

Estimating age-at-maturity for individual Atlantic bluefin tuna (*Thunnus thynnus*) from back-calculated growth trajectories

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ABSTRACT

We fit a biphasic Lester Model to back-calculated size-at-age data for Atlantic bluefin tuna (*Thunnus thynnus*) captured in the western Atlantic management area that had been genetically assigned to either the western (Gulf of Mexico) or eastern (Mediterranean) spawning stocks. We tested the hypothesis that spawning-stock variation exists in age-at-maturity for this species using a Bayesian approach to incorporate and compare the support for different growth models and maturity scenarios considered for the western spawning stock. The biphasic Lester Model out-performed the uniphasic von Bertalanffy model and showed good fits for describing individual growth variability in Atlantic bluefin tuna. The Lester Model provided estimates of individual age-at-maturity and spawning, from which spawning ogives were generated and compared to two reproductive scenarios currently considered for the western spawning stock; either an early (age at 50 % maturity at 4 years) or late maturity scenario (age at 50 % maturity at 10). The results derived from the Lester Model demonstrate a lack of stock-specific variation in reproductive dynamics for Atlantic bluefin tuna, and provide support for an early maturity scenario for the western spawning stock.

1. Introduction

Understanding growth and reproduction are central focuses of biology and natural resource management. In fisheries, growth and age-at-maturity are important inputs for stock assessment models, which support science advice for making management decisions (Lassen et al., 2001; Methot and Wetzel 2013). Sources of variation in such life-history parameters are often assessed for commercially important fish species, and stock-specific parameters are commonly used when between-population variation is observed. However, significant individual trait variation is common within fish populations as well, and whether the degree of between-individual variability in life-history traits is adequately incorporated into ecological models can affect the success of management strategies (Bolnick et al., 2003, 2011; Ward et al., 2016). Evaluating individual variation in growth and maturity within and between populations should provide strong foundations for science-based management strategies for commercially important fish species.

Life-history trade-offs between somatic growth and reproduction

have motivated increased efforts to incorporate maturity into growth models (Quince et al., 2008a; Mollet et al., 2010; Wilson et al., 2018). The vast majority of studies of vertebrate growth use uniphasic curves such as the von Bertalanffy growth model ("VB"; von Bertalanffy 1938), however, this model is often criticized (Schnute et al., 1981; Maunder et al., 2018). Among the main criticisms of the VB is that it does not incorporate the cost of reproduction at maturation into parameter estimation (Day and Taylor, 1997; Quince et al., 2008a). Several biphasic models have been developed that account for the physiological cost of reproduction and the potential trade-offs among a suite of growth-associated life-history traits (reviewed by Wilson et al., 2018), like the Lester Model (Lester et al., 2004). Biphasic growth models are often premised on the theory that a change in growth occurs at maturation following a redirection of energy from somatic growth during the juvenile phase, toward investment into reproduction following maturation (Charnov et al., 2001; Lester et al., 2004; Minto-Vera et al., 2016). Age-at-maturity (T_m) has therefore been treated as a potential breakpoint in individual growth trajectories in biphasic models and can either be preset in the model if known *a priori*, or estimated by the model

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(Wilson et al., 2018). Biphase models can provide more theory-driven descriptions of somatic growth compared to traditional models while also incorporating intrinsic life-history trade-offs to address uncertainty in T_m for certain species. The goal of the present study was to use a biphase model to address uncertainty in life-history parameters, namely T_m , for a fish species with complex reproductive dynamics.

The Atlantic bluefin tuna (ABFT; *Thunnus thynnus*) is a commercially important fish species for which there is uncertainty concerning the degree of variation in life-history parameters at the stock and individual levels. ABFT are one of the largest teleost fishes, with lengths exceeding 300 cm and weights exceeding 650 kg (COSEWIC, 2011). ABFT lifespan can exceed 30 years (Ailoud et al., 2017) and over that time ABFT will utilize most of the north Atlantic Ocean to satisfy foraging and reproductive requirements which can include sub-polar to sub-tropical habitats (Aarestrup et al., 2022). Historically, spawning site fidelity to the Gulf of Mexico or the Mediterranean Sea was the accepted paradigm, but a spawning ground identified in the Slope Sea and additional electronic tagging data support that ABFT spawning dynamics are more complicated (Richardson et al., 2016; Aalto et al., 2023). ABFT are managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT), which separates the eastern and western Atlantic management areas at a boundary of 45°W. ABFT migrate throughout the Atlantic Ocean and individuals from either spawning stock cross the 45°W boundary, consequently, the stock can be intermittently mixed and catches in either management area can be composed of individuals from either spawning stock (Rooper et al., 2014). Hereafter, we will refer to western and eastern ABFT as those fish that have uniquely western or eastern ancestry (following Puncher et al., 2018, 2022) and who are understood to have hatched and will presumably return to spawn in the Gulf of Mexico or the Mediterranean, respectively.

Uncertainty in life-history-based stock assessment inputs for ABFT is present in terms of both growth (Cort et al., 2018) and reproduction (Farley and Ohshima, 2019). Uncertainty in the life-history parameters of ABFT is partially the result of the complexity of ABFT migratory and stock mixing dynamics and the research challenges created by them. A long-standing component of the management of ABFT has been the idea that individuals belonging to the population that spawns in the Gulf of Mexico mature and spawn at later ages (between 9 – 15 years of age) than those that spawn in the Mediterranean (between 3 – 5 years of age). This characterization, particularly regarding ABFT reproductive dynamics in the western Atlantic, has been questioned based on evidence of spawning outside of these two spawning locations (Richardson et al., 2016; see reviews by Corriero et al., 2020; Medina, 2020). There is a stronger consensus among researchers concerning estimates of T_m for eastern ABFT compared to the western spawning stock. This high confidence in an early T_m for eastern ABFT is in part owing to the extensive sampling of ABFT gonads in the Mediterranean Sea (Medina et al., 2002; Corriero et al., 2005; Medina et al., 2022). T_m of ABFT spawning in the Slope Sea is not yet well understood, although Richardson et al. (2016) argues that it might be a spawning location for young (e.g., ages 4 – 5 years) western Atlantic individuals. However, Aalto et al. (2023) only identified electronic tag-based spawning behaviour in individuals greater than approximately 6 years of age. Currently, the ICCAT eastern management area ABFT stock assessment sets the estimated age at which 50 % of individuals mature at 4 years (Rouyer et al., 2022). The greater uncertainty of T_m for western ABFT in the western management area ABFT stock assessment is reflected by the consideration of two potential maturity scenarios within stock assessment frameworks; an early maturity scenario that matches the maturity ogive of the eastern assessment and a late maturity scenario where age at 50 % maturity is set at approximately 10 years (Tsukahara et al., 2021).

