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GROWTH OF ATLANTIC BLUEFIN TUNA: DIRECT AGE ESTIMATES

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SUMMARY

New models were fit for recent samples of Atlantic bluefin tuna on the basis of annulus interpretations in otoliths. Samples were specified further based upon whether individuals originated in western or eastern nursery systems using otolith stable isotope analysis. A model fit to recent year-classes (after 1970) for western captured, western-origin Atlantic bluefin tuna yielded von Bertalanffy coefficients of K=0.20; L_∞*=257; and* t_0*=0.83. These coefficients are substantially different than those from the Turner and Restrepo model (K=0.08;* L_∞*=382;* t_0*= -0.71), and predicts lengths at age which are similar to about age 12, but increasingly divergent at greater ages. Growth models were also fit for the eastern population, but coefficients were probably biased due to the small sample size. Given the established accuracy of direct age estimates from otoliths and the feasibility of complementary age and natal assignment determinations using the same prepared otoliths, we recommend future assessments be based upon direct ageing of otoliths over other approaches.*

KEYWORDS

Age Composition, Life History, Migration, Otoliths, Tuna Fisheries, Thunnus thynnus

Introduction

Here we provide von Bertalanffy growth models for Atlantic bluefin tuna based upon enumerating annuli in otoliths. Early efforts to provide such estimates (Hurley and Iles 1983) showed that interpretation of annuli in sectioned sagittal otoliths could be precise and lead to realistic growth estimates. Still, the central assumption that annulus counts were equivalent to age could not be validated at the time, which curtailed application of a direct ageing approach. For western Atlantic bluefin tuna (the main focus of this report), Turner et al. (1991) utilized tag-recapture estimates of growth increments to estimate L_∞, and K; and juvenile length frequency analysis (ages <3 years), which allowed the growth model to be scaled to t_0. For eastern Atlantic bluefin tuna, models were fit using direct age estimates from dorsal fin spines (Cort 1991), accepting the assumption of yearly annulus formation.

Three important scientific developments now permit improved estimates of age and growth for Atlantic bluefin tunas: (1) A manual on Atlantic bluefin tuna ageing methods was published by ICCAT, resulting in standard methods in otolith preparation and interpretation (Rodriguez-Marin et al. 2006). The ICCAT Direct Ageing Group that produced this manual also undertook increased sampling for otoliths throughout Europe. (2) A recent study on bomb radiocarbon dating of archived bluefin tuna otoliths provided strong evidence for yearly annulus formation, particularly in support of longevity estimates for the giant category (>205 curved fork length CFL) of bluefin tuna (Neilson and Campana 2006; in review). The same team that undertook this study developed an otolith reader set: a collection of otolith images calibrated against known age bluefin tuna and electronically annotated with annulus assignments.

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The reader set serves as a reference against which other investigators can evaluate accuracy. (3) Stable isotope ($\delta^{18}O$) composition of otoliths serves as a natural tag of natal origin for Atlantic bluefin tuna (Rooker et al. 2007). Composition can be measured in the otolith corresponding to the first year of life through micro-milling procedures, preserving the remaining otolith structure for ageing. This can allow an individual to be aged *and* assigned to its natal origin, reducing bias in population-specific growth models when stock mixing occurs.

Growth models were developed for sets of archived otoliths from US and Mediterranean fisheries on the basis of region of capture and natal population. We contrast model fits with those reported using other approaches.

Methods

Otolith preparation and interpretation procedures followed the standardized procedures adopted by the Direct Ageing Group (Rodriguez-Marin et al. 2006). Plastic-embedded sagittal otoliths were sectioned along the transverse plane that contained the core region (i.e., the volume circumscribing the first year of life). Stable isotope composition analysis required section thickness to be 1.5 mm for milling purposes. Micromilling within the region circumscribed by the first annulus occurred to 0.7 mm depth. Following the micro-milling procedure, otolith regions outside the first annulus were hand-polished with a lapping wheel (Secor et al. 1991), reducing the section thickness to 0.5-0.7 mm. In this way the same otolith used for population assignment could be subsequently interpreted for age determination.

