

RESEARCH ARTICLE

Bomb radiocarbon dating and age estimation of European eel (*Anguilla anguilla*) of Norway

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Received: 17 March 2024; **Revised:** 04 October 2024; **Accepted:** 22 October 2024; **First published online:** 27 January 2025

Keywords: anguilliformes; gas-AMS; lifespan; otoliths; Sargasso Sea

Abstract

Age estimates from bomb ¹⁴C dating conflict with a well-recognized age reading protocol (grinding, polishing and staining in the sagittal plane) for otoliths of European eel (*Anguilla anguilla*). Proper alignment of calculated hatch years for ¹⁴C measurements taken from the earliest otolith growth—among the smallest otolith extractions to date for successful ¹⁴C analysis due to the advent of gas-AMS—was not achieved using age estimates from an accepted method. The realignment of otolith ¹⁴C values to a tropical bomb ¹⁴C reference chronology, which is most applicable to the Sargasso Sea as the natal origin of European eel, led to an increase of the original age estimates by 8 to 32 years. A maximum age of approximately 46 years was determined for the European eel specimen with the most massive otolith, of which mass is a reasonable proxy for age and was instrumental in identifying age estimate discrepancies. By extending the otolith mass-to-age relationships from this study to the most massive otoliths available from archived otoliths of Norway, an increase of up to several decades from the original otolith age estimates was discovered, leading to support for a potential lifespan of 70–100 years in the natural environment.

Introduction

European eel (*Anguilla anguilla*) is an ecologically and commercially important species among Anguillid eels for which accurate estimation of age and growth is crucial for successful monitoring of population status and development of proper management strategies (Bevacqua et al. 2019; De Leo and Gatto 1995). It is a *critically endangered* species that is Red Listed by the IUCN (Pike et al. 2020), and yet stock assessment has been extremely challenging due to threat uncertainties and incomplete life history information, with one of the main difficulties being age estimation (ICES 2009a, 2011; OSPAR 2022). Methods exist but have not been validated through ontogeny—a requirement for a proper understanding of population dynamics (Campana 2001). *Anguilla anguilla* is one of 19 species, also known as freshwater eels, that have in common a facultative catadromous life history (Durif et al. 2023). For European eel, spawning occurs in the Sargasso Sea (Schmidt 1923), although most of its growth phase is spent in coastal and freshwater habitats of northern Africa and throughout Europe after migration across the North Atlantic (Figure 1). Because of this wide geographic distribution, there is an incredible variation in growth and reported lifespan, given they represent one genetic population (Als et al. 2011). Observations from otolith age estimation indicate they grow faster in the southern part of its distribution but live longer and achieve a greater age-at-maturation in the north (Durif et al. 2020; Vøllestad 1992). Estimated life-history parameters also vary according to sex and a choice of habitat that



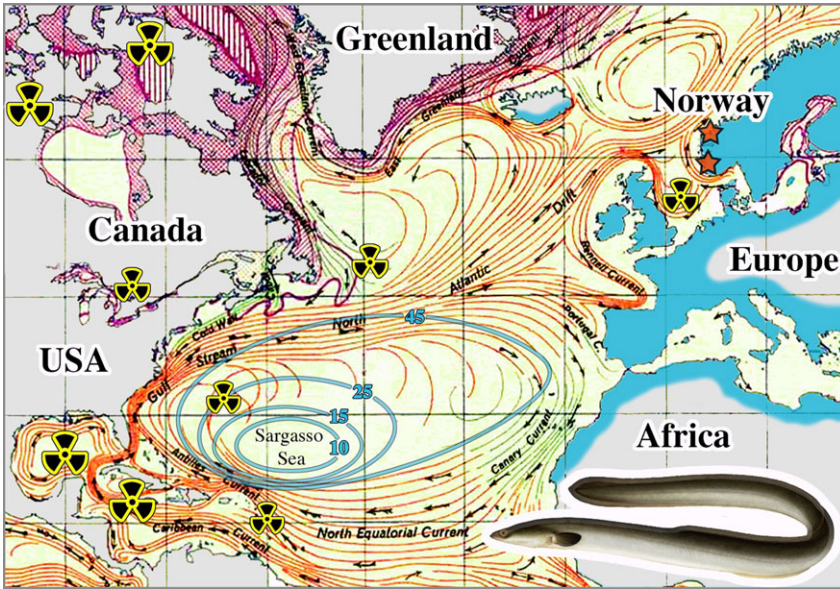


Figure 1. Map of North Atlantic with surface current patterns relative to the migration path of European eel, with collection locations in Norway (orange stars), and the selected bomb-produced ¹⁴C chronology locations from across the North Atlantic and North America (nuclear symbols; see Figure 2). Eggs hatch in the Sargasso Sea and *leptocephalus* migrate to inshore and continental habitats of northern Africa, throughout Europe, and north to Scandinavia (blue shaded edges). Radiating contours of 10-, 15-, 25-, and 45-mm TL are European eel length limits, within which nothing greater than that length exists in surface water collections and are indicative of the northeasterly migration pattern (Schmidt 1923). The most applicable bomb ¹⁴C reference records are from coral and otoliths in the western North Atlantic (Gulf of Mexico, Caribbean, Bermuda, Antilles) because they represent levels expected for the North Atlantic Gyre (Sargasso Sea) and waters advected as the migration path along the Gulf Stream to locations like Norway. A reliable clam shell record from the North Sea provides insight on ¹⁴C levels that are mixed with northern Europe runoff (waters that European eel would cross when migrating to Norway) and is intermediate to the timely ¹⁴C records of the Arctic and Laurentian lakes of North America (expected to be similar freshwater ¹⁴C records of Norway). Base map was rendered from a classic ocean circulation map produced by American Geographic Society (1943) that remains accurate for general flow patterns with indications of warm tropical (orange) and cooler marginal (green) currents (an otolith ¹⁴C record from cool waters of the Labrador Current off Canada provide an example of an attenuated bomb ¹⁴C signal for the Northwestern Atlantic; Figure 2).

covers marine to freshwater environments (Bertin 1956; Panfili and Ximémès 1994; Panfili et al. 2022; Rohtla et al. 2023).

