

BOMB ^{14}C DATING, AGE ESTIMATE REFINEMENT, AND GROWTH CHARACTERISTICS OF NORTH ATLANTIC ALBACORE (*THUNNUS ALALUNGA*) USING OTOLITHS

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SUMMARY

*A well-established bomb ^{14}C chronology was used to test the validity of age estimates for North Atlantic albacore tuna (*Thunnus alalunga*) in the by comparing ^{14}C values from otoliths of aged fish with the regional reference. Some age estimates were initially offset from the reference ^{14}C chronology. An investigation of daily increments and early length modes - coupled with information from the ^{14}C offsets and otolith mass growth - led to refined age-at-length estimates and an 18-year lifespan that was supported by bomb ^{14}C dating. A limited number of North Atlantic albacore otoliths were available for this study because they have not been routinely collected ($n = 54$); however, the combined set of specimens (smallest to largest and youngest to oldest otoliths) provided an opportunity to derive new age and growth parameter estimates ($L_{\infty} = 113.5$ cm CFL, $k = 0.367$, $t_0 = -0.767$) for the North Atlantic Ocean.*

RÉSUMÉ

*Une chronologie bien établie du carbone bombe radioactif ^{14}C a été utilisée pour vérifier la validité des estimations de l'âge du germon de l'Atlantique Nord (*Thunnus alalunga*) en comparant les valeurs du ^{14}C des otolithes de poissons dont l'âge a été déterminé avec la référence régionale. Certaines estimations de l'âge se sont initialement déviées de la chronologie de référence du ^{14}C . Une étude des incréments quotidiens et des modes de longueur des premières phases - associée aux informations issues des déviations du ^{14}C et de la croissance de la masse des otolithes - a permis d'affiner les estimations de l'âge par taille et d'établir une durée de vie de 18 ans, confirmée par la datation au carbone bombe radioactif ^{14}C . Le nombre d'otolithes de germon de l'Atlantique Nord disponibles pour cette étude était limité, car ils n'ont pas fait l'objet d'un prélèvement systématique ($n = 54$) ; toutefois, l'ensemble combiné de spécimens (des otolithes les plus petits aux plus grands et des plus jeunes aux plus anciens) a permis d'établir de nouvelles estimations des paramètres d'âge et de croissance ($L_{\infty} = 113,5$ cm CFL, $k = 0,367$, $t_0 = -0,767$) pour l'océan Atlantique Nord.*

RESUMEN

*Se utilizó una cronología bien establecida del ^{14}C de bomba para comprobar la validez de las estimaciones de edad del atún blanco del Atlántico norte (*Thunnus alalunga*), comparando los valores de ^{14}C de los otolitos de peces cuya edad se determinó con la referencia regional. Algunas estimaciones de edad se desviaron inicialmente con respecto a la cronología de referencia del ^{14}C . Un estudio de los incrementos diarios y las modas de talla de la fase*

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temprana —junto con la información obtenida de las desviaciones del ^{14}C y el crecimiento de la masa de los otolitos— permitió refinar las estimaciones de la edad en función de la talla y determinar una esperanza de vida de 18 años, respaldada por la datación con ^{14}C de bomba. Para este estudio se dispuso de un número limitado de otolitos de atún blanco del Atlántico norte, ya que no se han recogido de forma sistemática ($n = 54$); sin embargo, el conjunto combinado de ejemplares (otolitos de menor a mayor tamaño y de más jóvenes a mayores) brindó la oportunidad de obtener nuevas estimaciones de los parámetros de edad y crecimiento ($L_{\infty} = 113,5$ cm CFL, $k = 0,367$, $t_0 = -0,767$) para el océano Atlántico norte.

KEYWORDS

Scombridae, tuna, albacore, longevity, otolith, age validation, radiocarbon reference chronology

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1. Introduction

North Atlantic albacore (*Thunnus alalunga*) is one of six stocks for this globally distributed, temperate-tropical, tuna species. Despite ecological and economic importance, life history traits are described using untested age estimation techniques. While albacore support some of the world's most economically significant tuna fisheries, a comprehensive understanding of their age and growth is incomplete due to limited and contrasting life history traits described through time across their range (Nikolic et al., 2016). Accurate age and growth estimation is critical for effective monitoring and appropriate management frameworks. Estimates of age and growth for North Atlantic albacore remain uncertain because validation of otolith growth zone deposition (opaque and translucent) has not been rigorously evaluated (Santiago and Arrizabalaga, 2005). Otolith growth structure varies in clarity and definition in tropical and temperate tunas, leaving them vulnerable to misguided management.

As with many tuna species, the growth of albacore is described as rapid in its first few years with either, 1) a lack of asymptotic growth and short lifespan near 6 years, or 2) a sharp decrease in growth near maximum size with asymptotic growth and a longer lifespan to the mid-teens. In terms of validation, support for albacore age estimates is limited to tag-mark-recapture results from the South Pacific where otolith section ages were supported up to 14 years (Farley et al., 2013). Similarly, studies using comparable otolith age reading protocols in the North Pacific estimated ages up to 15 years (Wells et al., 2013). Numerous methods and structures have been used on North Atlantic albacore to estimate age and longevity — also true for albacore in other ocean basins (Nikolic et al., 2016) — resulting in maximum age estimates of 7–13 years as derived from scales, fin spines, vertebrae, and length-frequency analyses (Artetxe-Arrate et al., 2023; Macías et al., 2025). Absent from consideration to date is the comprehensive use of otoliths to determine the life history parameters of North Atlantic albacore. Previous studies on North Atlantic albacore age and growth relied heavily on dorsal fin spines and vertebrae, tissues that present challenges to age estimation of tuna species (Bard, 1981; Fernández et al., 1992). Fernández (1992), in particular, noted the promise of otoliths for growth analysis, but did not pursue direct validation using this structure.

The methods used to estimate age and determine growth characteristics of tuna species has evolved over the last few decades. Age estimation methods are typically based on growth zones visible in skeletal and non-skeletal parts, but otoliths have been deemed the most dependable because they form an inert record of growth containing environmental chemistry through ontogeny. Fish growth patterns are often reflected as annual growth zones in otoliths that stem from age estimate interpretations. The result quality depends on the readability of interpreting the growth zone structure, which can vary depending on the biology and environment of the species, as well as specimen preparation and age reader experience. An age reading protocol and the resultant age estimates must be validated in a manner that has some level of time specificity through ontogeny and otoliths offer unique opportunities (Reis-Santos et al., 2022).

