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A validated description of age and growth of western Atlantic bluefin tuna (*Thunnus thynnus*)

John D. Neilson and Steven E. Campana

Abstract: Current stock assessments of western Atlantic bluefin tuna (*Thunnus thynnus*) use age-structured population analyses, but the age assignment in the population model is made using an age–length relationship derived from mark and recapture studies largely completed during the 1970s. In our study, the deposition of bomb radiocarbon was used as a dated mark to validate age inferences of bluefin tuna and to compare the validated ages with those predicted from the age–length relationship. The results support the view that the age–length relationship currently in use for the assessment overestimates growth rate and the ultimate size of the fish. These findings have implications for the estimation of stock productivity and may negatively impact the rebuilding schedules established by fisheries managers.

Résumé : Les évaluations courantes des stocks de thons rouges (*Thunnus thynnus*) dans l'Atlantique ouest sont basées sur des analyses de populations structurées en fonction de l'âge, mais l'attribution des âges dans le modèle démographique se fait à partir de relations âge–longueur obtenues lors d'études de marquage et de recapture réalisées en grande partie dans les années 1970. Dans notre étude, nous utilisons les dépôts de radiocarbone provenant des essais nucléaires comme repères de date connue pour valider les estimations de l'âge chez les thons rouges et pour comparer ces âges validés à ceux prédits à partir des relations âge–longueur. Nos résultats appuient le point de vue qui veut que la relation âge–longueur en usage courant pour l'évaluation des stocks surestime le taux de croissance et la taille finale des poissons. Ces observations ont des conséquences sur l'estimation de la productivité des stocks et peuvent avoir un impact négatif sur les calendriers de reconstruction établis par les gestionnaires des pêches.

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Introduction

Atlantic bluefin tuna (*Thunnus thynnus*) are among the largest, most widely-ranging, and highly-valued members of the marine fish fauna. The responsible regional fisheries management agency (International Commission for the Conservation of Atlantic Tunas (ICCAT)) considers that there are two management units in the Atlantic (western Atlantic and Eastern Atlantic – Mediterranean). However, both Atlantic populations of bluefin tuna are considered to be severely overfished (Fromentin and Powers 2005), and there are growing concerns about their future, as indicated by the recent identification of the stock as a candidate species for special conservation measures by COSEWIC (Committee on the Status of Endangered Wildlife in Canada, www.cosewic.gc.ca/eng/sct3/sct3_1_e.cfm#4).

While direct age determination from hard parts such as otoliths have been attempted (i.e., Hurley and Iles 1983), such information has not been used in stock assessments because of the absence of validation that annulus counts corresponded with age. In the absence of direct estimates from hard parts, ages in the western Atlantic stock are currently assigned by empirical length modal separation for ages 1–3, then through application of a length–age relationship (ICCAT 2003). The growth model that informs the slicing is that of Turner and Restrepo (1994), who used mark and recapture information to provide estimates of L_∞ and K, following the von Bertalanffy growth equation, and modal analyses to provide an estimate of t_0.

However, the information used by Turner and Restrepo (1994) is now somewhat dated (about 89% of the available records included recaptures made before 1979; Turner et al. 1991), and there is a possibility that growth patterns observed in the past may no longer reflect the contemporary situation. More importantly, the data set used by Turner and Restrepo, while consisting of a large number of observations (N = 908), had relatively few (N = 11) observations of fish 250 cm or larger. The relatively few observations of larger fish may have impacted the estimation of L_∞. The impact of potential errors in age assignment for older fish could include errors in calculations of critical stock parameters, such as age at maturity and natural mortality.

We employed the bomb radiocarbon method to evaluate the accuracy of age interpretations from otoliths, a method considered to be one of the most accurate means available

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to obtain such validation (Baker and Wilson 2001). In brief, this method uses the observation that bomb-derived radiocarbon from nuclear testing conducted during the late 1950s resulted in elevated ^{14}C in the bony parts formed in marine organisms at the time. This deposition forms a dated reference that can be used to validate inferences of age (Campana 2001). Using ages validated with the radiocarbon method, we provide a description of the growth of bluefin tuna and contrast this with the model that has been used previously.