Age determination is the key to providing feedback on the long-term status of European eel as either recovering or declining, but doubts have been raised on the efficacy of age validation methods (Daverat et al. 2012). The accepted manner of age estimation for European eel is from an analysis of otoliths that exposes annuli (periods of fast and slow growth), of which observed growth zone structure may or may not be annual (ICES 2009a, 2011; Moriarty 1983; Svedäng et al. 1998). Estimates vary according to the methods used to reveal the annuli, which is especially true for older slow-growing eel in the north with lifespan estimates exceeding 50 years (Poole and Reynolds 1996, 1998)—one well-defined transverse otolith section aged to 55 years exemplifies the potential differences from use of the sagittal plane for age estimation (i.e., See otolith section image shown for a 77.4 cm TL European eel of Ireland on the cover and page 44 of the Otolith Manual from WKAREA 2009; ICES 2009b; Supplemental Material Figure 1). The

forms of age validation applied thus far are typically limited to the earliest otolith growth where the otolith margin type can be observed (Panfili and Ximémès 1994) or by tag and return of younger individuals (<12 years; ICES 2009a). There are unique records of individuals that were held captive for 43 years (Palstra et al. 2020) and over 100 years (Brantevik Eels of Sweden; Wikipedia.org), although it is unknown if such a great lifespan can occur naturally. European eel of Norway are among the oldest specimens for this species (Rohtla et al. 2023). Recently, European eel—thought to be on average 8 years old based on otolith readings—were re-estimated to an average of 19 years with certain individuals being aged to over 35 years (Durif et al. 2020). Although the more recently developed otolith processing method revealed more than twice as many annuli, validation of the annual periodicity of growth zone formation remains.

One of the most effective methods of determining accurate estimates of age, growth, and lifespan for fishes is bomb radiocarbon (^{14}C) dating of otoliths. This approach to age validation relies on a bomb-produced ^{14}C signal created by thermonuclear testing in the mid-1950s to the early 1960s (Hua et al. 2022). Because the calcium carbonate (CaCO_3) of otoliths is formed mostly from dissolved inorganic carbon (DIC), and therefore environmental levels are reflected in the inert biogenic aragonite, age determination is possible by comparison with regional aquatic ^{14}C reference chronologies (i.e., coral or known-age otolith material). The approach can be used to test the validity of ages from an estimation protocol, or it can provide an independent age estimate when quantifying growth zone structure that is inaccurate or poorly defined (e.g., Andrews and Schofield 2021; Andrews et al. 2018a, 2018b). The use of bomb ^{14}C dating for age validation of fishes has undergone steady refinement and innovation over the last 25–30 years (Andrews et al. 2013, 2019, 2024; Kalish 1993; Shervette et al. 2023), and the method has led to lifespan revelations and validated life history parameters that contribute to a better understanding of North Atlantic fisheries (e.g., Andrews et al. 2020; Dwyer et al. 2016; Friess and Sedberry 2011; Kalish et al. 2001; Neilson and Campana 2008).

European eel exhibits a migratory life history in the North Atlantic that would complicate otolith ^{14}C composition because uptake is derived from the environment at the time and location of the fish through ontogeny. They begin life in the warm waters of the Sargasso Sea in the North Atlantic after adults migrate from continental habitats to spawn. Eggs hatch and the leptocephali (so-called eel larvae) and glass eel (juvenile stage) drift within the Sargasso Sea and Gulf Stream for the first 1–2 years of life to continental waters, within which they will spend most of their growth phase (Bohemmeau et al. 2010; Lecomte-Finger 1992, 1994; Tesch 2003). Thus, it is expected that the ^{14}C content of core material formed in the first 1–2 years of life would be representative of tropical to subtropical marine environments of the North Atlantic. Material deposited in the following years is likely to represent recruitment to the inshore marine environment and onward to freshwater habitat, depending on the individual and location (Limburg et al. 2003; Rohtla et al. 2023). Hence, ^{14}C measurements from the earliest otolith growth must consider potential changes in the environmental ^{14}C levels during the migration period.

In this study, assays of ^{14}C levels were made from the earliest growth of the very small otoliths (3–10 mg) of European eel of Norway, with the aim of applying bomb ^{14}C dating to test estimates of age by alignment of measured values to a range of applicable bomb-produced ^{14}C reference chronologies. Ten previously aged European eel otoliths were selected from collections made in southern and central Norway (Nedstrand and Sunnmøre) to measure ^{14}C levels within the first 1–2 years of otolith growth (core extraction of ~100–200 μg CaCO_3), which was possible with the advent of gas-AMS (Synal et al 2007; Wacker et al. 2013a, 2013b). Estimated ages from counting annuli were 8–29 years for these specimens with corresponding hatch years spanning 1983–2005. The premise for this sample series was that if the age estimates were accurate, then the otolith core ^{14}C measurements would align with a reference chronology for the post-peak decline of bomb-produced ^{14}C , as defined at a minimum by atmospheric ^{14}C levels, and by coral and known-age otoliths of North Atlantic tropical seas. Because initial observations of otolith mass as a potential proxy for age provided an indication that age estimates were inconsistent and may not be accurate for some or all of the individuals, otolith mass was considered further as a tool in age estimate refinement on the basis of measured ^{14}C values and the potential years of reference chronology alignment.

Material and methods

Otoliths of European eel were considered from various collection locations across southern and central Norway that were previously aged using a standardized age reading protocol (grinding, polishing and staining in the sagittal plane; Durif et al. 2020). Two regions were selected (Sunnmøre and Nedstrand, Norway) with a range of ages and otolith masses to cover what may be an indication of age estimate inconsistency—the relationship for otolith mass to estimated age was poorly aligned because some younger fish had larger otoliths than older specimens by a considerable margin. The selected specimens had age estimates of 8 to 29 years, coupled with otolith masses that covered 3 to 10 mg because it is often a reasonable proxy for age (e.g., Andrews and Scofield 2021; Andrews et al. 2018a; Pacheco et al. 2021), to potentially reveal deficiencies in the age reading protocol (Table 1). In addition, the approach to bomb ^{14}C dating was to select a series of age estimates within a narrow collection period to trace the bomb ^{14}C signal back through time, thereby attributing the increases of otolith ^{14}C levels between individuals to progressively older hatch years. Hence, the selected collection years of 2012–2013 led to calculated hatch years of 1983–2005. Given the original age estimates are accurate, the measured ^{14}C values from the earliest otolith growth (core) were expected to be related to the post-peak bomb ^{14}C decline, with the earliest years being the most elevated because the fish were alive near the peak of bomb-produced ^{14}C in aquatic environments—see measured ^{14}C alignments in Andrews and Scofield (2021) and Hupfeld et al. (2023).

