

A complete otolith-based bomb radiocarbon chronology for the Baltic Sea and its use in the age validation of regional fishes

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Abstract

A complete bomb radiocarbon (^{14}C) chronology — covering an 80-year period (1938–2018) and reflecting thermonuclear testing in the 1950s and 1960s — was established using known-date otolith material to trace the signal in the Baltic Sea and to establish a tool in validating the age of regional fishes. Of particular interest were Baltic herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) that are estimated to live >20 years in the Baltic Sea, a longevity that is $\sim 2\times$ greater than determined for other locations. The new ^{14}C chronology was used to validate age estimates up to 22 years for herring and 18 years for sprat, although there was evidence of ^{14}C emissions from nuclear facilities, as well as deficiencies from other environmental factors. This work confirmed the accuracy of high-confidence age reading protocols used for decades and is a first step in establishing a valid basis for observed growth differences between northern-southern Baltic Sea populations. An exploration of ^{14}C in otoliths of coastal Baltic pike (*Esox lucius*), pikeperch (*Sander lucioperca*), and Baltic cod (*Gadus morhua*) lend support for broader use of bomb ^{14}C dating on marine and freshwater organisms of the Baltic Sea basin.

Keywords: Clupeidae; age estimation; longevity; carbon-14; Baltic cod; pike; pikeperch; gas-AMS

Introduction

The Baltic Sea is a brackish water basin with both freshwater and marine fish species that has provided seafood to northern Europe for millennia (Makowiecki 2008, Svedäng 2023). The pelagic food-web is relatively simple due to the dominance of three fish species: Baltic herring (*Clupea harengus*), sprat (*Sprattus sprattus*), and cod (*Gadus morhua*) constituting at 80% of the total fish biomass (Margonski et al. 2010). Recently, a fishery closure on both Baltic Sea cod stocks has led to commercial landings consisting of 95% herring and sprat (ICES 2024a). The Baltic Sea is heavily impacted by human activity and exhibits complex oceanography with strong abiotic gradients (Lehmann et al. 2002, Matthäus et al. 2008, Gröger et al. 2019). Hence, accurate life-history information on these vital fish stocks of the Baltic Sea in relation to abiotic factors is of paramount importance for understanding the interactive relationships between fishing, the ecosystem, and climate (Möllmann et al. 2014, Otero and Hidalgo 2023, Heimbrand and Limburg 2025). Central to this perspective is knowing the potential lifespan of fishery species, because misjudging life-history traits can contribute to harvest levels that exceed the population capacity to effectively replenish itself (Longhurst

2002). This can lead to shifts in population age structure, declines in fishery productivity, and reduced availability to the ecosystem (Pauly et al. 1998, Beamish et al. 2006, Longhurst 2010). Estimates of age for these dominant Baltic Sea fishes have been assessed for accuracy to differing degrees. While the lifespan of Baltic cod was addressed to an extent using elemental ratios in otoliths (Heimbrand et al. 2020), herring and sprat have not been thoroughly assessed in the Baltic Sea and yet lifespan estimates uniquely exceed 20 years (Ojaveer et al. 2003). Hence, it is important that the longevity of these small pelagic fishes be investigated to understand their fundamental life-history traits, like reproductive potential and natural mortality (Jennings and Beverton 1991).

The most common method of determining growth for teleost fishes involves counting growth zones in otoliths to estimate age (Campana et al. 1995). This approach can be challenging as the structure is often complex, and age determination ultimately depends on the preparation methods and reader interpretation and experience. A good example is with the otoliths of Baltic herring where age can be interpreted up to the mid-20s, but counts can differ due to splitting-grouping of growth zones or counting along alternate growth axes

(Fig. 1). Hence, otolith age reading is an acquired skill that depends on the development of a visual interpretation protocol (Kimura and Anderl 2005). This can only be achieved by repeated age estimation on numerous otoliths across all size and age classes. However, even well-established fish age estimation protocols must be rigorously validated — preferably through ontogeny for the species in question (Campana 2001) — and otoliths offer unique opportunities to accomplish this goal (Reis-Santos et al. 2022).

The use of bomb radiocarbon (^{14}C) dating on otoliths as a tool in the age validation of fishes has covered 30 years of progress. In many cases, a better understanding of fish biology and ecology has led to stronger life-history baselines for fishery sustainability and stock recovery (e.g. Andrews et al. 2024a,b, 2025, Kalish 1995, Cailliet and Andrews 2008, Sanchez et al. 2019). This method relies on a ^{14}C signal that was created in the 1950s and 1960s during Cold War era efforts to increase the efficiency and power of nuclear bombs (Hansen 1988). This sudden rise of bomb-produced ^{14}C from atmospheric nuclear tests can function as a time-specific marker in conserved growth structures, like tree rings and otolith growth zones (Cain and Suess 1976, Campana 1999, Kerr et al. 2004). While tree rings can be confirmed as annual with dendrochronology (Speer 2012), verifying the annual periodicity of otolith growths can be more challenging and requires a temporal reference (Reis-Santos et al. 2022). Hence, if the bomb ^{14}C signal can be detected in otoliths, then estimated ages can be compared to the timing of this known-date marker to determine its validity and whether adjustments to age reading protocols are required. This has been the case for some tropical fishes, like snapper and grouper of the Pacific and Atlantic oceans, where age was shown to be greatly underestimated, with consequent inaccurate growth parameters and stock assessments (e.g. Cook et al. 2009, Andrews et al. 2012, 2013a, 2019, 2020b, Sanchez et al. 2019).

Bomb ^{14}C dating most commonly uses the rise period of bomb-produced ^{14}C as a chronological reference in age validation studies, but recently collected fish would need hatch dates in the 1950s and 1960s or earlier, making them >50–60 years old (Fig. 2). While this approach remains suitable for some long-lived species, like cardinal snapper of the Caribbean Sea (*Pristipomoides macrophthalmus*; Baremore et al. 2025) and bigmouth buffalo of the Midwest US (*Ictiobus cyrinellus*, Lackmann et al. 2019), it is necessary to use the post-peak decline of ^{14}C levels for fish collected in recent years that live no more than a few decades. Examples of success with this approach are from North Atlantic yellowfin tuna (*Thunnus albacares*) and giant trevally (*Caranx ignobilis*) of Hawaii that were aged to respective lifespans of 18- and 25-years using otolith growth zone counting. For both species, there was a strong alignment of the otolith ^{14}C values with the regional coral ^{14}C chronology for the calculated hatch years, effectively validating the age estimates through ontogeny (Andrews et al. 2020c, Andrews 2020). While this approach can be a direct comparison of measurements to reference chronologies, its use can be challenging when natal origins are spatially variable or not well-known and as a result, oceanographic conditions can complicate the outcome (Andrews et al. 2024b, Fraile et al. 2024). Consequently, a regional bomb ^{14}C reference chronology is required for age validation studies and nothing to date has been recorded for the Baltic Sea.

To establish a similar age validation tool for fishes of the Baltic Sea, a ^{14}C reference chronology was assembled using

otoliths of (1) juvenile Baltic cod from the Baltic Sea proper and (2) young-of-the-year (YOY) sprat (age-0) from the northern Baltic Sea. This bomb ^{14}C chronology was examined for its shape and timing and then used to test the validity of age estimates for Baltic herring and sprat of the northern Baltic Sea that can exceed 20 years — life spans that are considerably greater than reported from other European regions and rarely exceeding 5 to 10 years (ICES 2024b). The approach was to determine if an overall alignment of ^{14}C values, across age classes of herring and sprat and among other species of interest, followed expected patterns through time or if there were differences that could be attributed to age reading errors or environmental factors. This first-time assessment of the bomb ^{14}C signal in the Baltic Sea intentionally covered different habitats and locations for a range of species to determine the suitability of the methodology.

