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Age validation of yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna of the northwestern Atlantic Ocean

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Abstract

The age and growth of yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna remain problematic because validation of growth zone deposition (opaque and transparent) hasn't been properly evaluated. Otolith growth structure (zone clarity) can be poorly defined for tropical tunas but the use of bomb radiocarbon dating has validated age estimates to 16–18 years for yellowfin and bigeye tuna. Use of the radiocarbon decline period — defined by regional coral and otoliths — provided valid ages through ontogeny. Yellowfin tuna aged 2–18 years (n = 34, 1029–1810 mm FL) and bigeye tuna aged 3–17 years (n = 12, 1280–1750 mm FL) led to birthyears that were coincident with the bomb radiocarbon decline. The results indicate there was no age reading bias for yellowfin tuna and that age estimates of previous studies were likely underestimated for both species.

Keywords: Scombridae, bomb radiocarbon, carbon-14, Gulf of Mexico, lifespan

Introduction

The age, growth, and potential lifespan of yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna (YFT and BET) remain problematic in that attempts to validate age estimates were typically incapable of evaluating maximum age. Recent estimates for the age and growth of YFT and BET indicate growth may be slower than previously estimated and maximum age may reach mid- to upper-teenage years (Farley et al. 2017; Lang et al. 2017). Work with length frequency analyses (LFA; Le Guen and Sakagawa 1973; Kikkawa and Cushing 2002; Zhu et al. 2009), tag-recapture data (Hampton and Fournier 2001; Hallier et al. 2005), daily increment counting in otoliths (Hallier et al. 2005; Schaefer and Fuller 2006; Shuford et al. 2007), and growth zone counting in otoliths (Farley et al 2006; Shih et al. 2013; Lang et al. 2017) and fin spines (Lessa and Duarte-Neto 2004) have led to wide ranging disparities in age and growth estimates for these species with inadequate findings in terms of age validation and maximum age. Tuna species with greater life spans have a higher probability of being overfished (Juan-Jorda et al. 2015), and growth patterns similar to what is being investigated here for YFT have been described for its closest relative, the neritic longtail tuna (*T. tonggol*), with a maximum age estimate of 19 years (Griffiths et al. 2010). Consequently, accurate estimates of age-at-length and potential lifespan need to be determined for tuna species because they are critical for determining natural mortality, one of the most influential stock assessment parameters (Then et al. 2015), and as a metric for evaluating age/size specific fecundity estimates (Birkeland and Dayton 2005).

Otolith growth zone structure can be complicated for tropical pelagic fishes because they live in a more aseasonal environment than higher latitude habitats, but marine chemistry and the sequestration of carbon to the otolith provides a unique tool in validating the age of fishes — bomb radiocarbon (^{14}C) dating. This method has evolved considerably over the last 25 years (Kalish 1993; Andrews et al. 2019) and takes advantage of the ocean mixed layer where air-sea diffusion of the bomb-produced ^{14}C signal from the 1950s and 1960s is shared among individuals living in this marine environment. It is this common record of the bomb-produced ^{14}C signal found in hermatypic coral and otoliths of tropical fishes that can be used to validate age (Campana 1999). The approach is well-founded and has been useful in life history studies at various tropical locations (e.g., Andrews et al. 2011, 2015, 2016*a*; DeMartini et al. 2018), including the Gulf of Mexico (Cook et al. 2009; Andrews et al. 2013; Barnett et al. 2018) and the pelagic environment (Andrews et al. 2018), including 3 species of bluefin tuna (Kalish et al. 1996; Neilson and Campana 2008; Ishihara et al. 2017).

For YFT and BET from the northwestern Atlantic - Gulf of Mexico region, it is reasonably certain that the earliest growth for these fishes was within the warm surface waters (Brill and Lutcavage 2001), where the ^{14}C signal would be contemporaneous and comparable to existing chronological references. This is consistent with other stable isotope assays that have traced natal origins for these species in the surface waters of the Pacific Ocean (e.g., Rooker et al. 2016). Because bomb ^{14}C dating is a well-established tool in providing valid birth years for fishes of tropical waters, the emphasis of this study is the use of bomb-produced ^{14}C in the earliest growth of adult otoliths to evaluate the validity of YFT and BET age estimates through ontogeny by alignment of measured values with the regional ^{14}C reference chronology. Further, because recent estimates approach 20 years for each species, the bomb ^{14}C decline period is potentially diagnostic for age and could easily differentiate age interpretation discrepancies that may have led to truncated estimates of growth and maximum age.