Annuli based age determination

Prior to processing, otoliths were weighed using a microbalance (Metler Toledo) to the nearest 0.001 mg. Either one of the two sagittal otoliths were prepared by grinding, etching, and staining, and age reading according to the described protocol (ICES 2009a, 2009b, 2011). The year-0 band was assigned as the first winter after the oceanic migration marking the beginning of the continental life stage. None of the otoliths had clear and regularly spaced annuli. Most presented numerous tight rings, unevenly spaced, which sometimes joined in a “bundle” or fused into one large annulus on the other side of the otolith. It was assumed that some of the marks forming a bundle represented false checks, caused for example by thermal stress outside of the typical winter annuli formation. Thus, one bundle represented one year. An age estimate was assigned but it was apparent that errors could be linked to (1) bundles and possible false checks and (2) outer rings that were not considered as they were not entirely embedded in the resin and polished (see sample EE009).

Micromilling

The core of the remaining whole sagittal otolith from each pair (one was aged previously) was extracted with a New Wave micromilling machine for ^{14}C analysis. Otoliths were prepared for milling by mounting them in Cytoseal 60 (Richard Allen Scientific Company) on glass microscope slides with the distal surface facing upward (sulcus side down). Because the distal surface shows mass accretion through ontogeny in transverse sections, and this external surface was hand ground (600 grit carbide wet-dry sandpaper) to a thickness that was just shy of the plane (sagittal) that is usually used for age reading. This approach effectively conserved the nuclear region for extraction of the earliest growth with the micromill. Core material, estimated as the first 1–2 years of growth, was determined using existing information on otolith size with age as shown in otolith sections for the selected specimens, as well as other well-illustrated references (e.g., ICES 2009a, 2009b, 2011; Durif et al. 2020). Otoliths from a migrating elver were measured as approximately $500 \times 600 \times 300 \mu\text{m}$ (width, height, depth; ICES 2009a, 2009b, 2011), dimensions that would yield just enough material for gas-AMS technology with reasonable precision ($\sim 150 \mu\text{g CaCO}_3$). Once the otolith thickness reached a dimension that indicated the earliest growth was exposed, a $300 \mu\text{m}$ carbide spherical cutting bur (Brasseler USA) was used to mill the core region, which was verified microscopically after the extraction. The mill

Table 1. European eel data for fish and otoliths used in this study that were collected in 2012–13 from Sunnmøre and Nedstrand, Norway, with estimated age from growth zone counting in sagittal otolith sections, readability score, measured ^{14}C from otolith cores, and alternate age scenarios based on ^{14}C reference records. Age from atmospheric chronology (Atm) are minimum ages and **bold** values are older than the original age estimates by at least the number of years in parenthesis. Data for EE009A/B are successive core extractions on same otolith specimen. The $F^{14}\text{C}$ values listed had a measurement error of ± 12 – 16% from sample masses of ~ 100 – $170\ \mu\text{g}\ \text{CaCO}_3$ that generated 12 – $20\ \mu\text{g}\ \text{C}$. The number of years added from original age (+yrs) and hatch year (hyr) are provided to show shifts in age based on alignments of measured ^{14}C values to each reference chronology

Lab #	TL (mm)	Otolith mass (mg)	Age (hyr)	Score	$F^{14}\text{C}$	Atm age (+yrs)	Tropical age (+yrs, hyr)	Oldest age (+yrs, hyr)
EE001	404	3.24	11 (2002)	1	1.107	16 (+5)	23 (+12)	23 (1990)
EE002	386	4.34	13 (1999)	1	NR	—	—	—
EE003	463	4.80	17 (1995)	1	1.116	17	25 (+8)	25 (1987)
EE004	415	5.59	22 (1990)	2	1.091 [†]	—	—	—
EE005	562	6.00	8 (2005)	1	1.119	19 (+11)	27 (+19)	27 (1986)
EE006	556	7.29	24 (1988)	1	1.146	21	34 (+10, 1978)	—
EE007	560	8.34	27 (1985)	2	1.152	22	37 (+10, 1975)	42 (+15, 1971)
EE008	568	9.75	29 (1983)	1	NR	—	—	—
EE009A	507	10.47	14 (1999)	2	1.138	21 (+7) [‡]	33 (+19, 1980)	46 (+32, 1968)
EE009B	—	—	—	—	1.177	25 (+11) [‡]	31	44

NR = Sample was not recovered from foil packet. [†] Coring included younger material that diluted the measurement ($F^{14}\text{C}$ much lower than expected and visually confirmed). [‡] The core sample (9A) cannot be younger than the second core sample (9B) that has a minimum age of 25 years due to ^{14}C level.

extractions were three passes of a 5-point surface scan to a depth of 100 μm on each pass. Each extraction is targeted within the first 1–2 years of growth. An additional extraction was performed on the largest otolith to sample growth years 3–4 by running two 100 μm deep passes along a 6-point scan that skirted the edge of the first core. The target mass for each extraction was approximately 100–200 μg of CaCO_3 . Each small pile of colloidal powder that was generated from each extraction was hand collected and placed in foil envelopes to be sent to ETH Zürich for ^{14}C analysis with gas-AMS.