There have often been problems with the use and misuse of age estimation and validation techniques (Campana et al., 2001). In some cases, age estimation methods for tuna were assumed to work past their utility, such as counting daily increments in otoliths well beyond the first 1–2 years of growth (Williams et al., 2013), or use of structures that do not reflect growth through ontogeny, such as the combined findings for southern bluefin tuna (*T. maccoyii*; see Kalish et al. (1996) and Gunn et al. (2008). In particular, the shortcomings of various methods were highlighted for yellowfin (*T. albacares*) and bigeye (*T. obesus*) tuna

in the Atlantic, Pacific and Indian Oceans where estimated maximum ages near 6–8 years were proven incorrect using bomb ^{14}C dating, which confirmed respective lifespans up to 16–18, 13–14, and 11 years, and supported the methods which estimated age from counting annual growth zones in transverse otolith sections (Andrews et al., 2020; 2024; Fraile et al., 2024). Hence, it is likely that the management efficacy of these species has been affected for decades due to incomplete or inaccurate life history information. The common thread in these revelations of otolith section-age validity and greater maximum ages is the use of bomb-produced ^{14}C to correct for age estimate errors and provide validated growth parameters (e.g., Pacicco et al., 2021; Waterhouse et al., 2022).

The use of bomb ^{14}C dating to age marine organisms relies on a time-specific signal — an observable increase in ^{14}C created by thermonuclear testing in the 1950s and 1960s — and its diffusion to the marine environment (Broecker and Peng, 1982; Nydal and Gislefoss, 1996). Although the bomb-produced ^{14}C rise period is limited to hatch years of fish that were alive during the late 1950s to mid-1960s, which is an obstacle to age validation of short-lived fishes that have no long-term otolith archives, the method was expanded to the post-peak bomb ^{14}C decline period, more recent than ~1980 (Andrews et al., 2013). This decline of environmental ^{14}C levels through more recent decades is consistent enough to provide a temporal reference for recently collected fishes that do not live beyond a few decades, like parrotfishes, giant trevally, small pelagic fishes, and tuna (Ishihara et al., 2017; DeMartini et al., 2018; Andrews, 2020; Andrews et al., 2020; 2024; 2025b; Fraile et al., 2024). Some of the most extensive records of bomb-produced ^{14}C in the marine environment are within the temperate-tropical North Atlantic, from which there are numerous fish age validation studies using both coral and otoliths (e.g., Baker and Wilson, 2001; Cook et al., 2009; Shervette et al., 2021; Baremore et al., 2025). The existing coral ^{14}C reference records cover a wide geographical range from the western to eastern North Atlantic and Caribbean Sea to the island of Bermuda (Druffel, 1989; Wagner, 2009; Fernandez et al., 2015; Paterne et al., 2023), some of which have complementary juvenile fish (known age and date of formation) as reference material (Andrews et al., 2013; Barnett et al., 2018; Shervette et al., 2021).

The aim of this project was to use otoliths of North Atlantic albacore to estimate age from thin sections and to assess the validity of the ages by alignment or misalignment with a regional bomb ^{14}C reference chronology. Age reading refinement was targeted by, 1) looking for adjusted growth zone counting, in relation to well-defined otoliths, which would properly align with the ^{14}C reference, and 2) using otolith mass as a proxy for age in determining where age estimate errors might exist. The age reading protocol was also refined using a few young-of-the-year (YOY) otoliths to establish a distance from the nuclear region to the first annulus. Finally, additional otoliths that were not measured for ^{14}C were sectioned and aged by referring to the first annulus distance, early age length modes, otolith mass growth, and otoliths with well-defined growth zone structure and strong alignment with the bomb ^{14}C reference chronology, hereafter referred to as “Rosetta Stone” otoliths due to their defining characteristics. This combined approach assisted with estimating ages for all fish that were consistent with the age reading protocol, especially for sections with ambiguous or poorly defined growth zone structure. The combined age-at-length data were used to establish otolith-based, growth parameter estimates for North Atlantic albacore.

2. Methods

2.1 Canvassing and Selection of Specimens

Most albacore samples were collected from the northwest Atlantic off the east coast of the United States by the Pelagic Fisheries Lab at the University of Maine aboard commercial pelagic longline vessels and a few were sourced from National Oceanic and Atmospheric Administration (NOAA) and Spanish National Research Council (CSIC; **Table 1**). Of the seventy albacore otoliths available at the University of Maine Pelagic Fisheries Lab, a series was selected from specimens aged 3 to 17 years, all of which were collected in 2019 (labeled MAB and SNE specimens; Mid-Atlantic Bight, Southern New England). Additional specimens were sought from numerous sources by canvassing academic and government institutions, leading to otoliths from five medium sized albacore (80–90 cm CFL) collected by the Panama City Lab (labeled as PCL specimens; SEFSC, NOAA) in 2010, 2013, and 2021 that were later aged as 3 to 8 years old. The very smallest fish were missing from the age and growth analyses and as a result of further queries, some YOY specimens were located at the CSIC. These otoliths were aged using counts of daily increments to establish a dimensional yardstick from the nuclear region that can be used to determine the location of the first annulus, similar to the method used for Atlantic bluefin tuna (Secor et al. 2014). This information was

used to create a better level of age reading consistency in both younger and older otoliths by placing the yardstick over the otolith section image, ranging from the nuclear region and along the growth axis. The 15 North Atlantic albacore that were sampled for ^{14}C covered lengths of 39 to 115 cm CFL, whole otolith masses of 0.0084 to 0.0840 g, and estimated ages of 0.5 to 17 years.

Table 1. North Atlantic albacore specimen details and ^{14}C results from otolith samples that were provided by the Pelagic Fisheries Lab at the University of Maine (MAB, SNE), Panama City Laboratory (PCL), and the Spanish Institute of Oceanography (CSIC). The details of additional aged otoliths used to characterize growth are listed elsewhere (**Table SM1**). Error (abs) is the mean absolute error for counts made in the determination of $F^{14}\text{C}$ via AMS.