Materials and methods

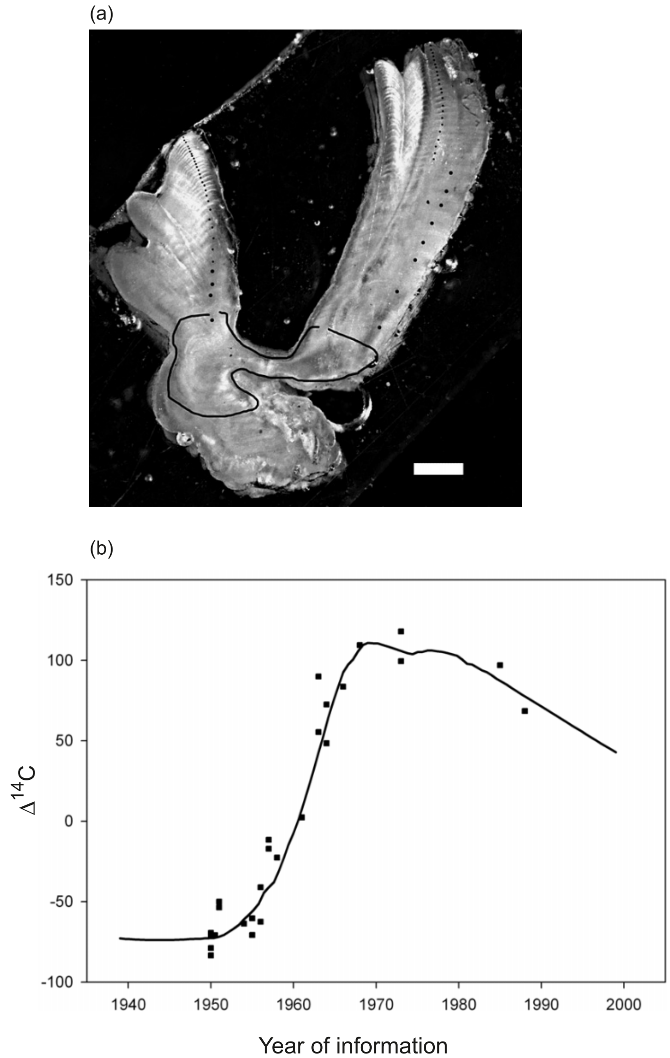
Bluefin tuna sagittal otoliths were collected from archived material stored at the St. Andrews Biological Station, Fisheries and Oceans Canada (St. Andrews, New Brunswick). Material selected for the study is listed in Supplemental Table S1[2]. Otoliths were only collected from the western Atlantic management unit and were generally collected during the 1970s and 1980s, with two exceptions. Samples were selected from that time period to include otoliths that were likely formed during the period of increasing radiocarbon and to be comparable with the material available to Turner and Restrepo (1994). The material was stored dry in coin envelopes, and details of the sampled fish were available from an electronic database. Consistent with the approach of Turner and Restrepo (1994), we report fish length as fork length. To do this, it was necessary to convert curved fork length (CFL) to fork length (FL) using the conversion factor used by the ICCAT (FL = 0.955 × CFL) for the majority of the samples.