Gas-AMS

Radiocarbon analysis of otolith calcium carbonate samples was performed by gas-AMS using the Mini Carbon Dating System (MICADAS) at the Laboratory of Ion Beam Physics, ETH Zürich, Switzerland (Synal et al. 2007). Samples were dissolved in phosphoric acid in the septum-sealed vials (Labco UK, Exetainer® 4.5 mL round-bottom borosilicate vials) under helium and CO_2 is released from the carbonates. In contrast to conventional graphite AMS analysis, where the liberated CO_2 is reduced to graphite and measurements are performed on solid targets (e.g., Wacker et al. 2013b), the CO_2 gas is concentrated by means of a zeolite trap and transferred with a helium gas carrier into a syringe in the gas interface system (Wacker 2013a). The gas sample is further diluted with helium and fed into the gas ion source of the AMS. A major advantage of the gas-AMS technique is, besides it being cost-effective and fast, that sample sizes required for the analysis are significantly smaller. Solid-AMS analysis typically requires 1 mg of CaCO_3 compared to less than 100 μg CaCO_3 needed for a gas analysis. With this approach, otolith carbonate samples were 10–20 times smaller compared to previous studies. Fossil and modern reference materials (IAEA-C1; Rozanski 1991) and an in-house coral standard (CSTD, nominal $F^{14}\text{C}$ value 0.9447 ± 0.0002 , G. Dos Santos, pers. comm.) were analyzed in concert with the samples. Data evaluation was performed with the “Beautiful AMS Tool of Switzerland” software (BATS), an analysis routine that functions as a reliable data reduction tool (Wacker et al. 2010). Radiocarbon data are reported as Fraction Modern ($F^{14}\text{C}$) according to Reimer et al. (2004).

Reference ^{14}C chronologies and age alignments

Five chronologies were selected to align the measured ^{14}C values from European eel otolith cores to the potential years of the otolith core formation. These chronologies ranged from atmospheric and freshwater records to locations across the North Atlantic that would function as a proxy for ^{14}C levels on the migration route used by European eel to reach Norway from the Sargasso Sea (Figure 1). The Northern Hemisphere atmospheric bomb ^{14}C record (NH1) describes the uptake and transport of bomb-produced ^{14}C throughout the Northern Hemisphere at latitudes greater than 40°N (Hua et al. 2022). This temporal reference represents the most recent date that an elevated bomb ^{14}C level can be sequestered by an otolith that formed in an aquatic environment at northern latitudes. Alignment of measured otolith ^{14}C values from a recently collected fish with this chronology provides an absolute minimum age limit (Figure 2).

A series of otolith ^{14}C measurements from fishes of Arctic and Laurentian lakes of North America (Campana et al. 2008; Casselman et al. 2019; Lackmann et al. 2019) was used as a proxy for freshwater ^{14}C levels in Norway. European eel used in this study eventually reached the freshwaters of Norway and would sequester to the otolith a similar near-atmospheric ^{14}C signal. There are no known water or fish otolith measurements of ^{14}C from freshwaters of Norway, but the ^{14}C records of North America should represent the precipitation ^{14}C signal (rain to river) across the well-mixed atmosphere of the Northern Hemisphere (Figure 2).

The most applicable ^{14}C reference chronology for hatch year otolith material of European eel is from tropical coral and otoliths covering the marine ^{14}C signal for North Atlantic waters, such as the natal origin of European eel, the Sargasso Sea. This collection of ^{14}C records covers a vast area ranging from western Gulf of Mexico and Caribbean Sea to Bermuda (Andrews et al 2013; Barnett et al. 2018;

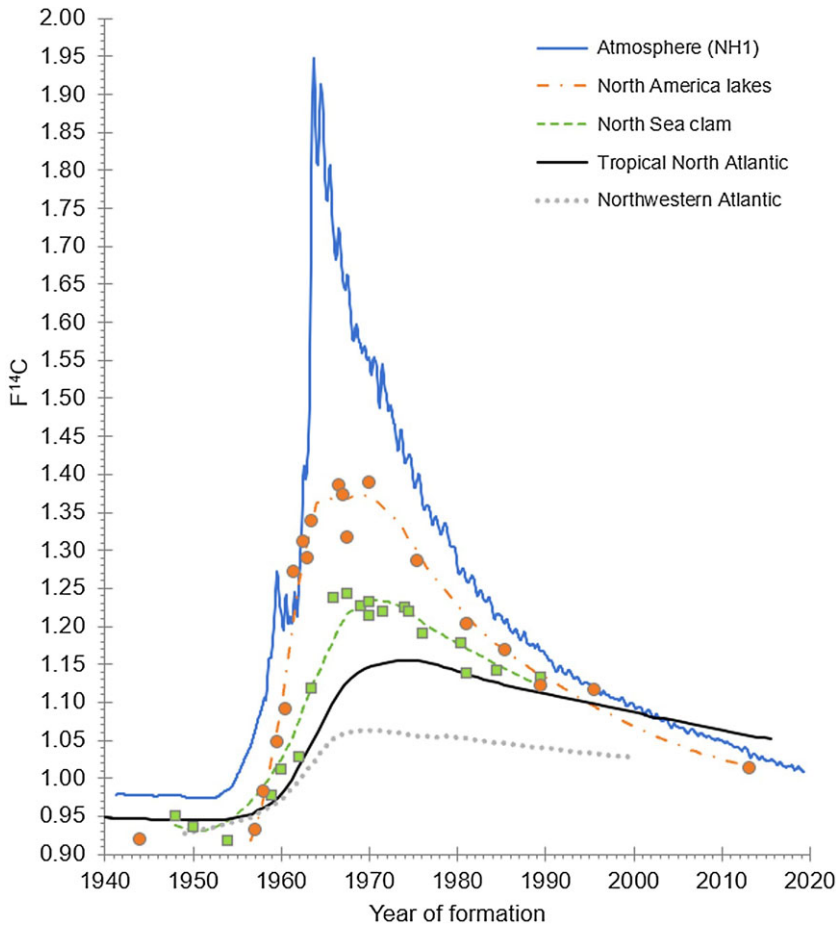


Figure 2. Selected bomb-produced ^{14}C chronologies from across the North Atlantic and the northern freshwater hydrosphere that are applicable to otolith formation during the migrational early life history of European eel. The atmospheric chronology for the Northern Hemisphere (NH1)—a composite of ^{14}C measurements from regions greater than 40°N latitude (Hua et al. 2022)—provides an absolute minimum age for the alignment of otolith ^{14}C values from recent capture years. The tropical North Atlantic chronology is considered the most reliable temporal reference for the earliest growth of European eel because it is a composite of ^{14}C references that would reflect the mean ^{14}C levels in the mixed layer of the Sargasso Sea, the known natal grounds for this species (Andrews et al. 2013, 2020, Barnett et al. 2018, Shervette et al. 2023). The North America Lakes freshwater chronology, established from otoliths of Arctic and Laurentian fishes (Campana et al. 2008; Casselman et al. 2019; Lackmann et al. 2019), is the best available proxy for the freshwaters of Norway. An intermediate record from the North Sea—established by an *Arctica islandica* clam shell in the mixed German Bight (Scourse et al. 2012)—provides a proxy for a mixed ^{14}C signal of North Atlantic waters that European eel would cross during migration to Norway. For a contrast in bomb ^{14}C signal strength, a northwestern Atlantic otolith chronology (Campana et al. 2008) shows the strong attenuation effects of mixed deep waters that are ^{14}C -deficient.