Methods

The regional ^{14}C reference used for the bomb ^{14}C dating of YFT and BET was a combination of hermatypic coral and otolith records of juvenile specimens (including other teleost fishes) from across the Gulf of Mexico. This record was established in a series of studies (Andrews et al. 2013; Barnett et al. 2018) and was further reinforced here with yearling YFT otoliths (aged 1+ and less than 2 years) as determined from a 1-year yardstick (a core to first annulus reference that was ascertained from daily increment counting; Lang et al. 2017) and the margin type (thick translucent) that is representative of growth beyond the first annulus (n = 8; Table S1). These data were fitted with a Loess curve to establish the central tendency of bomb-produced ^{14}C for the region. In anticipation of using the bomb ^{14}C decline period (1980s to 2010s), a linear regression of the ^{14}C reference values was used to calculate 95% prediction intervals, which were used to establish constraints on the validity of an age estimate from the birth year alignment or misalignment — birth years were determined as the difference between collection date and the number of growth zones counted for each individual. All otoliths were aged by counting presumed annual growth zones, defined as successive opaque and translucent zones where the opaque zone is counted under transmitted light (Fig. 1).

The otoliths selected for this study were from YFT and BET specimens that were collected by the National Marine Fisheries Service (NMFS) Pelagic Observer Program aboard commercial pelagic longline vessels, and both Louisiana state and NMFS port agents sampling recreational landings from the north-central Gulf of Mexico during 2011–2016. Selected yellowfin tuna otoliths (n = 34) were estimated to be 2 to 18 years of age with lengths of ~1000 to 1800 mm FL (Table S2). The first annulus in yellowfin tuna is particularly difficult to distinguish; therefore, the distance from the core to the proximal edge of the first annulus along the sulcus was measured and compared to similar measurements obtained through counting daily increments from Lang et al. (2017). Otoliths available for BET were fewer (n =

12) and were estimated to be 3 to 17 years of age with lengths of ~1300 to 1750 mm FL (Table S3). A range of older adult specimens that were collected in 2012 ± 1 year was the focus of the YFT series to provide corresponding birth years (calculated from the growth zone derived age estimate) that would cover the ^{14}C decline period (1980s to 2000s). This nearly common collection year would emphasize the relation of older fish to more elevated ^{14}C levels on earlier parts of the bomb ^{14}C decline. YFT and BET otoliths were collected opportunistically, and sex was recorded when possible. Sex ratio was close to 1:1 for both species despite a low sample size for BET. Whole otolith mass was considered for both species as a general proxy for age and a tool for eliminating potential age estimate outliers (Fig S1).

Radiocarbon measurements were performed on the earliest growth of the YFT and BET otoliths. Sample extractions were made in a series of steps that allowed the core of the whole otolith — estimated to be several months of growth — to be isolated manually (Fig S2). Several yearling otoliths that measured approximately 10–11 mm long by 2–3 mm wide by 1–2 mm thick with masses ~0.02–0.03 g provided guidance, to which the core extractions were well within these dimensions and mass (3.5 mm long by 1.1 mm wide by 0.5 mm thick with a mean extracted mass = 0.005 g). The extracted otolith samples were submitted as carbonate to the National Ocean Sciences Accelerator Mass Spectrometry Facility (NOSAMS, Woods Hole Oceanographic Institution in Woods Hole, Massachusetts) for standard hydrolysis analyses to determine sample ^{14}C levels (Tables S1–S3). Radiocarbon measurements were reported by NOSAMS as Fraction Modern — the measured deviation of the ^{14}C/^{12}C ratio from Modern. Modern is defined as 95% of the ^{14}C concentration of the National Bureau of Standards Oxalic Acid I (SRM 4990B) normalized to δ^{13}CVPDB (–19‰) in 1950 AD (VPDB = Vienna Pee Dee Belemnite geological standard). Radiocarbon results were corrected for isotopic fractionation using δ^{13}C measured concurrently during AMS analysis and are reported here as F^{14}C (Reimer et al. 2004). Stable isotope δ^{13}C measurements were made on a split of CO$_2$ taken from the CO$_2$ generated from acid hydrolysis.

Results

A total of 45 otolith sample extractions were made from adult YFT otoliths, and two were either lost during extraction (YFT-C09) or considered an unreliable extraction (YFT-C26). F^{14}C values ranged as expected, from a low F^{14}C of ~1.05 in 2015 to a high of ~1.10 in 1995 covering a span of 20 years and an expected monotonic decline of 2.5‰ per year (Tables S1, S2). Estimates of age from growth zone counting for YFT were supported by a consistent alignment of the ^{14}C values from otolith core material with the regional bomb ^{14}C reference curve (Fig. 2) — much greater ages were possible due to a potential alignment with the bomb ^{14}C rise but were highly unlikely.