Otoliths to be aged were first embedded in a slow-drying hard epoxy (Araldite epoxy GY502 and hardener HY956 in a 5:1 weight ratio). Otolith cores for bomb radiocarbon age validation were isolated from three adjacent transverse sections of the sagittae: a 1.2 mm central section through the core intended for micromilling and ~450 μm thick sections on either side for age determination. All sections were prepared with a single cut using multiple blades separated by spacers on an Isomet low-speed diamond-bladed saw. Sections were lightly polished to improve visibility of the growth sequence and then digitally photographed at 1280 × 1024 pixel resolution while under a binocular microscope at 16×–40× magnification using reflected light. Age interpretation was based on digitally-enhanced images, and counts were made along the longer of the two arms of the sectioned sagittae (Fig. 1*a*). The ages provided by the second author are referred to here as those from the "primary age reader" and are those used in the radiocarbon calibration and the von Bertalanffy growth curve. The electronic images were also supplied to two experts familiar with age determination using otoliths of bluefin tuna along with information on length at capture, who supplied independent estimates of ages. Those readers are referred to here as "secondary age readers". These additional age estimates provide an indication of the expected consistency of age interpretations possible with this species.

Otolith cores representing the first 2–3 years of life were isolated as solid pieces encompassing the innermost otolith annuli from the central thick section and one or both adjacent sections with a Merchantek computer-controlled micromilling machine using 300 μm diameter steel cutting bits and burrs. Although major error in isolating the otolith core is unlikely, any such error could only reduce the apparent age of the fish by incorporating more recently formed material. Thus the radiocarbon method assigns a minimum age to the fish.

Cores from both sections were sometimes required to

Fig. 1. (*a*) Polished transverse section of a sagittal otolith from sample No. 1536, aged as 31 years old. The specimen was photographed using reflected light, and the digital image was modified to enhance contrast. Black dots were added by the primary age reader to identify presumed annuli, and the otolith core sampled for radiocarbon analyses is also highlighted. The white scale bar is 0.5 mm in length. (*b*) $\Delta^{14}C$ in otolith cores of bluefin tuna (*Thunnus thynnus*) versus year of formation inferred from counts of presumed annuli. The $\Delta^{14}C$ chronology of the cores (■) was similar to that of a reference carbonate chronology (line smoothed with a LOESS curve), with the crucial feature being the period of rapid increase.



[2] Supplementary data for this article are available on the journal Web site (cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3778. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Fig. 2. (*a*) Paired comparisons of ages of the primary age reader with the two secondary age readers and the predicted ages from the Turner and Restrepo (1994) growth model. (*b*) Predicted relationship between length and age, from Turner and Restrepo (1994), shown as the gray line. The parameters of the von Bertalanffy fit to the Turner and Restrepo model were L_∞ = 382 cm, t_0 = –0.707, and K = 0.079. The estimated ages obtained by the primary age reader are shown (◆), and the fit to those data is shown by the black line, with the parameters L_∞ = 289 cm, t_0 = –0.06, and K = 0.116.