Shervette et al. 2021) and yet it provides a very consistent reference chronology that has become the ^{14}C reservoir by crossing the atmospheric ^{14}C record in the early 2000s (Figure 2). An intermediate chronology from a long-lived clam shell (*Arctica islandica*; Scourse et al. 2012) of the North Sea was selected as a good proxy for a mixed ^{14}C signal—tropical marine waters advected north by the Gulf

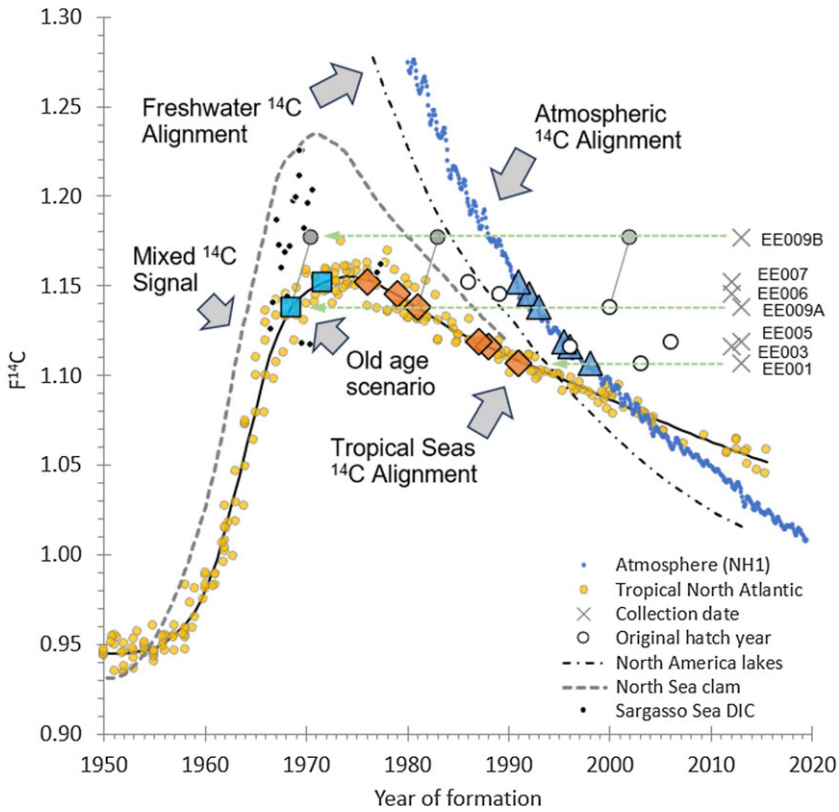


Figure 3. Alignments of ^{14}C data from European eel (*Anguilla anguilla*) otoliths relative to the collection years (X with sample ID) that are projected back to hatch year scenarios (green dashed arrows) as determined by: 1) the original otolith section age estimations (open circles); 2) the minimum ^{14}C age from an alignment with the atmospheric ^{14}C chronology (blue triangles); 3) the most applicable ^{14}C age from an alignment with the tropical seas chronology on the post-peak decline (orange diamonds); and 4) an extended ^{14}C age (old age scenario) from an alignment with the ^{14}C rise and peak period (blue squares). The grey circle connected to some data points is the second core from EE009 A/B (see Figure 5), the most massive otolith in the study and likely the oldest, as evidenced by the elevated ^{14}C levels noted in Sargasso Sea DIC measurements (Nydal et al. 1984). The freshwater and mixed ^{14}C chronologies are from North Sea and North America lakes as possible elevated alignment chronologies that depend on where this fish was during the otolith core formation period. The tropical seas chronology (Tropical North Atlantic) is also represented by the data from coral and otoliths (small yellow circles) to provide a visual on the variance associated with this ^{14}C record.

Stream to mix with freshwater influxes from Europe—as migrating European eel approach Norway (Figures 1, 2).

Hatch years were initially determined as the difference between capture year and the estimated age from annuli counting in the otolith sections. These hatch years were combined with the measured ^{14}C value from otolith core material and were plotted with the series of applicable bomb ^{14}C reference chronologies (Figure 3). Each hatch year was adjusted by +1 year to cover the mean year of formation for a more accurate alignment (2-year core) and all ages and collection dates were treated as years. When hatch years did not align with a given ^{14}C chronology, the year of formation was shifted by the number of years required to align with each reference curve. These shifts in time, rounded to nearest year, led to revised hatch years and ages that were used to provide insight on the age reading