Materials and methods

Bomb ^{14}C reference chronologies

The Baltic Sea has never been assessed fully for bomb-produced ^{14}C . To provide constraints on what to expect from a series of known-date otolith samples from this region, chronological ^{14}C records from other areas of the northern hemisphere were assembled (Fig. 2). Because bomb ^{14}C levels in aquatic ecosystems are primarily determined by the atmospheric signal (Nydal and Gislefoss 1996, Druffel et al. 2016), the most applicable compilation for the Baltic Sea is the Northern Hemisphere zone 1 (NH1) chronology because it represents northern latitudes (Hua et al. 2022). In a similar geographical perspective, ^{14}C measurements from fish otoliths of North American lakes were chosen as a proxy for the fresh-brackish water environments of the Baltic Sea basin because there are no other freshwater bomb ^{14}C chronologies. This chronology consists of otolith ^{14}C measurements from both aged (with confidence) and known-age fish (Campana et al. 2008, Casselman et al. 2019, Lackmann et al. 2019) from across the Canadian Shield (Arctic-Laurentian; Fig. 2), a geological region with few karst formations that might strongly attenuate bomb-produced ^{14}C levels that entered the system through atmospheric exchange and rain waters (e.g. Andrews et al. 2020a, Spiker 1980, Schuur et al. 2016, Hupfeld et al. 2023). Open ocean waters that would be reflected in the Baltic Sea due to inflow events (Holtermann et al. 2017) are represented by bomb ^{14}C chronologies of the tropical North Atlantic and the North Sea (Fig. 2). The collective tropical ^{14}C records cover both coral and otoliths of a vast area ranging from western Gulf of Mexico and Caribbean Sea to Bermuda (Andrews et al. 2013a, 2020c, Barnett et al. 2018, Shervette et al. 2021). The North Sea bomb ^{14}C signal is expected to become a mix of northern currents and terrestrial inputs from Europe and is represented by a long-lived clam shell (*Arctica islandica*; Scourse et al. 2012). The ^{14}C levels observed in these references may thus be reflected in the otoliths of Baltic Sea fishes that either migrated from open ocean waters or were influenced by inflow events.

Otolith archives and sample selections

Archived otoliths collected by the Swedish University of Agricultural Sciences (formerly Swedish Board of Fisheries) from the Baltic Sea covered decades and some were curated at The National Archives in Gothenburg, Sweden. The most compre-

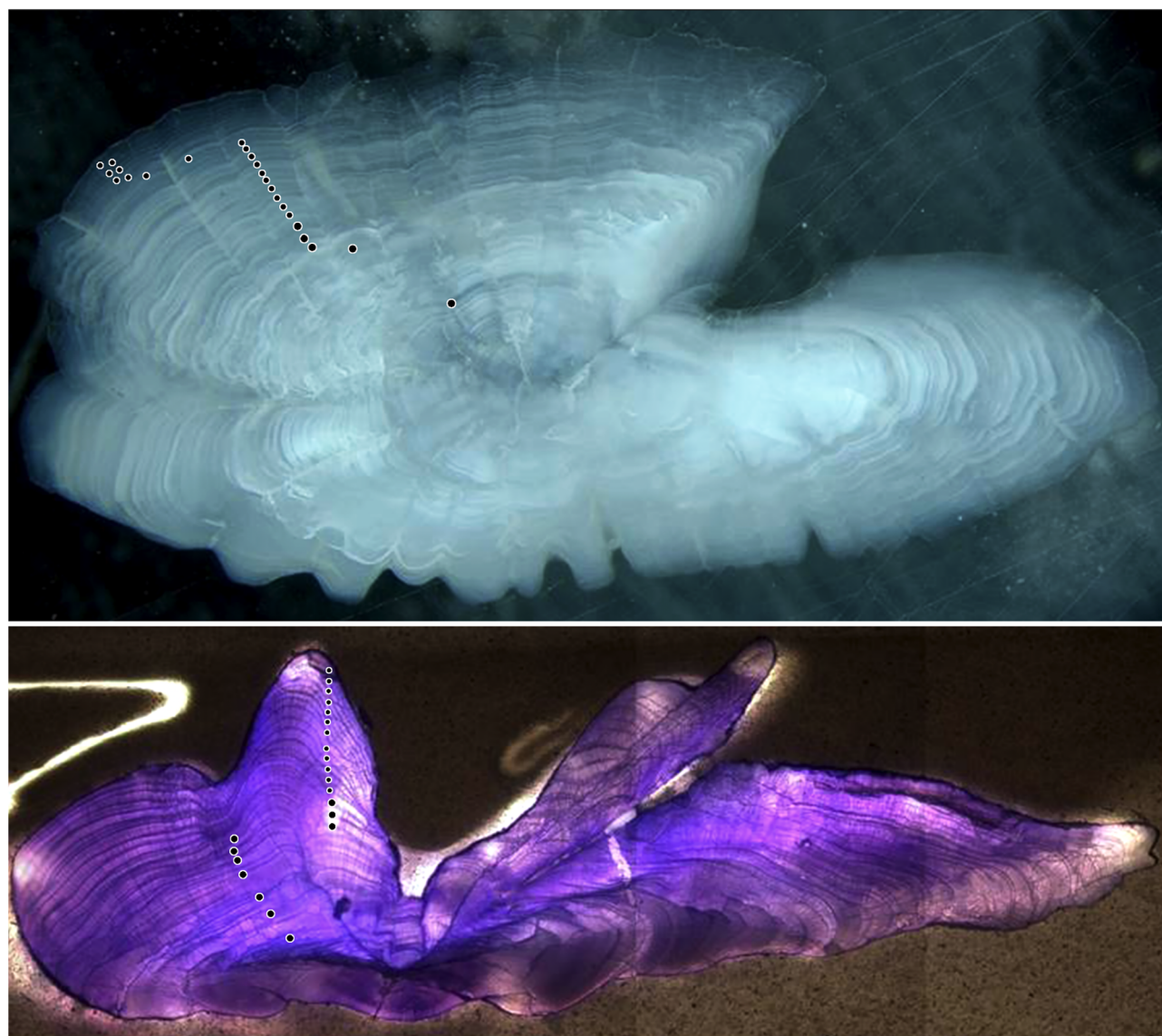


Figure 1. Otolith sections of a Baltic herring (*Clupea harengus*) that was aged to 23 years by counting the growth rings visible in both sagittal (top) and transverse (bottom) views. Note that the interpretation of these sections is subjective and other counting scenarios closer to 20 years are also possible due to variations in ring structure along alternate growth axes.

hensive collection in terms of covering the entire bomb ^{14}C period was Baltic cod with reliable samples dating back to the 1930s. The focal species, Baltic herring and sprat, covered more recent decades with reliable otolith collections made back to the 1970s. Other species of interest to further investigate the use of this methodology in the region were large specimens of Baltic pike and pikeperch from recent collections and two older cod that were previously aged in another study (Hembrand et al. 2020). These specimens were chosen as the most promising in terms of yielding information about age and how comprehensive age validation studies might evolve using bomb ^{14}C dating in the Baltic Sea basin. Extensive otolith collections exist for each of these species with records dating back to the 1970s that remain available for follow-up investigations.

