Improving growth estimates for western Atlantic Bluefin tuna using an integrated modeling approach.

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Abstract

Advances in modeling growth using tag-recapture data and progress in otolith ageing procedures allowed improved fitting of the western Atlantic bluefin tuna growth curve. Growth parameters were derived from an integrated analysis of tag-recapture data and otolith age-length data using the "Aires-da-Silva-Maunder-Schaefer-Fuller with correlation" (AMSFc) framework, which models growth such that parameter estimates from each data source are directly comparable. The otolith data consisted of a sample of 4,045 otoliths for which ages were estimated using tested and consistent protocols and conventions designed to avoid bias. Strict data quality control measures were applied to the tagging data for quality assurance and a subsample of 1,118 records were retained for use in the analysis. Two forms of the Schnute (1981) growth model were considered: the Richards model and the von Bertalanffy model. The Richards curve appears to provide a better fit. Both curves follow a similar trajectory until age 16, after which they diverge considerably. The Richards model supports a lower mean asymptotic length (L_∞= 271.0 cm FL) than the model currently used in the stock assessment (L_∞= 314.9 cm FL).

Keywords: Growth, *Thunnus thynnus*, fisheries stock assessment, otolith, tagging.

1. Introduction

Migratory pelagic fish present both opportunities and challenges in developing predictive growth models. Species such as Atlantic bluefin tuna *Thunnus thynnus* (ABT) attract substantial fishing effort, affording opportunities to access fish for tagging and collection of otoliths, which support parameterization of growth. Principal challenges include sufficient sampling, implementing quality control procedures to curtail biased observations throughout the stock's range, and making best use of combined age-length and tag-recapture data. Otolith data are used to estimate absolute ages and allow size-at-age functions to be modeled. For western ABT, these data are largely centered on the larger/older fish targeted by the recreational and commercial fisheries. Tagging data often have the opposite problem of lacking large fish and fish with long times at liberty. Each data source is also prone to various sources of observation error – mainly variability in age assignment across readers and measurement error in recorded fish lengths. It is therefore advantageous to estimate growth from both sources of data simultaneously to increase the size and representativeness of the sample and test the influence of each dataset on resulting parameter estimates (Maunder and Punt, 2013). We apply a new maximum likelihood approach to fit jointly direct age estimates, for a large sample of otoliths, with release and recapture lengths of conventionally-marked fish.

ABT is the largest member of the Scombridae family. It can reach weights exceeding 600 kg (Collette and Nauen, 1983) and live over 34 years (present study). The species is assessed and managed as two distinct stocks by the International Commission for the Conservation of Atlantic Tunas (ICCAT) under the assumption of no net mixing (ICCAT, 2014): the eastern stock (eastern Atlantic/Mediterranean) and the western stock (western Atlantic/Gulf of Mexico), with spawning grounds on opposite sides of the North Atlantic Ocean basin (Boustany et al., 2008; Carlsson et al., 2007; Riccioni et al., 2010; Richardson et al., 2016). Although these two stocks are conventionally separated by the 45°W meridian, tagging data indicate a high degree of transoceanic migration for animals of all ages, with significant mixing occurring on foraging grounds (Block et al., 2001, 2005; Sibert et al., 2006).

Following years of overfishing, ICCAT adopted rebuilding plans for the western and eastern stocks in 1998 and 2006, respectively, gradually tightening control measures over time, as the Commission strived to meet its objectives. According to the latest stock assessment, both stocks are showing signs of recovery. Still, considerable uncertainties remain in the assessment, particularly regarding maturity, growth dynamics and the level of mixing between the two stocks, making it difficult to draw definite conclusions about the current and future status of the stock (ICCAT, 2014).

Information on age and growth is needed to assess properly a depleted stock and define its rebuilding target. This holds especially true for bluefin tuna for which a growth curve is used to translate catch-at-size to catch-at-age through cohort slicing in the stock assessment process. Being a moderately long-lived, iteroparous species, bluefin tuna relies on the periodic production of strong year classes to persist through time (Secor, 2007). In this case, it becomes particularly important to characterize precisely the age structure of the stock, since having a truncated age structure (Siskey et al., 2016) and being the target of a highly age/size selective fishery (ICCAT, 2014) can severely compromise the sustainability of the fishery.

The growth parameters currently used in the assessment of western ABT (Restrepo et al., 2010) were derived from a combination of otolith-based age readings for large fish (n=146; Neilson and Campana, 2008; Secor et al., 2009) and modal analysis of length frequency data for small fish (1-3 years of age, 1970's US purse seine data). In their analysis, Restrepo et al. (2010) did not include information available in the ICCAT tagging database used to construct the former growth curve (Turner and Restrepo, 1994) due to data quality concerns and biases in the estimation process. Although the Restrepo et al. (2010) analysis was a significant improvement over the former growth curve, recent advances in integrative modeling and otolith age reading techniques highlights the need for an updated assessment of the current growth curve.