<i>Lab number</i>	<i>Specimen number</i>	<i>CFL cm</i>	<i>Sex</i>	<i>Otolith mass (g)</i>	<i>Date caught</i>	<i>Age</i>	<i>Hatch</i>	<i>$F^{14}\text{C}$</i>	<i>err (abs)</i>
ALB-001	MAB 2457	97	M	0.0407	4-Nov-19	4	2015.84	1.0483	0.0092
ALB-002	SNE 2442	97	M	0.0374	6-Oct-19	5	2014.76	1.0482	0.0075
ALB-003	MAB 2451	94	F	0.0456	4-Nov-19	4	2015.84	1.0418	0.0079
ALB-004	MAB 2448	99	--	0.0461	4-Nov-19	6	2013.84	1.0455	0.0080
ALB-005	MAB 2452	95	F	0.0361	4-Nov-19	4	2015.84	1.0412	0.0095
ALB-006	MAB 2456	111	M	0.0674	4-Nov-19	9	2010.84	1.0650	0.0085
ALB-007	MAB 2698	115	--	0.0648	12-Nov-19	11	2008.87	1.0745	0.0085
ALB-008	MAB 2621	112	--	0.0696	9-Nov-19	12	2007.86	1.0514	0.0081
ALB-009	MAB 2713	114	M	0.0780	14-Nov-19	13	2006.87	1.0619	0.0101
ALB-010	MAB 2474	111	--	0.0840	6-Nov-19	18	2001.85	1.0782	0.0083
ALB-011	PCL 2010 0001_01	92	--	0.0415	5-Sep-10	4	2006.68	1.0491	0.0123
ALB-012	PCL 2010 0002_01	88	--	Bkn-m	1-Aug-10	4	2006.58	1.0619	0.0096
ALB-013	PCL 2013 0003_04	83	--	0.0310	28-Jul-13	3	2010.57	1.0507	0.0093
ALB-014	PCL 2021 1003_03	89	U	0.0320	24-Jul-21	4	2017.56	1.0422	0.0096
ALB-015	PCL 2021 1003_02	86	U	0.0333	24-Jul-21	4	2017.56	1.0325	0.0104
ALB-016	CSIC ALB 08M2/14	39	U	0.0058	19-Aug-08	0.47	2008.17	1.0483	0.0092
ALB-017	CSIC ALB 08M2/15	43	U	0.0084	19-Aug-08	0.47	2008.07	1.0482	0.0075
ALB-018	CSIC ALB 08M2/12	44	U	0.0084	19-Aug-08	0.57	2008.07	1.0418	0.0079

Bkn-m = Broken and not weighed due to missing piece.

2.2 Otolith Processing and Age Estimation

Otolith samples were obtained from multiple laboratories that followed a relatively consistent approach for preparing sections. Methods varied slightly but the common process was embedding the whole otolith in clear epoxy resin and taking a thin transverse section that was polished and mounted to a glass slide. Age was initially determined by counting presumed annually deposited opaque zones, which were visualized using transmitted light illumination (**Figure 1**). Consecutive opaque and translucent zones creating annuli were assumed to represent 1 year of otolith growth. Age was estimated without a defined age reading protocol for North Atlantic albacore and relied on the increment structure observed in a few well-defined otolith sections. These initial age estimates provided guidance on how a refined age reading protocol could be developed based on bomb ^{14}C dating, an otolith mass-to-age relationship, a length mode analysis from the North Atlantic (Ortiz de Zárate et al., 2024), and verification of the first annual opaque zone from counting daily increments in YOY North Atlantic albacore. Once the refined age reading was established, an additional set of thirty-three otoliths (**Table SM1**) were aged using this approach to create an opportunity to model fish growth through ontogeny using a von Bertalanffy growth function.

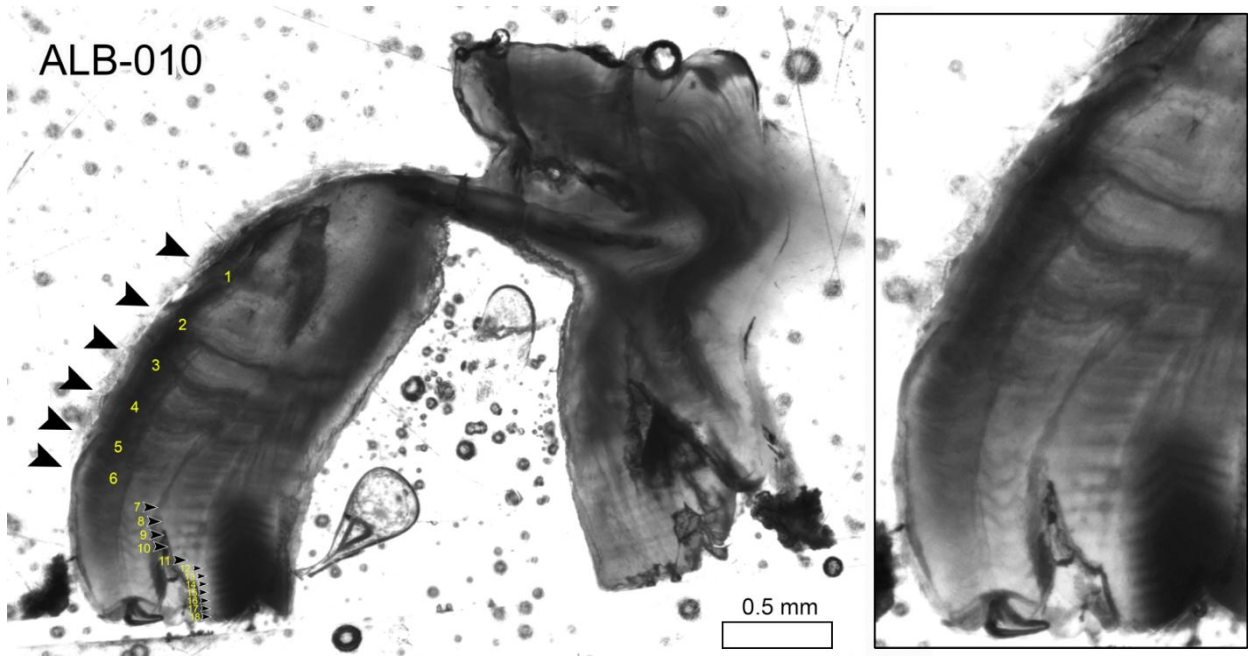


Figure 1. The transverse otolith section shown here was not only the oldest North Atlantic albacore at 18 years (ALB-010) but was considered to be one of the “Rosetta Stone” otoliths used in providing guidance for other otoliths that were not as well defined. Although the transverse section alignment is offset from the otolith center, growth zone definition was clearly defined. The zoomed in portion of the full otolith section on the right provides an unobstructed view of the subtle growth zone structure toward the latter years. This otolith was also the most massive for the sample series assessed with bomb ^{14}C dating (**Figure 2**) and the age of 18 years was well supported with an alignment to the bomb ^{14}C reference chronology (**Figure 3**).