Images were taken using an Olympus SZX12 stereoscope with transmitted light and an Olympus Camedia C-5050 digital camera (5 megapixal resolution). Blind counts of annuli were taken twice from the images using Adobe Photoshop CS2 Version 9.0. When counts differed by <2 years, the second count was accepted. When counts differed by >2 years (12% of overall sample), the image was inspected a third time along with the two previous annulus assignments.

A reader set of otoliths was provided by Fisheries and Oceans Canada (referred to subsequently as DFO by JDN and SEC) for calibration purposes. As indicated above this set was compared to bomb radiocarbon dates from Neilson and Campana (in review). The expected accuracy of this type of validation is 1-3 yrs (Campana 2001). The set included 29 digital images of otolith sections viewed under reflected light of principally giant category bluefin tuna (CFL>205 cm), but included three individuals 120-155 cm CFL. We randomly selected four images as a trainer set and retained the remaining images for a single blind test of accuracy. In the training exercise, the two investigators (DHS, RLW) from the University of Maryland (UM) tested their interpretations of individual annuli against interpretations by three experienced readers from Canada, Greece and Australia (projected as individual overlaid annotated images; see Figure 1). Once experience had been gained using the training set on interpretations of individual annuli, a single reader from UM undertook interpretations of the reader set (n=25) without reference to interpretations by other readers. The single blind trial showed slight but significant bias in UM interpretations. In comparison to experienced readers, negative biases ("under-counts") by UM readers were estimated to range between -1.1 to -2.3 years. This level of bias was slightly higher than the level of disagreement observed between experienced readers, which ranged from -0.6 to -1.2. In plots of UM versus experienced reader counts (Figure 2), deviations from the one-to-one slope indicated that the bias was greatest for the oldest individuals (>12 annuli). To adjust for this bias, we applied a correction for estimated ages > 12 years, based upon a regression of UM ages on the ages of the primary reader (Corrected Age = -3.0 + 1.288 (UM Age)). Patterns in the residuals indicated a linear fit ($R^2=0.89$) with no trends with increasing annulus number. This adjustment made to reconcile ages between UM and the reader set had relatively minor effects on fitted growth coefficients.

Samples

Most samples came from NOAA Fisheries sampling of US rod and reel catches during the late 1990s (the Large Pelagic Biological Survey), and recent directed sampling efforts by DHS and JRR in the Gulf of Maine and Spain (Table 1). In most instances, CFL was directly measured in cm but in some instances, conversions from total length or snout length measures were necessary. We emphasize our analysis of western-captured bluefin tuna because the aged Mediterranean sample size remains small. Estimated year-classes ranged from 1969 to 1999 (Table 1; Figure 3). US recreational fishery samples in addition to giant-category fish collected from Gulf of Maine commercial fisheries permitted us to fit growth models across most of the bluefin tuna's life span. Still, our youngest age estimates of bluefin tuna were four yearsand our oldest age estimate (33 years) was less than the maximum age estimated by Hurley and Iles (1983).

Natal population assignment was based upon otolith δ^{18}O composition corresponding to the first year of life. Some overlap between western and eastern population exists that can be resolved in assigning fractions of either group to a sample using stock a mixing algorithm (Rooker et al. in review), but such algorithms assign the population origin to a sample rather than individual bluefin tuna. Therefore, we adopted a conservative approach of minimal overlap, establishing thresholds where individuals were confidently assigned. This sometimes resulted in a substantial fraction of a sample (i.e., the US recreational fishery sample) that could not be confidently assigned to natal origin, which was omitted from these fitted models (Table 1).

Growth models were fit using Excel Solver © minimizing negative log likelihood estimates. Standard errors and the variance covariance matrix of the parameters were estimated from the Hessian matrix using a finite difference approximation (Solver macro MLESE).

Results

Age estimates for bluefin tuna ranged from 4 to 33 years old. For western-captured bluefin tuna, inclusion of only those western-captured individuals assigned to the western population (Table 2; Figure 4a,b) did not substantially change growth parameters ($K=0.20$; $L_\infty=257$; and $t_0=0.83$) or total variance explained. Similarly, fish assigned as eastern-origin (but captured in US fisheries) did not differ substantially in growth coefficients from western-origin fish (Figure 4c). Patterns in residuals with estimated age showed no systemic bias. Predicted size at age four was similar to length frequency modes assigned to age four (120-130 cm CFL) by Turner et al. (1991) for the period 1970-1988.