Here, we tested the hypothesis that spawning-stock variation exists in T_m for ABFT, as estimated by a biphase growth model. Given the historical paradigm for stock-level variation in T_m for this species, we predicted that western ABFT T_m would be higher than T_m for the eastern stock. To test this hypothesis, we estimated individual and stock-specific

T_m for western and eastern ABFT from individual back-calculated growth trajectories using the biphase Lester Model. Along with testing this hypothesis, related objectives included: comparing the performance of the Lester Model to the VB results for the same growth data, evaluating how biologically realistic the individual Lester Model life-history parameter estimates were, generating spawning ogives from the individual maturity estimates, and assessing the potential for time-varying growth based on mean growth parameters for a range of cohorts. The results demonstrate the utility of biphase models for addressing uncertainty in reproductive dynamics of a species

2. Methods

Although biphase growth curves with unknown T_m can be fit at the population level, they are best applied to individual growth trajectories (Mollet et al., 2010; Brunel et al., 2013). Mark-recapture data can be used to estimate individual growth parameters (Vincenzi et al., 2020). However, repeated size measurements are difficult to collect throughout the life of an individual for many species and can be subject to error, particularly for species like ABFT (Zhou, 2022). The challenges in obtaining comprehensive growth trajectory data for individuals makes back-calculation based on otolith measurements an attractive alternative to intensive and expensive field programs (Smart and Grammer, 2021). Applying biphase growth models to describe individual back-calculated growth trajectories has the potential to provide estimation of multiple life-history parameters at the individual level.

2.1. Data Collection

Our dataset was a subset of the ABFT data from Stewart et al. (2022). ABFT samples were collected from ABFT that were commercially landed in Atlantic Canadian provinces, including Nova Scotia, Prince Edward Island and Newfoundland and Labrador during 2013 – 2018. Stewart et al. (2022) back-calculated straight fork lengths generated from otolith annuli measurements collected following the most recent standardized ABFT aging methodology (Rodriguez-Marin et al., 2020) for ABFT ranging from ages 15 – 29 years at capture (Fig. 1). In the Stewart et al. (2022) dataset, integer ages were adjusted by adding 0.17 years to each age to represent the time period between the individuals' assumed time at hatch and the timing of opaque band formation. We adjusted this to instead add 0.5 years to each integer age, based on a recent marginal increment analysis which demonstrated that opaque band formation occurs later than previously thought (Rodriguez-Marin et al., 2022).

For the current analysis, a minimum age-at-capture threshold of 15 years was selected to ensure that the potential inflection point in an individuals' growth trajectory associated with T_m would be detectable. We selected individual ABFT that had been genetically assigned to either the eastern or western spawning stock. The genetic assignments came from Puncher et al. (2022), where a panel of 92 single-nucleotide polymorphisms (SNPs) was used to assign individual ABFT to the two main spawning areas. Puncher et al. (2022) based stock-assignments on genetic similarity to larvae and young-of-the-year from either the Gulf of Mexico or the Mediterranean (Puncher et al., 2018), and showed high levels of accuracy in these predictions. We did not include individuals that were assigned to an unknown stock in the Puncher et al. (2022) dataset, since we were primarily concerned with east-west comparisons in growth and maturity.

2.2. Growth Modeling

The purpose of this analysis was first to establish the suitability of a biphase model for describing growth of individual ABFT and then to use the biphase model to estimate individual life-history parameters and compare these parameters between stocks. To accomplish this, we compared the performance of two growth models for estimating individual growth trajectories for ABFT: the uniphase VB and the biphase

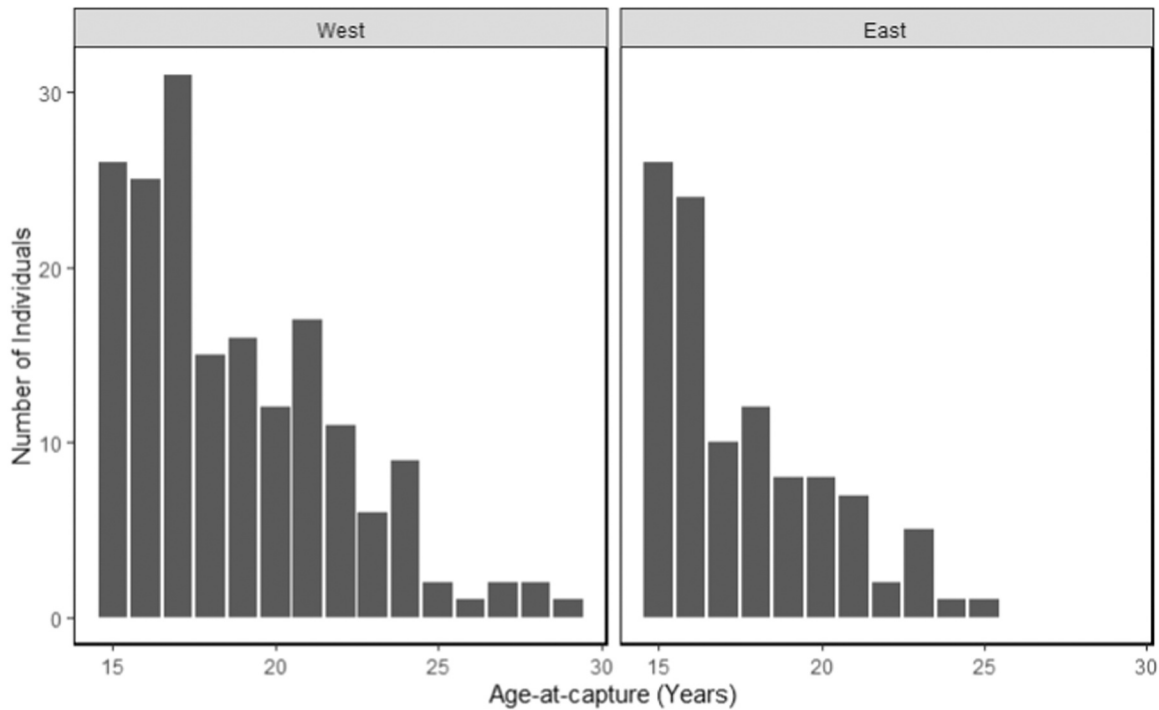


Fig. 1. Age-at-capture distribution for Atlantic bluefin tuna (*Thunnus thynnus*) included in the study that were genetically assigned to either spawning stock.

Lester Model.

We fit hierarchical Bayesian growth models with *runjags* (Denwood, 2016) in R (version 4.0.2; R Core Team 2022). Models were coded in JAGS (Version 4.3.1; Plummer, 2017) following methods described by Wilson et al. (2018) and were designed to estimate and compare individual and stock-specific parameters.

2.3. Definitions and assumptions

We fit formulations of both the VB and Lester Model to compare the performance of a uniphase and biphasic model fit to the same individual growth data. The VB had the following form for estimating straight fork length (cm, hereafter L) at age t (years) for individual i belonging to spawning stock j :

$$L_{ij}(t) = L_{\infty ij} (1 - e^{-K_{ij}(t-t_0)}) \quad (1)$$

where L_{∞} and K , the asymptotic length and the growth coefficient, respectively, were estimated at both the individual and stock levels, and t_0 , the theoretical age where L is 0, was estimated at the global level and fixed at that estimated value across individuals belonging to either spawning stock. The Lester Model was composed of the following equations, the first for describing juvenile growth, and the second for adult growth, using the same notation as above for i and j :

$$L_{ij}(t) = h_{ij}(t - t_1) \text{ when } t \leq T_{mij} \quad (2)$$

$$L_{ij}(t) = L_{\infty ij} (1 - e^{-K_{ij}(t-t_0)}) \text{ when } t > T_{mij} \quad (3)$$

cm change in L per year) is the juvenile growth rate for individual i in stock j , t_1 is the theoretical age where L is 0 for the juvenile growth phase, and T_m is the last immature age (Lester Model parameter for age-at-maturity). Since the adult growth phase is described by the VB growth function, L_{∞} , K and t_0 have the same definitions as in Eq. 1. Similar to the VB, t_1 was estimated at the global level and fixed at that estimated value for all individuals, while all other growth parameters were estimated at both the stock and individual level. Lester et al. (2004) further developed Eqs. 2 and 3 to incorporate trade-offs between growth and reproduction into the estimation of L_{∞} , K and t_0 (see Table 1 for equations),

Table 1

Biphasic Lester Model parameters and bounds fit to back-calculated Atlantic bluefin tuna (*Thunnus thynnus*) growth trajectories.