2.3 Age estimation refinement and validation

Otolith mass and the initial age estimates were used as a tool in describing the potential shortcomings of the age reading process. By plotting otolith mass as a proxy to predict age, a logical pattern should arise that shows a good correlation between increasing age and otolith mass (**Figure 2**). A wide range of otolith mass values for a given age suggests that age reading may be inconsistent in certain areas of the otolith section. Visual reference to Rosetta Stone otoliths can assist in identifying errors, such as early overcounting of subannual zones or miscounting of increments in older parts of large otoliths where fine growth structure is difficult to distinguish. Early overcounting is most clearly manifested as a wide range of ages for low mass otoliths and is revealed as subannual structure that is being mistakenly counted as annual (e.g., Baremore et al., 2025). Furthermore, use of length modes for the earliest years of growth can also assist with age refinement (i.e., Ortiz de Zárate et al., 2024). Erroneous counting in the largest otoliths from older individuals can be assessed with what may be a very wide range of age estimates for the greatest otolith masses (e.g., poor age estimate to otolith mass relationship for European eel (*Anguilla anguilla*); Andrews et al., 2025a). In each of these cases, a poor correlation can help discover interpretation inconsistencies; however, it is necessary to introduce some level of temporal calibration to know where the actual problems are for the initial age estimates. Two approaches were used for North Atlantic albacore: 1) a few otoliths of YOY (rare) were located and aged with daily increment counting, as was done with South Pacific and South Atlantic albacore (Lee and Yeh, 2007; Farley et al., 2021), and 2) bomb ^{14}C dating was applied using offsets in measured ^{14}C values to constrain age estimates, as was the case for snapper of Hawaii and the Caribbean Sea (Andrews and Scofield, 2021; Baremore et al., 2025).

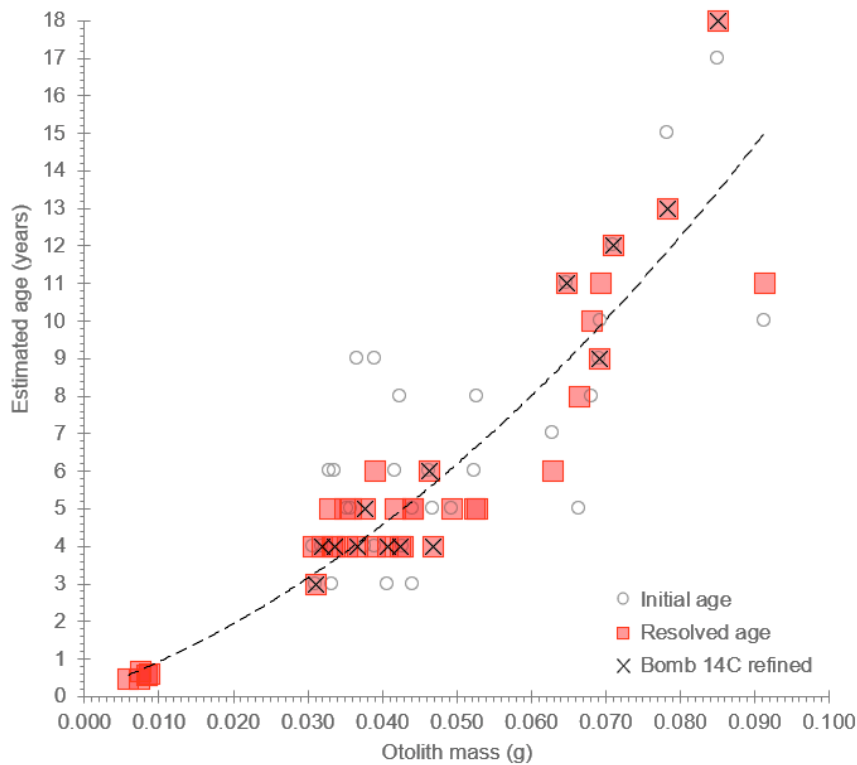


Figure 2. The initial age estimates for sectioned North Atlantic albacore can be seen as inconsistent relative to otoliths mass. Refinement of the age estimates (resolved age) using the first annulus yardstick (**Figure 1**) — along with the alignment of measured ^{14}C values to the bomb ^{14}C reference chronology (**Figure 3**) and early aged length classes — for the recalculated hatch years led to a tighter relationship in terms of otolith mass as a proxy for age. The exception was the most massive otolith available (ALB-026, 0.0913 g) that could not be confidently aged greater than 11 years. Overall, the approach boosted confidence for most of the findings from growth zone counting and the determination of growth parameters from the resolved ages (**Figure 4**).

2.4 Young-of-the-year otoliths

Otoliths of YOY North Atlantic albacore were rare and only six could be located from the Bay of Biscay in the eastern North Atlantic. These otoliths were assumed to provide a good proxy for establishing the first annulus of the older albacore from the western North Atlantic considering the common origin of albacore in the North Atlantic (Fraile et al., 2016). One of each sagittal otolith pair was used for daily increment age reading and the other was used to establish known date ^{14}C measurements. Prepared otoliths were read to a point of increment compression — typically up to ~250 days — that could be used to identify the first annulus. The mean distance to this compressed region was used to establish an index or “yardstick” that could be used as a tool to refine age estimates, such as evidence for early overcounting (subannual growth zone structure). This tool was combined with the, 1) Rosetta Stone otoliths, 2) early growth length modes (showing 3 clearly defined length modes for fish under 80 cm (SFL)), 3) otolith mass-to-age relationship, and 4) results from bomb ^{14}C dating to refine age estimates for the full range of North Atlantic albacore otoliths used in this study.