During a workshop aimed at standardizing otolith-based ageing protocols for ABT, Busawon et al. (2015) determined that the otoliths used by Restrepo et al. (2010) were significantly over-aged (average 3 years) due to errors in assignment of the first annulus. The problem was resolved using a standardized reference scale for the first annulus adopted by the laboratories involved in ageing studies (Secor et al., 2014a).

Improvements in both data quality control (Ailloud et al., 2014) and modeling techniques (Aires-da-Silva et al., 2015; Francis et al., 2016) now allow for the ICCAT tagging data to be incorporated in the growth analysis. Francis (1988) showed that growth parameters estimated from age-length data and tagging data have different interpretations when tagging data are analyzed by modeling growth increments through time (e.g., as done by Fabens, 1965). Comparing these estimates assumes that the expected annual growth of fish of age *A* (estimated from age-length data) is equivalent to the expected annual growth of fish whose length is equal to the mean length of fish of age *A* (estimated from tagging data), which is seldom the case (Francis, 1988). In recent years, maximum likelihood approaches have been developed that model the joint density of the release and recapture lengths as a function of age, making growth estimates age-based and thus avoiding the comparability problem (Laslett et al., 2002; Palmer et al., 1991; Wang et al., 1995). At the forefront of integrated methods is the so-called "Laslett-Eveson-Polacheck" (LEP) approach (Eveson et al., 2004), which models the release and recapture lengths as functions of age by treating age at tagging and asymptotic length, L_∞, as random variables. Though statistically attractive, this method can be difficult to implement due to its high computational demands and complicated error structures. A simpler alternative was developed by Aires-da-Silva et al. (2015) and later improved upon by Francis et al. (2016) by allowing correlation among deviates in tagging length: the AMSFc approach (Francis et al., 2016), named after Aires-da-Silva, Maunder, Schaefer and Fuller, where 'c' stands for correlation. Like the LEP approach, this method also treats pairs of observed lengths as a function of age, but treats L_∞ as a fixed parameter, greatly reducing the computational demands of the model (Aires-da-Silva et al., 2015). The AMSFc approach is applied here to fit and compare alternative growth models for the western stock of ABT.

2. Materials and Methods

2.1 Tagging data

The ICCAT conventional tagging database combines tag release and return information from several tagging studies conducted in various regions of the North Atlantic Ocean over the past 75 years. Of more than 85,000 releases, ICCAT recovered information for nearly 6,000 recaptures, of which 2,434 had complete and plausible data (e.g., non-negative times at liberty) on the date and length at release and recapture. Ailloud et al. (2014) demonstrated that the database contains valuable information for estimating growth of bluefin tuna (such as records of fish that were at liberty for many years and of old fish which appear to have reached their maximum sizes), but that extraction of the data must be done with care. Quality control measures employed in our analysis are detailed below (applied to data from the 06/30/2016 database update).

1) Animals at liberty for less than 105 days (~3.5 months) were excluded from the analysis (1,068 records) since, a) for fish with short times at liberty, the observed growth increments largely represent measurement error rather than somatic growth (Ailloud et al., 2014), and b) stress related to the tagging event could potentially have an adverse effect on growth in the short run.

2) Records showing the fastest and slowest 2% absolute growth per day were removed in an attempt to eliminate outliers (i.e., data entry misrecordings and large measurement errors) and improve growth parameter estimates (116 records dropped). To test the sensitivity of the results to these outliers, a separate run that included the outliers was performed.
3) Fish both captured and recaptured in the eastern Atlantic, as well as fish either captured or recaptured in the Mediterranean, were excluded from the analysis (132 records). This rule does not guarantee that fish of eastern origin are removed from the sample since considerable mixing is known to occur (Siskey et al., 2016), but it instead attempts to keep the tagging data sample focused on fish present in the western Atlantic, since growth is presumably linked to local conditions (e.g., prey abundance, water temperature and fish density).

The resulting dataset consisted of 1,118 records with lengths at tagging ranging from 36 cm FL to 259 cm FL, lengths at recapture ranging from 53 cm FL to 292 cm FL (Supplementary Fig. A1) and times at liberty ranging from 4.5 months to 16 years (median= 1 year). 53% of the records corresponded to fish tagged in the 1960's, another 43% corresponded to fish tagged in the 1970's and the remaining 4% were released between 1980 and 2011.