Estimated parameters			
Parameter	Definition	Prior	Bounds
t_1	Theoretical age where L is 0 for the juvenile growth phase (years)	$N(\mu = -1.0 \text{ years}, \sigma = 0.5 \text{ years})$	$-3 < t_1 < 0$
h	Juvenile growth rate (cm/year)	$N(\mu = 25 \text{ cm}^{-1} \text{ year}, \sigma = 20 \text{ cm}^{-1} \text{ year})$	$0 < h$
T_m	Last immature age (years)	$N(\mu = 5 \text{ years}, \sigma = 3 \text{ years})$	$2 < T_m < 15$
g	Proportional cost to somatic growth of maturation	$N(\mu = 0.21, \sigma = 0.10)$	$0 < g < 3/(T_m - t_1)$
Derived Parameters			
Parameter	Definition	Equation	
L_{∞}	Asymptotic length (cm)	$L_{\infty ij} = \frac{3h_{ij}}{g_{ij}}$	
K	Growth coefficient	$K_{ij} = \ln(1 + \frac{g_{ij}}{3})$	
t_0	Age at length = 0	$t_0 = T_{mij} + \frac{\ln(1 - \frac{g(T_{mij} - t_1)}{3})}{\ln(1 + \frac{g_{ij}}{3})}$	
L_m	Length at age = T_m	$T_{sij} = T_{mij} + 1$	
T_s	Age at spawning		
L_s	Length at age = T_s		

expressing L_{∞} and K as functions of g and h where g is the proportional cost to somatic growth of maturation, which has a mathematical upper limit of $3/(T_m - t_1)$. The Lester model assumes that after ageing beyond T_m , individuals divert energy toward reproduction so that the actual age-at-first spawning (T_s) occurs one year afterward ($T_s = T_m + 1$; Lester et al., 2004).

2.4. Prior justification and model comparison

Normally distributed priors (where μ is the mean and σ is the

standard deviation) for the VB were based on estimates of each parameter from Stewart et al. (2022): $L_{\infty} \sim N(\mu = 300.1 \text{ cm}, \sigma = 25 \text{ cm})$, $K \sim N(\mu = 0.11, \sigma = 0.5)$, and $t_0 \sim N(\mu = -1.0 \text{ years}, \sigma = 0.5 \text{ years})$.

Stock-level priors for the Lester Model were set to test the suitability of different maturity scenarios for ABFT. We used several different T_m priors for the Lester Model in preliminary runs to evaluate their influence on model performance and parameter estimates, including an early and late maturity scenario, in addition to a uniform prior on T_m . We found that all T_m priors that we considered converged on a common posterior mode. Our final T_m prior was $T_m \sim N(\mu = 5, \sigma = 3)$, which represents a middle ground between early and late maturity scenarios for ABFT. Preliminary analysis demonstrated that unrealistically low T_m estimates were estimated for individuals that lacked strongly defined inflections in growth unless a lower limit was set for T_m . We therefore limited posterior T_m estimates to fall between 2–15 years. This ensured that the first year of growth was always described by the juvenile growth equation and that the minimum T_s corresponded with the minimum observed age of mature individuals in the Mediterranean Sea (age 3; Corriero et al., 2005). The upper limit of 15 was selected based on higher T_m estimates for western ABFT (Porch and Hanke, 2018; Diaz et al., 2011). The other priors for the Lester Model were as follows: $h \sim N(\mu = 25 \text{ cm}^{-1} \text{ year}, \sigma = 20 \text{ cm}^{-1} \text{ year})$, $g \sim N(\mu = 0.21, \sigma = 0.10)$, and $t_1 \sim N(\mu = -1.0 \text{ years}, \sigma = 0.5 \text{ years})$. The entire model code is available in Supplemental Material 1.

After a burn-in of 75,000 iterations, the JAGS models were run for 100,000 iterations on 5 parallel chains. A thinning rate of 10 was used, resulting in 50,000 posterior samples from the combined chains. The performance and suitability of the VB and Lester Model were compared using efficient approximate leave-one-out cross validation (*loo*) in the *loo* package in R (Vehtari et al., 2022). The best performing model was determined to be the one which had the lowest expected log pointwise predictive density (ELPD).

2.5. Evaluation of the Lester Model results

We evaluated model performance using several methods. First, we visually inspected trace plots for Markov chain Monte Carlo (MCMC) chain convergence to identify whether independent chains sampled an overlapping, rather than divergent, posterior distribution and that posterior samples were not strongly autocorrelated. We also assessed potential scale reduction factors (PSRF) values for each parameter, where PSRF values < 1.1 indicated that the parameter had converged on a common posterior mode. The fit of the Lester Model was evaluated based on the standardized individual-level residuals of the mean posterior predicted values in relation to the corresponding observed length (back-calculated) and age data. We also used graphical posterior predictive checks to visually assess model performance by identifying posterior predictive samples that fell outside 95 % credible intervals (Wilson et al., 2019).

2.6. Post-hoc examination of individual parameters and spawning ogives

The distribution of individual T_s estimates were evaluated based on boxplots of T_s calculated for each individual from either spawning stock. To estimate spawning ogives, we first calculated T_s for each individual by adding one year to the posterior mean T_m estimates, following Lester et al. (2004). We estimated and plotted spawning ogives from the individual data using the “*Estimate_Age_Maturity*” function in the *AquaticLifeHistory* R package (Smart, 2023), which fits logistic ogives with a binomial error structure. We compared these spawning ogives with the ogives that are currently used in the ICCAT assessments for eastern and western ABFT. The variation in growth parameters through time was visually assessed between cohorts by plotting mean parameter estimates against each cohort year for either stock for cohort-stock groupings with at least 3 individuals. We then tested for potential cohort trends using generalized additive models (GAMs) using 4 knots for each model and

visually examine these trends using the “*geom_smooth*” function in *ggplot2*.

3. Results

Overall, the biphasic Lester Model provided a reasonable model fit to the stock- and individual-level variation in size-at-age and age-at-maturity. Model comparisons based on *loo-cv* indicate that the biphasic Lester Model fit the data better than the VB growth model, with the difference (and standard error) in the ELPD between the Lester Model and VB of $-1104.0 (\pm 78.5)$. MCMC trace plots for the Lester Model indicated that the chains were well mixed for each parameter (Supplemental Material 2) and the PSRFs were < 1.1 for each parameter indicating that model estimates converged on a common posterior mode. The individual-level residuals of the Lester Model were evenly distributed against observed (back-calculated) length and age (Fig. 2).

Graphical posterior predictive checks among individual-level growth curves indicated consistently strong fits to the data (example in Fig. 3, full results in Supplemental Material 3). However, the observed lengths of some individuals in their juvenile growth phase exceeded their 95 % credible intervals (e.g. ages 1 and 2 for individuals 229 and 231 in Fig. 3). Such instances could be attributed to the lack of flexibility caused by fixing t_1 at the individual level, whereas data within the mature phase of the model was almost always within the CIs (Supplemental Material 3).

