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Bomb-produced radiocarbon age validation of Greenland halibut (*Reinhardtius hippoglossoides*) suggests a new maximum longevity

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John D. Brogan[ab], Craig R. Kastelle[c], Thomas E. Helser[d], Delsa M. Anderl[e]

[a] Resource Ecology and Fisheries Management Division, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115-6349
john.brogan@noaa.gov

[c] Resource Ecology and Fisheries Management Division, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115-6349
craig.kastelle@noaa.gov

[d] Resource Ecology and Fisheries Management Division, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115-6349
thomas.helser@noaa.gov

[e] Resource Ecology and Fisheries Management Division, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115-6349
delsa.anderl.@noaa.gov

[b] Corresponding author: john.brogan@noaa.gov, (206)526-4219, Fax :(206)526-6723

Abstract

Bomb-produced radiocarbon (^{14}C) was used to validate age estimates of Greenland halibut (*Reinhardtius hippoglossoides*) using a stained otolith cross-section method. The $\Delta^{14}C$ in eastern Bering Sea (EBS) Greenland halibut otoliths was compared to both EBS and Gulf of Alaska (GOA) Pacific halibut (*Hippoglossoides stenolepis*) otolith reference chronologies to evaluate which reference chronology was most suitable, and to quantitatively estimate age determination bias. Using Bayesian analysis and a coupled-function model, the $\Delta^{14}C$ in the Greenland halibut showed greatest similarities to the $\Delta^{14}C$ in the GOA reference chronology. Although the model indicated under ageing, the bias was not large. Assigning an age less than the true age by more than a one year is about 73%, and less than the true age by more than 2 years is only about 25%. When considering the age at which Greenland halibut is only 7.5% of its maximum longevity (50+ years) and that the probability of underageing by 3 years being less than 5%, it is likely that between-age-reader variation will cancel out any systematic bias that exists in the age determination protocols. Prior to the use of stained cross-sections the maximum age was 38 years, now a maximum age of 53 years is supported.

Key Words

Age determination, age validation, Bering Sea, Gulf of Alaska, bomb-produced radiocarbon, Greenland halibut, otolith, Pacific halibut, coupled-function model, Bayesian analysis

1. Introduction

Greenland halibut (*Reinhardtius hippoglossoides*) is an important commercial species in both the North Atlantic and North Pacific oceans. In the North Pacific, Greenland halibut are found in the eastern Bering Sea (EBS) and along the Aleutian Islands chain (Alton et al., 1988). The commercial catch history ranges from a peak of 78,442 t in 1974 to a low of 1,656 t in 2014 (Bryan et al., 2019). Due to the commercial importance of Greenland halibut, age determination methods must be consistent so year classes can be successfully modeled for stock assessment purposes (Kimura and Anderl, 2005). Current otolith-based age estimates for Greenland halibut have low precision, and there is a general uncertainty about their accuracy in older fish (Gregg et al., 2006; Treble et al., 2008; Dwyer et al., 2016).

Most ageing attempts on Greenland halibut have historically used untreated surface patterns on whole otoliths. When this method is employed, the left otolith is used because the nucleus is more centric, and the annuli are more evenly separated than in the right otolith (Bowering, 1982; Bowering and Nedreaas, 2001; Gregg et al., 2006). Other commonly used methods to determine ages of Greenland halibut have included the use of otolith cross-sections, baking both left and right whole otoliths, grinding the distal surface of the left whole otolith, and transverse breaking and burning the left otolith (Gregg et al., 2006; Treble et al., 2008; Dwyer et al., 2016).

The importance of age validation studies is widely recognized, and many studies have shown that surface methods of ageing long-lived species often underestimate actual ages (Beamish and McFarlane, 1983; Campana, 2001). An age validation study on Greenland halibut in the North Atlantic showed that whole otolith and sectioned otolith methods underestimated ages by 1-15 years, with an average underestimation of 6 years (Treble et al., 2008). Albert (2016), using OTC tag and recapture, found that a whole otolith ageing protocol was reasonably accurate for determining mid-age growth zones (5-10 years), but likely it underestimated ages of older fish (>10 years).

Gregg et al. (2006) developed a new method for ageing Greenland halibut (Figure 1). This method involves embedding the left sagitta in polyester resin, making a single cut through the core of the otolith, and staining the cross-section with a solution of 1% Aniline Blue WS (no. B362-03, Mallincrodt Baker Inc., Phillipsburg, NJ) in 1% acetic acid. However, this new age determination method has not been validated for its accuracy. Prior to using stained cross-sections, the surface of the otoliths were commonly viewed for age determination (Gregg et al., 2006).

Bomb-produced radiocarbon age validation is widely recognized as one of the best methods to determine the accuracy of fish ages (Campana, 2001; Wischniowski et al., 2015). Recent studies have used the bomb radiocarbon method to validate ages in many species including Dover sole (*Microstomus pacificus*) (Kastelle et al., 2008a), Pacific ocean perch (*Sebastes alutus*) (Kastelle et al., 2008b), Pacific halibut (*Hipploglossus stenolepis*) (Piner and Wischniowski, 2004), bocaccio rockfish (*S. paucispinis*) (Andrews et al., 2005; Piner et al., 2006), canary rockfish (*S. pinniger*) (Piner et al., 2005; Andrews et al., 2007), quillback rockfish (*S. malinger*) (Kerr et al., 2005), and the white shark (*Carcharodon carcharias*) (Kerr et al., 2006).

Beginning in the early 1950s, above-ground testing of atomic bombs produced an increase of ^{14}C in the atmosphere and marine environment. This testing, which continued into the middle of the 1960s, caused a swift increase in marine ^{14}C that plateaued about

1970. The increase in ^{14}C was recorded in corals, other calcified marine organisms, and fish otoliths and provides a time reference of ^{14}C uptake. When an exact time frame of ^{14}C uptake for a species is known, a “reference chronology” is provided that can be compared to ^{14}C uptake for the species to be validated (Kalish, 1993; Kastelle et al., 2008a; Helser et al., 2014; Wischniowski et al., 2015). When the uptake for both the reference and validation species are synchronous, the ages from the validation species are usually considered accurate or validated. For the North Pacific Ocean, two reference chronologies have been developed: one from Pacific halibut in the Gulf of Alaska (GOA) (Piner and Wischniowski, 2004) and one from Pacific halibut in the (EBS) (Wischniowski et al., 2015). Due to the lack of young Greenland halibut from the bomb-produced radiocarbon era in the EBS, there is no conspecific species reference chronology.

Two assumptions are important when using the bomb radiocarbon method to validate fish ages (Piner and Wischniowski, 2004; Piner et al., 2005; Kastelle et al., 2008a). The first is that the species to be validated must be biologically and ecologically similar to the species of the reference chronology in the first few years of life (Campana and Jones, 1998). When both species receive their ^{14}C from the same sources, the timing and magnitude of the ^{14}C increase should be similar (Campana and Jones, 1998; Andrews et al., 2007). The second assumption is that the otolith cores used for the ^{14}C analysis must be uncontaminated and must constitute a closed system. This second assumption requires that the otolith core be extracted without contamination from other carbon sources or otolith material from outside the desired core (Kastelle et al., 2008a). Since two reference chronologies are currently available for Greenland halibut, and owing to the complex circulation patterns of the Bering Sea, it was not immediately clear which reference chronology should be chosen for this species.