The series of yearling YFT otoliths, aged using daily increment measurements from YOY to identify the first annulus, were selected as reference material which further supported the existing ^{14}C decline pattern with consistent values through to 2015 (Table S1). The combined ^{14}C decline relationship from coral, other juvenile otolith samples, and the YFT juveniles is now well-supported through 2015 as a reference for otolith material from cored adult fishes of the region (Fig. 2). A regression of all ^{14}C decline reference data from 1989 to 2015 ($F^{14}C = -0.00242 \cdot (\text{year}) + 5.92$; $R^2 = 0.949$) was nearly coincident with the Loess curve fit (Fig. 3), as would be expected from a monotonic decline of post-peak bomb ^{14}C in the Gulf of Mexico.

Older YFT aged 2 to 18 years (n = 34, 1029 to 1810 mm FL) were validated by residing within the 95% prediction intervals of the ^{14}C decline scenario, with the exception of one individual that was marginal (Fig. 3). The oldest fish typically had the most massive otoliths, approaching or exceeding 0.15 g (Fig. S1). A regression of all YFT birth years provided a relationship that was similar to a regression of the ^{14}C decline reference (YFT adults 1995 to 2011: $F^{14}C = -0.0250 \cdot (\text{year}) + 6.079$; $R^2 = 0.883$) — the YFT birth year slope was consistent with the reference providing a monotonic ^{14}C decline of 2.50‰ per year (2.37–2.70‰, 1SE; Barnett et al. 2018), and the slopes were not significantly different ($t_{0.05(2),66} = 1.995$, $t_{\text{crit}} = 1.680$). An age bias analysis of YFT birth years relative to the central tendency of the F^{14}C reference, by minimizing the sum of squared residuals (SSR; Kastelle et al. 2008), revealed age estimates from growth zone counting were accurate overall with a minor bias of –0.5 years (number of intentionally biased years (SSR value): –2 (197), –1 (124), –0.5 (**112**), 0 (118), +0.5 (141), +1 (181)).

A total of 12 otolith sample extractions were made from aged BET otoliths. F^{14}C values ranged as expected, from a low F^{14}C of ~1.06 in 2011 to a high of ~1.10 in 1995 covering a span of 16 years and an expected monotonic decline of 2.5‰ per year (Table S3). Limited data for BET precluded a meaningful age bias analysis but age estimates were supported from 3 to 17 years (n = 12, 1280 to 1750 mm FL), with the exception of two marginal individuals (Fig. 3). The oldest fish of 17 years had the most massive otolith, approaching 0.18 g, while otoliths of fish aged 11–12 years were near 0.12–0.14 g (Fig. S1). The marginal fish were reassessed for age and found to be 1 year older (5 vs. 4 years) and unchanged for the 12-year-old (Table S3) — unintentional extraction of more recently formed material could explain the lower than expected value for the 12-year-old, but habitat-related differences of BET relative to YFT, like daily vertical migration patterns (Brill and Lutcavage 2001), were also considered.

Overall, the F^{14}C values from otolith core material for both species were remarkably consistent with the birthdates expected from the bomb F^{14}C decline for a period covering ~20 years (Fig. 3). The findings effectively validate a lifespan of 16–18 years, along with the age reading protocol through ontogeny, for both YFT and BET (Fig. 1).

Discussion

Bomb ^{14}C dating successfully validated an otolith age reading protocol that enumerated more growth zones than most other studies on YFT and BET — the potential lifespan of each species is 16–18 years in the northwestern Atlantic Ocean. The maximum validated ages for YFT from this study were for six fish aged 16–18 years (1390–1810 mm FL), and fish near 1500 mm FL could be as young as 5 years illustrating a decoupling of length from age (e.g., Andrews et al. 2016*a*). The maximum ages reported here are consistent with a preliminary estimate of 15 years from the northern Gulf of Mexico (Lang et al. 2017), results that were initially considered preliminary due to an absence of age validation (ICCAT 2017). Overall, YFT aged 2 to 18 years (n = 34, 1029–1810 mm FL) revealed birth years that were coincident with the bomb ^{14}C decline reference. Similar to YFT, the maximum validated age from bomb ^{14}C dating for BET was 17 years (1626 mm FL), a length for which fish could be as young as 7 years. This finding is consistent with those of the Indian Ocean and southwestern Pacific Ocean off Australia where purported annual otolith growth zones revealed maximum estimated ages of 15–16 years for BET (Farley et al. 2006), and other regions of the western and central Pacific provided similar otolith growth structure (Farley et al. 2017, 2018). Overall, BET aged 3 to 17 years (n = 12, 1280–1750 mm FL) were fewer but also in agreement with the bomb ^{14}C decline reference.