2.5 Bomb ^{14}C reference chronology

Existing ^{14}C measurements from age-dated coral cores and individual measurements from young or known-age otoliths were compiled to create a ^{14}C reference chronology for the tropical North Atlantic (**Figure 3**). These records of bomb-produced ^{14}C cover decades of studies throughout the tropical North Atlantic, which provides the sum product for ^{14}C levels expected from otoliths that formed across this region (Andrews et al., 2013; 2020; Barnett et al., 2018; Shervette et al., 2021). The reference chronologies exhibit slightly different slopes of $-2.1\text{‰}\cdot\text{yr}^{-1}$ for the Caribbean Sea region and $-2.4\text{‰}\cdot\text{yr}^{-1}$ for more northerly locations in the tropical western North Atlantic. This collective reference chronology was used to make comparative alignments of measured ^{14}C values for the calculated hatch years of aged North Atlantic albacore. An offset coral ^{14}C record from Cape Verde Islands in the eastern North Atlantic exemplifies the effect of ^{14}C -deficient waters in eastern boundary currents (Fernandez et al., 2015; Toggweiler et al., 2019; Paterne et al., 2023).

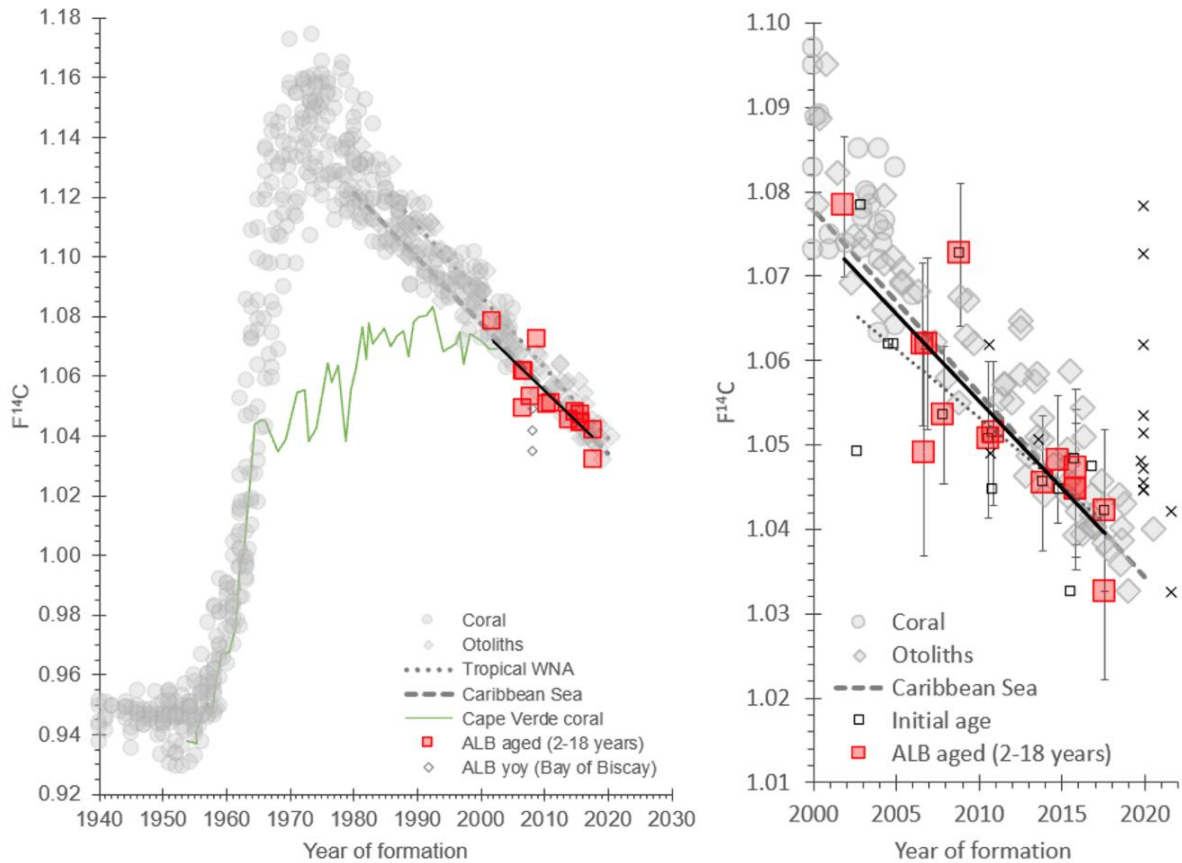


Figure 3. Otolith ^{14}C data from the cores of aged albacore from the western North Atlantic for fish aged 3–18 years are plotted as hatch years (red squares) relative to the ^{14}C reference chronology (gray symbols). The ages were the result of refinement from use of Rosetta Stone otoliths (**Figure 1**), otolith mass as a proxy for age (**Figure 2**), and early-age length modes (Ortiz de Zárate et al. 2024), coupled with observations of offset hatch dates from the post-peak decline (initial age in right panel as squares). Coral and otolith ^{14}C records from the tropical western North Atlantic Ocean are shown as the comprehensive (pre-bomb to post-peak decline) reference chronology (right). The Caribbean Sea (dashed line; -2.1‰ per year) exhibits a lower slope than the more fortified tropical western North Atlantic (dotted line; -2.4‰ per year). The fit and slope to the resolved North Atlantic albacore hatch years was similar to the Caribbean Sea at -2.1‰ per year ($R^2 = 0.710$), an improvement over the low slope of -1.6‰ per year with greater scatter ($R^2 = 0.498$) from the initial reads. Some of the known-age albacore (YOY) from Bay of Biscay may have been ^{14}C -deficient due to early movement to the eastern North Atlantic (Fraile et al. 2016), a region affected by eastern boundary currents (upwelled water sources), like the unusual ^{14}C record from a Cape Verde Islands coral. Vertical error bars represent the mean absolute error.