Eastern Bering Sea Greenland halibut have been aged since the early 1980s and age compositions are currently integrated into stock assessments (Bryan et al., 2019). However, age estimates have yet to be evaluated for their reliability and ageing bias, or to determine which bomb radiocarbon reference chronology is most appropriate. Therefore, Bayesian methods with Markov Chain Monte Carlo (MCMC) simulation can provide a natural framework for hypothesis testing and a probabilistic framework for estimating ageing bias (Kastelle et. al. 2016). The central goal of this study was to evaluate which is the most suitable reference $\Delta^{14}C$ chronology for comparison to Greenland halibut, and then to quantitatively estimate age determination bias, if it exists.

2. Materials and Methods

2.1. Otolith Selection and Coring Procedures

The Greenland halibut otoliths used in our validation study were selected from collections archived at the Alaska Fisheries Science Center (AFSC). The sample universe consisted of 845 specimens from where two independent cross-section age estimates existed (a read age and a test age), and from which age reading precision (percent agreement, CV, etc. see Kimura and Anderl, 2005) was available. We chose samples collected by both commercial fisheries observers and fishery-independent surveys in the Aleutian Islands and EBS during 1979 and 1982 (Figure 2). These two years were used to provide a reasonable likelihood that the posited hatch years (combination of average age of reader and tester, and catch date) would fall between 1951 and 1973, coinciding with the increasing ^{14}C levels. Beyond these two years, data from over 8000 Greenland halibut specimens, aged using the new cross-section technique (Gregg et al., 2006) were available at the AFSC for reference in this study. Subsamples for coring and subsequent bomb radiocarbon analysis (n = 32) were selected based on relative consistency between age estimates from two independent analysts, and such that the posited hatch years were evenly distributed between 1951 and 1973 (Table 1).

The otoliths were removed at sea, stored dry, and cataloged for future age determination. Prior to being aged, they were rehydrated for one month with a glycerin and thymol mixture. This mixture was not expected to be a contaminant in the ^{14}C measurements (Campana et al., 2003). Once rehydrated, the left, or blind side, otolith was embedded, cut, and stained using the method described by Gregg et al. (2006). Specimens were viewed under a dissecting microscope, up to 60×, using transmitted light. Posited annual marks (constituting paired translucent and opaque growth zones) were identified and counted (Figure 1) by two expert age readers. Because the small innermost core representing the first year did not provide enough material for a ^{14}C assay, a 2-year core was extracted from the eyed-side (i.e., right side) otoliths. A Buehler® EcoMet® (Buehler Ltd., Lake Bluff, IL) grinder with 320 grit sandpaper was used to produce cores. First, material was removed on the perimeter from the dorsal-ventral and anterior-posterior axes. Next, material was removed from the proximal and distal surfaces. This process made the 2nd annulus easier to see which allowed it to be a guide for the final core. Finally, the otolith was ground to the size and shape of the 2nd annulus. To prevent contamination, the sandpaper was changed for every specimen. The dimensions and weights of the finished cores were compared to dimensions and weights of known 2-year-old Greenland halibut otoliths. The finished cores were cleaned in an ultrasonic bath, dried, weighed, and stored in acid-washed vials to be shipped for ^{14}C analysis.

2.2. ^{14}C Analysis

The samples were sent to the National Ocean Sciences Accelerator Mass Spectrometry Facility at the Woods Hole Oceanographic Institution, Woods Hole, MA for ^{14}C and ^{13}C measurements. There, a routine acid hydrolysis procedure was used to produce a graphite target which was analyzed using accelerator mass spectrometry. Results are reported as $\Delta^{14}C$, which is defined as the relative difference between an international standard (base year 1950) and sample activity. The $\Delta^{14}C$ is normalized to 1950, corrected for isotopic fractionation with the $\delta^{13}C$ measurement, and normalized to a $\delta^{13}C_{VPDB}$ value of -25‰ (https://www.whoi.edu/nosams/radiocarbon-data-calculations, last accessed May 18, 2020). For the purposes of this analysis, a midpoint of otolith deposition for every individual was used. Hence, the birth year of each test validation specimen was adjusted by +1 year to account for the 2-year core, and the Pacific halibut birth years were adjusted by + 0.5 years to account for using whole otoliths from 1-year-old juveniles (Kastelle et al., 2016). Making these adjustments assumed that deposition of otolith material is consistent during the course of a year.

To evaluate age reading bias, $\Delta^{14}C$ from Greenland halibut otolith cores was compared to two known age $\Delta^{14}C$ reference chronologies: a GOA Pacific halibut (*Hippoglossus stenolepis*) (Piner and Wischniowski, 2004) and an EBS Pacific halibut (Wischniowski et al., 2015). Since we did not have an a priori reason to believe which reference curve was appropriate, the Greenland halibut validation samples were compared to both reference chronologies to make an initial assessment for further quantitative analysis. We used a coupled-function model (product of Gaussian and exponential models) (Hamel et al., 2008; Kastelle et al., 2016) to fit parametric models to the $\Delta^{14}C$ data, given as

$$\hat{y}_x = \lambda + ke^{\left[(\mu \cdot r)+\frac{(\sigma^2 \cdot r^2)}{2}\right]} \times e^{(-r \cdot x)}\Phi(\mu + \sigma^2 \cdot r, \sigma, x) + \sigma_e^2 ,$$

where, $\hat{y}_x$ = estimated $\Delta^{14}C$ and x = birth year. The model parameters are λ = average pre-bomb $\Delta^{14}C$ value (predicted lower asymptote), k = the predicted total increase of $\Delta^{14}C$ to reach the upper asymptote, μ = estimated mean or peak year of radiocarbon Gaussian pulse curve (which is the birth year corresponding to the midpoint, 50%, of the $\Delta^{14}C$ increase), σ = standard deviation of the Gaussian pulse curve, r = post-peak exponential decay rate (per year), and σ^2_e = the error variance. The symbol Φ signifies the cumulative normal function. The difference between the predicted μ of the reference chronology (R) and that of the test validation sample (V), μ_R - μ_V, is a dissimilarity in the years of 50% increase of the two curves, and therefore, bias in the age reading (Kastelle et al., 2016).

Bayesian methods (Gelman et al., 2003) were used to fit the models using Markov Chain Monte Carlo (MCMC) simulation (4,000,000 samples, burn-in = 500,000, thinned at 2,000) and the converged posterior sample, n = 2000, was used to compute the probability of age determination bias. Sample chains of the parameter space were generated using a random walk Metropolis-Hastings method with a heavy-tailed t-distribution as the proposal distribution. In general, we used diffuse conjugate prior distribution specifications for the Bayesian models which assumes [λ, K, u, r], conditioned on σ^2_e, are normally distributed. The prior on the parameter σ was specified as a uniform distribution [0, 10e^{6}] and the prior on the precision parameter $h = \sigma^{-2}$ is the inverse gamma specified by the shape (0.001) and scale parameter (0.001). Full specification of the likelihood, conditional posterior and priors will not be reiterated here but can be found in Helser et al. (2012) or Kastelle et al. (2016). Convergence to the target joint posterior distribution was evaluated visually using trace, autocorrelation and posterior density plots, and quantitatively using Gweke and Heidelberger statistics.