While studies of age and growth for YFT and BET span nearly every region of the Atlantic, Pacific, and Indian oceans, the common thread among these studies is a lack of an applicable method to provide validated age through ontogeny. Studies that noted a maximum age of 6–10 years using daily increments in otoliths or annual growth zones in fin spines for Atlantic YFT (Lessa and Duarte-Neto 2004; Shuford et al. 2007) — in comparison with other methods like length frequency analysis (LFA) and outdated scale ring counting — exemplify the limits of other methods when addressing population age structure and lifespan. These limits may be a factor in underestimating the maximum age of YFT in other ocean basins where ages from related methods revealed similar lifespan estimates, such as the Indian Ocean with maximum ages of 6–10 years (Stéquert et al. 1996; Shih et al. 2014), and the Pacific Ocean where the latest preliminary observations were up to 13 years (Farley et al. 2018). Yellowfin longevity based on tag-recapture are generally inconsistent with the length at age estimates from Lang et al. (2017). For the Atlantic Ocean, the maximum age was 11 years from the ICCAT historical tagging dataset and time at liberty (ICCAT 2009). For the western and central Pacific Ocean, the yellowfin assessment (Tremblay-Boyer et al. 2017) has a maximum age estimate of 7.5 years from a fish that was tagged in the western

Pacific at an age of ~1 year and was at liberty for 6.5 years. For the Eastern Pacific Ocean, the IATTC indicated that maximum age may be 8 years from a tagged fish that was at liberty for 5 years and estimated to be 3 years old at tagging (K. Schaefer, IATTC; pers. comm.) — the potential problem with this observation is the estimated age of the fish at capture, as well as the potential for greater time at liberty. For BET, purported annual growth zone counts in otoliths were validated to 8 years using mark-recapture and included estimates to 10 years off eastern Australia (Clear et al. 2000), but potential problems with other age estimation methods (as described for YFT) are possible for BET, as well. Fin spines provided age estimates up to 9–10 years in the Atlantic and Pacific (Sun et al. 2001; Duarte-Neto et al. 2012), and daily increment counts were shown to be limited to the first 2 to 4 years of growth, depending on the use of transverse or longitudinal sectioning techniques (Farley et al. 2006, 2018; Schaefer and Fuller 2006). Furthermore, both species were noted to have the potential for early over-estimation of age because daily increments were needed to validate the first one or two annual growth zones, but most applicable to the findings presented here was that daily increments underestimate age beyond the first 1–2 years (Williams et al. 2013; see Figure 11 of Farley et al. (2017)). In general, this kind of problem with daily increments, as well as other methods like LFA, would be expected due to reduced resolution and a decoupling of length with increasing age — these are well-known limitations among numerous fishes with asymptotic growth that can be addressed with bomb ^{14}C dating, from which numerous species have been shown to be longer-lived than previously estimated (Campana 2001).

The progression of youngest to oldest YFT birth years rising up the bomb-produced ^{14}C decline supports age estimates from 2 to 18 years. There was remarkable consistency of the otolith ^{14}C values from a wide-range of aged YFT with the coral-otolith ^{14}C decline reference — estimated birth years covered 15 years of the ^{14}C decline period (1995–2010). At the upper end of this relationship, fish aged as 16–18 years would be at most 1–3 years younger based on the upper limit of the 95% prediction intervals of the ^{14}C decline relationship. In addition, the consistency of yearling YFT ^{14}C measurements with the ^{14}C decline series provides support for these observations — the juvenile phase of each cored adult would be expected to occupy similar surface water habitat that is reflected in the coral-otolith ^{14}C reference record through time. The well-established use of the bomb-produced ^{14}C record in the Gulf of Mexico is one that covers a vast oceanographic region and has been used to age other teleost fishes through ontogeny to ages exceeding 40–50 years, with first-time use of the decline period to validate the age of younger fishes (i.e., Andrews et al. 2013; Barnett et al. 2018). Hence, the proven utility of this record provides strong support for its use in testing the validity of YFT age estimates.