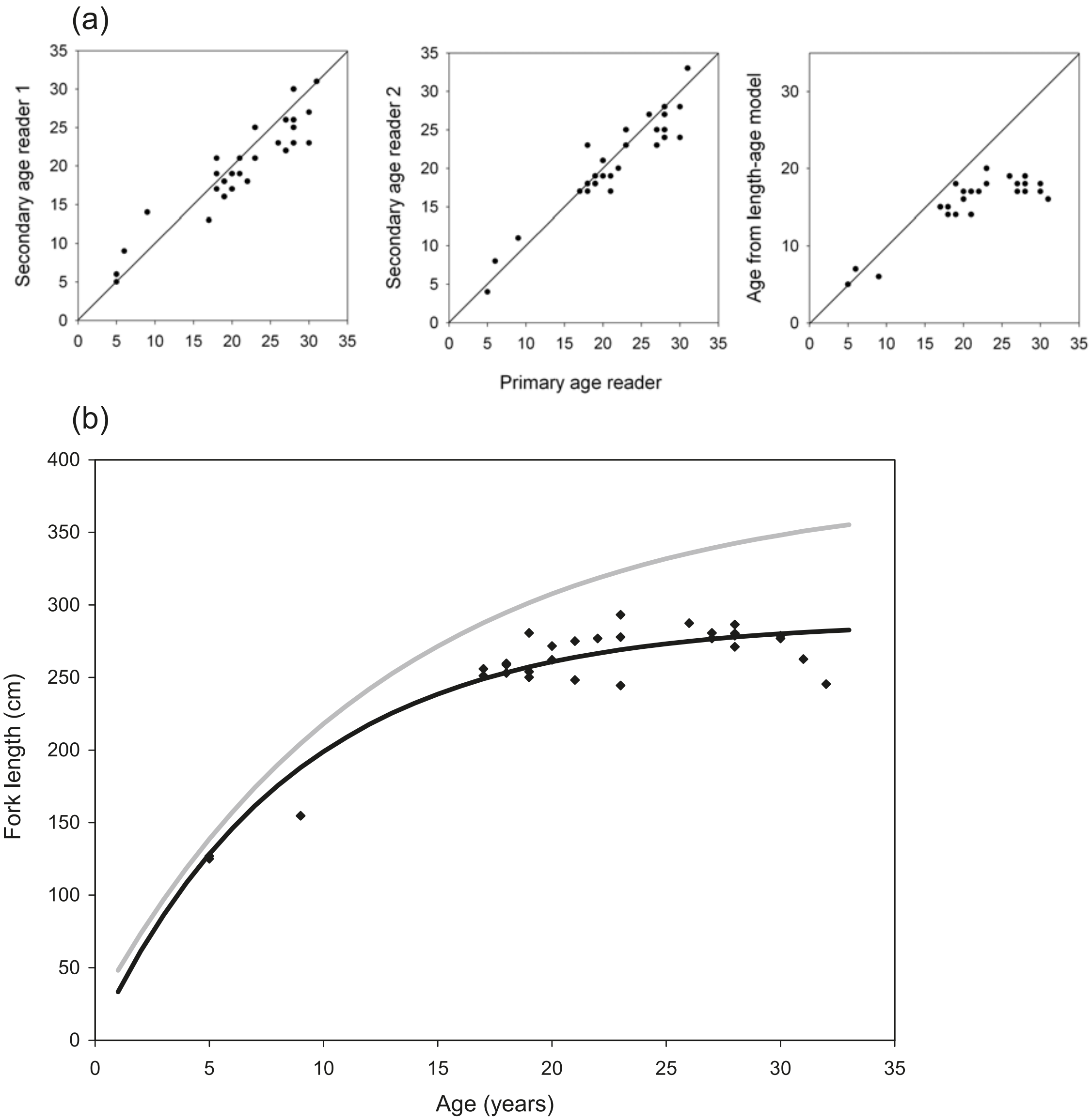


Table 1. Parameters of the von Bertalanffy growth equation, fitted using age interpretations from the three age readers or from the primary age reader only.

	L_∞		K		t_0		CV	
	Mean	SD	Mean	SD	Mean	SD	Length error	Age error
All readers	304.0	15.2	0.098	0.021	–0.15	1.03	0.06	0.12
Primary reader only	289.0	16.9	0.116	0.040	–0.06	1.56	0.10	

Note: CV, coefficient of variation; SD, standard deviation.

bring the sample weight up to the minimum of 3 mg necessary for radiocarbon assay. The date of sample formation was calculated as the year of fish collection minus the number of increments between the otolith edge and the midpoint of the growth increments extracted in the core. After sonification in Super Q water and drying, the sample was weighed to the nearest 0.1 mg in preparation for ^{14}C assay with accelerator mass spectrometry (AMS). AMS assays also provided $\delta^{13}C$ (‰) values, which were used to correct for isotopic fractionation effects and provide information on the source of the carbon. Radiocarbon values were subsequently reported as $\Delta^{14}C$, which is the per mil (‰) deviation of the sample from the radiocarbon concentration of 19th-century wood, corrected for sample decay prior to 1950 according to methods outlined by Stuiver and Polach (1977). The mean standard deviation of the individual radiocarbon assays was about 5‰.