Mediterranean-captured fish in comparison to the western-captured sample were fitted with higher K (0.27) and a relatively high t_0 (3.1)); L_∞ was similar to the western samples (Table 2; Figure 5a). The high t_0 probably indicates a poor fit in comparison to data fit to the western population. Inclusion of eastern samples assigned to have originated in the Mediterranean further increased K (0.3) and t_0 (3.4) (Figure 5b). For both fitted models, predicted size at age 4 gave an unrealistically low estimate (<60 cm CFL).

Discussion

Across the two western samples, growth model coefficients and predicted lengths at age were substantially different than those used in current SCRS bluefin tuna assessments (Tables 2; 3; Figure 6a). For western bluefin tuna, estimated K (0.2) was approximately two-fold higher than the K estimated by Turner and Restrepo (1994). In turn, estimated L_∞ was substantially lower (255-257 cm) than the previous model (382 cm). Predicted sizes at several benchmark ages (4, 8, 12, 16 and 20 years) indicated very little difference in sizes at ages 4 and 8 between direct ageing and the Turner and Restrepo (1994) predictions, consistent with the extensive use of small fish in the Turner and Restrepo model. However, the discrepancy between the UM and Turner et al. models increased beyond age 12, and became particularly marked after age 16 (Figure 6a; Table 3). Regardless of which sub-sample model was chosen (Table 2), very gross errors or biases would be required to reconcile the direct ageing estimates of growth with those estimated previously with mark-recapture data at estimated ages >12 years.

To model growth from tag-recapture data, Turner et al. (1991) faced several difficult issues. Despite a large initial sample of released individuals (n=3,261), only 37 were >150 cm CFL (19 were >200 cm CFL), curtailing the fitted distribution of growth rates across the entire adult life span. Although care was taken to identify bias in how fish lengths were estimated at release and recapture, difficult decisions were required on how to capture measurement error in the analysis, and perhaps more critically, how to deal with observed negative growth rates and anomalously high growth rates. Careful length modal analysis by Turner et al. (1991) gave support for scaling the observed growth increments (t_0 estimation), but L_∞ and K will be very sensitive to the measurement errors in size.

In comparison to growth parameters currently used by SCRS (SCRS 2003), parameters fitted here for the western population are more similar to those estimated through direct ageing on a smaller sample set of Canadian bluefin tuna otoliths by Neilson and Campana (in review) (Tables 2; 3; Figure 6b). Most bluefin tuna in that study were giant category fish, well above 205 cm CFL, such that L_∞ may have been well modeled (274 cm). On the other hand, limited data for adolescents may have affected estimates of K and t_0, which were lower (K=0.12; t_0=-0.1) to values reported here for US samples. Overlaying size-at-age data upon the growth model fit by Neilson and Campana (in review) showed positive residuals at estimated ages 4-10 but negatives ones at estimated ages > 15. We feel that these differences were due to underlying sample structure, where the Canadian sample was weighted towards giant bluefin tuna, and the US sample was weighted more towards school and medium size-classes. Never-the-less, predicted sizes at benchmark ages were similar between this and the previous study (Table 3).

For the western population, we recommend adopting the model fit to western-captured, western-origin data. In the present analysis of western samples, stipulation of sub-samples based upon population origin had little influence but this could change as we look at a larger and more representative sample.

For the eastern population, we recommend additional age determinations prior to adoption of a growth model based on direct ageing. In particular school and medium size categories should be emphasized in future ageing studies. Our sample only included adults, which may have biased the fit, particularly t_0. The currently accepted growth model (Cort 1991; Figure 6c), based upon direct ageing of dorsal fin spines, yields similar predicted size at age as the current western growth model (Table 3).