Baltic Sea ^{14}C chronology

The otoliths of YOY and juvenile Baltic cod were randomly, as well as opportunistically, selected as a subset from 1000s of archived specimens to create a full bomb ^{14}C chronology. Collection dates covered the pre-bomb (prior to ~1958), rise and peak (late 1950s through the 1970s), and post-peak decline (after early 1980s) periods and were primarily from the eastern Baltic cod stock (ICES SD25; Fig. SM1). To further investigate the bomb ^{14}C signal and provide support for alignments of the older sprat and herring of the Bothnian Sea (ICES SD30), the otoliths of YOY sprat were randomly selected from the most comprehensive collection area (northern Baltic Sea proper; ICES SD29) to cover the most informative years of the post-peak decline (Fig. SM1).

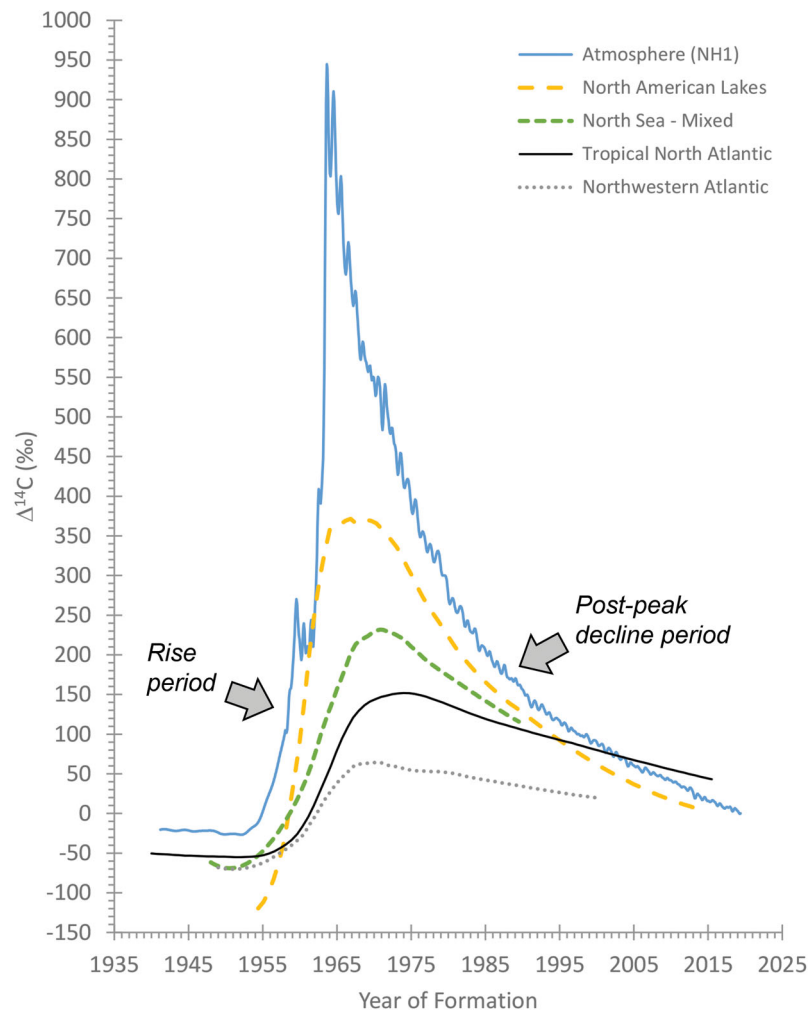


Figure 2. Bomb-produced radiocarbon in the atmosphere is reflected in reference chronologies stored in known-age coral and otoliths of marine and freshwater environments that can be used to test estimates of age for aquatic organisms where life history is not well known. Each temporal reference for measured ^{14}C values is regionally specific and dictated by the influence of environmental factors on the exchange of CO_2 from the atmosphere within a given aquatic ecosystem. For northern latitudes, like the Baltic Sea basin, a composite chronology for the atmosphere (NH1, solid line that approaches 1000 per mille) is the most applicable (Hua *et al.* 2022). The freshwater chronology for North American lakes (wide dashed line), established from otoliths of Arctic-Laurentian fishes (Campana *et al.* 2008, Casselman *et al.* 2019, Lackmann *et al.* 2019), is the best available proxy for the freshwaters of the Baltic Sea basin because no other records exist. Influxes of marine waters from the tropical North Atlantic (solid line that reaches 150 per mille; Andrews *et al.* 2013a, 2020c, Barnett *et al.* 2018, Shervette *et al.* 2021), via mixed waters of the North Sea (narrow dashed line; Scourse *et al.* 2012), to the Baltic Sea will combine with freshwaters during inflow events to form the stratified, brackish ecosystem of the Baltic Sea. An example of ^{14}C -deficient waters due to open ocean upwelling of deep waters of the northwestern Atlantic (small dotted line) provides an example of a greatly attenuated bomb ^{14}C signal (Campana *et al.* 2008).

Small pelagic fishes

To capture the near-monotonic ^{14}C decline, focus was placed on a collection year that allowed a direct relationship of increased sample age to an increase in ^{14}C back through time (successively earlier hatch years). The collections for both herring and sprat that could be 20+ years old were limited to the southern Bothnian Sea (ICES SD30; Fig. SM1), whereas ages were mid-teens at the greatest in other areas of the Baltic Sea.

The selected otoliths for the reference chronology and older-aged small pelagic fishes were subsampled in a manner that was suitable for each species based on otolith shape and mass. In each case, the earliest otolith growth was accessed by grinding away more recently formed material (i.e. flattened in the sagittal plane), cutting with a scalpel by hand or with a micromill (i.e. hand slicing under a dissecting microscope or a series of extractions around the core with the

micromill), or some combination of these steps. Otolith core material (within the first year) was extracted in each case by focusing microscopically on the growth zone structure visible in whole, and progressively ground down, otoliths. The exception to some of these handling procedures were YOY sprat and otolith edge material of juvenile cod that were used as reference material. The YOY samples were often analyzed as whole otoliths because the mass was low and clearly represented growth within the first year of life. Edge material was sampled by snapping off a small piece from the rostrum tip, with a follow up inspection under the microscope and weighing, to make certain the material would be only the most recent growth. Older fish used for age validation had more massive otoliths with the core material buried within, which were mounted with Cytoseal 60 (Richard Allen Scientific Company) to glass slides for grinding and in

some cases cutting with a scalpel or low-speed saw (Buehler Isomet).

The Baltic herring and sprat specimens used for age validation had all been previously aged using well-established methods. Due to the purportedly slower growth rate of herring in the Bothnian Sea (ICES SD30), age was estimated from counting annual growth zones in transverse cross sections of otoliths stained with toluidine blue (Fig. 1, bottom panel). Whole untreated otoliths viewed in the sagittal plane were used for age estimation of apparently faster growing herring from the southern Baltic Sea (ICES SD25; Fig. 1, upper panel). Whole untreated otoliths were used for age estimation of sprat from all areas in the Baltic Sea. The otoliths of each species that had high confidence in the age reading were selected over low-confidence otoliths to avoid uncertain age estimates that suffer from poor preparation and increment visibility. To extract the core of herring otoliths, the distal surface was ground down to just above the core by hand using a glass slide mount. The flattened otolith was then flipped and remounted to the glass slide proximal side up to grind off this surface to the thickness of YOY otoliths (0.30–0.35 mm). Once the proper thickness was reached, the material deposited outside the first year of life (the core, as determined from the smallest otoliths) was cut away with a New Wave micromilling machine by following the concentric growth zone structure. A similar approach was taken for the much smaller otoliths of sprat (max mass 1.5 *cf.* 8.5 mg), but the extractions were made by hand after flattening to the proper YOY thickness (~0.3 mm). Each core was isolated using a scalpel while viewed under a dissecting microscope (variable magnification levels that depended on what needed to be seen) to the dimensions of the YOY otoliths using the ocular micrometer, marks on the slide, or a combination of the two. The isolated cores of each species were removed from the slide with either a scalpel or solvent, cleaned in additional solvent and detergent-water, and air dried for placement in sample vials.