2.2 Otolith data

The otolith data consisted of samples collected from the Gulf of Mexico (n=305), the southeastern USA (n=55), the USA Mid-Atlantic Bight (n=1,141) and the Northeastern USA/Canada (n=2,512) (Supplementary Fig. A2). The large majority of otoliths (85%) was collected between 2009 and 2015. Snout lengths and curved fork lengths (CFL) were converted to straight fork lengths (FL) using conversion factors from Secor et al. (2014b) and Rodriguez-Marin et al. (2015), respectively. In the few cases where no length measurements were taken (3.5% of records), round weights were converted to FL using monthly conversion factors from Rodriguez-Marin et al. (2015). Sizes ranged from 48 cm FL to 300 cm FL (Supplementary Fig. A1) and age estimates from 1 to 34 years.

Neilson and Campana (2008) validated absolute age in large/old bluefin tuna using bomb radiocarbon dating and Siskey et al. (2016) confirmed the annual periodicity of growth increments, validating otolith ageing for the species. Otolith samples were prepared and read by experts following the standardized protocol outlined in Secor et al. (2014a) and Busawon et al. (2015) which, among other things, prescribes using a reference scale to identify the first annulus and performing multiple reads per otolith to detect any inconsistencies and reduce ageing error. Using a reference set of otoliths (n=100), Busawon et al. (2015) estimated that ageing error was low among readers and detected no systematic bias. Each sample was assigned an integer age based on annuli counts of either opaque of translucent bands, which was then adjusted (a_{adj}) to account for the timing of band formation (i.e. when counting opaque bands, one year was added to the age if the fish was caught between January and June; when counting translucent bands, one year was deducted from the age if the fish was caught between July and December. The estimated age was then assigned a decimal age (a_{final}) that accounted for the time elapsed between birth month (*b)* and month of capture (*c*) using the following equation:

$$a_{final} = a_{adj} + (c - b)/12 \quad (1)$$

To test the influence of outliers on the resulting parameter estimates, a sensitivity run analysis was performed by excluding otolith records whose length observations fell beyond 3 standard deviations from the mean for each age (33 records). Additionally, because of the possibility that the size composition of the first few age groups was positively biased by a combination of size selectivity of the fishery (only the largest individuals at age 1 and 2 are caught owing to a minimum size limit of 6.4 kg established in 1975) and timing of capture (all fish ages 1 and 2 were captured in the summer months when growth is thought to be fastest; Supplementary Fig. A2) the growth models were refitted without age groups 1 and 2.

2.3 The AMSFc approach

We used the AMSFc approach of Francis et al. (2016) to analyze the otolith and tagging data simultaneously. This maximum likelihood method has two likelihood components, one for each data source, both of which model length as a function of age. For the tagging data, this entails modeling the joint distribution of the lengths-at-release and –at-recapture (with correlation ρ) as a function of age at tagging (A_{tag}) and time at liberty (Δt). Since A_{tag} is unknown, it is treated as a random effect with an assumed probability distribution whose parameters are estimated in the maximum likelihood framework. For each component, a common growth function is specified to describe the relationship between mean length and age, and variability in length-at-age is defined.

2.4 The growth function

Two growth models were considered to describe the functional relationship between fish length (*L*) and age (*a*): the Richards (1959) model and the von Bertalanffy (1938) model. The von Bertalanffy model was chosen to allow for a direct comparison of the results to the growth curve currently used in the stock assessment (i.e., Restrepo et al., 2010) and the Richards model was chosen for its increased flexibility in fitting data. The Richards function has an additional shape parameter (*p*) that allows it to take on a sigmoidal form. Let A_1 and A_2 be two reference ages (pre-specified by the modeler) with corresponding mean lengths L_1 and L_2, respectively, and *p* be a shape parameter ($p \leq 1$). Then, both models can be expressed as special cases of the Schnute (1981) model, as follows:

$$L_a = f(a; \theta = \{p, K, A_1, A_2, L_1, L_2\}) \tag{2}$$

where,

$$f(a;\theta) = [{L_1}^p + ({L_2}^p - {L_1}^p)\frac{1 - e^{-K(a-A_1)}}{1 - e^{-K(A_2-A_1)}}]^{1/p} \tag{3}$$