A significant advantage in adopting otolith-based ageing will be improved comparability between western and eastern population stock assessments. Further, as highlighted above, analysis of otoliths can permit both population assignment and age determination. A substantial number of otoliths have already been archived by National Marine Fisheries Service (n>900) and the ICCAT Direct Ageing Group, which should receive priority for ageing and complementary population assignment analysis. Future research on western population tuna should also include age determinations for the large archived sample of Canadian fish, which represent estimated year-classes from 1947-1970 (Figure 2) and would permit larger and presumably older fish to be included in the western growth model but also test whether growth has changed during the past 50 years (see Polacheck et al. 2003). Important areas of population mixing such as the Central Atlantic also deserve emphasis in terms of otolith sampling, age determinations, and population assignment.

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Table 1. Sample size and attributes by region of collection. Otolith samples were contributed by NOAA SEFSC (S. Turner), Texas A&M, Chesapeake Biological Laboratory, and Stanford University (J. Rooker, D. Secor, and B. Block). Gulf of Mexico fish were sampled from the long-line fishery where they are captured as by-catch. Nova Scotia and US Coast samples were primarily from rod and reel commercial and recreational fisheries. Mediterranean samples were collected from cages; fish were initially harvested in the eastern Mediterranean during summer months.

Location	**Total (n)**	**Age Estimate (years)**	**West (n)**	**East (n)**
Gulf of Mexico	41	8-33	34	3
US Coast	157	4-33	87	37
Mediterranean	37	6-20	5	25
Sub Totals	235	4-33	126	65

Table 2. von Bertanlanffy growth models fitted to certain sets of aged Atlantic bluefin tuna. Also included in the table are growth models reported by Turner and Restrepo (1994); Neilson and Campana (in review); and Cort (1991). Eastern Capture=sampled in Mediterranean; Western Capture=sampled west of 45 W Meridian.

Sample/Study	**N**	**L_∞ (SE)**	**K (SE)**	**t_0 (SE)**
Western Capture	198	255 (2.0)	0.20 (0.01)	1.1 (0.17)
Western Capture-Western origin	121	257 (2.0)	0.20 (0.01)	0.83 (0.22)
Turner and Restrepo (1994)	?	382	0.079	-0.71
Neilson and Campana (in review)	28	289	0.116	-0.06
Eastern Capture	37	263 (2.3)	0.27 (0.02)	3.08 (0.19)
Eastern Capture-Eastern origin	25	257 (2.1)	0.30 (0.02)	3.38 (0.15)
Cort (1991)	?	318.9	0.093	-0.97

Table 3. Predicted CFL (cm) at age predicted by growth models for Atlantic bluefin tuna. See Table 2 for growth model sources and coefficients.

Sample/Study		**Predict CFL @age:**				
	N	4 years	8 years	12 years	16 years	20 years
Western Capture	198	113	192	227	242	249
Western Capture- Western origin	121	118	193	227	242	249
Turner and Restrepo 94	?	119	192	244	282	309
Neilson and Campana in review	28	111	179	221	247	263
Eastern Capture	37	58	193	239	255	260
Eastern Capture-Eastern origin	25	44	193	238	251	255
Cort 1991	?	115	177	220	250	271