There was substantial life-history variation among individuals despite no substantial differences among western or eastern ABFT stocks. For example, posterior mean estimates for h (juvenile growth rate) and g (proportion of energy allocated to reproduction) among all individuals was $30.13 \text{ cm} \cdot \text{year}^{-1}$ (range: $22.23 - 45.20 \text{ cm} \cdot \text{year}^{-1}$) and $0.28 (0.14 - 0.42)$, respectively (Fig. 4). Posterior mean estimates for T_s ranged between $3.05 - 10.24$ years among individuals, with the overall individual posterior mean being approximately 4 years for each stock (4.23 and 4.13 for western and eastern individuals, respectively; Fig. 4). In general, the stock-specific estimates of T_m did not indicate major differences in the growth-associated life-history traits between eastern (Mediterranean) or western (Gulf of Mexico) stocks (Table 2). For example, posterior mean estimates of T_m at the stock-level were 2.10 ± 0.091 and 2.13 ± 0.120 for ABFT from western and eastern stocks, respectively (Table 2). Both posterior mean stock-specific T_m estimates were therefore near the lower bound of 2 years that was established based on observations of spawning individuals in the Mediterranean (Corriero et al., 2005). The posterior mean estimates for stock-specific h and g and the corresponding stock-specific growth curves were also very similar between stocks (Table 2; Fig. 5).

Furthermore, the estimated spawning ogives for eastern and western individual ABFT were very similar (Fig. 6). Age at 50 % and 95 % spawning (and standard errors) were estimated as 4.31 ± 0.06 years and 6.12 ± 0.11 years for western ABFT individuals, and 4.23 ± 0.07 and 5.74 ± 0.13 years for eastern individuals, respectively. L_s ranged between approximately $72 - 226 \text{ cm}$, however, most of the data were concentrated between $100 - 150 \text{ cm}$ (Fig. 5). L_{∞} estimates were slightly higher than expected for some individuals, with L_{∞} ranging between $231 - 481 \text{ cm}$. We caution that some individuals had unrealistically high estimates for L_{∞} ; however, most estimates were between approximately $300 - 330 \text{ cm}$ (Fig. 4).

Potential cohort-specific variation in growth parameters estimated by the Lester Model was assessed post-hoc by evaluating trends in posterior mean parameters for individuals among cohorts and stock (for cohort-stock groupings with at least 5 individuals). Observed and estimated life-history traits for each cohort between 1989–2003 were fit with a GAM to visually assess potential trends (Fig. 7). For western cohorts, L_{∞} gradually increased from 1989–1994 before levelling off at approximately 325 cm . There was a general decline in T_s for western cohorts between 1989 and 2003, from nearly 5 years to less than 4 years on average. For western cohorts, h generally increased from 1989 until

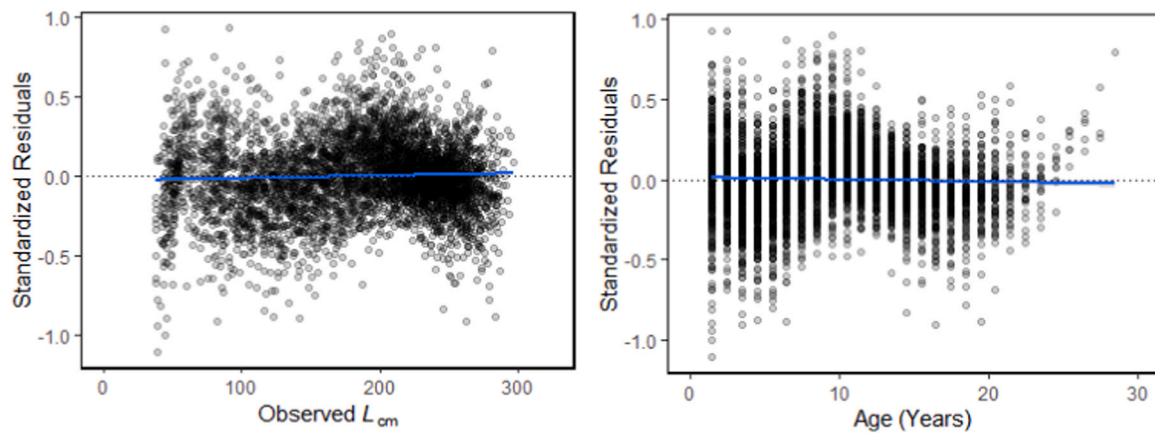


Fig. 2. Lester Model standardized individual-level residuals plotted against observed (back-calculated) length, and age of Atlantic bluefin tuna individuals ($n = 280$). The blue line on each plot was fit with a linear regression using the “geom_smooth” function in *ggplot2*.