While growth models are typically parameterized in terms of L_∞ and t_0 (the theoretical age at size 0), the Schnute model is parameterized in terms of two reference ages, A_1 and A_2, representing the youngest and oldest fish in the sample, respectively. This parameterization reduces the correlation between the estimates of parameters, unlike models parameterized in terms of L_∞ and K, which are otherwise highly correlated. The shape parameter, p, is related to the ratio of the length at the inflection point to the mean asymptotic length (L_∞). When $p = 1$, there is no inflection point and the model reverts to a von Bertalanffy curve. When $p < 1$ it takes on the shape of a Richards curve, with the inflection point moving up along the age-length curve as p decreases. K has units time^{-1}, when an inflection point exists, its inverse, $1/K$, is related to the age associated with the inflection point on the curve. For the von Bertalanffy model, K relates to the rate of approach to the asymptote. Schnute (1981) provides the following equations to obtain L_∞ and t_0 from the parameters of the Schnute model:

$$L_\infty = [\frac{e^{KA_2}{L_2}^p - e^{KA_1}{L_1}^p}{e^{KA_2} - e^{KA_1}}]^{1/p} \tag{4}$$

$$t_0 = A_1 + A_2 - \frac{1}{K}\ln[\frac{e^{KA_2}{L_2}^p - e^{KA_1}{L_1}^p}{{L_2}^p - {L_1}^p}] \tag{5}$$

Variability about the mean length-at-age was modelled as the sum of process error (i.e. true variability around the mean curve resulting from individual variability in growth) and observation error (i.e. resulting from estimated or converted length measurements). As in Aires-da-Silva et al. (2015), true variability around the mean curve (hereafter referred to as "variability in length at age") was defined as a linear function of length with intercept a^* and slope b,

$$\sigma_{L_a} = a^* + bL_a \tag{6}$$

while observation error, σ_{obs}, was defined as,

$$\sigma_{obs} = \sigma_{obs}\, I_i \tag{7}$$

where I_i is an indicator variable that takes on the value 1 if a length record was either estimated or converted from another length/weight measurement and 0 if it was directly measured as straight FL.

2.5 Otolith likelihood

The log-likelihood for the otolith data, $\ln(\lambda_{oto})$, was expressed as the sum of the log-likelihood contributions from each fish. Length-at-age was assumed to be normally distributed with expected length given by (1). To avoid computational problems, the linear relationship of the variability in length-at-age with length (eq. 7) was parameterized in terms of the reference lengths $L_1$and L_2 (estimated by the model), as follows (Schnute and Fournier, 1980):

$$\sigma_{L_a} = \sigma_{L_1} + \left(\sigma_{L_2} - \sigma_{L_1}\right)\frac{E[L_a] - L_1}{L_2 - L_1} + \sigma_{obs}I_i \tag{8}$$

2.6 Tag-recapture likelihood

Lengths-at-tagging and –at-recapture were modeled following a bivariate normal distribution with correlation, ρ. The expected length at age of individual fish was defined by the expected lengths at tagging (L_{tag}) and recapture (L_{rec}), given the unknown age at tagging (A_{tag}) and time spent at liberty between each capture event (Δt) (i.e., $f()$ given in eq.2):

$$E[L_{tag}|A_{tag} = a] = f(A_{tag} = a; \theta) \tag{9.1}$$

$$E[L_{rec}|a + \Delta t] = f(a + \Delta t; \theta) \tag{9.2}$$

The random effects for the age-at-tagging (A_{tag}) were assumed to follow a lognormal distribution with mean ($\mu_{logA_{tag}}$) and standard deviation ($\sigma_{logA_{tag}}$) of A_{tag} estimated on the log scale. The lognormal distribution was chosen because it seemed to provide a reasonable approximation to the distribution of lengths-at-release. Given the small sizes and narrow size range observed in the length-at-release, we expected a relatively linear relationship between length-at-age and length-at-release. As with the otolith data, the standard deviations associated with each length were defined as:

$$\sigma_{L_{tag}} = \sigma_{L_1} + (\sigma_{L_2} - \sigma_{L_1})\frac{E[L_{tag}|a] - L_1}{L_2 - L_1} + \sigma_{obs}I_i \tag{10.1}$$

$$\sigma_{L_{rec}} = \sigma_{L_1} + (\sigma_{L_2} - \sigma_{L_1})\frac{E[L_{rec}|a + \Delta t] - L_1}{L_2 - L_1} + \sigma_{obs}I_i \tag{10.2}$$

As Francis et al. (2016) demonstrated, lengths-at-tagging and –at-recapture are likely to be more highly correlated when time-at-liberty is short (cor(L_{tag},L_{rec}) close to 1), with correlation decreasing with increasing time at liberty. Thus, the correlation coefficient, ρ, was modeled as a simple decreasing function of Δt (Francis et al., 2016):

$$\rho = 1 - \frac{1-\rho_0}{1-\rho_0+\rho_0 e^{(-k_\rho \Delta t)}} \tag{11}$$

where ρ_0 ($0<\rho_0<1$) is the correlation between L_{tag} and L_{rec} when Δt=0, and k_ρ ($k_\rho > 0$) is related to the steepness of the slope defining the relationship between ρ and Δt (the higher the value of k_ρ, the faster the correlation coefficient will decline to zero).