One potential complicating factor for adult YFT is unknown natal origin. Some studies indicate there is a low probability for this kind of problem (Pecoraro et al. 2018), but there is conflicting information from other studies (Kitchens 2017; Kitchens et al. 2018) that indicate adults of the Gulf of Mexico could come from other parts of the Atlantic. Unfortunately, there are no bomb ^{14}C records from off west Africa in the proximity of the Gulf of Guinea, but it is reasonable to assume that otolith core values for fish from this region would be depleted because of the effects of upwelled waters of western boundary currents, which could lead to underestimated age from the ^{14}C decline relationship. With regard to other parts of the North Atlantic, the reference records range from nearly coincident to slightly attenuated for the decline period (~5–10‰ according to coral records reported by Kilbourne et al. (2007) and Wagner (2009)). For the YFT analyzed in the current study, the fact that none of these fish were 5–10‰ lower than the 95% prediction interval indicates it is unlikely that any of these fish began life in distant regions, unless they were from an area where reference records overlap. In addition, this offset in tropical ^{14}C reference records tend to dovetail on the decline as dates become more recent (both Atlantic and Pacific Oceans; Grottoli and Eakin 2007, Andrews et al, 2018). It is also important to mention that a projection of the measured YFT values to the ^{14}C rise period (1950s and 1960s) is possible (Fig. 2) but highly improbable in this case because the fish would be on the order of 40–50 years old with an unrealistic age-at-length growth pattern. With the decline period as the well-defined reference in this study, it is the consistency of the monotonic ^{14}C decline rate from YFT otoliths (n = 34 from 1995 to 2011) with the regional ^{14}C reference (–2.50‰ yr^{-1} *cf.* –2.42‰ yr^{-1}) — coupled with a low age estimate bias of –0.5 years overall — that are perhaps the most compelling elements of the study. Therefore, age-at-length for YFT as defined by the age reading performed for this study is valid within the narrow temporal constraints of the bomb ^{14}C decline period.

The findings for BET were less informative overall because fewer specimens were available but use of the bomb ^{14}C decline indicated age estimates for most fish were accurate to within a few years for fish aged 3–17 years. Relative to the YFT findings, BET may have suffered from either lower age estimate precision or a habitat depth-related factor that could lead to reduced ^{14}C uptake. As a result, BET specimens with corresponding birth years that were initially offset from the ^{14}C decline (outside the 95% prediction intervals) were reinvestigated for estimated age from growth zone counting. One fish with a minor elevated ^{14}C offset, initially aged 4 years from zone counting (BET-C01), was recounted by three age reading experts from two separate institutions as one year older and was then within the ^{14}C decline prediction interval — otolith mass also provided an indication this fish was slightly older (Fig. S1). This suggests the possibility that otolith mass, coupled with bomb ^{14}C dating, can be used as a tool to increase precision, especially in difficult to age species like tropical tunas. The BET specimen with the greatest

^{14}C offset was lower than expected and one of the second oldest fish at 12 years (BET-C10), although two other fish aged 11–12 years agreed with the decline reference (BET-C11, C12). The offset fish was consistently aged to 12 years and remains below the 95% prediction interval minimum by 2.1‰, but the measurement error of ±2.2‰ includes the predicted range of decline values. Because BET exhibits greater daily vertical migration than YFT, and that deeper forays were not limited for BET juveniles (the region of otolith growth sampled) due to body size (Brill and Lutcavage 2001; Brill et al. 2005), uptake of ^{14}C to the otolith could be reduced — deeper waters of the mixed layer are ^{14}C-depleted in the tropics due to advection and diffusion of deep waters that are unaffected by bomb-produced ^{14}C (e.g., Druffel et al. 2008; Kumamoto et al. 2013). It is likely that some variability in the measured ^{14}C levels from otoliths among BET individuals would occur due to this depth-related factor, but the bomb ^{14}C signal was recorded to have penetrated the tropical waters of the North Atlantic to depths of 400–700 m during the 1990s and 2000s (Druffel et al. 2008) and does not appear to be a factor for most of the BET specimens studied here. With this in mind, it is important to consider that this concern is a depletion factor and would only contribute to an underestimate of age from bomb ^{14}C dating when comparing measured values to an alignment with the decline reference (^{14}C values would need an upward adjustment due to dilution). Therefore, the oldest BET aged 17 years from growth zone counting would be at most 2–3 years younger (upper limit of the 95% prediction interval) and would be even older if ^{14}C-depletion due to depth-related forays were considered a normal factor for the otoliths of this species.

Of the various members in the family Scombridae, three species of bluefin tuna (BFT) have been studied for validated age and growth using bomb ^{14}C dating. The first was an early study that was conducted on the southern BFT (*T. maccoyii*) from Australia (Kalish et al. 1996). While the method was in its infancy and had far less to consider for bomb ^{14}C references, age estimates from growth zone counting to ~30 years were well-supported by the alignment of ^{14}C values that were expected for bomb-produced ^{14}C in the regional marine environment. Work on the Atlantic BFT (*T. thynnus*) was the next success using bomb ^{14}C dating with validated ages exceeding 30 years (Neilson and Campana 2008). At that time, the approach was becoming well-established and more ^{14}C reference records were available for temporal alignments along the full bomb-produced ^{14}C signal (from the rise through to the decline in a general manner). Most recently, Pacific BFT (*T. orientalis*) was evaluated with a modern form of bomb ^{14}C dating that uses well-established decline period records (post-peak; Andrews et al. 2016b) to validate ages approaching 30 years (Ishihara et al. 2017). This innovative approach makes it possible to validate the age of younger and more recently collected fishes because the bomb ^{14}C rise period is in the 1950s and 1960s — otolith collections for fish with birth years during this early period often do not exist. This innovation was of central importance to the current study on YFT and BET because these species were thought to live less than 10–20 years and otoliths available for this research were exclusively from recent collections.