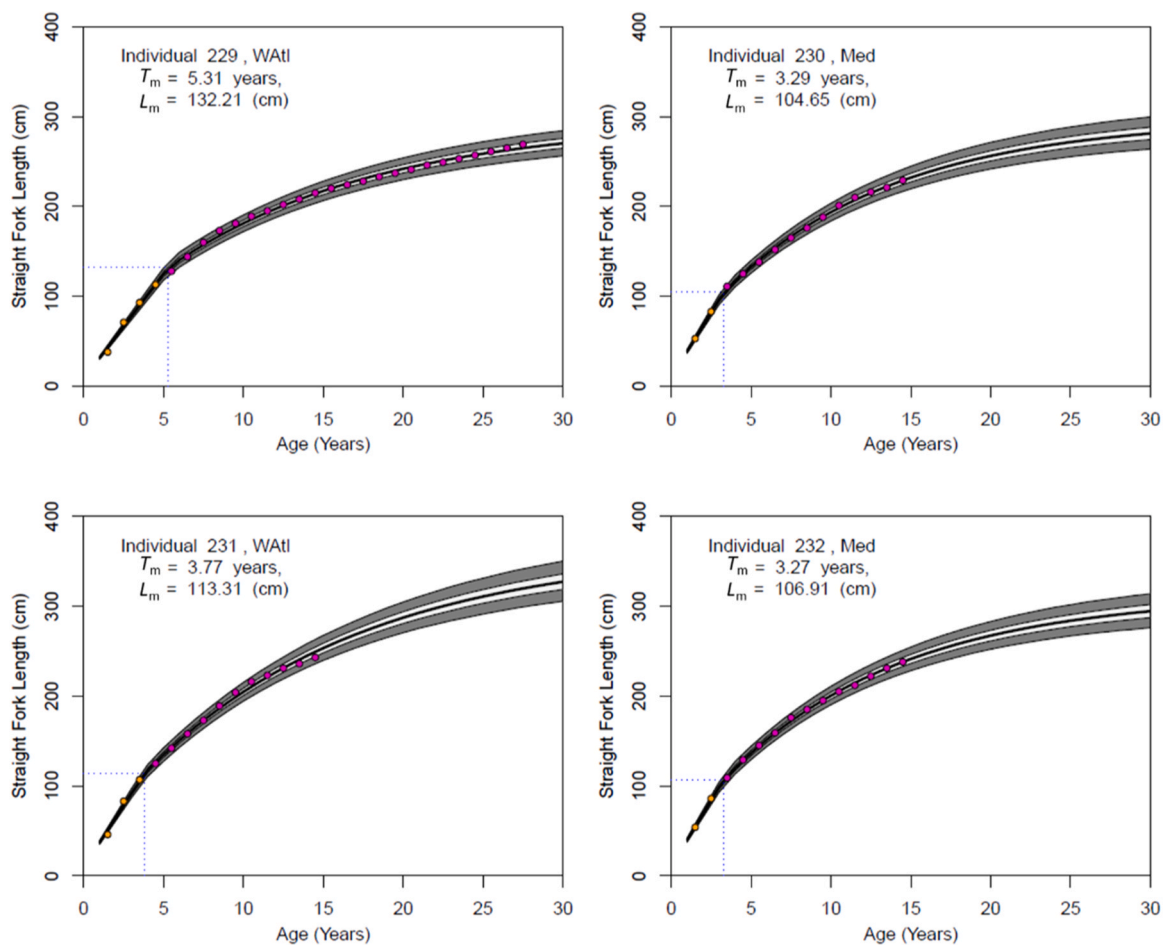


Fig. 3. Examples of Lester Model posterior-predictive check results for four individual Atlantic bluefin tuna; two from either spawning stock. Individual lengths at age were generated through back-calculation. Immature lengths-at-ages below the individuals posterior median T_m are orange and those above are purple. T_m and corresponding L_m are indicated by dotted vertical and horizontal lines, respectively.

1998, after which h tended to decline. For the western ABFT cohorts, g fluctuated near 0.28, with a peak of approximately 0.30 for the 1998 cohort (Fig. 7). Fewer cohorts were represented for eastern ABFT, so potential temporal trends in growth parameters were less clear. Both h and g were strongly positively correlated (Supplemental Material 4). Since individual g and L_∞ were fairly strongly negatively correlated, the results suggest that as ABFT investment in reproduction increased, the

maximum size of fish decreased. Estimation of g may be driving the individual growth curve estimation, given that g was correlated with both h and T_m (Supplemental Material 4).

4. Discussion

This study provides estimates for the age- and length-at-maturity of

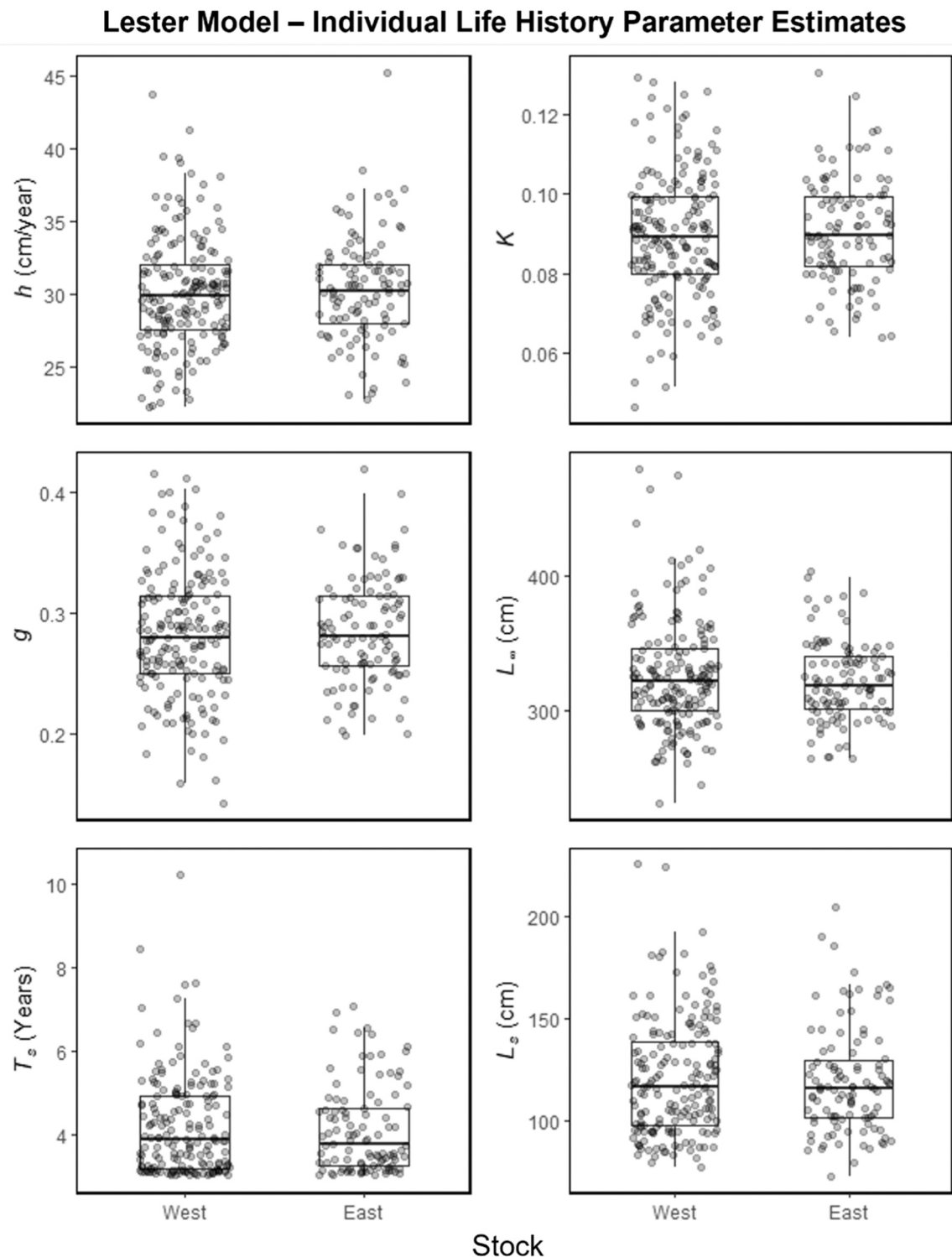


Fig. 4. Boxplots showing the 25th, 50th and 75th quantiles of median posterior individual parameter estimates derived from a Lester Model fit to back-calculated length-at-age data for Atlantic bluefin tuna (*Thunnus thynnus*; $n = 280$ individuals). T_s values were derived from individual posterior estimates of $T_m + 1$ year.

individual ABFT from two genetically distinct spawning stocks through an analysis of back-calculated length-at-age data. The hypothesis that spawning-stock variation exists in T_m for ABFT was not supported by the results of the current study, nor was our prediction that T_m would be greater for western compared to eastern-origin ABFT. Overall, posterior distributions of T_m were similar for ABFT individuals genetically assigned to either spawning stock at both at the stock and individual levels (Table 2, Fig. 4). Previous analysis has demonstrated a lack of

difference in growth parameters between individuals genetically assigned to either spawning stock (Stewart et al., 2022) and other authors have suggested that reproduction and maturation dynamics might be more similar between western and eastern ABFT than previously thought (Richardson et al., 2016; Corriero et al., 2020; Medina, 2020). Our study adds to a body of work concerning western ABFT reproductive biology that draws on different methodologies and provides different estimates of the minimum age- and length-at-maturity and spawning for

Table 2

Posterior median and 95% credible intervals for stock-level parameter estimates for fixed effects in the biphasic Lester Model.

Parameter	Mean	SD	2.50 %	50 %	97.50 %
T_m (West)	2.10	0.091	2.00	2.08	2.34
T_m (East)	2.13	0.120	2.00	2.10	2.45
h (West)	30.06	0.271	29.53	30.06	30.60
h (East)	30.45	0.630	29.24	30.45	31.69
g (West)	0.28	0.004	0.27	0.28	0.29
g (East)	0.30	0.008	0.29	0.30	0.32
t_1	-0.22	0.008	-0.24	-0.22	-0.21

ABFT in the western Atlantic.