First, Bayesian models were used to evaluate which Pacific halibut reference chronology was most suitable to assess the bias of the Greenland halibut validation Δ^{14}C. Further, a possible reduction in the number of parameters, by sharing parameters between reference and validation samples, was evaluated using the deviance information criteria (ΔDIC) (Spiegalhalter et al*.,* 2002). Second, once a suitable reference chronology was determined, the marginal posterior density of the converged MCMC sample was used to derive an estimation of ageing bias = $\mu_R - \mu_V$ as described in Kastelle et al. (2016). Here, if the MCMC probability density of $\mu_R - \mu_V$ is centered on zero, then the estimated ages (and hence age determination methods) of the test validation specimens can be considered accurate. Age determination bias can be determined probabilistically by calculating the tail probability of the posterior sample as being greater or less than zero; that is, $Prob[\mu_R - \mu_V] = (> 0 \text{ or } < 0)$.

3. Results

3.1. Otolith Selection and Coring Procedures

Since 2006, over 8,442 Greenland halibut age estimates have been generated at the AFSC using the new stained cross-sectioned method which has revealed ages older than previously estimated. Based on this large sample, the maximum longevity of Greenland halibut is greater than 50 years of age, compared to a previous maximum age of 38 years. Age determination precision from the sample (n=845) used to select the bomb radiocarbon otoliths indicated that between age reader agreement is generally low at 25% (+/- zero years) although agreement increases considerably to 68% when the margin of error to +/- one year of age (Figure 3). Data also show a relatively high CV of 12.9% between two readers which, beyond age 1, stays relatively constant (Figure 3). To target the era of bomb radiocarbon rise, specimens collected in 79 and 82, n=845, were aged by two independent readers and 32 were chosen for use in the ^{14}C validation study. All 32 specimens were cored successfully with an average core weight of 10.3 mg (±2 mg standard error) and an average size of 3.46 × 2.75 × 0.53 mm. This core size was smaller than the known 2-year-old otoliths that were used as a guide. Two independent age estimates were in exact agreement for 4 of the 32 specimens chosen. The remaining sample age estimates, not in agreement, were averaged for further use in the analysis. Ages from this sample ranged from a low of 8 to a high of 32 years of age and generally consistent with the dispersion of the larger sample (Figure 3).

3.2. ^{14}C Analysis

In our Greenland halibut validation specimens, the $\Delta^{14}C$ followed a general pattern of low $\Delta^{14}C$ levels before atmospheric nuclear testing with levels rising after testing began (Table 1; Figure 4). However, the level and variability in the $\Delta^{14}C$ increased after about 1958, which is typically expected as the enhanced bomb radiocarbon becomes mixed and circulated in the world’s oceans. We compared the

Greenland halibut validation samples to two Pacific halibut reference curves, the EBS and the GOA, as they show a similar increase in the level and variability of $\Delta^{14}C$ through the same time period. Given that Greenland halibut is a Bering Sea species of flatfish, we were surprised to see that the general pattern of the $\Delta^{14}C$ in the Greenland halibut was subjectively more similar to the pattern of the GOA Pacific halibut reference curve (Table 2; Figure 4). The median pre-bomb levels of $\Delta^{14}C$ for GOA Pacific halibut (-106.6‰, 1956 and prior) and Greenland halibut (-116.4‰, 1956 and prior) were similar while the EBS Pacific halibut was much higher (-87.8‰, 1956 and prior). Most of the Greenland halibut otolith cores estimated to have formed after 1958 show an increase in $\Delta^{14}C$ into the mid-1960s that followed the pattern of the GOA Pacific halibut reference curve, but there were some outliers that remained low in the mid-1960s. Pacific halibut reached a plateau by about 1970 at about 90‰ $\Delta^{14}C$. Although the Greenland halibut displayed more variability, on average they also reached a plateau at about 1970. While following the general pattern of the GOA Pacific halibut reference curve, the Greenland halibut values appear subjectively to be shifted later in time by about 2 years.

MCMC diagnostics confirm the reliability of the modeling approach to these data sets, and demonstrated that the coupled-function model fit the observed data well. The MCMC simulation was computationally efficient in traversing the parameter space. The mean of the trace plots showed stability over entire width of the chain, and evidence of good mixing was shown by smooth kernel density plots of the marginal posterior density of each parameter. Effective samples sizes were close to the thinned number of samples in the chain (n=2000) indicating low autocorrelation. Moreover, Gweke statistics for all parameters were greater than $|z| > 0.05$ and all parameters passed the Heidelberger tests.

Hence, we conclude that there is reasonable evidence that the MCMC chain converged to a stationary distribution with which to compute summary statistics, and develop a framework for hypothesis tests.

Modeling results confirmed our initial interpretation that Greenland halibut was more consistent with the GOA Pacific halibut reference than to the basin-similar EBS Pacific halibut reference. First, in Greenland halibut and GOA Pacific halibut a post-peak decay rate, *r*, was not supported by the data; their highest posterior densities (HPD) encompassed zero (Table 2). The EBS Pacific halibut reference $\Delta^{14}C$ clearly shows a declining level after 1967 which is not apparent in the other two data sets (Figure 4). Pre-bomb $\Delta^{14}C$ levels, represented by the parameter λ, for Greenland halibut (-90.6 ‰) are more or less equidistant between the GOA (-108.5 ‰) and EBS (-82.5 ‰) Pacific halibut, but show lack of substantial differences when considering the variability (HPD) in that parameter. Most notably, however, the asymptotic parameter *k*, the total rise in $\Delta^{14}C$ was substantially greater for EBS Pacific Halibut (268.1 ‰) than for either the GOA Pacific halibut (178.8 ‰) or similar Greenland halibut (176.7 ‰) (Table 2).

The qualitative modeling results above support the argument that the GOA Pacific halibut reference is the most appropriate data set for quantitative evaluation of age determination bias in Greenland halibut. As such, a new model specification for comparing these data sets to derive a probabilistic estimate of ageing bias consisted of a decay rate parameter (*r*) fixed at 0, shared total $\Delta^{14}C$ rise parameter (*k*) among the reference and validation data sets, and a single share error variance (σ^2_e) (Table 2). The reason for the shared parameter *k* is that the Δ DIC between a model with and without separate values was only 1.34 (less than 5 is the general guidance for lack of substantial support Gelman et al. 1995). The marginal posterior density of our estimate of ageing bias, μ_R - μ_V, was centered on 1.5 years, and it does suggest that current age determination protocols are under ageing Greenland halibut (Figure 5). Here, 97% of the posterior density is less than zero; however, considering the spread of the probability density, under ageing is not as severe when considering the longevity of a species such as Greenland halibut. For instance, the probability of assigning an age less than the true age by more than a 1 year is about 73% and of assigning an age less than the true age by more than 2 years was only about 25%. When considering the age at which Greenland halibut is only 7% of its maximum longevity (50+ years), and the probability of under ageing by more than 3 years is less than 5%, age data are more accurate than they are precise based on current age determination protocols.