2.6 Otolith core sampling

Extraction of the earliest growth (core material as calcium carbonate) was targeted for ^{14}C measurements in otoliths of both YOY and older albacore specimens. Otoliths were prepared specifically as illustrated in the supplementary material of Andrews et al. (2020). Microscopic examination of the extracted otolith cores, coupled with containment using a flexible mounting medium (Cytoseal 60, Richard Allen Scientific Company), provided confidence that the earliest growth was isolated and collected for ^{14}C measurements. Observations of daily increments in the otolith core region, along with measured dimensions of approximately 2.0 mm L x 1.5 mm W x 0.4 mm D that were smaller than known-age YOY, were used as confirmation that sampling was within the first year of life. Core samples were liberated from the mounting medium with toluene, cleaned in detergent, rinsed in deionized water, and air dried.

2.7 Accelerator mass spectrometry

The calcium carbonate samples were analyzed by gas-accelerator mass spectrometry (AMS) for carbon isotopes using the Mini Carbon Dating System (MICADAS; Synal et al., 2007). Samples were placed in AMS-ready, septum-sealed vials (Labco Exetainer 4.5 mL #948) and purged of ambient CO_2 with a Helium carrier. Sample CO_2 was subsequently generated with 80% phosphoric acid and injected into the AMS via syringe on the gas interface. Fossil and modern reference materials (IAEA-C1; Rozanski 1991) and an in-house coral standard (CSTD, nominal F^{14}C value 0.9447 ± 0.0002 , G. Dos Santos, pers. comm.) were analyzed in parallel with the samples. The “Beautiful AMS Tool of Switzerland” software (BATS) was used as the reliable data reduction tool (Wacker et al., 2010). Radiocarbon results were reported as fraction modern (F^{14}C), the fractionation-corrected sample activity (Reimer et al., 2004).

2.8 Bomb ^{14}C dating

Measured ^{14}C values from the otoliths of aged North Atlantic albacore were aligned based on the calculated hatch date (age subtracted from capture date). An adjustment of +0.25 years for the hatch date was used to correct for a 6-month core formation period. Alignment or misalignment of the values was used to inform potential adjustments to the original estimated ages, as well as the age reading protocol used to age each fish. This approach was combined with the otolith mass-to-age relationship, early growth length modes, a selection of age-validated Rosetta Stone otoliths, and a reinvestigation of early growth zone counting with the delineation of the first annulus using the daily increment yardstick.

3. Results

The initial estimates of age from thin sectioned otoliths of North Atlantic albacore were read several times with little reference, aside from a few well-defined otolith sections. The most massive otolith from the first set of specimens that were considered was fortuitously one of the best otolith sections and was the oldest estimated age of 17 years. This otolith was considered a Rosetta Stone in refining the initial age reading for the other sections that were not as well defined or had ambiguous growth zone structure that was difficult to read; however, it was later determined based on observations of the otolith section that the orientation of the transverse sections in this set of otoliths was away from the primordium. This resulted in a modification of the counting in these sections in terms of identifying the first annulus, which led to an increase of the estimated age by one year to 18 years for this oldest fish (**Figure 1**). The use of otolith mass as a general proxy for age served as an initial indication that the age reading might be inconsistent due to a weak otolith mass-to-age relationship (**Figure 2**). The scatter of age estimates for a given otolith mass was wide ranging and thought to be an indication that early overcounting of subannual growth zones was occurring. This scattered relationship was refined using otolith mass, coupled with daily growth increment information, early growth length modes, and bomb ^{14}C dating relationships (**Figure 3**).

Daily increment counting in the smallest otoliths provided guidance for the location of the first annulus. The distance to the inner edge of the first annulus was on average 0.75 mm from the nuclear region. This distance was translated into a yardstick that could be used as an overlay in other otolith sections. Use of this information reduced the initial age estimates for some low-mass otoliths by precluding counts made in the area of rapid otolith growth. However, otolith sections that were offset from the nuclear region had to be considered more carefully due to a reduction in the distance to the first annulus. Use of these tools led to a more constrained otolith mass-to-age relationship (**Figure 2**).

Bomb ^{14}C dating was used to further support or refine the adjusted age estimates and the reading protocol by revealing an offset of some calculated hatch years from the bomb ^{14}C reference chronology (**Figure 3**). While the ^{14}C values increased as expected for older hatch years along the post-peak decline using the initial age estimates, the relationship was poor with a skew toward lower ^{14}C values through time. In general, the slope was lower than expected (-1.6 ‰/year), relative to the two overlapping regional ^{14}C records for the Caribbean (-2.1 ‰/year) and tropical western North Atlantic (-2.4 ‰/year). Adjusted ages, using the first annulus yardstick, early length modes, and Rosetta Stone otoliths, in conjunction with otolith mass-to-age relationship, led to iterative age estimate changes that achieved the best alignments. The finalized age estimates were consensus counts made by two experienced age readers, along with some that were adjusted to counts that provided better conformity to each of the tools being considered. The resolved ages led to hatch years that were more closely aligned with the Caribbean Sea bomb ^{14}C reference chronology with a slope of -2.1 ‰ per year (**Figure 3**).

Two of the three reference otolith ^{14}C measurements were lower than expected (**Figure 3**). North Atlantic albacore of this size (39–44 mm CFL) were rare and none were available from the western North Atlantic. Hence, these fish collected from the Bay of Biscay in the eastern North Atlantic were used assuming their natal origins were similar. Evidence for early movement to the eastern North Atlantic from spawning grounds in the southern Sargasso Sea (Fraile et al., 2024) may provide an explanation for the ^{14}C -deficient values for some YOY and cored older adults.