The results of the current study support individual age-at-first spawning ranging from approximately ages 3 – 10 years and 3 – 7 years for the western and eastern stocks, respectively, with medians of approximately 4 years for both stocks (Fig. 4). This corresponds to a length-at-first spawning (L_s) ranging from approximately 70 – 225 cm across both stocks and a median of approximately 116 cm (Fig. 4). The extremes of the range in L_s are likely unrealistic given that the smallest documented ripe male and female ABFT recently caught in the Mediterranean were 117 and 119 cm SFL (Medina et al., 2022). The quantiles of L_s indicate that 50 % of individual L_s estimates fell between 99 – 137 cm, which represent a more realistic range of estimates for first spawning events based on spawning data for ABFT in the Mediterranean (Corriero et al., 2005; Medina et al., 2022). These results rely on the strength of the model fit to the back-calculated growth trajectories, the similarity of the estimated spawning ogive to that of the eastern-stock spawning in the Mediterranean (Corriero et al., 2005) and the results of previous studies that provide evidence for an early maturity scenario for western ABFT (Baglin, 1976; Heinisch et al., 2014). We will discuss each of these factors in the consideration of ABFT spawning dynamics in the western Atlantic as well as limitations of our approach and future tests of the proposed spawning ogives.

4.1. Support for the biphasic model

The biphasic Lester Model provided better fitting estimates of individual growth trajectories than the uniphasic VB for ABFT. The suitability of the biphasic model was supported based on the results of a *loo* comparison, where the Lester Model outperformed the VB. There have been mixed conclusions across previous studies concerning whether ABFT and other *Thunnus* species' growth is best modeled by biphasic or uniphasic curves. Hearn and Polacheck (2003) report that the

length-at-age relationship for southern bluefin tuna (*Thunnus maccoyii*) was best described by biphasic curves compared to a traditional uniphasic VB. The authors attributed such a shift in growth to changes in foraging behaviour of juvenile versus mature southern bluefin tuna, although they also note that maturity is associated with a significant change in energy expenditure that could account for changes in growth (Hearn and Polacheck, 2003). Additional explanations for biphasic growth in fishes are summarized by Wilson et al. (2018), including ontogenetic or habitat-related shifts in growth. Wang et al. (2017) modeled Pacific bluefin tuna (*Thunnus orientalis*) growth using the biphasic model provided by Quince et al. (2008a,b), assuming that juvenile growth is linear and adult growth can be modeled using a VB curve. Ailloud et al. (2014), however, evaluated residuals for growth estimated from tagging data for ABFT and concluded that there was no evidence in support of biphasic growth. More recently, a morphological analysis identified a breakpoint in the length-weight relationship for ABFT that was best described using a biphasic model (Bello et al., 2021), which was attributed to a maturity-related diversion of resources toward physiological preparation for spawning. In the case of the current study, the strong performance of the Lester Model likely involved its increased flexibility to account for individual variability in growth trajectories for ABFT. Some individuals showed strong inflection points (e.g., individuals 9, 11 and 12), while some other individual trajectories could be better described entirely by a VB curve (e.g., individuals 1, 3 and 4), leading to an estimate of T_m that hit the lower threshold of our allowable range (approximately 2 years).

An important assumption in our inferences concerning spawning dynamics for ABFT is the link between an inflection in growth and maturity, followed by spawning, as theorized by Lester et al. (2004). Such a link has been well-developed theoretically (Quince et al., 2008a; Wilson et al., 2018) and supported empirically (Quince et al., 2008b). Our results indicate that such a shift happens for most individual ABFT between ages 2 – 4, corresponding to first spawning events at ages 3 – 5 (Fig. 4), using the addition of 1 year between maturation and spawning proposed by Lester et al. (2004).

The Lester Model is useful in providing not only T_m information, but also information on a number of biological characteristics of an individual's growth, including juvenile growth rate, investment in reproduction, and VB growth parameters (Tables 1, 2; Fig. 5). The relationships between these features highlight trade-offs between the cost of reproduction, fecundity and individual fitness (Lester et al., 2004). The relationships between g , h , L_∞ and T_m observed in this study indicate that ABFT that mature at younger ages also have the fastest juvenile

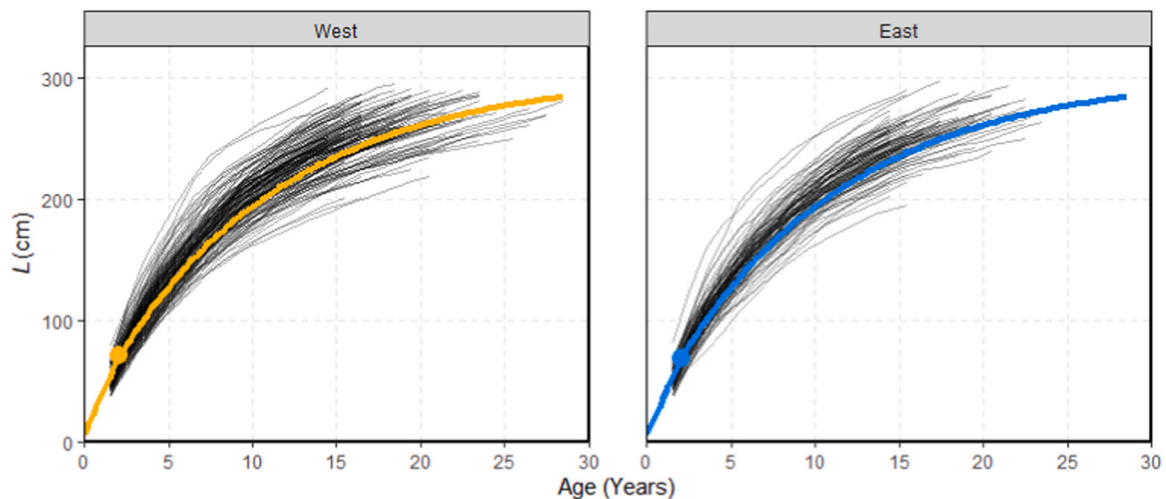


Fig. 5. Posterior median stock-level Lester Model growth curves for Atlantic bluefin tuna genetically assigned to either the western ($n = 176$) or eastern ($n = 104$) spawning stocks. Individual back-calculated growth trajectories are shown underneath the growth curves, and median stock-level age-at-maturity estimates from the biphasic model are shown as single dots.

