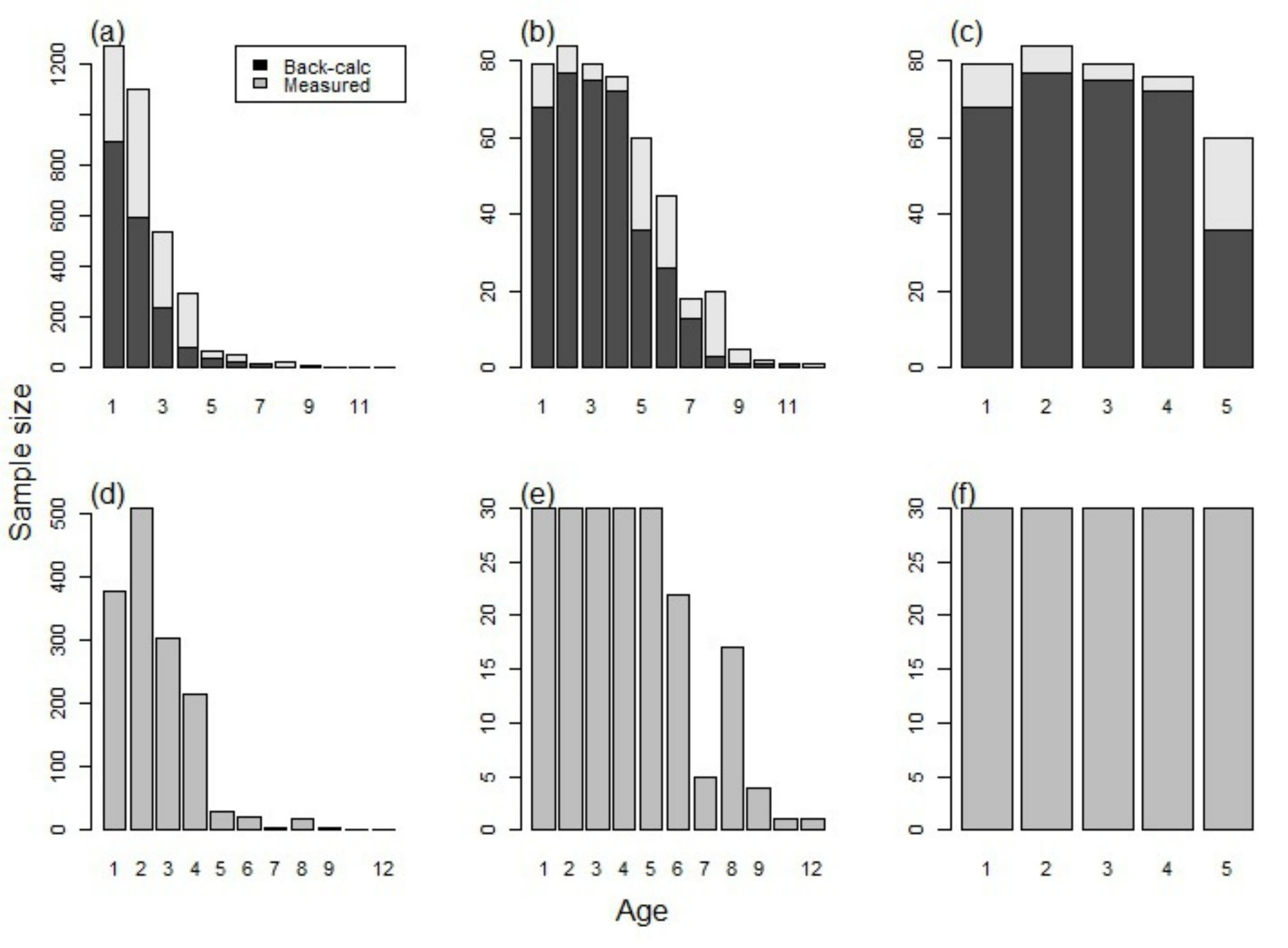
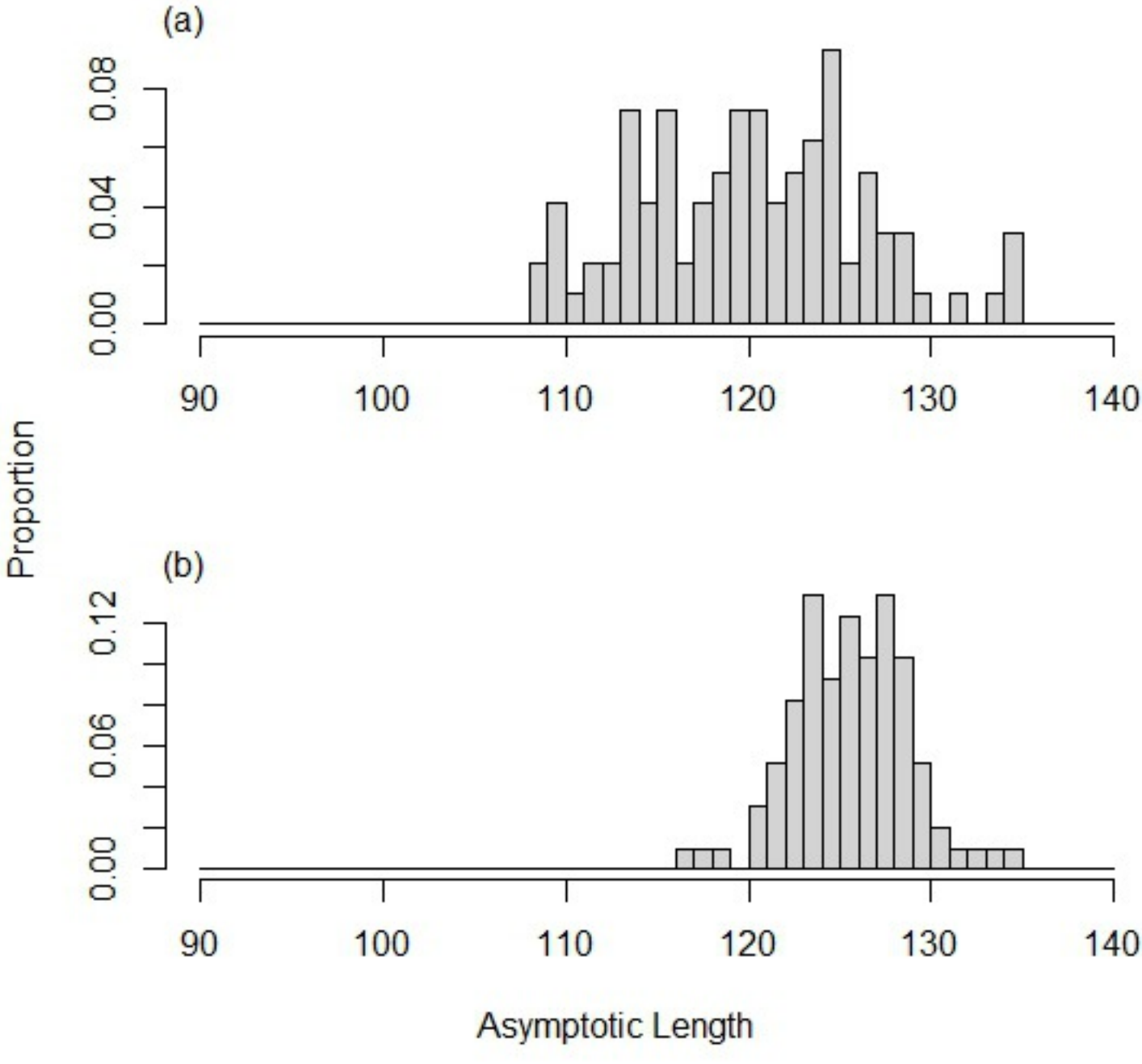
15°0'0"O
10°0'0"O
5°0'0"O
50°0'0"N
45°0'0"N
40°0'0"N
N
W
E
S
Years
2011
2012


Frequency
0
10
20
30
40
40
60
80
100
120
Fork length (cm)


(a)
Residual
15
5
0
-10
-20
40
60
80
100
120
Predicted value
(b)
Observed quantile
15
5
0
-10
-20