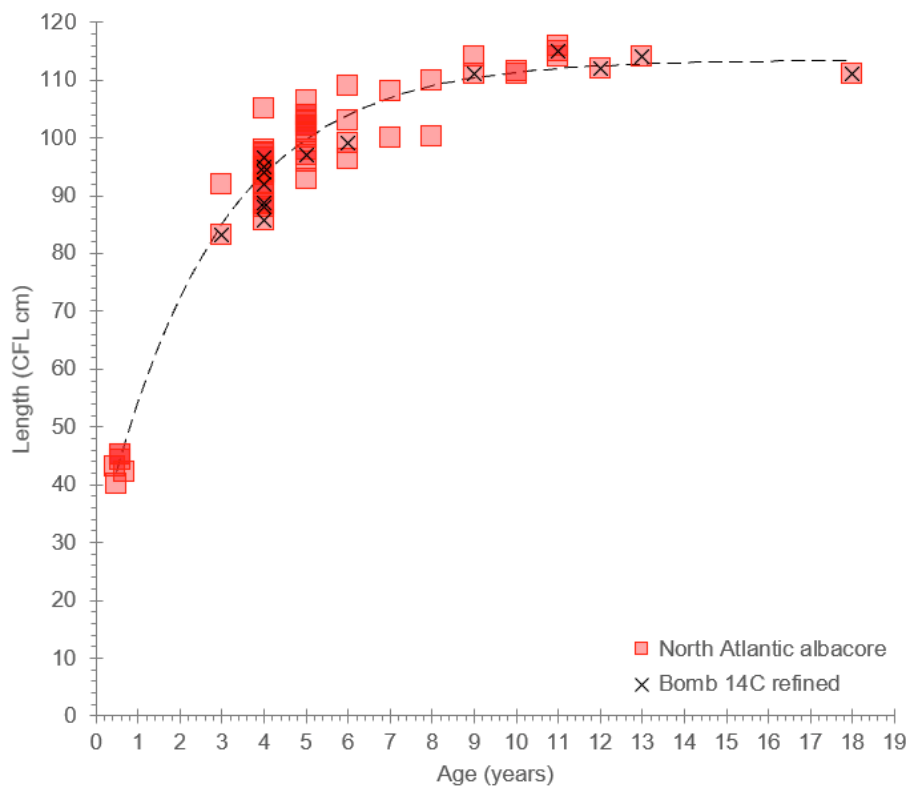


Figure 4. Curve fit of the von Bertalanffy growth function to the resolved age-at-length data for North Atlantic albacore. The bomb ^{14}C dated (used in refining the reading protocols, $n = 15$), additional sectioned ($n = 34$), and daily counted ($n = 5$) otoliths resulted in a total of 54 aged specimens. The resulting parameters describe growth characteristics that are more rapid with a greater longevity than other studies on albacore across its geographical range ($L_{\infty} = 113.5\text{ cm CFL}$, $k = 0.367$, $t_0 = -0.767$).

The concluding result was a set of 54 aged North Atlantic albacore otoliths with a von Bertalanffy growth function fitted to these results as the first otolith-based age-at-length assessment (**Figure 4**). Growth characteristics exhibit rapid initial growth in the first 3–5 years of life followed by asymptotic growth through to a potential maximum age of 18 years ($L_{\infty} = 113.5\text{ cm CFL}$, $k = 0.367\text{ yr}^{-1}$, $t_0 = -0.767\text{ yr}$).

4. Discussion

This work represents the first example of an exclusively otolith-based age and growth study conducted on North Atlantic albacore that incorporates direct age validation. A maximum age of 18 years for North Atlantic albacore was well supported on the basis of well-defined otolith growth zone structure and an alignment of the measured ^{14}C value to the bomb ^{14}C reference chronology (ALB-010). While the oldest estimated albacore in the Atlantic until now was 13 years, ICCAT recognizes the more comprehensive and validated otolith-based work conducted in the Pacific and has assumed a maximum longevity of 15 years for the North Atlantic (Wells et al., 2013; Farley et al., 2013; 2021; Artetxe-Arrate et al., 2023). This highlights the importance of validating and standardizing methodologies across ocean basins, as stock assessments and the ICCAT Standing Committee Research and Statistics (SCRS) use growth models from Bard (1981) and Santiago and Arrizabalaga (2005), both of which use ages based on fin spine derived counts and tag-recapture data. A recent work on the reproductive biology for the North Atlantic albacore stock revealed a maximum estimated age of 11 years with life history traits derived from fin spine sections (Macías et al., 2025), which highlights the need for an exploration of otolith-spine age reading relationships.

Asymptotic growth is apparent as the fish in this group approach maximum size in the first 5–6 years of life, exhibiting a strong decoupling of length from otolith-derived age — similar sized fish can differ in age by up to 10 years. Growth for this albacore stock is rapid in the first few years of life and appears to be greater than described for other albacore stocks. Studies of the southern and northern Pacific albacore stocks describe growth that is slower growing than described here for the North Atlantic ($k = 0.172\text{--}0.317$ cf. 0.367; J. Farley, pers. comm., Snodgrass et al. 2025). While there is uncertainty about how albacore grow during early life history for the South Pacific, the age and growth estimates were well supported and refined (Farley et al., 2013; 2021). This work led to a recent exploration to establish an epigenetic clock — a non-lethal method of estimating age — with a reported maximum age of nearly 18 years (Chevrier et al. 2026), similar to the longevity determined here from a well-defined otolith of the North Atlantic (**Figure 1**). Of note are results from the first annulus determination using daily increment counting and the tag-recapture of a few key North Atlantic albacore. Refinement of the age reading protocol was similar to this study by locating the first year of growth at the inner annulus edge near 0.7 mm from the inflexion or nuclear region, and the section images closely resemble those acquired for otoliths of the North Atlantic. Otolith mass was deemed an effective tool in resolving age estimate discrepancies for North Atlantic albacore, particularly when coupled with the identification of the first annulus using daily increments, comparisons with early-age length modes, and the alignment of ^{14}C values to the reference chronology.

The ^{14}C data from the otolith cores of aged North Atlantic albacore otoliths that were collected by the Pelagic Fisheries Lab at the University of Maine and NOAA had calculated hatch years that were almost entirely aligned with the post-peak decline. The measured ^{14}C values for the series of North Atlantic albacore otoliths covered a wide range that would be expected from recently collected fish with calculated hatch years dating back to the early 2000s. The focus was initially on recently collected otoliths in the year 2019 to create a series of measurements that would follow the post-peak decline over a period of ~20 years, which was near the maximum estimated age from this data set, in an approach similar to what was used for yellowfin tuna of the North Atlantic (Andrews et al., 2020). The ^{14}C levels from the North Atlantic albacore cores in this initial set decreased as expected toward younger individuals for fish initially aged 2–17 years ($F^{14}\text{C} = 1.0418$ to 1.0782). Additional otoliths from albacore aged 3–8 years by PCL were added to the data set with collection dates covering different years. Most otoliths aligned with the reference chronology once section age and fish size for early age classes, coupled with otolith mass, were considered. Because the youngest specimens were absent, a set of YOY that were collected by CSIC from the Bay of Biscay were provided for the study. It is certain that these fish were YOY based on the small body size and daily increment counts that confirmed ages near 0.5 years (daily ages ranged from 0.47 to 0.68 years for the YOY samples (39cm to 44 cm)); however, the alignment of the ^{14}C values from these known-age otoliths did not entirely agree with the reference chronology for two of the three samples, each of which fell below the reference chronology. Collection dates were verified for the sample set and as a result, other explanations for the low values were sought. No sample handling or sample mass limits could be attributed to the lower-than-expected values; therefore, additional consideration was given to the oceanography of the collection location and potential natal grounds of albacore across the North Atlantic. The Bay of Biscay is located at the eastern boundary of the North Atlantic and fish originating from this region are more likely to have been exposed to ^{14}C -deficient waters, as opposed to the western boundary areas that exhibit pooling effects of warm tropical waters (Toggweiler et al., 2019). Evidence for an early transit to the eastern North Atlantic could explain uptake of reduced ^{14}C levels for the otolith formation period that was sampled in the core extraction. This could also