4. Discussion

The overall similarities between the $\Delta^{14}C$ in the GOA Pacific halibut reference curve and the Greenland halibut samples indicate a general accuracy in the Greenland halibut ages. Our samples spanned an age range of 8 to 32 years, from which samples were available for ^{14}C analysis. However, there is no reason to assume that even older ages of Greenland halibut are any less accurate or less precise as they are aged with the same methods used here. Normally such an extrapolation is not recommended, but because the methods are the same and the CV is constant with age (Figure. 3), this extrapolation seems reasonable. The results of the Bayesian analysis with MCMC estimates of μ_R - μ_V indicate a median under ageing bias of 1.5 years existed; that is, the distribution of μ_R - μ_V was centered on -1.5 years, though, there was only a 25%

probability of under ageing by more than 2 years. Nevertheless, because of the high amount of variability in the Greenland halibut data points, compared to both reference chronologies, there could be an imprecision associated with specifying a probability of under ageing. This variability could be the result of two factors. First, a range in ^{14}C encountered when the Greenland halibut were juveniles due to potential variation in geographical settlement areas, depth of settlement, or variation in water mass experienced through the EBS current systems. This factor is discussed further below. Second, in situations where the reference curve and samples are conspecific and from the same geographic area (Campana et al., 2002; Piner and Wischniowski, 2004; Helser et al., 2014; Wischniowski et al., 2015), this variability can be attributed to inconsistent ageing error. However, in this study, we cannot decisively distinguish between ageing error and a violation of assumption 1, which states that the species to be validated must be biologically and ecologically similar to the species of the reference chronology in the first few years of life (Campana and Jones, 1998; Helser et al., 2014; Kastelle et al., 2016).

One theory for the variability in the Greenland halibut $\Delta^{14}C$ values involves the oceanographic conditions in the EBS and how these conditions influence the mixing of atmospheric ^{14}C into the water column. The mixing of different water masses, via currents, freshwater input, or upwelling was shown to be a variable that can influence the bomb-produced $\Delta^{14}C$ (Haltuch et al., 2013; Helser et al., 2014; Wischniowski et al., 2015). The EBS shelf is relatively shallow and is one of the largest continental shelves in the world (Schumacher and Stabeno, 1998). The water column is well mixed up to a depth of 50 m for most of the year and there is a large influx of fresh water from rivers (Schumacher and Stabeno, 1998). Continental freshwater ^{14}C values are thought to closely represent levels in the atmosphere, which increases several years earlier, at a faster rate, and to a greater level than in marine environments (Nydal, 1993; Campana and Jones, 1998). The southeastern and central areas of the EBS shelf can be divided into three hydrographic domains with distinct vertical structures (Schumacher and Stabeno, 1998). In the coastal domain (< 50 m depth), the combination of tidal and wind mixing results in a weakly stratified or mixed layer (Schumacher and Stabeno, 1998). The limitation of intermixing between the top and bottom layers in the middle domain (50-100 m depth) results in a two-layered water column during weaker summertime wind mixing. If ice is not present during the fall and winter, the entire water column can be mixed (Schumacher and Stabeno, 1998). The outer shelf domain (101-200 m) is oceanic in nature, with mixed upper and lower layers that have little exchange between them (Coachman and Charnell, 1979). The northern section of the EBS shelf is characterized by relatively shallow depths (< 50 m) and large inputs of fresh water from the Yukon River. The influx of fresh water can lead to stratification in depths as shallow as 20 m in some areas of the northern shelf (Schumacher and Stabeno, 1998). This variety of oceanographic conditions, along with considerations about the location of juvenile Greenland halibut settlement areas, can further the understanding of their $\Delta^{14}C$ variability.

Greenland halibut settle over a large geographic area. Alton et al. (1988) reported catches of young Greenland halibut over a wide area of the EBS shelf and at variable depths (50-184 m). Catches were reported from southwest of St. Lawrence Island to Bristol Bay, with the highest concentration being caught south and west of St. Matthew Island (Alton et al., 1988; Sohn et al., 2010). This area covers the entire southeastern, central, and northern sections of the EBS shelf. Greenland halibut have a pelagic larval stage, before settling on the bottom, during which they are advected northwestward by the flow of the Bering Slope Current (BSC) (Alton et al., 1988; Sohn et al., 2010; Sohn et al., 2016). Importantly, the $\Delta^{14}C$ values in our 2-year cores represent uptake from the pelagic and bottom phases, and it is also possible that the specimens used in our study settled as juveniles in a range of areas (or domains), each with unique oceanographic conditions and mixing rates. If this was the case for correctly aged specimens, individuals who settled in shallow well-mixed areas would have $\Delta^{14}C$ values to the left and above the Pacific halibut reference curve, and those who settled in deeper areas that are not well-mixed would have $\Delta^{14}C$ values to the right and below the Pacific halibut reference curve. Hence, a range of settlement areas could be a further possible explanation for the $\Delta^{14}C$ variability.

We had two reference chronologies available for the comparison (Bayesian analysis with MCMC) to the Greenland halibut. The first is based on GOA Pacific halibut juveniles (Piner and Wischniowski, 2004) and the second is based on EBS Pacific halibut juveniles (Wischniowski et al., 2015). The GOA Pacific halibut reference chronology was chosen for several reasons. First, the $\Delta DIC_{(full-reduced)}$ of 1.34 supports a null hypothesis of a single (reduced) model fitting both the Greenland halibut and the GOA reference chronologies. In general, a ΔDIC less than 5 suggests a lack of substantial support for separate models (Gelman et al., 1995). Second, subjectively a similarity between the EBS Pacific halibut reference and the Greenland halibut chronologies is notable; this is shown in Figure 4, and by the estimated model parameters given in Table 2. The EBS Pacific halibut reference's peak rises much higher than the EBS Greenland halibut's, and then has a notable post-peak decline. These differences are indicative of a biological or environmental difference between these two species, and a violation of assumption 1. Third, there may be an oceanographic connection between the GOA Pacific halibut and the EBS Greenland halibut populations through the BSC. Understanding the source of bomb-produced ^{14}C in the marine environment is critical when attempting an age validation of this type; oceanographic processes such as currents or upwelling play a role in supplying or diluting ^{14}C (Haltuch et al., 2013; Helser et al., 2014; Wischniowski et al., 2015). The source of the BSC's northwestward flow over the EBS slope is largely water from the GOA flowing through Aleutian Island passes, such as Unimak Pass and Amchitka Pass. In turn, the westward flow of the Alaska Stream and Alaska Coastal Current in the GOA, are the source of the flow through passes (Reed and Stabeno, 1999; Stabeno et al., 1999; Sohn et al., 2010). These currents and flows through island passes are illustrated concisely by Sohn et al. (2010) and Wischniowski et al. (2015). According to Sohn et al. (2010) and Sohn et al. (2016) Greenland halibut pre-flexion larvae are known to occur just north of Unimak Pass and are transported northwest by the BSC where they are found as young-of-the-year or age-1 juveniles settled near St. Matthew Island. They typically settle at depths of 50 to 100 m, but migrate soon to deeper regions of the continental slope (Alton et al., 1988; Sohn et al., 2010; Sohn et al., 2016). As age-1 year juveniles the Greenland halibut can often be found at depths of 100 -200 m (Sohn et al., 2010). The oceanographic connection between the GOA Pacific halibut and the EBS Greenland halibut comes from the fact that juvenile Pacific halibut in the GOA are [typically found in shallow nearshore areas (Norcross et al., 1995; Abookire et al., 2001)] in waters of the Alaska Stream and Alaska