-3
-2
-1
0
1
2
3
Theoretical quantile
(c)
Residual
0.2
0.1
0.0
-0.1
-0.2
3.8
4.0
4.2
4.4
4.6
4.8
Predicted value
(d)
Observed quantile
0.2
0.1
0.0
-0.1
-0.2
-3
-2
-1
0
1
2
3
Theoretical quantile


(a)
GMR
log-GMR
log-regression
(b)
Measured
Predicted
(c)
(d)
Fork length (cm)
Spine diameter (mm)
40
60
80
100
120
2
3
4
5
6
7


(a)
(b)
(c)
(d)
(e)
(f)
Back-calc
Measured
Sample size
Age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0.00
0.04
0.08
90
100
110
120
130
140
Proportion
(b)
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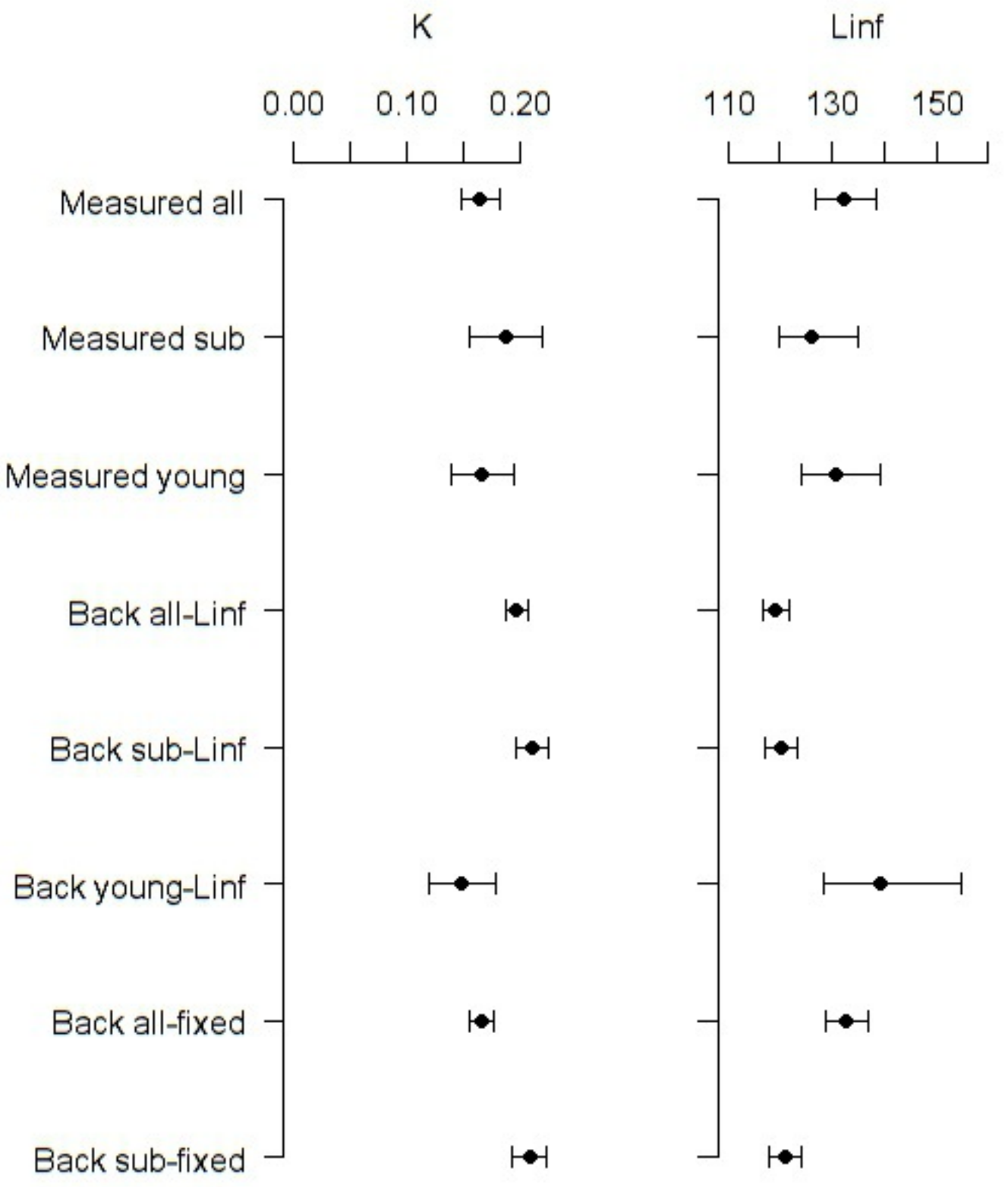
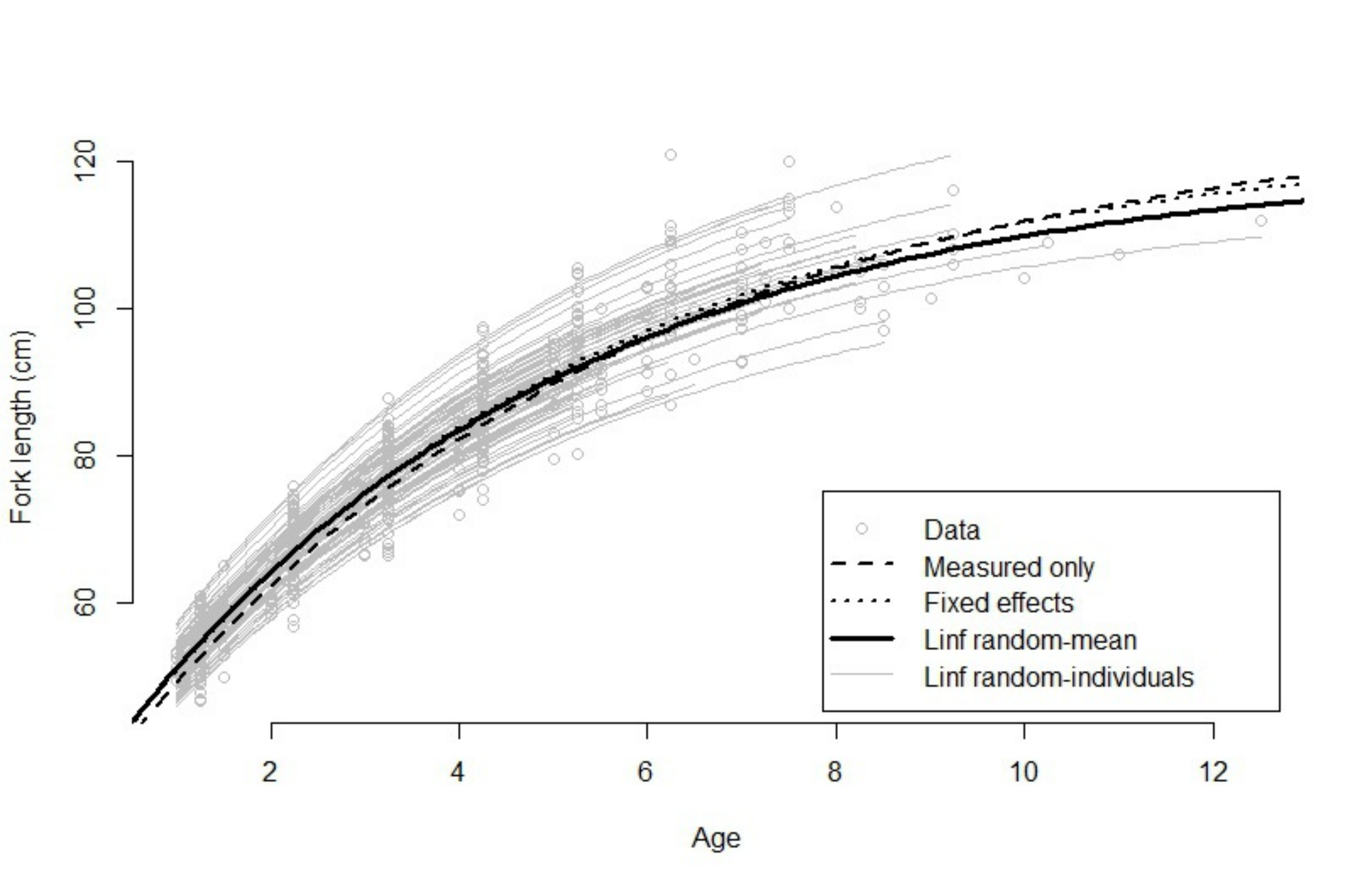
0.06
0.12
90
100
110
120
130
140
Asymptotic Length


K
0.00
0.10
0.20
Linf
110
130
150
Measured all
Measured sub
Measured young
Back all-Linf
Back sub-Linf
Back young-Linf
Back all-fixed
Back sub-fixed


Fork length (cm)
60
80
100
120
2
4
6
8
10
12
Age
Data
Measured only
Fixed effects
Linf random-mean
Linf random-individuals