Statistical analyses

The goal of this study was to evaluate if the otolith age reading protocols, as established by the most well-defined (highest confidence) otoliths, were accurate in terms of the significantly greater age estimates of >20 years for Baltic sprat and herring. To do so, the ^{14}C data for the older aged sprat and herring specimens were first visually checked for consistency with the reference ^{14}C data by plotting the measurements as hatch dates (determined as capture date minus otolith age) with the Baltic Sea reference data from known-age otolith material (Baltic cod and sprat). Any large and consistent bias in the age estimates (i.e. growth zones being over or under counted) would be apparent as a systematic offset of the validation data from the reference data (e.g. Andrews and Scofield 2021). More formal evaluations to compare the validation and reference data were then performed using an analysis of the ^{14}C activity ($F^{14}\text{C}$) domain with an analysis of the age data (year CE) domain — an age calibration of the older aged sprat and herring ^{14}C data to an age calibration curve based on the otolith-based Baltic Sea ^{14}C chronology (as established here), coupled with a Monte Carlo simulation to quantify age offsets (in years CE) and the associated uncertainties.

Age calibration

The otolith-based Baltic Sea ^{14}C chronology, including measurement uncertainties, was used to construct a post-peak bomb ^{14}C calibration curve. This calibration curve was constructed using the Undatable age-depth modelling software (Lougheed and Obrochta 2019), which considers the measurement uncertainty associated with each data point contained in the otolith-based ^{14}C series. By default, Undatable implements a Bayesian prior that assumes a positive sedimentation rate through time (age increases with depth). In this case, the focus was not on modelling age vs sediment depth, but as an analogy by using age vs ^{14}C activity through time, which can fluctuate both upwards and downwards through time. Hence, the aforementioned Bayesian prior was disabled, thus allowing ^{14}C activity to fluctuate bidirectionally with time. The age modelling software was run using 10^5 iterations, which resulted in ~95% of the underlying ^{14}C reference data falling within the 2σ uncertainty bounds of the calibration curve, without any need for bootstrapping in this case. To avoid spurious calibration of the sprat and herring ^{14}C data to the rise period of the ^{14}C bomb curve (1950s and 1960s), the calibration curve was cropped to data in only the peak and post-peak decline periods, in this case January 1968 to December 2020.

This post-peak ^{14}C calibration curve was used to compute a calibrated age probability distribution from each sprat and herring ^{14}C activity for the validation specimens, with measurement uncertainty, using the MatCal calibration software (Lougheed et al. 2016). This approach employs a standard ^{14}C calibration routine described in Bronk-Ramsey (2008). This calibration process enables a like-for-like comparison, whereby the estimated DoF (years CE) for each sprat and herring specimen can be compared to its ^{14}C -calibrated age (also in years CE).

To determine how well ^{14}C -calibrated age and DoF were in general agreement at the population level, two Monte Carlo procedures were carried out, one for the sprat population and a second for the herring population. For both populations, weighted random sampling was carried out on the calibrated age probability distributions for each specimen, and each randomly sampled age was subtracted from the DoF. This process was repeated 10^5 times for each specimen, and the specimen results for each population were amalgamated into a histogram with the associated central tendency statistics.

Other Baltic Sea fishes

Otoliths of some of the largest Baltic pike, pikeperch, and cod available were included in this study to make an initial assessment for future studies. For Baltic pike, the fish used were fortuitous collections by local fishers. Two smaller pike were collected from an enclosed bay on the southwestern coast of the Bothnian Sea (Ängskärsviken, Hållnäs, Sweden), 10 km north of Forsmark Nuclear Power Plant (NPP). The largest pike (Pike-003) was from an enclosed coastal bay (Granfjärden, Sweden), along with the large pikeperch (77 cm; Gös-001) on the same day (2 June 2023), a location 30 km inland from the Åland Sea and away from the Forsmark NPP. Fish lengths were measured or calculated from head length due to predation (Fig. SM2).

Otoliths of the pike and pikeperch were mounted to glass slides distal side up to allow grinding that would expose the core (earliest growth). This was verified microscopically and the core was extracted with a New Wave micromilling ma-

chine in a manner similar to previous studies (i.e. Andrews *et al.* 2013a). The Baltic cod otoliths were treated differently because each was used previously in a laser-ablation inductively-coupled plasma mass spectrometry (LA-ICP-MS) study (Heimbrand *et al.* 2020). The otolith was previously mounted in a resin block, cut in the transverse plane and polished to the nucleus. Core extraction was made with the micromill down into the otolith within the first visible annulus to a depth of 0.6 mm. Age was estimated for each fish specimen using wing bones (mesopterygoid, small pike), a transverse otolith section (large pike and pikeperch; Figs SM3, SM4), and from otolith elemental profiles (cod; Heimbrand *et al.* 2020).

Bomb ^{14}C dating

The reference material from Baltic cod and sprat otoliths, and the extracted otolith cores of older aged fish, were analyzed as calcium carbonate samples for ^{14}C at ETH Zürich using gas-AMS (accelerator mass spectrometry, MICADAS; Synal *et al.* 2007). This time-efficient, on-line approach involves placing sample material in septa-sealed vials (Exetainer #948, Labco Ltd, UK), evacuation of ambient atmosphere with helium, liberation of sample CO_2 with 85% phosphoric acid, and direct injection to the gas ion source. Measured $^{14}\text{C}/^{12}\text{C}$ ratios are reported as F^{14}C (fraction modern; Reimer *et al.* 2004) and $\Delta^{14}\text{C}$ (age corrected F^{14}C ; Stuiver and Polach 1977) and were compared with the Baltic Sea ^{14}C chronology that was developed as part of this study. Alignment of ^{14}C values from fish with estimated ages were made by plotting the calculated hatch year in comparison with new and existing bomb ^{14}C chronologies.

Results

Baltic Sea ^{14}C chronology

Eighty-two of the 151 juvenile Baltic cod otoliths were ultimately selected for AMS to establish the ^{14}C time series with a focus on replicating years for a better understanding of variability (Table SM1). Within this set of samples, three suffered from low sample recovery during AMS (low ^{14}C counts) and one otolith core sample was lost. A total of 78 AMS runs were successful. The remaining 69 otolith samples, extracted in advance while the specimens were in hand, are ready for ^{14}C analyses in further establishing this Baltic Sea chronology. An 80-year span (1938–2018) was established using the Baltic cod otoliths and the ^{14}C values cover the full range expected (Table SM1). This time series effectively establishes a complete record for the Baltic Sea proper (SD25; Fig. SM1) and reflects the pattern shown for North American lakes (Fig. 3a). Pre-bomb levels were similar to, and slightly lower than, many marine and freshwater environments (mean $\Delta^{14}\text{C} = -71.6\text{‰}$), with a calculated reservoir age of 413 ± 88 years [ΔR ; 1937–1957 in comparison to NH1 pre-bomb (Hua *et al.* 2022)]. Radiocarbon then rises and approaches 400‰ with a range of 312–363‰ $\Delta^{14}\text{C}$ from the reference Baltic cod otoliths. While the rise time of the chronologies shown is similar (1958), the rise rate may be slower for the Baltic cod record, attaining peak levels a few years later than shown for North American lakes (1965–1966 *cf.* 1962–1963; Fig. 3a). Peak levels were similar on average (338‰ *cf.* 341‰), although the North American lakes record is based on fewer individuals with a different timespan ($n = 18$, 1967–1975 *cf.* $n = 7$, 1962–1970). In addition, a gap in collection years for the Baltic cod chronol-

ogy between 1975 and 1982 makes the timepoint for the initial decline difficult to determine, but the first measured values that decreased significantly in 1982 (222.2 and 243.0‰) were unexpectedly more in sync with the atmospheric ^{14}C reference (NH1) during the post-peak decline, as opposed to the slightly attenuated North American lakes chronology (lower by $\sim 45\text{‰}$ in 1982).