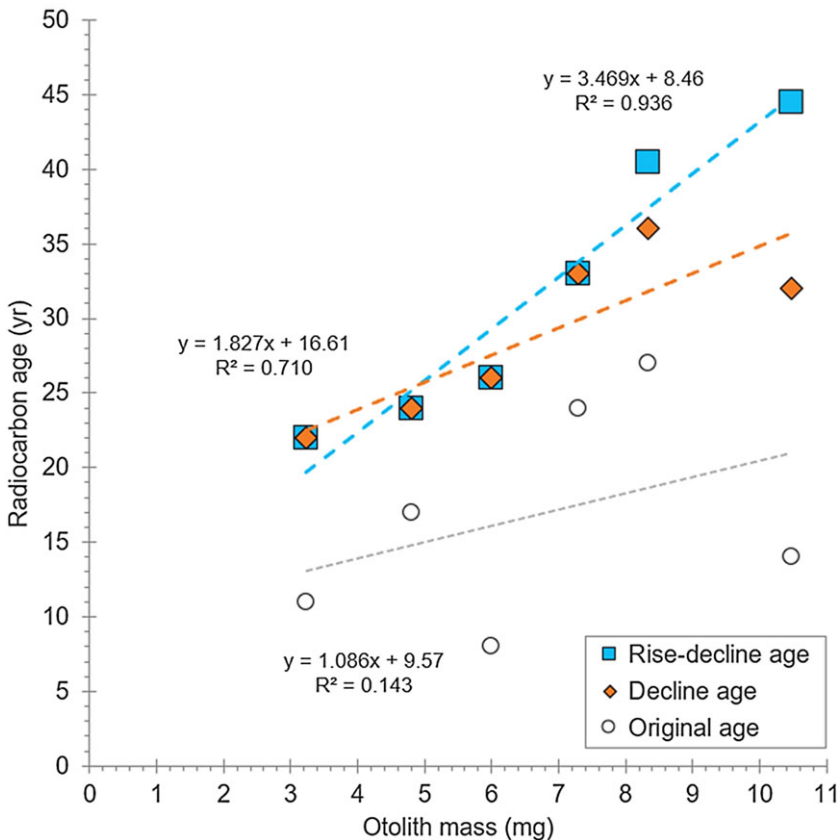


Figure 4. Plots of European eel (*Anguilla anguilla*) age estimates versus otolith mass for the otoliths used in this study that provided an opportunity to investigate relationships for three age estimation scenarios (original age = annuli counting; decline age = alignment of ^{14}C values to the post-peak decline; rise-decline age = an extension of the two most massive otoliths to the upper ^{14}C rise and peak period). Because otolith mass is often a reasonably good proxy for age, these comparisons can provide insight on what age estimates are more likely to be accurate in the absence of known age otoliths. The original age estimates (open circles) provided the poorest fit with large inconsistencies in otolith mass accretion rates and an unrealistic intercept. Alignment of the otolith ^{14}C values to the post-peak decline led to ages that made otolith mass a better proxy for age, but the best fit was when the two most massive otoliths were shifted to upper bomb ^{14}C rise and intermediate peak positions (Figure 3).

of European eel otoliths. In addition, otolith mass can function as a proxy for age and was used as a guide in making decisions about greater age scenarios relative to the applicable ^{14}C reference chronologies.

Results

Calcium carbonate samples were successfully extracted from the otoliths of European eel, which may be the smallest ever used in bomb ^{14}C dating. Otolith core material that was extracted with a micromilling machine was 100–170 μg from whole otoliths that weighed 3.24–10.47 mg (Table 1). The initial comparison of otolith mass to estimated age revealed differences in otolith mass-growth through time and a poor correlation among individuals (Figure 4). These differences were further highlighted with the corresponding ^{14}C measurements and reference chronology inferences and alignments.

Radiocarbon measurements for European eel were successful for eight of the 10 specimens because two samples were not successfully recovered from the foil envelopes (Table 1). The measured $F^{14}C$ values were 1.091–1.177 and followed a generally increasing pattern with increasing otolith mass and age (as hatch year decreases (increasing age) within the last few decades, the bomb-produced ^{14}C values should increase systematically toward peak values); however, the calculated hatch years for the otolith measurements led to a mix of within and outside the absolute minimum age for hatch years set by the atmospheric reference chronology (Figure 3).

Minimum age from bomb ^{14}C

The hatch years from annuli estimates for three specimens resided well outside the atmospheric ^{14}C chronology (Figure 3). Therefore, ages must have been underestimated by at least 5 to 11 years (EE001 = 11 *cf.* 16 years, EE005 = 8 *cf.* 19 years, EE009A = 14 *cf.* 21 years) from the otolith core measurements and by at least 16 years for the second core (EE009B = 14 *cf.* 25 years; Table 1). The age of 25 years for EE009B, being the most elevated value of the EE009A/B measurement pair, trumps the minimum age of 21 years for EE009A because the core cannot be younger than a sample extracted from more recently formed material. Furthermore, these ages are strictly the minimum age for each fish from the alignment of each year of formation with the atmospheric ^{14}C chronology. The true age of each specimen is likely older than determined by this limitation because only freshwater aquatic habitats tend to be nearly in synch with the atmosphere due to timely aquatic deposition via precipitation (e.g., Figure 2).

The other four otolith core ^{14}C values were within the range of possible ^{14}C values as prescribed by the various reference chronologies (Figure 3). One specimen had a ^{14}C value that aligned with the atmospheric reference at an age of 17 years (EE003), but this fish is likely older for reasons stated previously. Two fish were aged in their mid-20s with calculated hatch years later than the minimum age set by the atmospheric ^{14}C reference (EE006 = 24 *cf.* 21 years, EE007 = 27 *cf.* 22 years; Table 1). One measurement (EE004), however, was suspected to be contaminated because the ^{14}C value was considerably lower than expected relative to the other sample findings (Table 1). Upon inspection of the cored otolith and referring to laboratory notes, this sample most likely included a significant amount of mass from other parts of the otolith that were formed more recently (cracks formed during milling with missing micro-pieces mixed into the sample). Inclusion of material away from the core would reduce the apparent core ^{14}C value, as indicated by being the lowest ^{14}C value ($F^{14}C = 1.091$), because of the decrease of environmental ^{14}C over the lifespan of the fish. Hence, this sample was deemed unreliable and is not considered further.

Bomb ^{14}C age

Annuli-based age estimates provided a range of formation years that were either reasonable or unreasonable in terms of the limits set by bomb-produced ^{14}C (Table 1). The earliest otolith growth was expected to be formed primarily from DIC of the tropical waters of the Sargasso Sea through to the northern extent of the Gulf Stream near the North Sea (Figure 1). Hence, the most applicable temporal reference for measured ^{14}C values from European eel otolith cores is the tropical coral and otolith chronology that covers much of the marine mixed-layer ^{14}C signal for the North Atlantic but must also consider the North Sea reference chronology as a mix of oceanic and continental freshwater sources (Figures 2, 3). Beginning with the smallest otolith (EE001, 3.24 mg) at a minimum age of 16 years from alignment to the atmospheric chronology, a realignment of the measured ^{14}C values to the tropical chronology leads to an age of 23 years and a hatch year of 1990 (Figure 3). This is an increase of 12 years from the annuli count estimate of 11 years. Following this approach, EE003 and EE005 are the next most massive otoliths (4.80 and 6.00 mg) with minimum ages from alignment to the atmospheric chronology of 17 and 19 years, respectively. While the annuli-based year of formation for EE003 aligns

with the atmospheric ^{14}C record, the actual age would be 8 years older for an age of 25 years and a hatch year of 1987 based on the tropical North Atlantic chronology. For EE005 the original age estimate of 8 years was underaged by at least 11 years according to the atmospheric record and would have been 27 years old by aligning with the tropical ^{14}C chronology, an increase of 19 years for a hatch year of 1986.