Coastal Current that eventually contribute to the BSC. Whereas, the EBS juvenile Pacific halibut are typically found in shallower areas of the inner shelf adjacent to the Alaska Peninsula, between Bristol Bay and Nunivak Island, and near the Pribilof Islands in depths < 50 m (Sohn et al., 2016). Indeed, the EBS Pacific halibut juveniles used in the reference chronology were largely from the Bristol Bay area with depths < 50 m (Wischniowski et al., 2015) Here, mixing throughout the water column and large river systems supplying fresh water to the EBS and Bristol Bay area also add to differences in the supply of ^{14}C when compared to the GOA. These conditions can reasonably be expected to cause an early and greater increase in $\Delta^{14}C$ compared to the GOA Pacific halibut (Wischniowski et al., 2015). Therefore, we suggest that it is possible that GOA Pacific halibut and EBS Greenland halibut are experiencing connected water masses, and it is reasonable to make comparisons between the GOA Pacific halibut and the EBS Greenland halibut for this age validation study. Hence, we further suggest that due to a different early life shallower residence in a different shallower oceanographic system, the EBS Pacific halibut are less oceanographically connected to the EBS Greenland halibut.

Our results can be compared to those from previous bomb-produced $\Delta^{14}C$ age validation studies done on Greenland halibut from the North Atlantic. Using otolith cross-sections and bomb-produced ^{14}C, Treble et al. (2008) estimated that their specimens were under aged by an average of 6 years and had a maximum bias of 15 years. The maximum age in our study samples using the Gregg et al. (2006) method was 32 years, with the $\Delta^{14}C$ indicating better accuracy, under ageing only by 1.5 years. A more recent study by Dwyer et al. (2016), also using bomb-produced $\Delta^{14}C$ on Greenland halibut from the same area in the North Atlantic as Treble et al. (2008), indicated a general accuracy of cross-section ages. Although, the validation samples in this second study demonstrated a large range of values around the reference chronology, and they did not make estimates of ages, or ageing bias, based on the $\Delta^{14}C$ reference, as Treble et al. (2008) and others, on different species, have done (Andrews et al., 2016). There are several notable differences between these two North Atlantic studies and ours. First, their reference chronology was composed of the juveniles from the same species and from the same area; this is a notable advantage in their studies. Second, we had a larger number of validation samples and hence were able to use Bayesian methods and MCMC simulation to estimate the probability of age determination bias. Finally, the population of fish we studied in the EBS has older individuals, with a maximum age of 53 years (https://www.fisheries.noaa.gov/alaska/commercial-fishing/fish-species-maximum-age-data, accessed 6/24/2020), compared to a maximum of 35 years in the North Atlantic (Dwyer et al., 2016). It is probable that the stained cross-section method (Gregg et al., 2006) employed here provides better resolution and contrast when interpreting the fine, closely packed growth zones, and hence older ages which are less biased.

5. Conclusion

This study validated that EBS Greenland halibut ages produced using the Gregg et al. (2006) method were reasonably accurate. The Bayesian methods and MCMC simulation demonstrated that the probability of assigning an age less than the true age by more than 1 year was about 73% and of assigning an age less than the true age by more than 2 years was only about 25%. Such probabilistic statements of ageing bias illustrates the advantages of using Bayesian inference because functions of parameters; that is, μ_R -

μ_V, can be easily calculated from the posterior distribution. The Gregg et al. (2006) method of assigning age used in this study provided a maximum growth zone-based age of 32 years in the test samples, and a maximum age of 53 years from otoliths aged since the early 1980s. Because the age determination methods were the same and the CV was constant with age, we consider such a maximum age was supported by the data and analysis. Prior to the use of the staining method, the maximum age of EBS Greenland halibut using a surface ageing protocol was 38 years. This is not surprising because the Albert (2016) study also showed that the surface ageing protocol under estimated the ages of older fish. The Gregg et al. (2006) staining method makes it easier to see compressed growth zones in otoliths from older fish. This is an important consideration in stock assessments where allowable biological catches (ABC) are estimated. Accurate older ages lead to correct estimates of lower natural mortality, and a more conservative ABC estimate. Our conclusions are similar to that of Treble et al. (2008) who suggested they were under ageing by an average of 6 years, although our estimates of bias from EBS Greenland halibut was substantially less. Given that we were only under aging by an average of 1.5 years, it is unlikely that the Gregg et al. (2006) method used in production ageing will not change. Rather, stock assessment models can now explicitly incorporate age reading bias and ageing uncertainty (Methot and Wetzel, 2013; Punt et al., 2008).

The bomb-produced radiocarbon validation method relies on similarities between the species to be validated and the species used for the reference chronology. The GOA and EBS may differ in regards to the environmental mixing properties of bomb-produced ^{14}C into the marine environment. However, after considering the potential similarities in the water masses experienced by EBS Greenland halibut and GOA Pacific halibut through the influence of the BSC, there was rationality in using the GOA reference. We believe these results show that the ages generated by stained cross-sections are reliable and only minor adjustments are necessary when interpreting growth zones.

CRediT authorship contribution statement

John D. Brogan: Conceptualization, Methodology, Writing - original draft, Visualization. **Craig R. Kastelle:** Project administration, Conceptualization, Methodology, Visualization, Writing - original draft, Writing - review and editing. **Thomas E. Helser:** Conceptualization, Formal analysis, Methodology, Writing - review & editing, Visualization. **Delsa M. Anderl:** Conceptualization, Methodology, Visualization.

Declaration of Competing Interest

The authors report no declarations of interest

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Table 1. Age estimates and radiocarbon measurements for Greenland halibut (*Reinhardtius hippoglossoides*) from the eastern Bering Sea and Aleutian Islands. The average age estimates were determined from otolith growth zone counts of two expert age readers (i.e., a reader and a tester). The estimated birth years were determined from the average age estimates (reader and tester) and catch year. The carbon measurements were made at Woods Hole Oceanographic Institution, National Ocean Sciences Accelerator Mass Spectrometry Facility.