Two Baltic cod ^{14}C values from 1983 were notably elevated (Bcod-047 and 048; Fig. 3a), but overall, the time series largely aligns with the atmospheric reference until after the crossover of the tropical North Atlantic chronology (ocean becomes the ^{14}C reservoir over atmospheric levels). The lowest values on the decline were in the final two years of sampling (2017–18), covering a 45‰ range, from an alignment with the tropical North Atlantic chronology to less than the atmospheric chronology.

The ^{14}C measurements from 27 YOY sprat otoliths covered a range of high to low values (241.4‰ to 55.6‰), as expected for this 27-year chronology (1978–2005), that cover much of the post-peak decline period (Table SM2). The alignment of most of the YOY sprat ^{14}C measurements of the northern Baltic Sea (ICES SD29) reveals a close correspondence to the Baltic cod measurements for a similar range of years (Fig. 3b). Exceptions were two fish collected in 1978 — dubiously associated with Baltic Sea collections due to incomplete records — were far lower than expected and closer to the North Sea reference chronology and 60‰ lower than the otolith pair collected just two years later (Fig. 3b). One specimen revealed an elevated ^{14}C value in 1990, similar to two Baltic cod in 1983. One sprat value in 1998 was marginally lower, similar to what was observed for Baltic cod in 1991.

Small pelagic fishes and bomb ^{14}C dating

A total of 28 sprat covering estimated ages of 2 to 18 years were chosen for analysis from two collection years (1991 and 2012; Table SM3). Specimens were chosen from the Bothnian Sea (ICES SD30) because previous age estimates exceeded 20 years in this region, but sprat older than 18 years were not available because collected specimens were missing from the archive collection. The best years of alignment across the post-peak decline were for samples from 1991 for a focus on the upper (steepest) part of the decline, covering potential hatch years of 1976 to 1989 and age classes 2 through 16 years ($n = 6$). Samples from 2012 covered age-classes of 2 to 18 years ($n = 22$) with hatch years of 1994 to 2010. The alignment was good for the 1991 series to the post-peak decline reference (Fig. 4a) with a steady decrease in ^{14}C from oldest to youngest sprat (344.6 to 154.2‰) — this is a confirmation that age reading is accurate to within a few years for sections that were well-defined based on the low median offset that falls within the σ and RMSE values, indicating statistical significance. With this in mind, the most elevated ^{14}C sample from one of the two oldest sprat was aged as a year older from growth zone counts (follow up counting within this study), which was consistent with a more massive otolith (1.385 *cf.* 1.317 mg; Table SM3). The more recently collected 2012 series also exhibited steadily increasing ^{14}C levels from youngest to oldest (31.4 to 124.2‰) and a close alignment to the reference chronology, with the exception of one lower value for an age-10 fish with low ^{14}C counts from the AMS (error was not great enough to classify as unreliable; Table SM3). The overall alignment provides strong support for the age reading

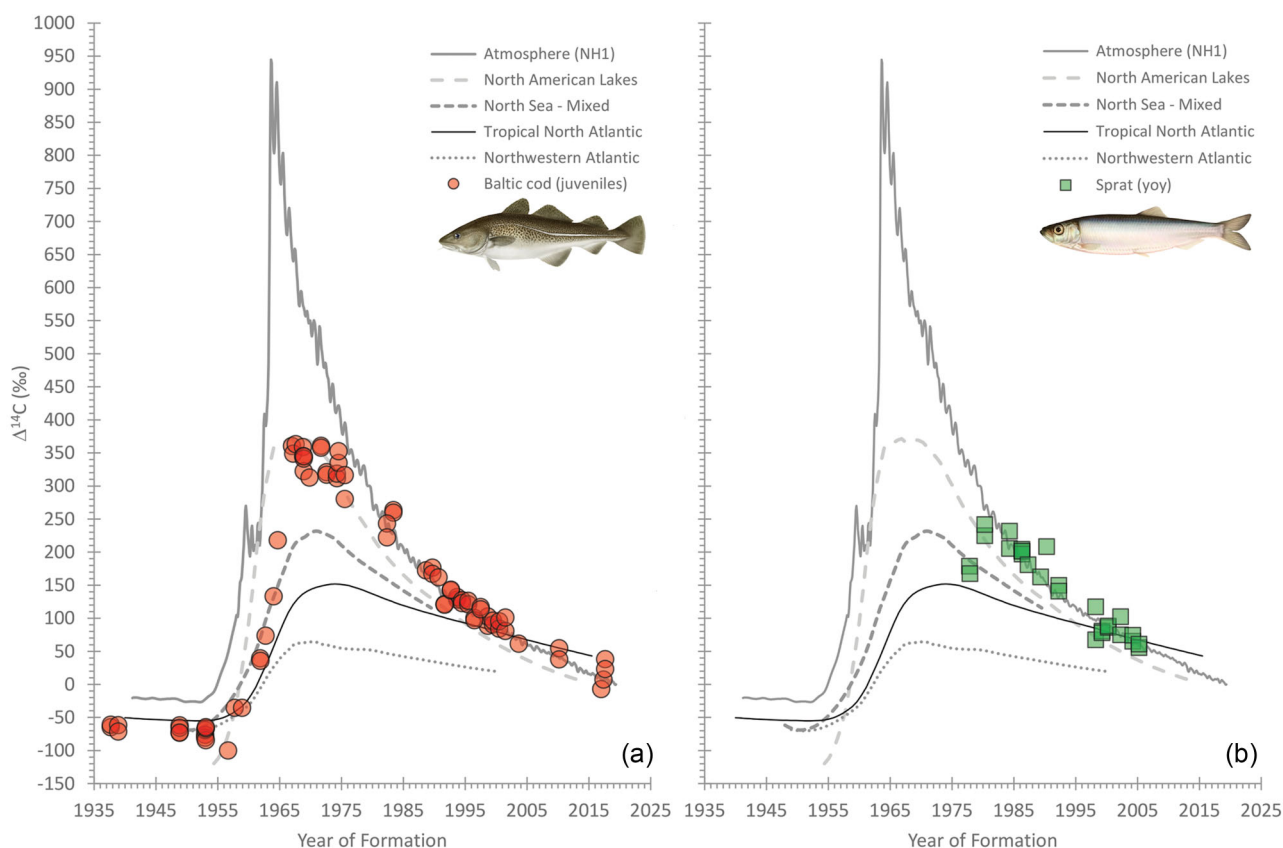


Figure 3. New records of bomb-produced radiocarbon in the Baltic Sea that were traced through time with known-age otolith material of juvenile Baltic cod (a) of the Baltic Sea proper and young-of-the-year sprat (b) of the northern Baltic Sea (Fig. SM1). The Baltic cod chronology covers the full bomb ^{14}C period ranging from pre-bomb levels in the 1930s to 1950s, to a steep rise of ^{14}C beginning in 1958 that reaches peak levels that are similar to the North American lakes chronology, and into the post-peak decline in unison with the atmospheric ^{14}C chronology. The sprat chronology is limited to the post-peak decline and falls largely in unison with both the atmospheric and Baltic cod chronologies. Deviations in the alignment of each record that are shown as slight outliers may be due to other anthropogenic ^{14}C sources in the Baltic Sea basin (elevated) or incomplete collection location information and inflow events (lower than expected).

protocol and age estimates for sprat aged to 18 years, despite minor variances due to environmental factors.