As an interesting anecdote, the most recent findings for Pacific BFT revealed a ^{14}C decline relationship that was slightly depleted relative to reference records for the adult otolith cores. This was attributed to an inclusion of material in the extracted otolith core that formed in either deeper or more geographically distant waters that were ^{14}C-depleted (Ishihara et al. 2017). While this factor can also be interpreted as overestimation of age for adult Pacific BFT, the known life history of this species and evidence of ^{14}C levels from regions and depths where Pacific BFT travel provided a plausible explanation for the attenuated ^{14}C signal. Hence, the findings were deemed a success for validation of the age reading. Given a greater number and range of aged adult BET from the northwestern Atlantic - Gulf of Mexico region, it is possible there would be a similar circumstance in the overall ^{14}C decline relationship due to daily depth migrations, but some fish may be more in synch with the surface ^{14}C signal due to individual variability of depth movement behavior (differing amounts of time in and out of deeper waters).

In general, age reading the otoliths of YFT and BET is difficult and future studies in other regions should employ techniques that are capable of assessing maximum age. The findings presented here support the observation that techniques used to determine age structure, like daily increments and LFA, are limited to the earliest and most rapid growth and may truncate the estimated age structure of the population. Methods relying on an interpretation of patterns that may be difficult to discern at advanced ages should be accompanied by age validation techniques like bomb ^{14}C dating to properly describe age-at-length interpretations toward maximum sizes and ages.

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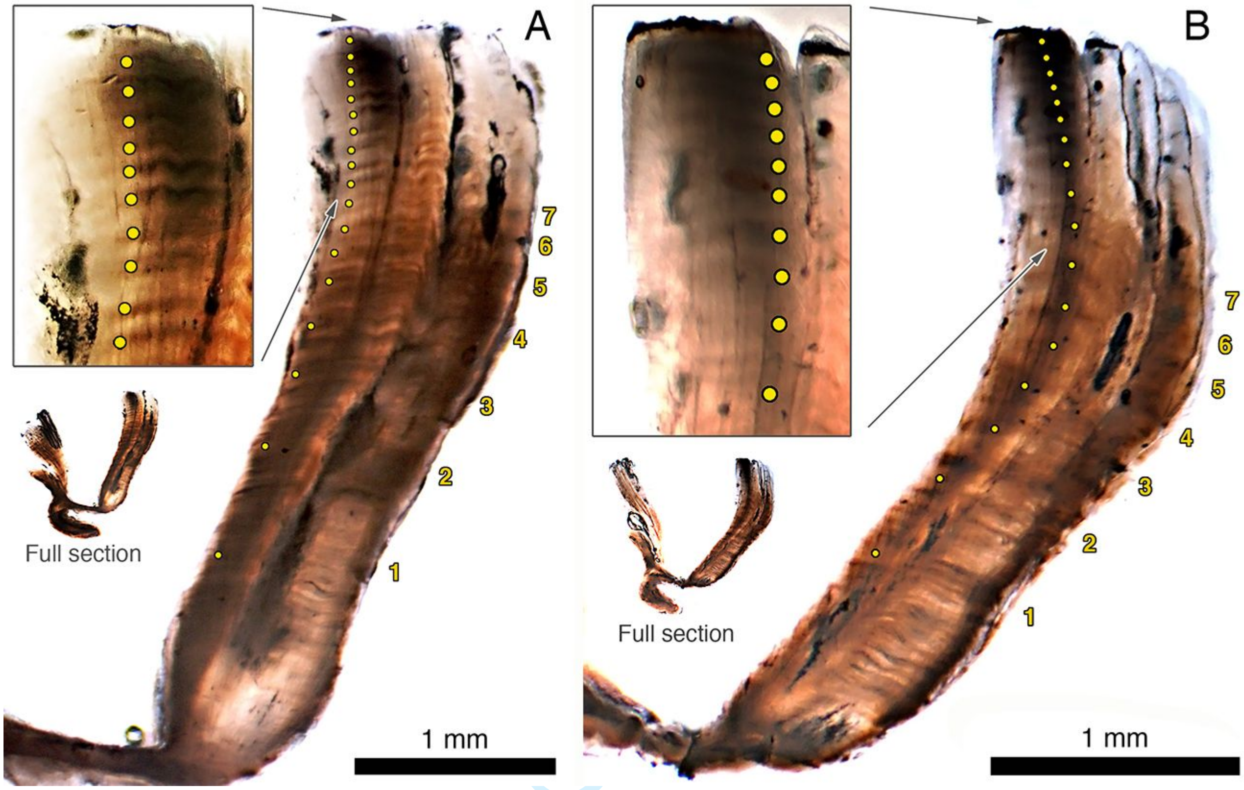