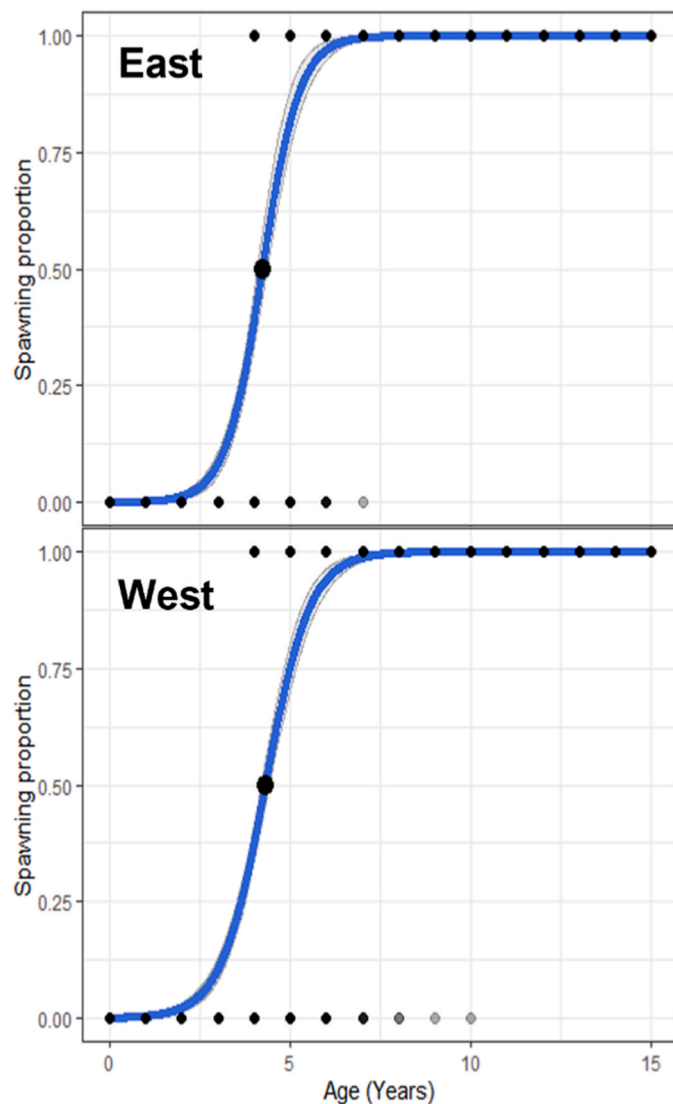


Fig. 6. Spawning ogives based on posterior median individual estimates of age-at-spawning for Atlantic bluefin tuna (*Thunnus thynnus*) based on a Lester Model.

growth rates and invest more energy in reproduction, resulting in lower maximum size. These observations are consistent with life-history theory (Hutchings, 2021) and open the door to further work exploring the degree to which genetic and environmental factors drive these relationships. Trends in the mean individual estimates of the Lester Model parameters for cohort years suggests a significant time-varying component to the dynamics of the population that should be considered in projections of stock biomass under alternative harvest scenarios. Identifying the functional relationship between the variability in these parameters and environmental variables will allow for a more realistic modeling of the effects of these factors on stock dynamics and will help to support management advice conditioned on the predicted future trends of the environment.

4.2. Comparison of spawning estimates to other studies

The results from the biphasic model indicate that the spawning ogives of individual ABFT of western and eastern origin are similar (Fig. 6). The estimated spawning ogive for individuals genetically assigned to the eastern stock closely matches the ogive used by ICCAT for describing the maturity of the eastern stock (Rouyer et al., 2022),

which was based on gonad analysis of individuals aged 3 – 5 years (examined individuals between 60 – 270 cm caught in the Mediterranean; Corriero et al., 2005). The similarity between our results and the well-supported spawning ogive for eastern ABFT supports the estimates derived from the biphasic Lester Model.

The correspondence of the eastern ABFT ogives developed from samples from opposite sides of the Atlantic Ocean informs on their complex life history. Other authors have suggested, based on tagging and otolith data, that there is a tendency for younger eastern ABFT to spend several years in the western Atlantic before returning to the Mediterranean Sea around age 9 (Rooker et al., 2008; Teo and Boustany, 2016). Our dataset includes individuals older than 15 years (maximum age 25) that were caught in the western Atlantic and assigned to the eastern stock that spawned between ages 3 and 7, based on the Lester Model estimates. The spawning locations of these individuals is unknown. Increased electronic tagging efforts with long-lasting multi-year tags for individuals of a greater size range is needed to explain the life-history of older eastern-origin ABFT caught in the western Atlantic.

While it is likely that ABFT with a common ancestry have similar T_m , it is not obvious where the spawning occurs in each year of their life. The age-at-maturity and spawning estimates derived from the growth trajectories of older eastern-origin ABFT individuals could be a product of spawning events in the Mediterranean, the Slope Sea or other ‘alternative’ spawning grounds. Richardson et al. (2016) provide evidence of ABFT spawning in the Slope Sea based on the presence of ABFT larvae and argue that the area might serve as a spawning ground for younger ABFT (ages 4 – 5, corresponding to lengths of 120 – 140 cm), and suggest that ABFT may exhibit size-segregated spawning similar to Pacific bluefin tuna (Itoh, 2006). The argument made by Richardson et al. (2016) for the Slope Sea as a spawning ground for young ABFT was based on catch data demonstrating that small individuals occupy this area during periods when ocean conditions are suitable for spawning. Spawning by young (< age 5) ABFT in the Slope Sea was previously supported by evidence of ripe male and female ABFT caught in the area during a research cruise in 1957 (Baglin, 1976; Mather et al., 1995). Heinisch et al. (2014) demonstrated that ABFT > 134 cm in length had hormonal profiles characteristic of sexual maturity; however, they lacked hormonal data for individuals between 38 – 134 to establish a minimum length at which hormonal profiles indicate maturity in the western Atlantic. More recently, Aalto et al. (2023) assessed electronic-tag-based depth profiles of 250 ABFT between 95 – 313 cm, and identified potential Slope Sea spawning behaviour in 24 individuals between 165 cm – 284 cm in length. Aalto et al. (2023) note that their tagging efforts were biased toward larger ABFT, however, overall they state that their results do not provide evidence of spawning in the Slope Sea at such young ages as those argued for by Richardson et al. (2016). Our results are therefore in greater agreement with the younger maturity scenario for ABFT in the western Atlantic provided by Richardson et al. (2016).

The maturity and spawning estimates for the western ABFT stock in the current study contrast with previous studies that were based on catch data from the Gulf of Mexico which estimated the fraction spawning to be 50 % by age 10–12 with 10 % spawning at ages 6–9 (Diaz, 2011; Porch and Hanke, 2018). The landings data on which the contrasting estimates are based indicate that ABFT less than 120 cm or younger than age 8 do not appear in the Gulf of Mexico landings of either Japan, Mexico or the USA, and consequently could not support large spawning fractions at younger ages. These landings data and subsequent analyses may be subject to gear selectivity as well as the spatial and temporal extent of the fishing activity relative to spawning location. Basing western ABFT spawning ogives on only Gulf of Mexico catch data may also be flawed due to the potential for size segregated spawning of ABFT (as argued for by Richardson et al., 2016).