A total of 31 herring otoliths covering estimated ages up to 22 years were chosen for analysis in a narrow series of collection years (Table SM4). Specimens of the Bothnian Sea (ICES SD30) were chosen for maximum ages exceeding 20 years. In this case, four herring otoliths aged 20 years or more were located for the study. The most comprehensive collection year for alignment through the post-peak decline was 2007 with an extension to 2008–09 to include more of the oldest fish. These specimens had potential hatch years of 1987 to 2008 for age classes 0 through 22 years ($n = 21$). In addition, a smaller sample set from the Baltic Sea proper (ICES SD25) was selected to consider younger ages from large fish and potentially address either age reading discrepancies or different growth rates and lifespan between regions (Table SM5). These fish were aged 3 to 14 years ($n = 8$) with lengths of 230 to 275 mm TL and potential hatch years of 1993 to 2004. Alignment of the ^{14}C measurements from herring of the Bothnian Sea increased in general from youngest to oldest with some variation (Fig. 4b): ^{14}C levels ranged from 62.6 and 59.6‰, for respective ages 0 and 3 years, to 209.5 and 177.3‰ for respective ages 21 and 22 years. Some of the offset for the maximum values for a given hatch year may be accounted for by the later collection year (2009 vs 2007) because of the steep annual decline in ^{14}C

levels. Two values (Table SM4) were elevated in a similar manner to some that were observed in the reference chronologies: H30-062 was measured at 180.2‰ for a hatch year of 1995 (aged to 13 years) and H30-010 was measured at 180.8‰ for a hatch year of 1991, both of which are noticeably greater than the atmospheric record (Fig. 4b). The alignment of the herring specimens from ICES SD25 was generally in line or slightly lower than the herring from ICES SD30. One was lower than expected in a similar manner to a sprat from a similar year (Fig. 4). Overall, the alignments indicate the age reading is accurate.

Statistical results

The age calibration method and Monte Carlo simulation (Fig. 5a–c) approach provided support for an agreement between the ^{14}C -derived ages and the estimated ages from growth zone counting for the sprat and herring validation specimens. The curve fit to the post-peak decline ^{14}C data from Baltic cod and sprat resulted in an undulating pattern with sufficiently large confidence intervals that consider possible uncertainties associated with data gaps and potentially elevated or depleted ^{14}C levels from other circumstances (NPP emissions or inflow events; Fig. 5a). In most cases, the 68% range of a specimen's the ^{14}C -calibrated age distribution overlapped with the 1:1 line of ^{14}C -calibrated age vs estimated age,

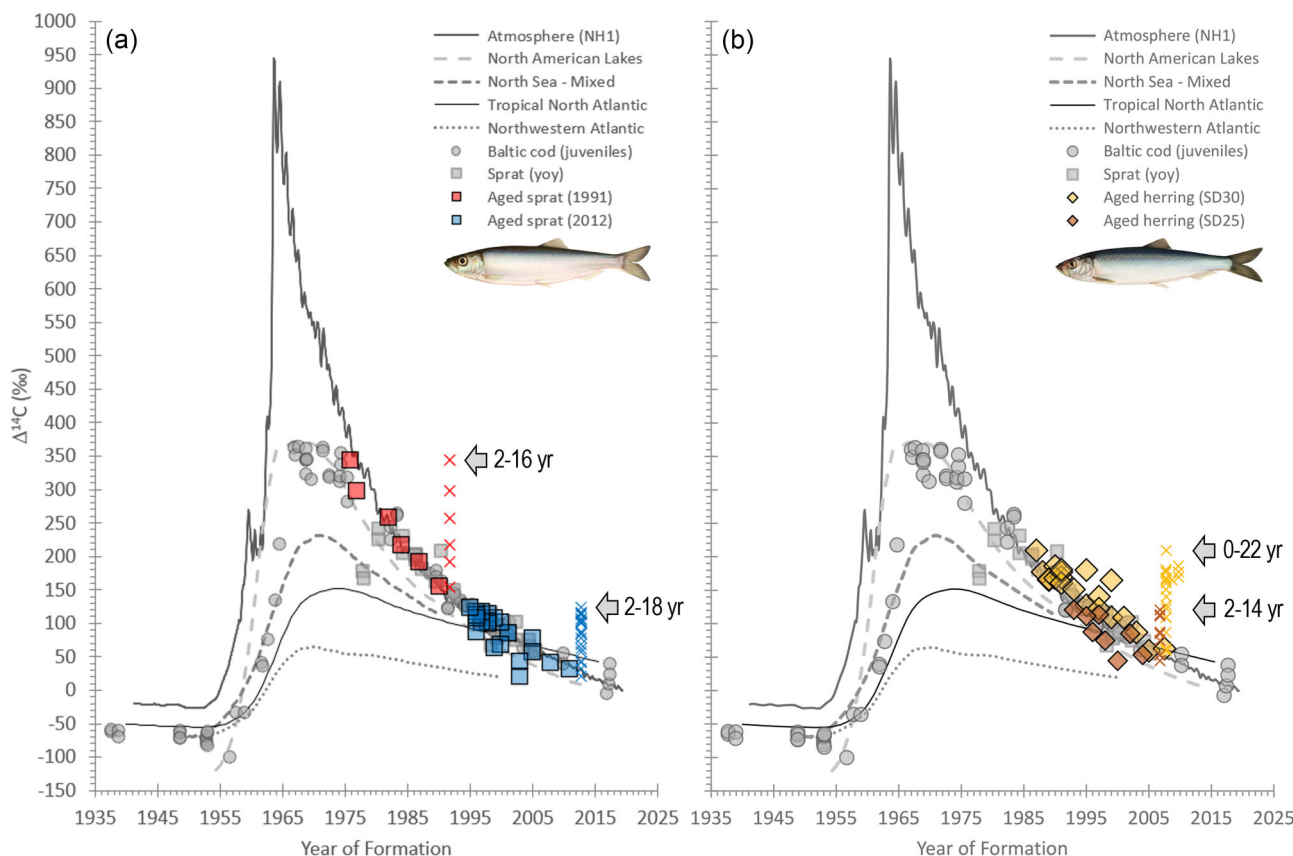


Figure 4. Alignment of the ^{14}C measurements from sprat (a) and herring (b) otolith cores for the calculated hatch years—determined from sprat otoliths estimated to be 2–18 years old and herring estimated to be 0–22 years old as the difference from the collection date (X's)—with the Baltic Sea chronological reference have effectively validated the age reading protocols with a caveat. Some otoliths were clearly affected by processes that either elevated or reduced ^{14}C levels, as shown in the reference time series established here for the Baltic Sea (Fig. 3), and these differences are attributed to environmental variation and not estimated age because the specimens could not be reasonably aligned to younger or older dates based on otolith mass being either too high or low for a given age adjustment of a few years. The aged sprat were collected in 1991 and 2012 to cover more of the post-peak decline and aged herring were primarily collected in 2006–07 from the Bothnian Sea (SD30) with a subset from the apparently younger southern population (SD25).

indicating agreement across age classes (Fig. 5b). As expected at the 68% level, some specimens within the sprat and herring populations do not overlap the 1:1 line; however, analysis at the population level using the Monte Carlo procedure shows agreement between the ^{14}C method and the estimated growth zone age (Fig. 5c), with the median offset between the two methods being -0.46 years for sprat and 0.96 years for herring. These small offsets are insignificant, falling within the precision of the ^{14}C method at the population level, which is suggested to be 4.2 years (1σ) for sprat and herring. The impact of NPP emissions and inflow events on the Baltic Sea cannot be considered at a more precise level due to the limited nature of the sampling thus far.