Specimen number	Average birth year	Average age (yr)	$\delta^{13}C$ ‰	$\Delta^{14}C$ ‰	$\Delta^{14}C$ 95% CI
1	1960.5	21.50	-1.21	-98.2	6.46
2	1963	19.00	-1.37	-41.8	6.46
3	1969.5	12.50	-1.41	12.3	6.65
4	1960.5	21.50	-2.11	-109.9	6.65
5	1970.5	11.50	-2.16	62.9	7.23
6	1951	31.00	-2.06	-124	6.07
7	1953	29.00	-1.53	-114	6.27
8	1973	9.00	-1.83	174.9	8.01
9	1956	26.00	-1.56	-48.4	6.85
10	1971.5	10.50	-1.47	103.9	6.65
11	1971	11.00	-2.52	157.3	7.04
12	1959	23.00	-1.86	5.3	6.46
13	1969.5	12.50	-1.71	50.4	7.82
14	1957	25.00	-1.31	-92.9	6.27
15	1969	13.00	-1.74	38.7	7.04
16	1972	10.00	-1.81	45	7.43
17	1958.5	23.50	-1.08	-115.9	5.88
18	1971	11.00	-2.16	11.7	6.06
19	1964.5	17.50	-1.74	44.9	7.24
20	1964.5	17.50	-0.64	28.4	6.45
22	1959	23.00	-1.5	-33.8	6.65
23	1956.5	25.50	-1.21	-66.3	6.46
24	1962	20.00	-1.34	-75.6	5.87
25	1964	18.00	-1.49	-48.6	5.87
27	1963	19.00	-1.32	5.3	6.06
28	1968.5	13.50	-1.56	6.4	6.06
29	1971.5	10.50	-2.26	16.7	6.84
30	1964	15.00	-1.49	5.8	6.07
31	1969	10.00	-2.06	92.1	6.45
32	1967	12.00	-2.19	119.9	7.63
33	1964	15.00	-1.61	-63.4	6.65
34	1952.5	29.50	-1.38	-118.7	6.07

Table 2. Coupled-function model parameters, with HPD (highest posterior density) for EBS Greenland halibut (*Reinhardtius hippoglossoides*) and Pacific halibut (*Hippoglossus stenolepis*) estimated with Bayesian methods and using Markov Chain Monte Carlo simulation. A) Fit to all three data sets individually. B) Fit with shared parameters for the Absolute $\Delta^{14}C$ rise and the error variance.

A

		GOA Pacific halibut reference (*n*=36)		EBS Pacific halibut reference (n=34)		Greenland halibut (*n*=32)	
Model parameter	Model attribute	Median	95% HPD	Median	95% HPD	Median	95% HPD
λ(‰)	Pre-bomb $\Delta^{14}C$	-108.5	-123.6, -94.2	-82.5	-102.4, -64.5	-90.6	-132.3, -52.6
k	Absolute $\Delta^{14}C$ rise	178.8	167.6, 207.0	268.1	226.1, 309.9	176.7	115.7, 237.5
μ (year)	Year of 50% rise	1963.1	1962.4, 1963.8	1962.4	1961.8, 1963.0	1965.5	1962.3, 1969.5
σ	Pulse curve S.D.	2.71	1.68, 3.72	1.83	0.93, 2.77	3.49	1.12, 4.96
r (year^{-1})	Decay rate	0.004	-0.015, -0.025	0.036	0.021 0.053	0.02	-.091, 0.08
σ^2_e	Error variance	385.3	206.2, 613.3	651.0	345.2, 1027.8	1059.0	675.1, 1934.4

B

		GOA Pacific halibut reference (*n*=36)		Greenland halibut (*n*=32)	
Model parameter	Model attribute	Median	95% HPD	Median	95% HPD
λ(‰)	Pre-bomb $\Delta^{14}C$	-107.5	-132.8, -80.6	-96.3	-124.6, -69.5
k^{**}	Absolute $\Delta^{14}C$ rise	184.1	150.0, 215.0	-	-
μ (year)	Year of 50% rise	1963.1	1961.6, 1964.6	1965.4	1963.2 1968.1
σ	Pulse curve S.D.	2.82	1.05, 4.99	3.49	1.89, 4.99
r (year^{-1})*	Decay rate	-	-	-	-
σ^{2**}_e	Error variance	658.9	245.7, 1043.2	-	-
	$\Delta DIC_{Full\text{ - }reduced} = 1.34^{***}$				

* Parameter not estimated and set = 0.
** Parameter estimated but shared between reference and validation species.
*** Δ DIC less than 5 indicates lack of support to specify separate full and reduced models.

Figure 1. An image of an example Greenland halibut (*Reinhardtius hippoglossoides*) otolith aged 49 years using the Gregg et al. (2006) age reading method, but not a specimen analyzed here for $\Delta^{14}C$.

Figure 2. Map of the North Pacific Ocean showing capture locations for Greenland halibut (*Reinhardtius hippoglossoides*) validation specimens and Pacific halibut (*Hippoglossus stenolepis*) reference chronology specimens in the Eastern Bering Sea (EBS) and Gulf of Alaska (GOA)

Figure 3. A) Age bias plot graphically showing a long-term example of the precision between two independent ages (i.e., a read age and test age). The data represents all Greenland halibut (*Reinhardtius hippoglossoides*) aged at the Alaska Fisheries Science Center, collected by observers in the commercial fisheries and fishery-independent surveys in 1979 and 1982 (n=845). The gray circles represent all $\Delta^{14}C$ candidates that were aged and tested. The stars are samples chosen for $\Delta^{14}C$ analysis, the dashed 45° line represents agreement between test age and read age. B) Percent CV by age for all samples from the same fishery-independent surveys. The CV at age 25 represents a weighted average of ages 25+ for the sample.

Figure 4. Greenland halibut (*Reinhardtius hippoglossoides*) $\Delta^{14}C$ ‰ dashed lines and black circles with A) Pacific halibut (*Hippoglossus stenolepis*) $\Delta^{14}C$ ‰ eastern Bering Sea solid line and gray squares and B) Gulf of Alaska solid line and gray squares using the model with shared parameters. The Year of deposition is the average age from two

expert readers (i.e., a reader and tester) and represents a 2-year otolith core, and therefore is the posited midpoint of deposition. The error bars are the 95% confidence intervals of the average ages.

Figure 5. Markov Chain Monte Carlo (MCMC) simulation results showing marginal probability density of ageing bias, μ_R - μ_V, and cumulative probability curves of ageing bias in Greenland halibut (*Reinhardtius hippoglossoides*).

Figure 1.