The overall tagging log-likelihood, $\ln(\lambda_{tag})$, was the sum of the bivariate normal log-likelihood of L_{tag} and L_{rec} and the lognormal log-likelihood of the random effects.

2.7 Objective function

The log-likelihoods of the tagging data and otolith data were added together into one objective function to be optimized:

$$\Lambda = \ln(\lambda_{oto}) + \ln(\lambda_{tag}) \tag{12}$$

The optimization was carried out in ADMB-RE (Fournier et al., 2012) using the separable functions feature to reduce memory requirements and computational demand of the random effects (Skaug and Fournier, 2015). The program's default convergence criterion (maximum gradient component < 10-4) was used to evaluate convergence at the optimal solution. Due to differences in sample sizes between the two datasets, the otolith data carried more weight than the tagging data on the overall analysis. A sensitivity run was therefore conducted to test whether down-weighting the influence of the otolith data caused any noticeable changes to the results. The otolith log-likelihood was multiplied by a factor of 0.27, the inverse of the 3.7 times as many otolith records as tagging records.

2.8 Model diagnostics

Goodness of fit was first determined by visual inspection of the data plotted against the fitted curve. For the otolith data, a scatterplot of the standardized residuals was produced to look for any indication of poor model fit. Interpreting the residuals of the tagging component was complicated by the correlation between the lengths-at-tagging and –at-recapture. Instead a comparison was made between the observed lengths-at-recapture and their expected distributions given the parameters estimated in the model. This was done by calculating the conditional cumulative distribution function (c.d.f.) of L_{rec} given L_{tag} and Δt using the following approximation (see Appendix in Francis et al. (2016) for a detailed derivation):

$$F_{L_{rec,i}}\left(L_{rec} \middle| L_{tag} = L_{tag,i}, \Delta t = \Delta t_i\right) \approx \frac{\sum_j \left[F_{L_{rec,i}}\left(L_{rec} \middle| L_{tag} = L_{tag,i}, \Delta t = \Delta t_i, A_{tag} = A_j\right) f_{L_{tag,i}}\left(L_{tag} \middle| A_{tag} = A_j\right) f_{A_{tag}}(A_j)\right]}{\sum_j \left[f_{L_{tag}}\left(L_{tag} \middle| A_{tag} = A_j\right) f_{A_{tag,i}}(A_j)\right]} \tag{13}$$

where F_X denotes the c.d.f. of X, f_X denotes the probability density function (p.d.f.) of X, i refers to individual fish in the dataset, and $\{A_j\}$ is a large set of equally spaced numbers covering the expected range of ages at tagging. If the model fits the tagging data, we would expect the quantiles of the conditional distribution to be evenly distributed over the interval (0,1). A Kolmogorov-Smirnov test was also carried out to formally compare the quantiles with that of a uniform distribution.

Finally, a log likelihood ratio test (with 1 degree of freedom and a significance level of α=0.05) was used to determine whether the addition of the shape parameter in the Richards model provided a significant improvement in fit over the simpler von Bertalanffy model.

3. Results

The two models generally follow similar growth trajectories until age 16 (~250cm FL), with the Richards model predicting slightly larger lengths for fish of ages 7 to 16 compared to the von Bertalanffy model (Table 1; Supplementary Fig. A3). Beyond age 16, the two curves begin to diverge considerably, with the von Bertalanffy model predicting a higher mean asymptotic length (L_∞ = 318.9 cm FL) than the Richards model (L_∞ = 271.0 cm FL) (Supplementary Fig. A3). There were also notable differences in the estimates of variability in length-at-age between the two models: the von Bertalanffy model predicted smaller variability in length-at-age for younger fish (σ_{L_1}= 5.0 < 7.7 cm FL) and higher variability in length-at-age for older fish (σ_{L_2}= 29.1 > 21.0 cm FL), compared with the Richards model. The von Bertalanffy growth curve currently used in the western ABT stock assessment (Restrepo et al., 2010) was very similar to that estimated here (Supplementary Fig. A3).

Visual inspection of the fitted curve against the otolith data (Fig. 1) indicated that the Richards model was a better fit than the von Bertalanffy model. Although the data show evidence of an asymptote, the von Bertalanffy model is not able to adequately capture the bend in the curve (Fig. 1). The scatterplot of residuals (Fig. 2) confirms this. The von Bertalanffy model displays a strong negative pattern in the residuals beyond age 18 (Fig. 2) that is only weakly apparent in the residual plot of the Richards model (beyond age 22; Fig. 2). There is a noticeable lack of very young fish in the otolith data (Fig. 1), and both model fits show a positive trend in the residuals of fish aged 1-3, that is slightly more pronounced in the Richards model (Fig. 2). In the von Bertalanffy fit, there is a negative pattern to the residuals for fish of ages 4-6 followed by a positive pattern in the residuals of fish ages 7-16.