Other Baltic Sea fishes and bomb ^{14}C dating

Radiocarbon levels were successfully measured for three other species of the Baltic Sea basin using otolith core material (Table SM6). Measurements from three Baltic pike otoliths revealed two different ^{14}C alignments in time relative to the Baltic Sea chronology and ^{14}C proxies in other aquatic environments (Fig. SM3). The two smaller fish (Pike-001 and 002), aged 3 and 7 years with the wing bones, aligned with the Baltic Sea reference, but the ^{14}C value from the 20-year-old pike (Pike-003) from a coastal bay, well away from the Fors-

mark NPP, aligned with the freshwater reference chronology of North American lakes (Fig. SM3). This fish was aged confidently with a well-defined growth zone pattern (Fig. SM4). Similarly, the ^{14}C values from the 15-year-old pikeperch (Gös-001) aligned with the North American lakes reference. The pikeperch was also aged with confidence due to well-defined growth zones (Fig. SM5). The older Baltic cod otolith ^{14}C measurements aligned with the Baltic Sea reference chronology when the ages of 6 years, as determined from elemental cyclicity, were used to calculate hatch dates (Fig. SM3).

Discussion

Baltic Sea ^{14}C chronology

The time series of otolith ^{14}C measurements is the first-ever portrayal of the full bomb-produced ^{14}C signal for the Baltic Sea — a comprehensive bomb ^{14}C reference chronology that covers an 80-year period (1938–2018) using known-age otolith material of Baltic cod and sprat. The ^{14}C records for these species exhibit strong similarities to each other, as well as the atmospheric ^{14}C signal, during the post-peak decline period. While the rise of bomb-produced ^{14}C — as established by Baltic cod otoliths — can be used for age validation alignments of older-aged fishes and organisms of the Baltic Sea

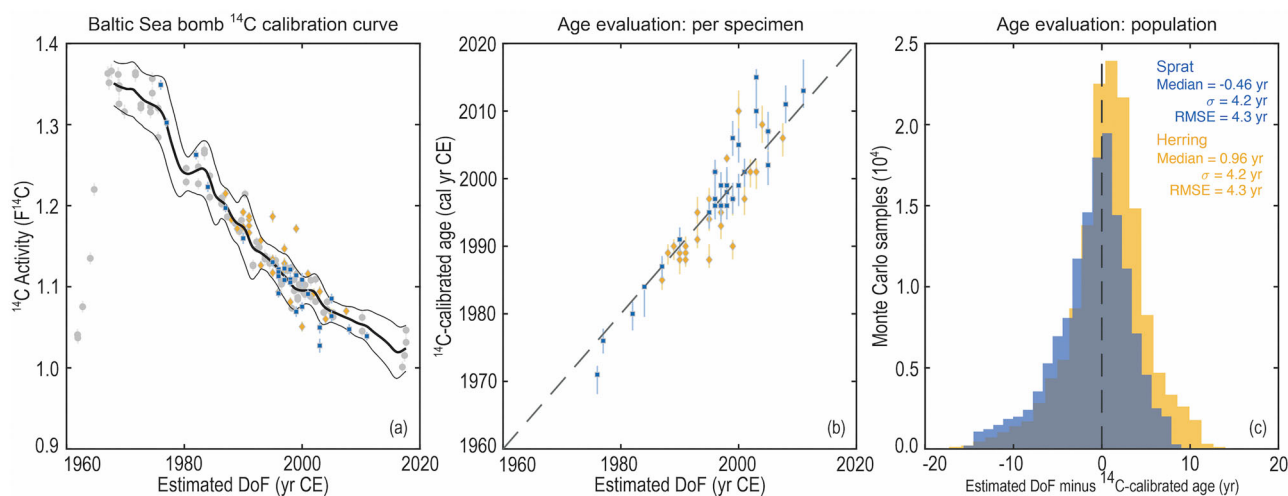


Figure 5. Panel (a): Baltic Sea bomb ^{14}C reference series, as generated by known age otolith material from Baltic cod and sprat (grey circles), with the estimated date of formation (DoF) hatch years as calculated for the older sprat and herring (blue squares and yellow diamonds) that were aged from otolith age reading (vertical bars are 1σ measurement errors). A calibration curve was fitted to the reference ^{14}C data covering 1967 to 2017 (thick black line) with $\pm 1\sigma$ sigma intervals (thin black lines). Panel (b): the ^{14}C -calibrated age distributions for sprat and herring were evaluated on a per specimen basis with vertical bars denoting the 68% credible range (calculated using highest posterior density) of the calibrated age distribution. Shown for reference is a 1:1 line (dashed line) that indicates perfect agreement between ^{14}C -calibrated age and the estimated DoF. Panel (c): Results plotted as a histogram of the Monte Carlo procedure that was carried out on ^{14}C -calibrated age distributions of sprat (yellow) and herring (blue) to evaluate any offsets between the ^{14}C -calibrated ages and the estimated DoF. Shown for reference agreement is a dashed line at zero offset.

(hatch or formation years in the 1950s and 1960s or during the pre-bomb period), the alignment of both Baltic cod and sprat otolith measurements with the atmospheric ^{14}C chronology is unusual. Aquatic environments are normally characterized by an attenuated ^{14}C signal due to time lags, mixing with ^{14}C -deficient waters, and remineralization processes (e.g. Spiker 1980, Nydal and Gislefoss 1996, Keaveney et al. 2015). Caveats to the use of this post-peak chronology for age validation of regional fishes come from variation in ^{14}C values due to (1) releases of ^{14}C from NPP, or nuclear research, repository, and reprocessing facilities (Lindgren et al. 2001, Stenström and Mattsson 2022, Bjarheim et al. 2025), or (2) mixing of ^{14}C -deficient waters from the North Atlantic (Scourse et al. 2012, Morholz 2018), freshwater reservoir effects (e.g. input from Trave River, Germany: levels of $\text{DIC F}^{14}\text{C} = 0.076\text{--}0.086$; Philippsen 2013), and the contribution of ^{14}C -free carbon from limestone (Lougheed et al. 2013, Lougheed et al. 2016). Despite these cautionary notes, the Baltic Sea ^{14}C reference chronology provided strong support for the sprat and herring age reading protocols through ontogeny that led to age estimates exceeding 20 years for the Bothnian Sea.