explain some of the older adults that were slightly ^{14}C -deficient. This eastern region exhibits highly variable ^{14}C levels due to upwelling — as shown by the attenuated bomb ^{14}C signal at Cape Verde (Fernandez et al., 2015; **Figure 3a**) and coupled with low ^{14}C values measured in historic DIC assays off the northwest Africa (Nydal et al., 1984) — is a reasonable explanation for the ^{14}C deficiency.

The initial age reading of annual growth zone structure in thin-sectioned otoliths of North Atlantic albacore was effectively adjusted for errors in age estimation using otolith mass, lengths for early age classes, daily increment counting, and bomb ^{14}C dating. Reconsideration of the initial age estimates for some fish based on low otolith mass or small fish size led to better alignments, especially when considering the location of the first annulus and alignment of the ^{14}C values from otolith cores to the regional bomb ^{14}C reference chronology. The circular approach to considering various alignments in an iterative manner reinforced the final age determinations, but the remaining uncertainty for some otolith sections that were offset from the nucleus is something that should be addressed in a follow up otolith-based age estimation study. While the number of fish considered in this study is much lower than for comparable albacore stocks, like the South and North Pacific Oceans, the age reading protocols were refined and validated to an extent in this study. It is recommended that further study of North Atlantic albacore be conducted by collecting otoliths, coupled with fin spines to evaluate the level of agreement, across all size- and age-classes for a more comprehensive study of validated age and growth.

The use of ^{14}C results on consensus age estimate interpretations, coupled with other forms of age-related information, to refine age estimates is a different approach to the normal application of bomb ^{14}C dating — a direct evaluation of age estimate validity. This multifaceted approach, as applied here to North Atlantic albacore as an investigative tool, could be useful in developing valid life history characteristics for other stocks and species where no previous otolith age reading has been undertaken.

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Supplemental Materials - BOMB ¹⁴C DATING, AGE ESTIMATE REFINEMENT, AND GROWTH CHARACTERISTICS OF NORTH ATLANTIC ALBACORE (*THUNNUS ALALUNGA*) USING OTOLITHS

Table SM1. Additional North Atlantic albacore specimens that were aged using revised age reading protocols.

<i>Lab number</i>	<i>Specimen number</i>	<i>CFL cm</i>	<i>Sex</i>	<i>Otolith mass (g)</i>	<i>Date caught</i>	<i>Age</i>
ALB-019	SMAB 2041	108	M		21-Nov-20	7
ALB-020	SMAB 2060	116	M	0.0693	25-Nov-20	11
ALB-021	SMAB 2064	109	M	0.0629	25-Nov-20	6
ALB-022	SMAB 2065	98	M		25-Nov-20	5
ALB-023	SMAB 2097	110	M	0.0661	27-Nov-20	8
ALB-024	SMAB 2114	102	M	0.0494	29-Nov-20	5
ALB-025	MAB 2464	100		0.0358	5-Nov-19	5
ALB-026	MAB 2471	114	M	0.0913	6-Nov-19	11
ALB-027	MAB 2479	97.5	M	0.0427	6-Nov-19	4
ALB-028	MAB 2583	105		0.0390	7-Nov-19	4
ALB-029	MAB 2590	106.5	M	0.0442	7-Nov-19	5
ALB-030	MAB 2591	91		0.0353	7-Nov-19	4
ALB-031	MAB 2597	111.5	M	0.0682	9-Nov-19	10
ALB-032	MAB 2600	101	M	0.0441	9-Nov-19	5
ALB-033	MAB 2677	102		0.0524	11-Nov-19	5
ALB-034	MAB 2699	103			12-Nov-19	6
ALB-035	MAB 2700	114	M		13-Nov-19	9
ALB-036	MAB 2701	104			14-Nov-19	5
ALB-038	MAB 2714	104	M	0.0528	14-Nov-19	5
ALB-039	MAB 2653	111	M		10-Nov-19	10
ALB-040	PCL 2010 0006_0001	96.4		0.0390	14-Aug-10	6
ALB-041	PCL 2013 0001_0002	92.1		0.0307	28-Jul-13	4
ALB-042	PCL 2020 1000_0001	102.8		0.0418	23-Aug-20	5
ALB-043	PCL 2020 1002_0003	98			6-Sep-20	4
ALB-044	PCL 2021 1000_0002	100			23-Oct-21	7
ALB-045	PCL 2021 1000_0003	95.8		0.0330	23-Oct-21	5
ALB-046	PCL 2021 1000_0004	94			23-Oct-21	4
ALB-047	2021ALB1000_0005	92			23-Oct-21	3
ALB-048	2021ALB1001_0002	100.3			15-Oct-21	8
ALB-049	2021ALB1002_0001	93.6		0.0332	7-Aug-21	4
ALB-050	2021ALB1002_0002	92.8		0.0349	7-Aug-21	5
ALB-051	2021ALB1003_0004	88.4			24-Jul-21	4
ALB-052	2021ALB1003_0005	97.3			24-Jul-21	4
ALB-060a	CSIC ALB 08M2/2	43		0.0074	19-Aug-2008	0.47
ALB-060b	CSIC ALB 08M2/6	42		0.0076	19-Aug-2008	0.68
ALB-060c	CSIC ALB 08M2/17	45		0.0088	19-Aug-2008	0.59