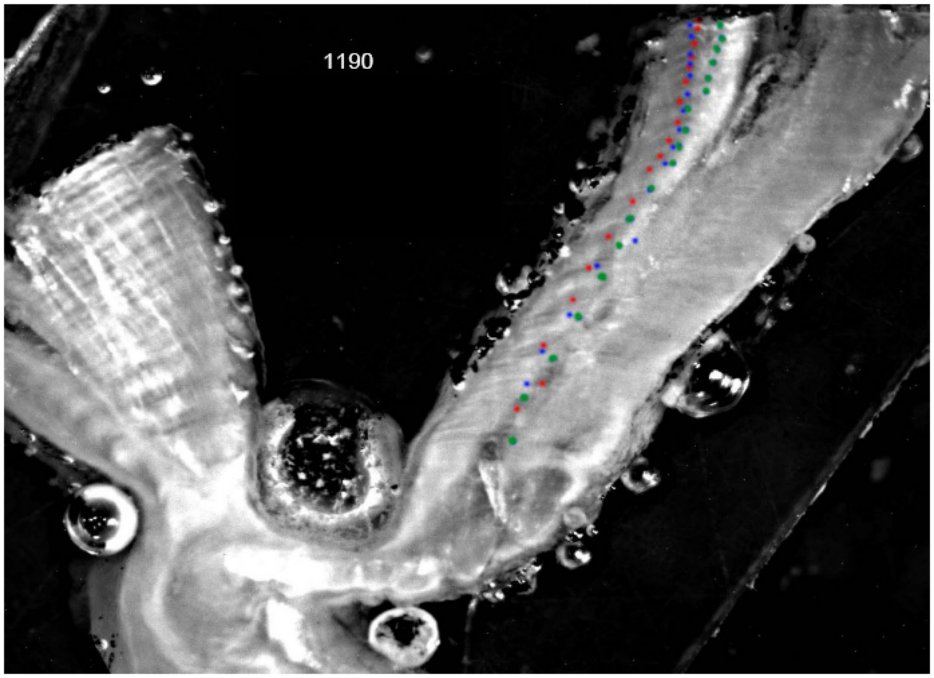


Figure 1. Annulus assignments by three experienced readers and UM (in red) for an otolith within the DFO reader set. Age estimates ranged 17-18 years.

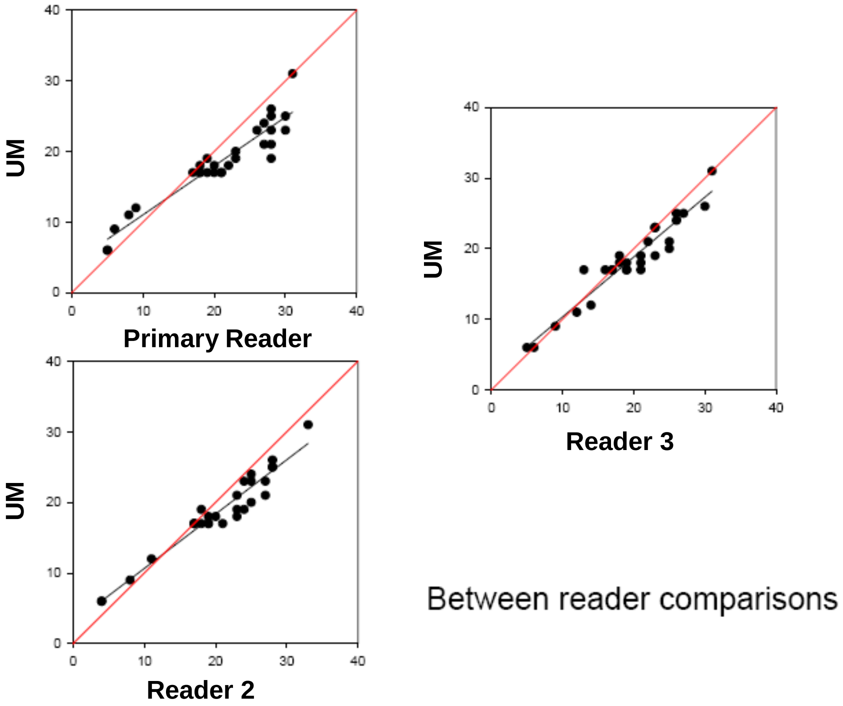


Figure 2. Age comparison plots between UM estimates and those of experienced readers. Red line indicates expected identity slope.