Following this trend of using the tropical reference chronology to reassess age, the three most massive otoliths that also had the most elevated F^{14}C values were revised to ages of 33 to 37 years with hatch years of 1975–1980 (Table 1). These ages are 10–19 years older than the original age estimates. For EE009A/B, the ^{14}C value for the second sample core rises above the tropical ^{14}C reference and is estimated to be 2 years more recent than the first otolith core. The timing for this measurement aligns with a combination of the freshwater proxy for ^{14}C (North America lakes) and the levels expected for the North Sea (Figure 3), as expected if this individual had moved into the coastal waterways of Norway by this time in the formation of the otolith. This elevated F^{14}C value provides support for the alignment of the first otolith core with the tropical North Atlantic chronology because placement in time with the North Sea or freshwater proxy is limited and leads to a less plausible alignment to, or outside, the atmospheric chronology.

The alignment of the three most massive otoliths focused on the post-peak ^{14}C decline but because of their proximity to peak ^{14}C levels during this period, the measurements could have formed further back in time and still agree with the tropical ^{14}C chronology. By comparing otolith mass to age there is support for greater ages to EE007 and EE009 because mass becomes a better proxy for age (Figure 4). Hence, the most massive otolith may be associated with the late rise of bomb ^{14}C , prior to reaching peak levels, by assuming only the first 2–3 years of growth were sampled. Alignment to the bomb-produced ^{14}C rise increases the age of EE009A to 46 years with a hatch year of 1968, which consequently places the elevated second core in 1970 and near peak levels, possibly representing uptake of ^{14}C from a combination of the tropical seas and mixed North Sea waters while in transit to the northeast (Figure 3). Consideration of historic ^{14}C measurements made in DIC from the Sargasso Sea during the peak period (Nydal et al. 1984) might explain some of the slightly elevated ^{14}C level of the second measurement, relative to the more averaged chronology that is derived from coral and otolith samples, but it seems more likely that the elevated levels reflect a mix of the ^{14}C chronologies to the northeast and its arrival in the freshwaters of Norway (Figure 3). It is important to note that DIC measurements are typically much more variable than coral and otolith samples (months or even a year of accretionary growth) because each DIC measurement is instantaneous. For EE007, the hatch year alignment is not as well defined because the measured ^{14}C value from the core is similar to peak bomb ^{14}C levels, but an estimated hatch year of 1971 was applied in this case (toward the top of the rise period, although it could be a few years younger) for an age of 42 years (Figure 3). These alignments are an increase of 15 and 32 years to the original age estimates (Table 1).

The successive ^{14}C measurements made for the most massive otolith (EE009 at 10.47 mg) exemplify the successful process used to extract core material from European eel otoliths. The first extraction (Core 1) targeted the first two years of growth and the second (Core 2) targeted a few more years beyond the core (Figure 5A). Based on the original counting to 14 years (marked), Core 1 extracted the first year of growth and Core 2 covered most of years 2–3 based on an overlay of the cutting paths (Figure 5B). However, because the first two growth zones are tightly coupled and not originally counted separately, it is possible that Core 1 sampled years 1–2 and Core 2 sampled years 3–4. Alignments were similar for the other single-extraction otolith cores by being within what is interpreted here as the first 2 years of growth.

Discussion

Bomb ^{14}C dating of European eel otoliths has revealed that an accepted otolith age reading protocol can significantly underestimate true age. The temporal constraints that are set by environmental ^{14}C reference chronologies indicate the age of some individuals was older by at least 5–11 years and by up to

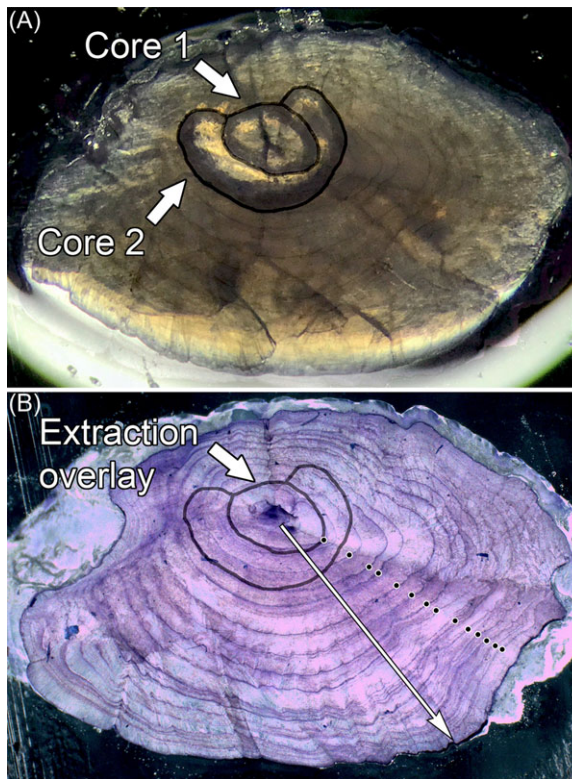


Figure 5. Sagittal otolith sections from the European eel (EE009) with the most massive otolith (10.47 mg) showing (A) the core extractions and (B) the growth zone counting marked to attain the original age estimate of 14 years. The otolith core was extracted twice (A) with core 1 centered on the first 2 years of growth and core 2 as a concentric extraction to remove years 3 and 4. The overlay (B) shows how this specimen and the other otoliths were verified by tracing a microscopic view of the extraction area on the aged otoliths. An older age reading scenario that may account for the much greater age of 46 years is indicated with the white arrow extending from the nucleus to the edge, along which there are numerous finer increments that are currently considered subannual.

a few decades when aligned with the most applicable bomb ^{14}C chronology. Because the natal origin of European eel is the Sargasso Sea, use of the coral-otolith ^{14}C reference for the tropical North Atlantic was the most trustworthy for the alignment of measured ^{14}C values from otolith cores because of the shared water mass sources (Figure 1). Discrepancies in how age was determined were highlighted by changes in the otolith mass-to-age relationship as estimates of age increased with the more applicable ^{14}C reference alignments. Because otolith mass usually functions as a reasonable proxy for age (e.g., Andrews and Scofield 2021; Andrews et al. 2018a; Pacheco et al. 2021), it was evident that there were problems with the accepted age estimates because otolith mass-to-age provided a poor correlation. Once minimum ages were determined from the atmospheric ^{14}C chronology, and then further projected to the tropical seas ^{14}C record, the otolith mass-to-age relationship improved and supported ages approaching 50 years (Figure 4).