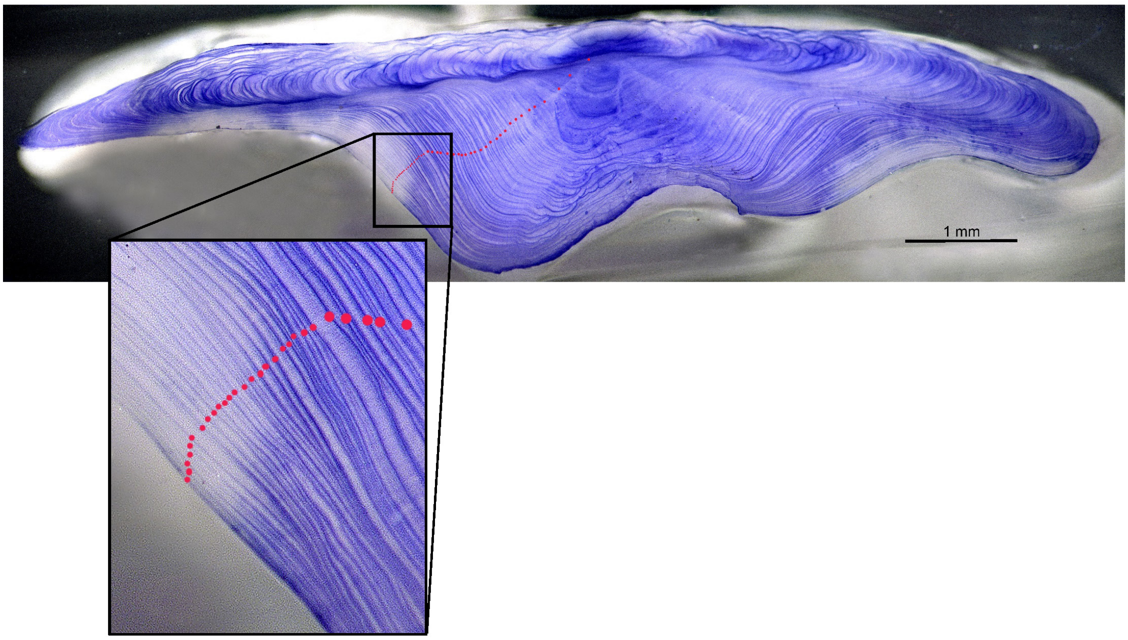


Figure 2.

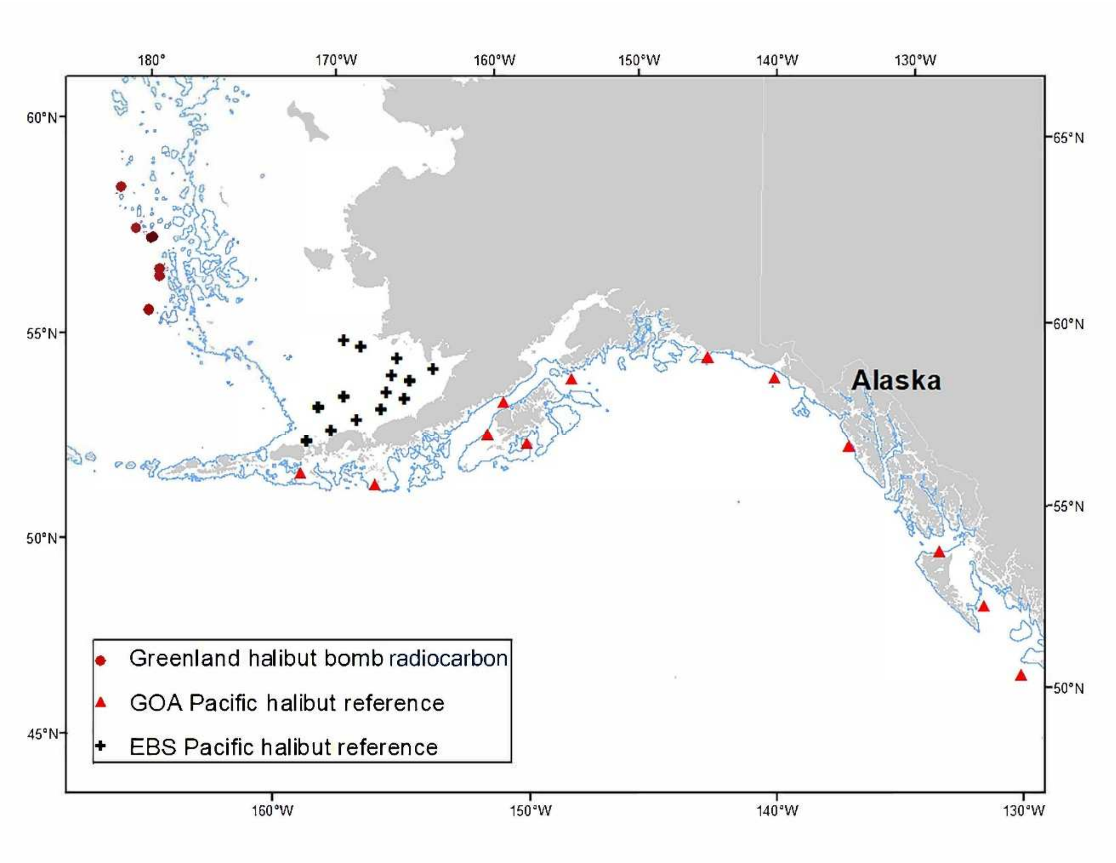

180°
170°W
160°W
150°W
140°W
130°W
60°N
55°N
50°N
45°N
65°N
60°N
55°N
50°N
Alaska
Greenland halibut bomb radiocarbon
GOA Pacific halibut reference
EBS Pacific halibut reference
160°W
150°W
140°W
130°W

Figure 3.

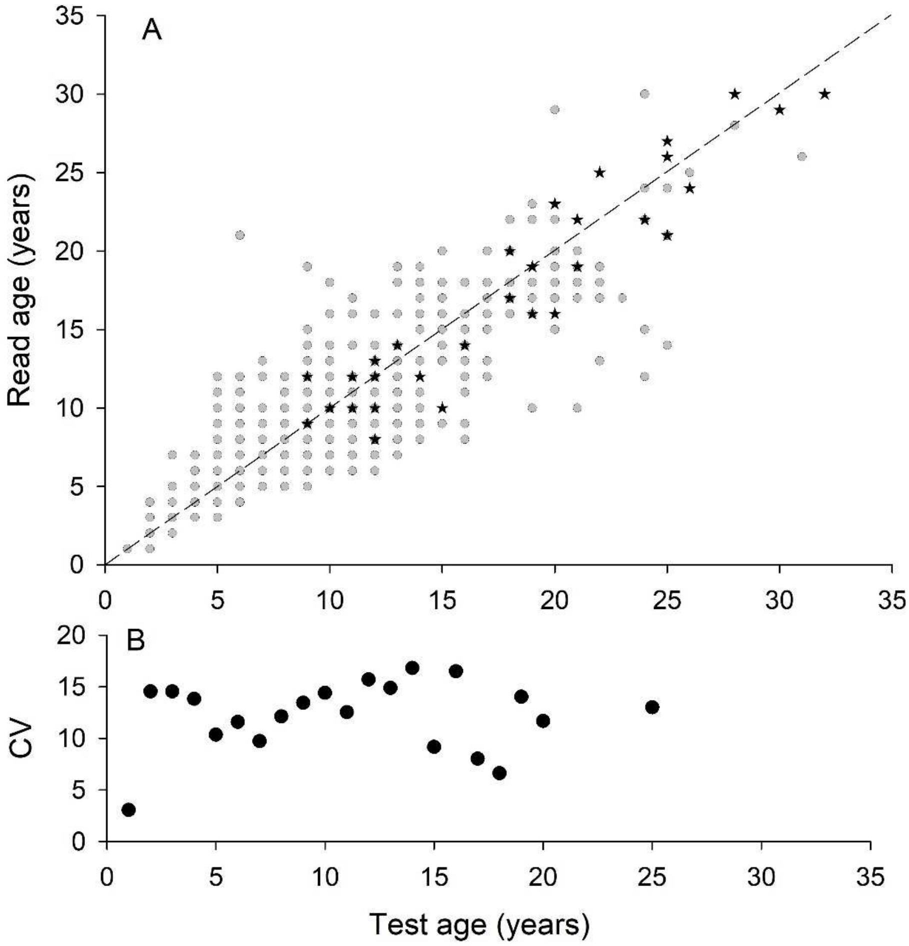


Figure 4.