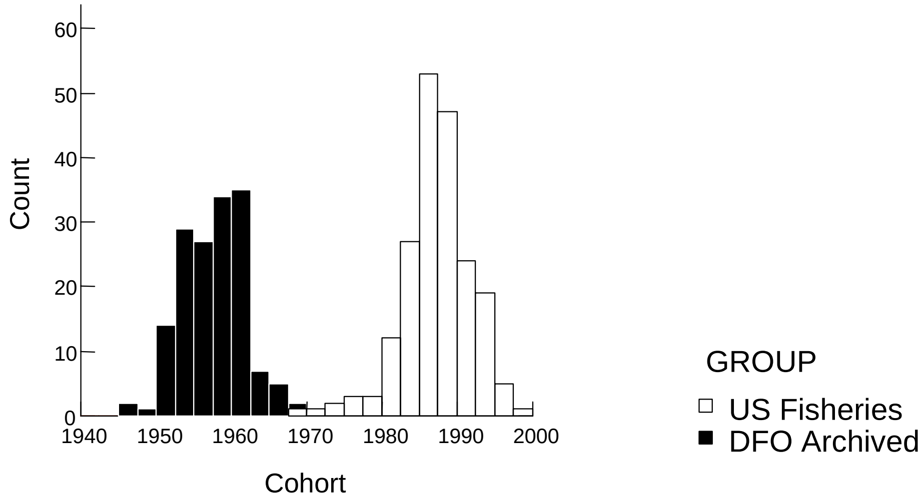
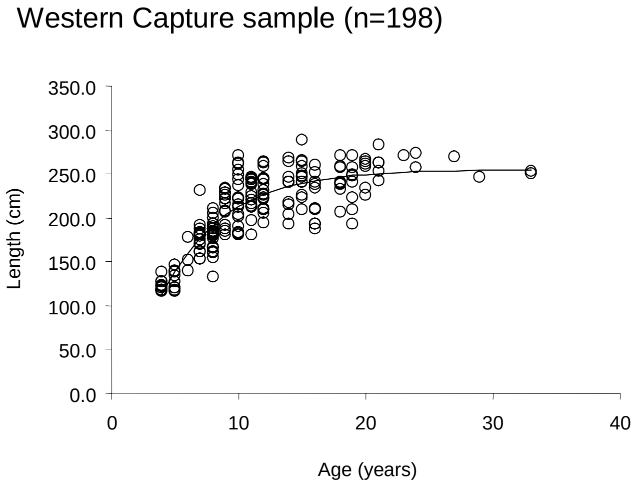
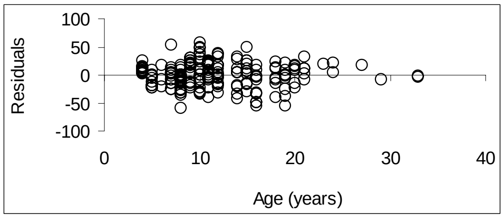


Figure 3. Year-class (cohort) representation in aged samples of western-captured individuals. US Fisheries are included in the current study. DFO archived samples are shown to exhibit sample attributes of this valuable data set. Year-classes for DFO sample were estimated many years ago by DFO staff but will need to be re-analyzed according to currently accepted practices.

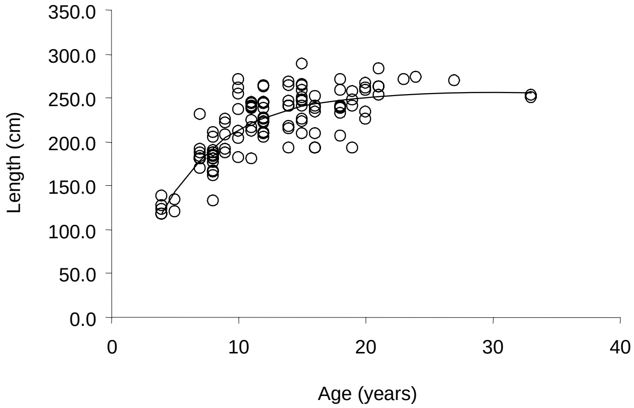


Parameters		SE
L(inf)	254.9	2
K	0.2	0.01
t0	1.1	0.17
sigma	453.9	

Figure 4a. Fitted length at age for Atlantic bluefin tuna based upon otolith annuli interpretation. Sample, growth model parameters, and residual plot are presented.



Western Capture, Western Origin (n=121)