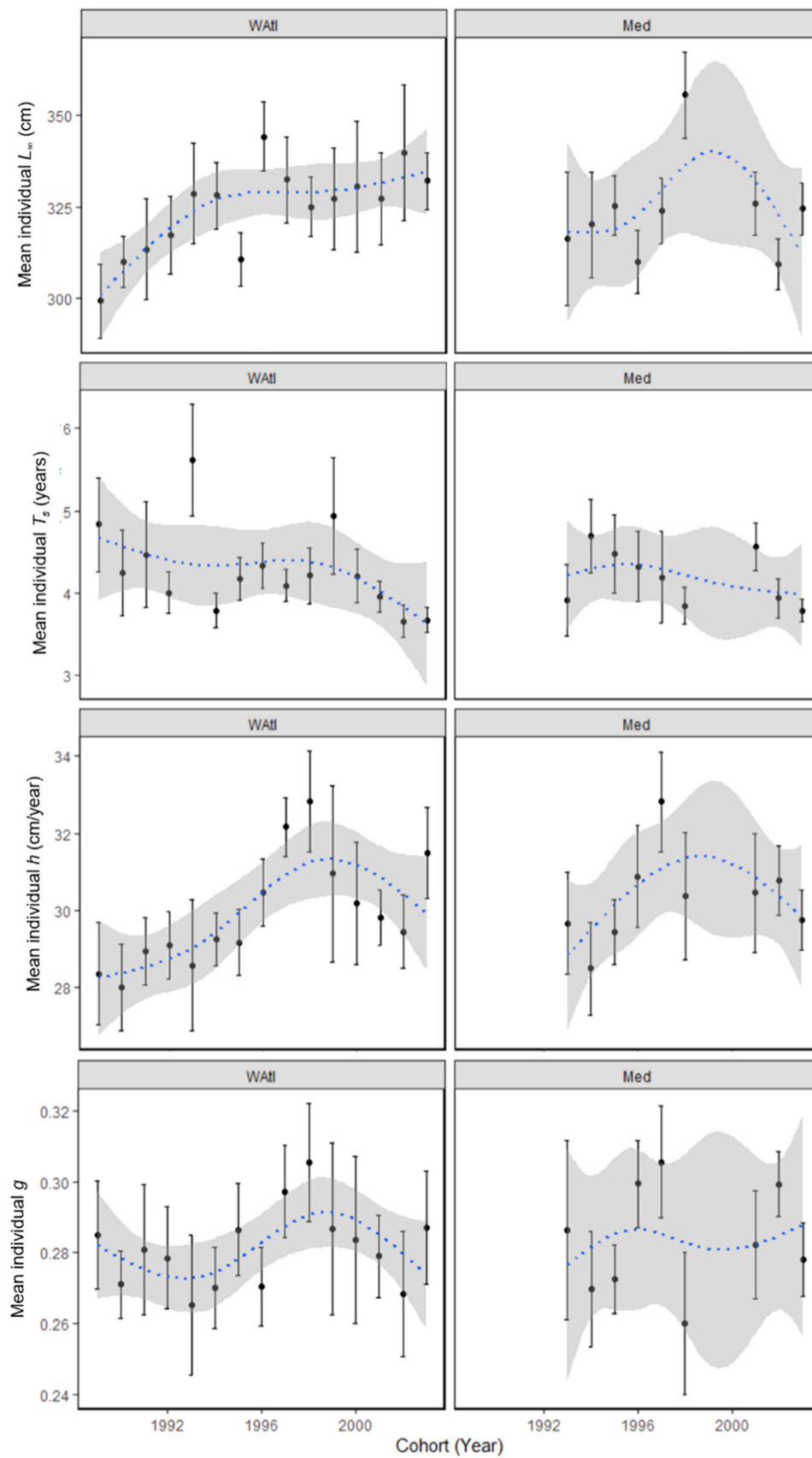


Fig. 7. Cohort-specific means and standard errors for Atlantic bluefin tuna (*Thunnus thynnus*) life history traits estimated by a biphasic growth model for individuals from two distinct spawning stocks. Points represent median posterior estimates for asymptotic length (L_{∞}), age at spawning (T_s), juvenile growth rate (h) and investment in reproduction (g). The dotted blue line on each plot was fit with a generalized additive model (GAM) using the “geom_smooth” function in *ggplot2*.

4.3. Limitations and Next Steps

In the current study, we used a somatic growth model based on life history theory to derive estimates of maturity and spawning for ABFT belonging to genetically distinct spawning stocks. This work relies on the validity of the stock-of-origin assignments using SNPs (Puncher et al., 2018; 2022). Future applications of biphasic modeling approaches for this species could instead use otolith stable isotope based geographic-origin assignments, or newly developed genetic markers of origin, since the complexities of stock-mixing and ancestry in ABFT is an ongoing area of research.

Analysis of growth increments, collected either from tag-recapture or otolith-based measurements, has supported multiple studies on ABFT (Santamaria et al., 2009; Ailloud et al., 2017; Stewart et al., 2022; Zhou, 2022). While back-calculation is highly useful in expanding size-at-age datasets, there are important potential sources of error in back-calculation, such as improperly applied back-calculation functions or Lee's Phenomenon (Francis, 1990). The back-calculation dataset used in the current study was validated using a within-cohort comparison of observed and back-calculated lengths-at-age to increase confidence in estimated lengths at earlier ages (Stewart et al., 2022). Incremental growth analysis for ABFT could continue to be facilitated by routine data collection if annuli measurement is incorporated into aging protocols, such as those described by Rodriguez-Marin et al. (2020). Linking growth increments to annual environmental variables would be highly informative for predicting future growth, and other life-history characteristics, of ABFT under different climate change scenarios. While the results of the current study support the younger age-at-maturity scenario for ABFT in the western Atlantic, we acknowledge that this important aspect of ABFT biology will be best resolved through future collections of gonad samples from smaller ABFT caught in the northwest Atlantic for empirical analysis of reproductive dynamics.

5. Conclusions

The individual and stock-level ABFT maturity and spawning estimates are inferences based on a modeling approach applied to back-calculated length-at-age data rather than direct histological examination of gonads from fish collected at a range of ages and months of the year. However, the statistical approach applied here has the advantage of having fewer issues associated with the logistical challenges of sampling all ABFT life stages, particularly those within the range of potential lengths at first maturity (e.g., ages 2–4 years). However, regardless of the approach, it should be emphasized that evidence of maturation does not strictly demonstrate that an individual ABFT has contributed to stock productivity through spawning (Farley and Ohshimo, 2019). Consequently, some consideration should be given to quantifying the appropriate length of time to allow between maturation and spawning estimated and inferred from the growth model.

The results presented here add to the body of evidence for understanding the complex life-history dynamics of ABFT and support the early maturity scenario currently considered for ABFT within the stock-assessment framework used by ICCAT. Establishing that the spawning ogives for the eastern and western ABFT stocks are similar would also greatly simplify the management strategy evaluation (MSE) process which is currently being used to generate total allowable catch (TAC) advice by reducing the number of known uncertainties. Validation of the conclusions of this study will depend on the outcomes of ongoing research projects for western ABFT, such as increased efforts to collect gonad tissue samples from younger ABFT females landed in Atlantic Canadian provinces for analysis of atretic follicles indicative of past spawning events. An additional test of the validity of the proposed spawning ogives will come from the close-kin-mark-recapture (CKMR) program for western ABFT, which is aimed at estimating population size of the western stock via genetic identification of parent-offspring pairs (McDowell et al., 2022). While still in its early stages, the CKMR

program has the potential to link western ABFT larvae with young spawners (e.g., ages 3–5 years). Finding such young parents depends on expanding the scope of the ABFT larval sampling to beyond the Gulf of Mexico, which appears to primarily provide grounds for large spawners (Porch and Hanke, 2018). Increased ABFT larval sampling in the Slope Sea may yield such pairs if the hypothesis that this region supports the spawning of smaller western ABFT is accurate. The modeling approach that we applied here to back-calculated data is powerful and can be used to examine trade-offs between reproduction and somatic growth, as well as estimating individual age-at-first-spawning, for other commercially and ecologically important fish species.

CRediT authorship contribution statement

Alex Hanke: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Kyle Wilson:** Writing – review & editing, Writing – original draft, Supervision, Methodology. **Nathan Stewart:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2024.107102.

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