The fit to the tagging data seemed adequate and similar between the two models (Fig. 3). Trajectories of fish with long times at liberty were in agreement with the general trajectory of the growth curve (Fig. 3) and both models estimated similar values for the parameters of the lognormal distribution of the unknown ages at tagging (Table 1, Fig. 4). The few records of fish that were relatively large at the time of release may have been under-aged (Fig. 3) but their influence on the results was negligible since they represented just 1% of the total tagging data sample. The histograms of quantiles of the conditional distribution of $(L_{rec}|L_{tag}, \Delta t)$ (Fig. 5) indicated that the von Bertalanffy model provided a slightly better fit to the tagging data than the Richards model. The differences in fit were a result of fish being assigned slightly younger ages at tagging under the von Bertalanffy model compared to the Richards model. Nonetheless, results from the Kolmogorov-Smirnov tests indicated that both models had some level of misfit since the quantile distributions associated with each model were both significantly different from a uniform distribution (p-value<0.01). These differences in fit between the two models are relatively unimportant when compared to the differences in fits observed in the otolith data. Trends in the otolith residuals resulting from the von Bertalanffy model were indicative of a much greater problem. Results from the likelihood ratio test likewise indicated that the Richards parameterization was a better fit to the data than the simpler von Bertanffy parameterization (p-value<0.001). Therefore, the Richards curve appears to be superior to the von Bertalanffy curve for modelling the growth of western ABT.

Down-weighting the otolith component of the likelihood did not make an appreciable difference in the resulting curve for either model (Supplementary Fig. A4, Table A1). This indicates that the otolith and tagging data are complementary and in agreement with one another. What did change as a result of shifting the weight away from the otolith data were changes in the estimates of variability in length-at-age estimates. The Richards model with down-weighted otolith component estimated smaller variability in length at young ages (σ_{L_1}= 2.03 $\pm$ 0.5 < 7.7 $\pm$ 0.6) and larger variability at older ages (σ_{L_2}= 27.9 $\pm$ 1.2 > σ_{L_2}= 21.0 $\pm$ 0.7) compared to the Richards model without weights (Supplementary Table A1).

The decision to exclude tagging records of fish showing the slowest and fastest 2% growth did not make any appreciable difference to the results (Supplementary Table A1). For the otolith data, the results were not sensitive to the impact of potential outliers, nor were they sensitive to biased samples of fish ages 1 and 2. In both cases, excluding these records changed estimates of K and L_∞ by less than half a percentage point compared with their original values (Supplementary Table A1).

4.Discussion

Growth parameterization for the western stock of Atlantic bluefin tuna was substantially improved by (1) adopting ageing protocols and data filtering criteria that reduced bias in both length increment data and otolith-based ageing, (2) a large and more representative sample of age estimates than existed historically, and (3) application of the AMSFc maximum likelihood approach, which allowed robust weighting of tagging and otolith data (i.e., the results were not sensitive the relative weights placed on the tagging and otolith likelihoods) in their combined use in parameterization of growth models. Further, applying the more general Schnute model fitting approach allowed us to identify past process error associated with adopting the traditional von Bertalanffy model. Because the observation and process errors identified in our study are general to other migratory stocks, we suggest the complement of approaches taken here for the western stock of ABT may serve to improve growth parameterization across a range of exploited species.

Our new assessment of the ICCAT tag recapture data set and improvements to the growth curve indicate that western ABT attain lower mean asymptotic sizes than previously thought. The Richards parameterization of the Schnute model led to a better fit to the data. The shape parameter allowed it more flexibility in fitting to the older ages, resulting in a lower estimate of L_∞ (271.0 cm FL) compared to the von Bertalanffy parameterization (318.9 cm FL). This new estimate of the average size of fish in the oldest age group appears to be in agreement with the range of maximum sizes reported in the literature. In a recent meta-analysis of historical size data, Cort et al. (2013) uncovered a collection of maximum sizes recorded during recreational fisheries competitions that took place between 1870 and 1979, and found record sizes of landed fish ranging from 210 to 320 cm FL (mean=269cm FL; where the 320cm measurement was estimated from weight). Cort et al. (2013) also showed that records of fish with lengths greater than 330cm FL in the ICCAT tagging database did not agree with the accepted length-weight relationship, and were most likely the result of estimation errors or data misrecordings. Looking exclusively at measured lengths, the 20 largest fish present in the database ranged from 246 to 295cm FL. According to the Richards model fit, an estimated variability in size-at-age of 21 cm near the maximum age means we should expect 95% of old fish to reach sizes between 229 and 313 cm FL. This result appears to be a more reasonable finding than that suggested by the von Bertalanffy fit which implies that the oldest fish commonly reach maximum sizes between 261 and 377 cm FL.