Parameters		**SE**
L(inf)	256.7	2
K	0.2	0.01
t0	0.83	0.22
sigma	470.2	

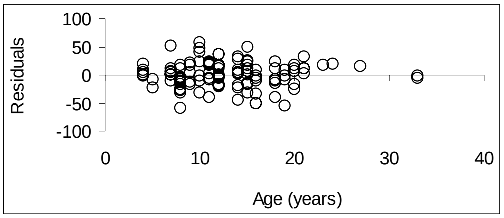
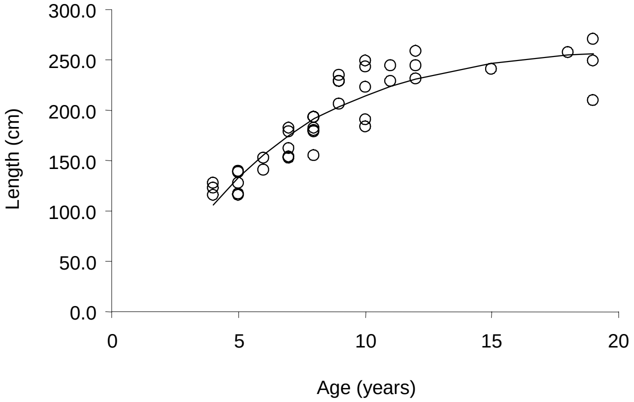


Figure 4b. Fitted length at age for Atlantic bluefin tuna based upon otolith annuli interpretation. Sample, growth model parameters, and residual plot are presented.

Western Capture, Eastern Origin (n=40)



Parameters		**SE**
L(inf)	265.4	2.9
K	0.19	0.01
t0	1.36	0.13
sigma	359.2	

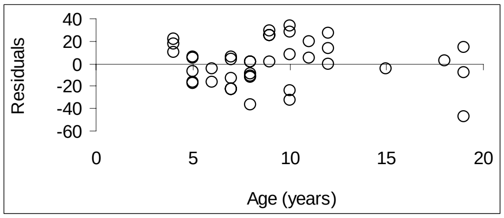
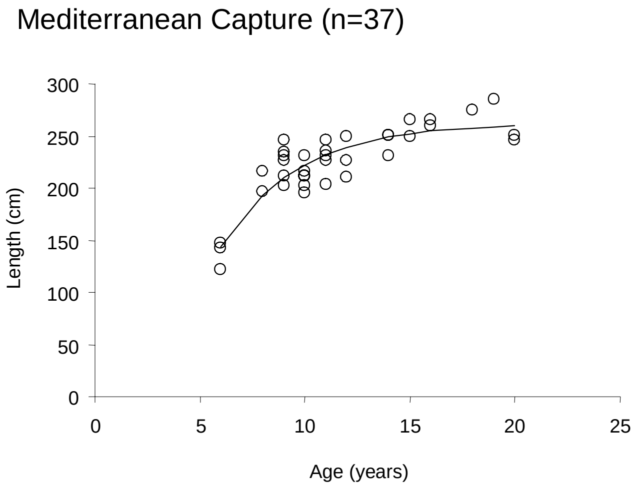
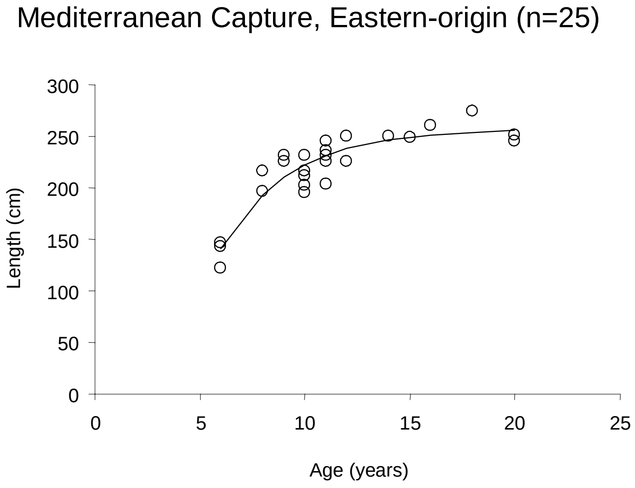


Figure 4c. Fitted length at age for Atlantic bluefin tuna based upon otolith annuli interpretation. Sample, growth model parameters, and residual plot are presented.



Parameters		SE
L(inf)	262.5	2.3
K	0.27	0.02
t0	3.08	0.19
sigma	252.9	

Figure 5a. Fitted length at age for Atlantic bluefin tuna based upon otolith annuli interpretation. Sample, growth model parameters, and residual plot are presented.