To assign dates of core deposition for the bluefin tuna otoliths, we compared the tuna $\Delta^{14}C$ data to a $\Delta^{14}C$ chronology based on known-age material (a reference chronology) for the northwest Atlantic derived from known-age fish otoliths formed between 1949 and 2000 (Campana et al. 2008). The $\Delta^{14}C$ chronology of fish otoliths in the Northwest Atlantic parallels that of North Atlantic corals and bivalves (Campana 1997), so it is a good proxy for the $\Delta^{14}C$ dissolved inorganic carbon history of the tuna environment assuming that the tuna spent at least part of their first 2–3 years of life in the upper 200 m of the water column.

Estimation of the parameters of the von Bertalanffy growth equation were made using nonlinear estimation approaches, described in Cope and Punt (2007). Those authors have also developed random effects methods that allow for multiple age readings from the same fish and thereby provide estimates of ageing error.

Results and discussion

An example of a transverse section is shown, demonstrating the periodic banding that we assumed to represent annuli (Fig. 1*a*). Based on our experience, these annuli were relatively straightforward to identify and count compared with other species.

The results of the radiocarbon assays are shown, in comparison with the reference chronology for the Northwest Atlantic (Fig. 1*b*). The distribution of the radiocarbon results appears consistent with the reference chronology, implying that the age determinations of the primary age reader are accurate. Consistent age underestimation or overestimation would have been clearly evident as a shift of the entire fitted curve to the left or the right of the reference chronology. Campana (2001) has indicated that the expected precision of ages validated with the bomb radiocarbon approach is 1–3 years.

There was, however, a slight but not significant (paired t test, $p > 0.01$) tendency for the secondary age readers to underage relative to the primary reader (Fig. 2*a*), but those differences were small in relation to the predicted values from age–length model of Turner and Restrepo (1994). Age underestimation from the Turner and Restrepo (1994) model was evident at ages greater than 7 years, but was most acute at ages exceeding 18 years.

Although the sample size is small and the collection generally skewed towards larger fish, we fitted the available data to a von Bertalanffy growth equation using a standard nonlinear fit (Table 1). Using the ages obtained by all three age readers, we also fitted the growth equation using the random effects method described by Cope and Punt (2007).

The von Bertalanffy curve for the primary reader is plotted along with the Turner and Restrepo (1994) fit currently used in the assessment (Fig. 2*b*). On the basis of the validated age determinations, it appears that the older analysis has overestimated L_∞ and the growth rate, despite the fact that the bluefin tuna samples used in our analysis were contemporaneous with those used in the Turner and Restrepo (1994) analysis. As noted by Restrepo et al. (2007), the estimation of the von Bertalanffy growth parameters may be influenced by the size and age ranges included in the analyses, and the differences between our results and those of Turner and Restrepo (1994) are probably related to this, at least in part. Our results present an estimate of L_∞ that is more comparable with those of Hurley and Iles (1983) (L_∞ of 278 and 266 cm for males and females, respectively). Hurley and Iles (1983) also raised the issue of frequency of formation of apparent annuli as a possible source of error. Our results provide evidence that the structures considered to be annuli are indeed formed annually.

The coefficient of variation for the multiple ages is also relatively low (0.12) compared with most of the values reported by Cope and Punt (2007) for other taxa, suggesting that the secondary age readers were able to obtain ages that were reasonably consistent when compared with the primary reader.

While our results provide a more realistic estimate of L_∞ than was available previously, more work is required to refine the estimate of t_0, as relatively few small fish are included here. Furthermore, the applicability of our description of bluefin growth to the current situation remains unknown, as our samples were necessarily taken from older collections to ensure that the ages included in the validation included the period of rapidly increasing radiocarbon. However, our results, which include electronically annotated images of the material used in this study, form a valuable reference set for future age and growth studies of bluefin tuna. The validation results completed here, along with the observations that the periodic structures of bluefin tuna are readily observed and consistently counted, provide a basis for routine age determinations in the future.

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