Because otolith samples used in our analysis were largely obtained during fishery dependent surveys, they are expected to reflect the selectivity of the fishery from which they were obtained (Kolody et al. 2016; Schueller et al. 2014). Some of this sampling bias may have been lessened by large sample size, particularly in comparison to Restrepo et al. (2010). Still, there was a noticeable lack of very young fish in the otolith data (Fig. 1) that was likely due, in part, to the presence of a minimum weight regulation of 30kg (~115cm FL) in the commercial fishery (in place since 1991) and, in part, to difficulties associated with sampling the recreational fishery. Similarly, the positive trend in the residuals of fish aged 1-3 apparent in both model fits (Fig. 2) could be a reflection of regulations placed on the recreational fishery, which prohibits landing fish <27” curved fork length (~70cm FL). It is also likely to be a reflection of seasonal growth. All samples for fish ages 1-3 were obtained in the summer months (July-October for ages 1 and 2, and May-October for age 3) compared with other ages where, depending on the age, 1-50% of samples were obtained during the winter months (Supplementary Fig. A2). Faster growth in the summer has been recorded in the closely related species of southern bluefin tuna (Eveson et al., 2004) for which seasonality in growth has been modeled, and is thus likely to occur in ABT as well. Since seasonal changes in growth are most prominent in younger ages when fish undergo rapid growth, it is likely that the positive trend in residuals is linked to the clustering of samples age 1 and 2 around months of fastest growth.

Growth parameter estimates play a central role in the stock assessment of western Atlantic bluefin tuna. They are needed to convert historical catch-at-size data into catch-at-age data, using cohort slicing, and to estimate weight at age (ICCAT, 2014). Moreover, estimates of variability in size-at-age could be used to improve the cohort slicing procedure by adjusting the length bounds used to assign ages to individual fish. Preliminary analyses comparing cohort slicing results using growth parameters from the two different models showed that the use of the Richards growth parameter estimates resulted in higher contributions of very young and very old fish in the catch-at-age estimates compared with estimates obtained using von Bertalanffy growth parameters. The extent to which this will have an impact on the evaluation of the stock status is of prime interest and will need to be investigated. Growth parameter estimates are also used to calculate spawning potential ratio and biological reference points.

Though a recent study by Siskey et al. (2016) suggests western ABT may have experienced subtle differences in growth rates during the past four decades, it was unclear how much of the observed changes might be due to fisheries selection or differences in sample coverage between decades (i.e., the relative number of small vs. large fish in the sample). Further investigation into that issue is warranted as using time-varying growth curves may help decrease uncertainty in the catch-at-age estimates used in the assessment, particularly with retrospective approaches such as catch-at-age-analysis. However, until balanced samples for each time period become available (perhaps through data mining of length frequency data), it is best to continue the use a single growth curve in the stock assessment of western ABT that is representative of the time period covered by the assessment as a whole.

Finally, there have been discussions in ICCAT about possibly moving towards a length-based integrated assessment (ICCAT, 2014). If and when that happens, having good estimates of the average length of the oldest age-class in the model (L_2) and variability in size at age will become crucial since these parameters can play an important role in determining management outcomes (Aires-da-Silva et al., 2015; Zhu et al. 2016). The observed differences in mean asymptotic length estimates are also likely to affect assessment results. Having reliable estimates of L_∞ is particularly important for determining stock productivity and associated reference points used for management advice (Aires-da-Silva et al., 2015; Aires-da-Silva and Maunder, 2011) so further investigation should be carried out to determine the importance of such a change.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at ….

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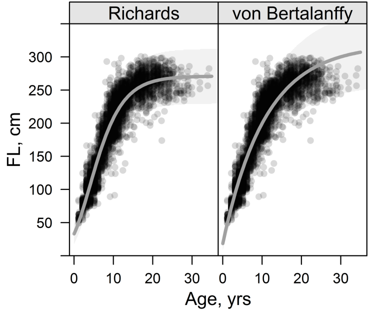
Figure 1. Otolith data plotted against the fitted Richards and von Bertalanffy curves (grey solid lines). In each panel, the shaded area represents the 2.5 and 97.5 percentiles of the distribution of the fitted length at age.