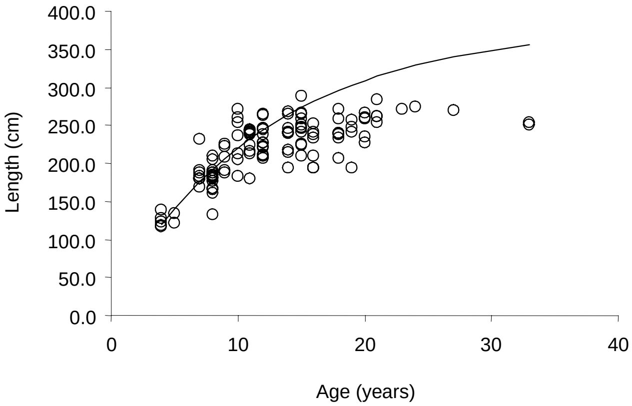


Parameters		SE
L(inf)	257.1	2.1
K	0.3	0.02
t0	3.38	0.15
sigma	198.9	

Figure 5b. Fitted length at age for Atlantic bluefin tuna based upon otolith annuli interpretation. Sample, growth model parameters, and residual plot are presented.

Turner et al. (1991) fit to Western Capture,
Western Origin (n=121)

Parameters	
L(inf)	382
K	0.08
t0	-0.71
sigma	1588



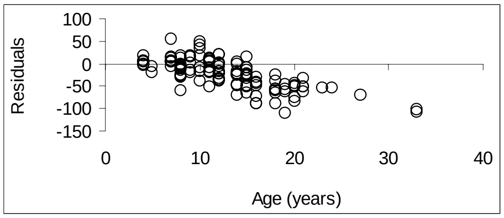


Figure 6a. Fitted length at age for Atlantic bluefin tuna based upon otolith annuli interpretation. Sample, growth model parameters, and residual plot are presented.

Neilson and Campana (in review) fit to Western Capture,
Western Origin (n=121)

Parameters	
L(inf)	289
K	0.12
t0	-0.06
sigma	585

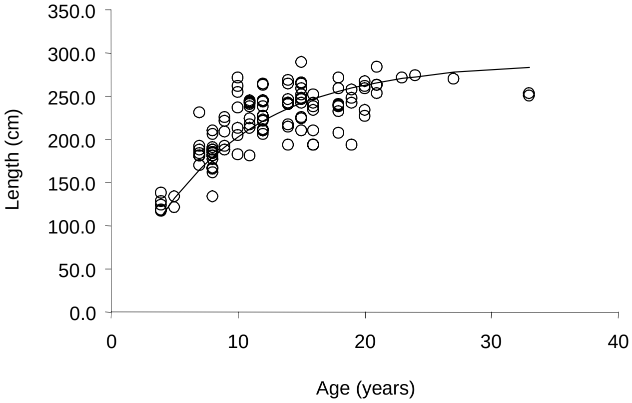
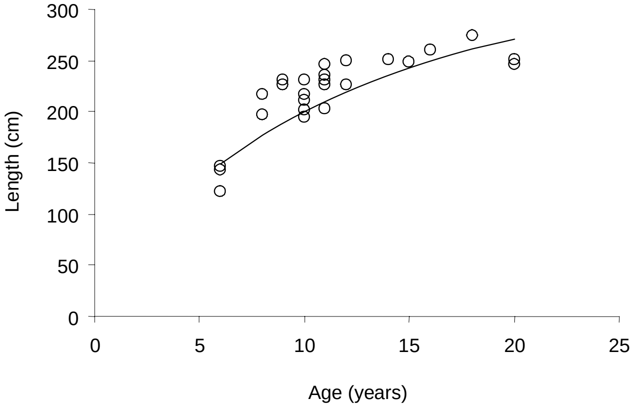


Figure 6b. Fitted length at age for Atlantic bluefin tuna based upon otolith annuli interpretation. Sample, growth model parameters, and residual plot are presented.



Cort (1991) fit to Eastern Capture, Eastern Origin (n=25)

Parameters	
L(inf)	318.9
K	0.09
t0	-0.97
sigma	419.9

Figure 6c. Fitted length at age for Atlantic bluefin tuna based upon otolith annuli interpretation. Sample, growth model parameters, and residual plot are presented.