The specimen with the greatest age estimate discrepancy was for the European eel with the greatest otolith mass at 10.47 mg. Age was initially estimated to be 14 years from what appears to be a well-defined age reading protocol, but ^{14}C levels indicated the fish was much older. The otolith for this fish was successively sampled (two core extractions) to investigate changes in ^{14}C uptake through the early years of growth. From otolith section image overlays, the first core was likely the first 1–2 years of

growth and the second core (a ring around the first core) was material that may have formed during ages 3–4, given early ring counts are accurate—one closely set ring to the first was considered year-2 but may have been part of the first ring (Figure 5). The ^{14}C levels measured for this sample pair revealed a pattern that may reflect a habitat transition or a longer lifespan. Because the core ^{14}C value was lower than the second core ($F^{14}\text{C} = 1.138$ cf. 1.177), the increase in ^{14}C could represent movement from tropical marine (Sargasso Sea and Gulf Stream) to freshwater influenced habitats of the eastern North Atlantic, like the North Sea, or rivers and streams of Norway (e.g., Arctic-Laurentian freshwater habitats of North America by proxy). For this scenario, alignment of sample EE009A with the post-peak ^{14}C decline of tropical seas leads to placement of the elevated sample EE009B on a date that reflects a mix of North Sea and freshwater habitat ^{14}C levels (Figure 3), as expected with a 1–2-year migration to Norway. This alignment leads to an age of 33 years, which is 19 years older than the original age estimate.

While it is known that this species begins life in the Sargasso Sea and would continue to sequester ^{14}C levels representative of the North Atlantic tropical seas through to northern latitudes of the North Atlantic, the formation time and location within the sampled otolith was not known. Hence, the estimated age may have incorporated levels that are represented by the North Sea chronology during the latter formation period of the core sample. However, the successive measurements made on the largest otolith provided important insight by limiting the alignment of the core to the tropical North Atlantic chronology by placement of the second core as a mix of the freshwater and North Sea chronologies. This observation provides support for the age of recruits, as they reach Scandinavian habitats by crossing the greatest distance traveled, is a few years old in order to complete the migration from the Sargasso Sea (Bonhommeau et al. 2010; Kettle and Haines 2006; Lecomte-Finiger 1992).

The long-lifespan interpretation for the largest otolith, however, is equally viable and places the hatch year on the upper rise of bomb-produced ^{14}C in 1968 for an age of 46 years (Figure 3). This leads to placement of the second measurement in 1970 near peak ^{14}C levels. While this elevated value is above the range of peak ^{14}C values from the tropical chronology, it can be explained by either the measurement uncertainty (± 12 – 16%) or more elevated ^{14}C levels during this time that are unaccounted for from the gyre waters of the Sargasso Sea (Nydal et al. 1984). In addition, otolith mass provides better support for the older age interpretation because this otolith would have been the oldest, as opposed to second oldest based on an alignment to the post-peak decline. The age of 46 years for the most massive otolith, and a marginally greater age of 42 years for the next most massive otolith (EE007) as having formed during the peak period, significantly improved the otolith mass-to-age relationship (Figure 4). This finding is more in line with what was expected and may be an indication that otolith mass can function as an effective proxy for European eel age.

Taking the findings of this study one step further, it is possible to estimate the maximum age of European eel in Norway. An examination of otolith archives for Norway revealed that otoliths can attain masses that are nearly 3 times greater than the largest otolith of this study (10 mg cf. 28 mg). By applying the older age scenarios for otolith mass-to-age, it is possible to speculate that European eel in Norway may reach a 70- to 100-year lifespan, considerably older than an estimate of 34 years from annuli counting in the 28 mg otolith. Clearly, this series of estimates is based on a few data points and should be considered with caution, but it is suggested that these otolith mass-to-age relationships be used to design a follow up study to further explore ^{14}C in European eel otoliths. The temporal alignment of additional European eel otolith measurements to bomb ^{14}C chronologies, with further investigation of how otoliths are interpreted for age estimation, should lead to better age-at-length estimates that provide a validated basis for accurate life history parameters and population longevity.

Conclusions

European eel of Norway are longer lived than previously estimated using an accepted age reading protocol. The offset of hatch years for ^{14}C values measured in the earliest otolith growth from bomb-produced ^{14}C chronologies provide compelling temporal constraints on the actual age. Age estimation

from otoliths should be revisited to discover patterns of otolith growth that might correct for the discrepancies exhibited here. Specifically, it is recommended that transverse sections be investigated for increment structure that may not be present in the sagittal plane, as well as comparisons with other methods, like burnt and cracked otoliths. It is also recommended that a follow up study be conducted using bomb ^{14}C dating on otoliths from Norway and other regions, using otolith mass as guidance in the experimental design, to further investigate the development of a validated age estimation method. Overall, if otolith mass can be considered a reasonable proxy for age and the ages generated from the bomb ^{14}C alignments in this study are nearly accurate, then the lifespan of European eel may approach 100 years in the natural environment.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/RDC.2024.134>.

Acknowledgments. Thank you to Negar Haghipour (AMS sample processing) along with Lukas Wacker, Marcus Christl, and Arno Synal (project support) from the Laboratory of Ion Beam Physics at ETH Zürich. Thanks to Russell Poole (Fisheries Ecosystems Advisory Services, Marine Institute, Newport, Ireland) for providing access to otolith age estimates and masses for European eel of Ireland. This work was supported in part for A.H. Andrews under the August T. Larsson Guest Researcher Programme at Sveriges Lantbruksuniversitet (Swedish University of Agricultural Sciences). This study was funded by the Norwegian Research Council (MAREEL; grant/award number: 280658) and by the Institute of Marine Research's Coastal Ecosystems Program.

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