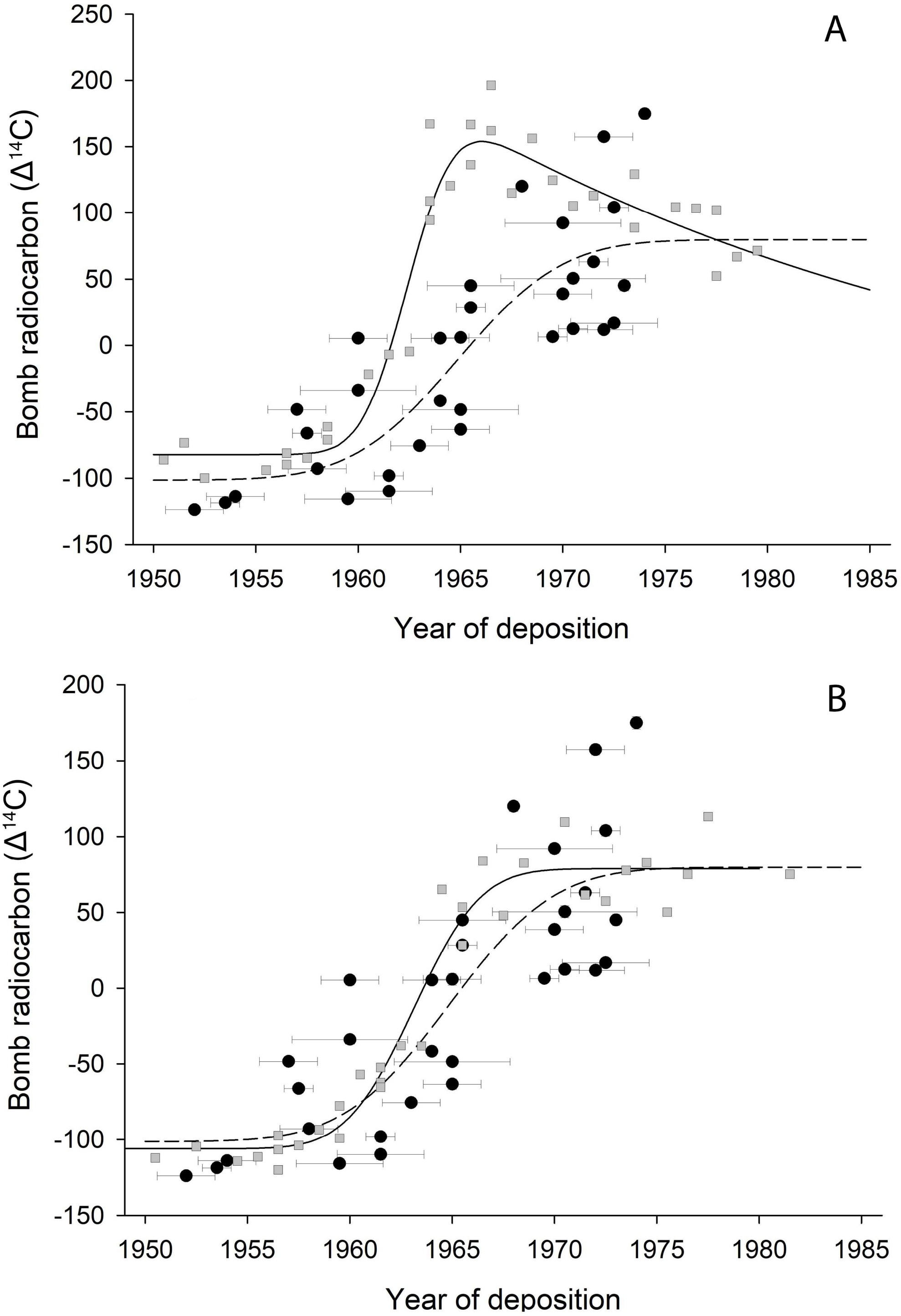
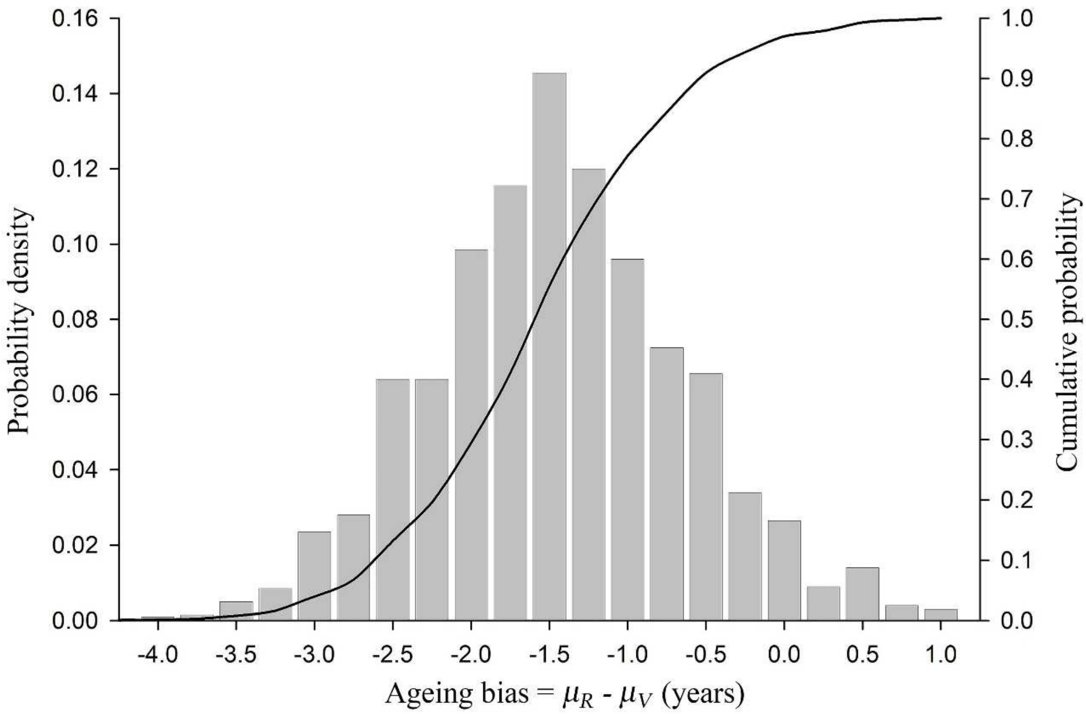

A
Bomb radiocarbon (Δ14C)
250
200
150
100
50
0
-50
-100
-150
1950
1955
1960
1965
1970
1975
1980
1985
Year of deposition
B
Bomb radiocarbon (Δ14C)
200
150
100
50
0
-50
-100
-150
1950
1955
1960
1965
1970
1975
1980
1985
Year of deposition

Figure 5.



0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Probability density
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Cumulative probability
-4.0
-3.5
-3.0
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
Ageing bias = μ_R - μ_V (years)