Figure 2. Scatterplot of otolith standardized residuals resulting from the Richards and von Bertalanffy model fits. A loess line (grey solid line) was fitted to the residuals in each panel to investigate trends. For reference, horizontal dotted lines are drawn at 0 and ± 2 standardized residuals.

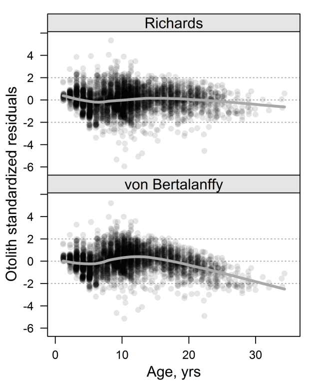
Figure 3. Tagging data plotted against the fitted Richards and von Bertalanffy curves (grey solid lines). Each vector represents the growth trajectory of a fish given its known length at release, length at recapture, time spent at liberty and estimated age at tagging (estimated using empirical Bayes methods). In each panel, the shaded area represents the 2.5 and 97.5 percentiles of the distribution of the fitted length at age.

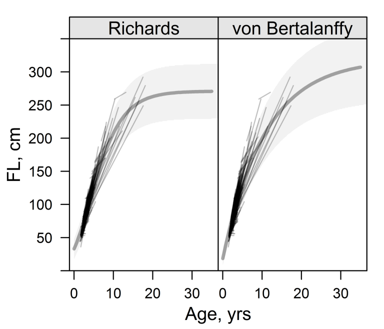
Figure 4. Estimated frequency (histogram) and probability density function (grey solid line) of the lognormal distribution of the random effects for the Richards and the von Bertalanffy models.

Figure 5. Quantiles in distribution of $(L_{rec}|L_{tag},\Delta t)$ for the Richards and von Bertalanffy models. If the data were well fitted, the histogram of quantiles would follow an approximately uniform distribution and lie close to the horizontal dotted line.

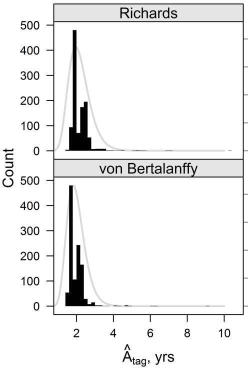


Richards
von Bertalanffy
FL, cm
300
250
200
150
100
50
0
10
20
30
Age, yrs


Richards
von Bertalanffy
Otolith standardized residuals
Age, yrs
4
2
0
-2
-4
-6
10
20
30



Richards
von Bertalanffy
FL, cm
300
250
200
150
100
50
0
10
20
30
Age, yrs


Richards
von Bertalanffy
Count
Density
$\hat{A}_{tag}$, yrs
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
2
4
6
8
10

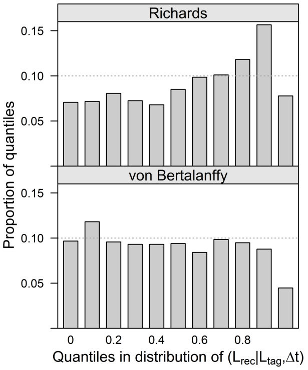

Richards
von Bertalanffy
Proportion of quantiles
0.15
0.10
0.05
0
0.2
0.4
0.6
0.8
Quantiles in distribution of ($L_{rec}|L_{tag},\Delta t$)

Table 1. Maximum likelihood estimates for the parameters of the Richards and von Bertalanffy growth models. Note: the K parameters of the Schnute parameterization of the Richards and von Bertalanffy models have different interpretations (see methods section 2.4).

	Richards (Schnute with p <1)		**Von Bertalanffy** (Schnute with p =1)	
	Value	**S.E.**	**Value**	**S.E.**
Fixed parameters				
A_1	0	-	0	-
A_2	34	-	34	-
p	-	-	1	-
Estimated parameters				
L_1	33.0	0.74	18.5	1.1
L_2	270.6	1.3	305.9	1.8
K	0.22	0.01	0.09	0.002
p	-0.12	0.05	-	-
k_ρ	1.5	0.18	0.97	0.15
ρ_0	0.97	0.01	0.94	0.01
σ_{obs}	3.6	0.46	2.8	0.44
σ_{L_1}	7.7	0.60	5.0	0.66
σ_{L_2}	21.0	0.69	29.1	0.91
$\mu_{logAtag}$	0.74	0.02	0.66	0.02
$\sigma_{logAtag}$	-1.3	0.04	-1.4	0.05
Derived parameters				
L_∞	271.0	1.39	318.9	2.56
t_0	0	-	-0.65	0.05
a^*	5.84	0.69	3.5	0.75
b	0.06	0.004	0.08	0.004
Negative log-likelihood	19597.1		19884.7	