Fig. 1. Yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna otolith sections viewed with transmitted light for the oldest specimens YFT-C32 (A) and BET-C03 (B). The age reading protocol was defined by growth zone structure that has some level of subjectivity (typically ±1 year), but overall the counts were 18 years for YFT-C32 and 17 years for BET-C03. Age reading out to 5 years appeared as broad, diffuse bands that traverse the section and can be used as a tool for lumping the subannual growth structure of early growth. Finer zone structure begins after a bend in the growth axis and can be difficult to resolve (inset images). Age reading for each species was delineated along the ventral arm as shown and enumerated here and was consistent with the age reading protocol presented in recent studies of each species (Lang et al. 2017; Farley et al. 2017).

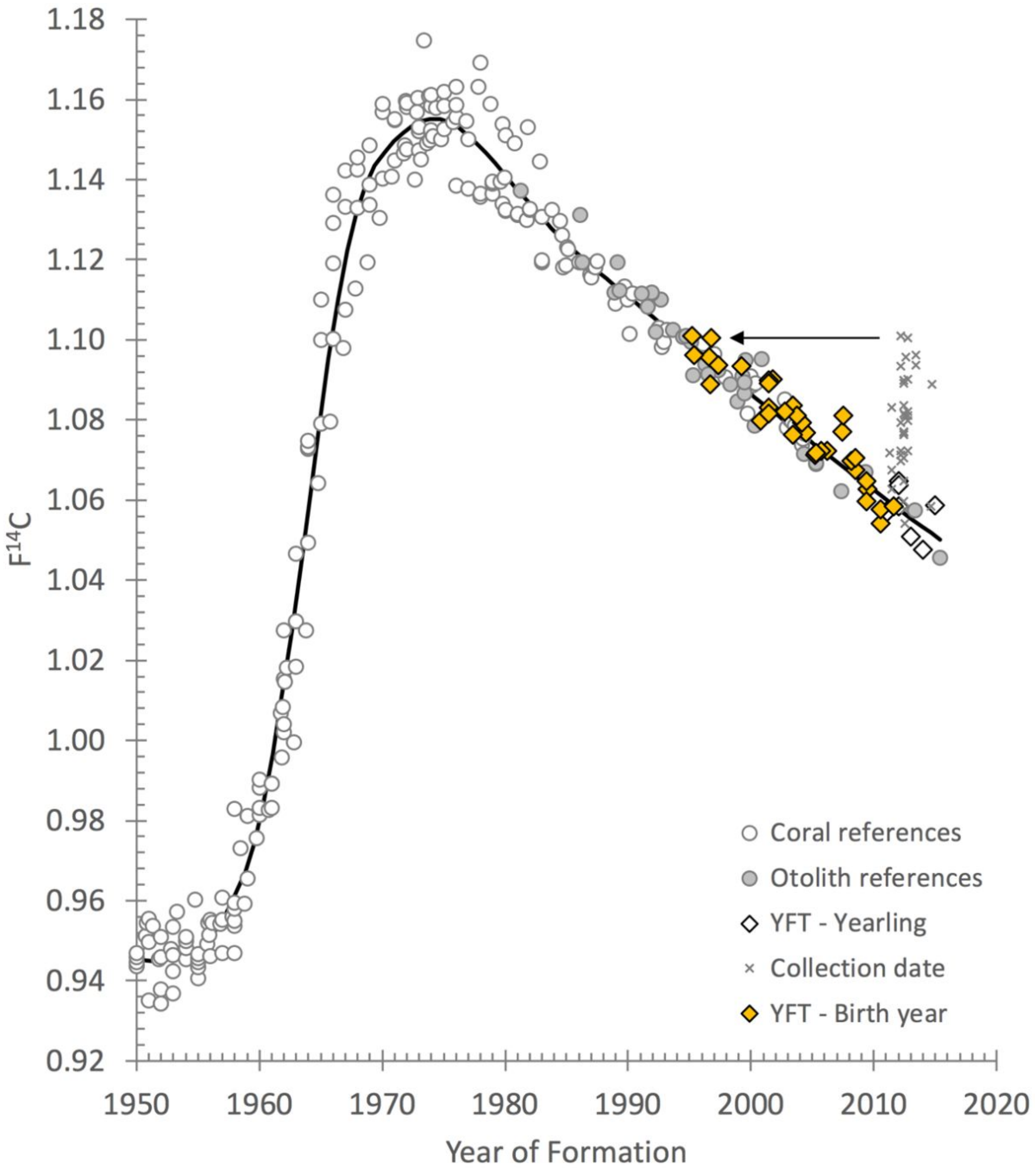

Fig. 2. Aged yellowfin tuna (*Thunnus albacares*) that were cored (sampled within first year of growth) and measured for ^{14}C are plotted relative to the Loess curve that was used to describe the central tendency of the entire bomb ^{14}C reference record for the Gulf of Mexico (coral and otolith records with known dates of formation; Andrews et al. 2013; Barnett et al. 2018), including yearling YFT. The ^{14}C values for YFT are plotted at the collection date (x-symbol) and then as a projected birth year based on age from otolith growth zone counting (estimated 2–18 years). Note that a correlation of otolith values to the ^{14}C rise (1950s to 1960s) is possible but would lead to unreasonable ages on the order of 40–50 years and an unrealistic age-at-length structure through ontogeny. See supplemental material for yearling and older YFT otolith data (Tables S1 and S2).

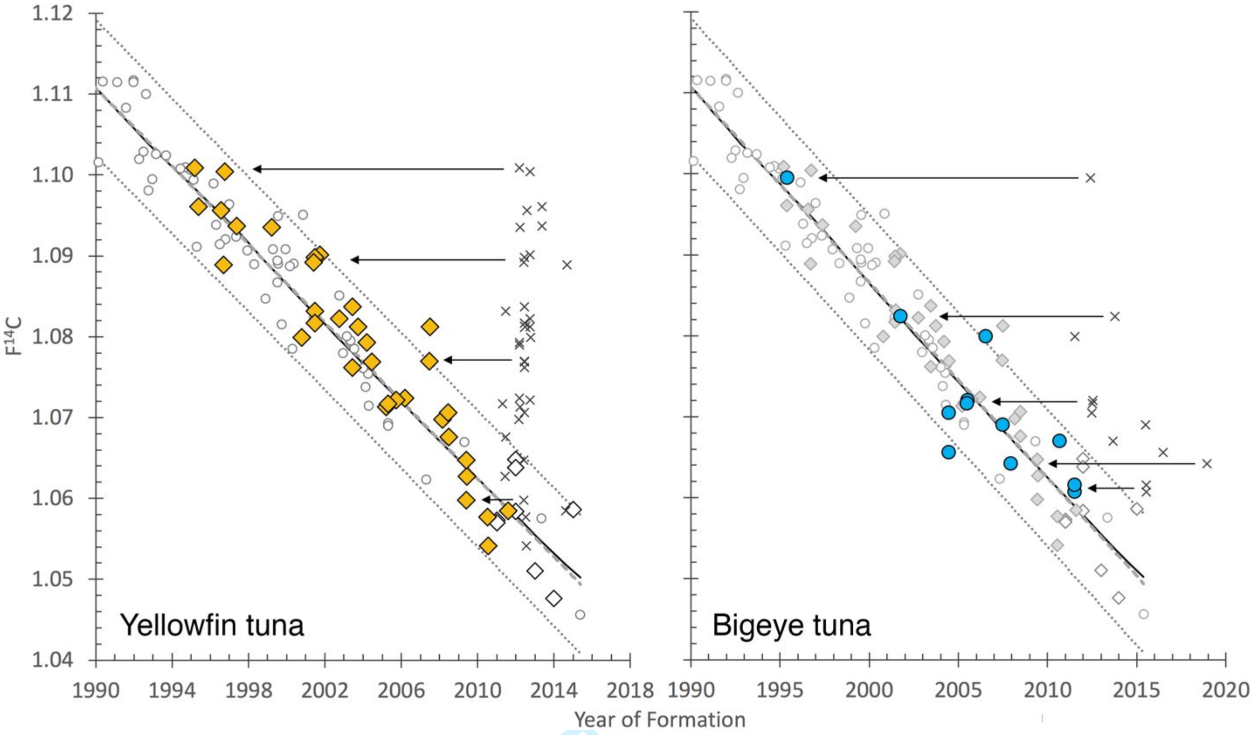

Fig. 3. Close up of the bomb ^{14}C decline period that focuses on the alignment of measured ^{14}C values from otolith cores of older yellowfin tuna (filled diamonds) and bigeye tuna (filled circles) with the Gulf of Mexico ^{14}C reference record (open circles) by projecting the estimated age from growth zone counting back to the calculated birth year from the collection date (x symbols). The Loess curve fitted to the ^{14}C reference record (solid line), including the yearling YFT (open diamonds), was coincident with a linear regression (dashed line). The 95% prediction intervals (dotted lines) from the linear regression indicated all age estimates, except two or three, were within the natural variability of the monotonic ^{14}C decline.