The strong ^{14}C signal of the Baltic Sea is similar to freshwater and brackish chronologies established for some watersheds of North America where peak bomb-produced ^{14}C levels are in the 300–500‰ $\Delta^{14}\text{C}$ range (Campana and Jones 1998, Campana et al. 2008, Casselman et al. 2019, Lackmann et al. 2019, Daugherty et al. 2020). In addition, recent work in the Kattegat on the shells of *Mytilus edulis* revealed similarly elevated levels for the peak period (Bjarheim et al. 2025). This contrasts with peak-level observations from oceanic waters that are on the order of 100–200‰ $\Delta^{14}\text{C}$ and typically associated with the surface waters of tropical gyres (Broecker and Peng 1982). Peak levels of this magnitude can be attributed to direct deposition from the atmosphere with low effects from benthic respiration or remineralization (Spiker et al. 1980, Keaveney et al. 2015). The elevated ^{14}C levels across

the post-peak decline period that align with, and sometimes exceed, the atmospheric record may be due to consistent releases of radionuclides to the Baltic Sea, such as the Forsmark NPP on the Bothnian Sea (Vesa-Pekka 2023). While monitoring of ^{14}C in the Baltic Sea has not been performed, and ^{14}C data from NPPs as a liquid discharge are sparse (Magnusson et al. 2008, Svetlik et al. 2017), the release of other radionuclides (i.e. Caesium-137, ^{137}Cs) is a reasonable proxy for some level of ^{14}C release to the environment (Mattsson et al. 2022). Levels of both ^{137}Cs and ^{14}C that were sourced from other nuclear facilities have been traced in marine environments of the eastern North Atlantic, such as the Sellafield reprocessing facility in the UK where emissions were traced to uptake by local marine mammals (Tierney et al. 2017). In addition, brown algae (*Fucus* spp.) along the Swedish coast show localized ^{14}C spikes and overall elevated levels (i.e. Ringhals NPP; Bjarheim et al. 2025), as well as potential influence from inflow waters to the Baltic Sea from external nuclear facilities, like the La Hague reprocessing facility in France (Mattsson et al. 2022, Stenström and Mattsson 2022). Measurements from brown algae of the Baltic Sea also revealed a post-peak decline pattern for collection sites away from point sources that are consistent with the Baltic cod and sprat otolith chronology in the mid-1980s to 1990s but it becomes more elevated after the mid-2000s (Stenström and Mattsson 2022, Bjarheim et al. 2025). Hence, this assessment of bomb-produced ^{14}C in otoliths of the Baltic Sea provides a promising baseline for further study using known-age materials to trace the various signals and strengths in many environments of the region.

Small pelagic fishes and bomb ^{14}C dating

The potential lifespan for Baltic herring and sprat, as estimated from growth zone counting in otoliths, is validated using bomb ^{14}C dating on individual otolith cores to >20 years. This is a longevity considerably greater than estimated in other

parts of the world for these wide-ranging, small-pelagic fishes, and may reflect different ecotypes, such as the recent discovery of piscivorous herring in the Bothnian Sea (Goodall *et al.* 2024). In the western North Atlantic, bomb ^{14}C dating provided support for herring age estimates to approximately 14 years. The approach used year-class tracking across age classes and confirmed that age is often underestimated for fish aged >6 years (Melvin and Campana 2010). In that study, pooling of otolith cores (earliest otolith growth) from 2–5 fish was used to obtain enough mass for ^{14}C analyses (~ 3 mg), as recommended by most AMS facilities at the time for good precision. Advances in AMS technology have increased ^{14}C measurement capacity to a point where individual otolith cores from herring — as well as the much smaller otoliths of sprat (the maximum mass for fish near 20 years of age in this study was 1.5 mg vs 8.5 mg for herring) — can provide reliable ^{14}C values from 100–200 μg of calcium carbonate. This is 10–20 times smaller than typically used in previous studies. Hence, the current study avoided the assumptions necessary for combining otolith samples of different fish of a similar age to get a ^{14}C value. In contrast, existing support for sprat age estimates and protocols, normally reported up to 6–8 years, are not known to date. Only a workshop report that used methods most appropriate for the earliest otolith growth was located that addressed age validation for sprat in any form (Torstensen *et al.* 2004).

Due to the number of fish across size and age classes — coupled with successive alignments to the Baltic Sea ^{14}C chronology that were statistically supported — the findings provide strong support for the current age reading protocols, as determined by well-defined otoliths, for Baltic sprat and herring. In some cases, offsets from the reference chronology have given indications of age estimate bias or occasional offsets due to significant under or over estimation of age from growth zone counting (Campana 2001, Andrews and Scofield 2021, Andrews *et al.* 2025). Although there were no signs of such a scenario within the minor offsets that are more likely attributed to environmental factors, like seasonal influx of freshwater and mixing to the Baltic Sea. The strongest alignments for sprat were observed in the older collections of 1991, for which the annual change in ^{14}C was greatest overtime. For this series, the otolith with the greatest mass was aged to 16 years by counting well-defined growth zones, placing it at peak ^{14}C levels as shown in the Baltic Sea chronology. In addition, sprat otoliths were reassessed for age in this study and found to be well-defined and within ± 1 year from original age estimate. The more recent 2012 sprat collections also aligned well with the reference chronology up to 18 years, although there were some individuals on the low side of the ^{14}C reference chronology — reinvestigating the age reading, along with an otolith mass-to-age relationship, could not explain these offsets. Hence, it was concluded that some fish may have been in waters affected by inflow events from the North Sea or ^{14}C -deficient freshwater sources, as evidenced by similar variability that was observed in the most recent years of the Baltic Sea ^{14}C reference chronology.

The circumstances were similar for hatch year alignments of herring aged up to 22 years. Both sample sets were from similar collection years but different regions — southern Baltic proper (ICES SD25) vs Bothnian Sea (ICES SD30) — and aligned well with the Baltic Sea chronology, with a few outliers that could not be explained by age estimate errors or an otolith mass-to-age relationship. Two elevated samples were

most likely affected by another anthropogenic ^{14}C source in the Bothnian Sea, such as emissions to the Baltic Sea from NPPs or other nuclear facilities, as exemplified by a few elevated reference chronology samples. One reduced ^{14}C value was unlikely to have been younger based on the otolith mass-to-age relationship, although it is noted that one of the most massive otoliths could have been a few years older and would still align with the reference. Despite the minor offsets of a few otoliths, it is apparent and statistically supported that the age reading of herring otoliths is correct and that there are actual growth differences between regions (northern-southern Baltic Sea) as observed for age-at-length and maximum age (14 *cf.* 22 years).

Other Baltic Sea fishes and bomb ^{14}C dating

The use of otoliths from other Baltic fishes revealed contrasting chronological alignments, as well as support for follow-up age validation studies. Baltic pike and pikeperch, restricted to less saline environments for reproduction and recruitment than cod, sprat, and herring, would be expected to reflect ^{14}C levels of a freshwater environment. However, measurements from two younger pike from enclosed coastal Baltic waters — aged 3 and 7 years from wing bone growth zone counts — aligned well with the Baltic Sea reference chronology. The much larger and older pike and pikeperch from a semi-enclosed coastal bay farther to the south — aged 20 and 15 years, respectively, from well-defined otolith sections (Figs SM4, SM5) — had ^{14}C values that aligned with the North American freshwater chronology by being slightly attenuated from atmospheric levels. Alignment of the two smaller pike to a similar freshwater trend could mean the fish were underaged by a few years but the age reading of these younger wing bones was well defined. It is likely that the earliest growth for the smaller pike were formed in waters influenced by nearby emissions from the Forsmark NPP and that the older pike and pikeperch began life in waters that were not affected. Previous studies described different ecotypes for Baltic pike, from lifetime residency in brackish water to anadromy and residency in freshwater, with intermediary behaviors connecting those extremes (Nordahl *et al.* 2019, Sunde *et al.* 2022, Rittweg *et al.* 2024). These alignments are an indication that semi-isolated coastal bays with high freshwater input to the Baltic Sea may follow the slightly attenuated North American lakes record in terms of future age estimate alignments and validation efforts. The assessments performed here on two older Baltic cod aligned with the Baltic Sea bomb ^{14}C chronology when an age of 6 years — as determined previously using annual elemental cyclicity from LA-ICP-MS for each specimen (Heimbrand *et al.* 2020) — was used to calculate hatch years, whereas alternate age estimates of 7 and 11 years from growth zone counting did not align as well. It was expected that the Baltic Sea bomb ^{14}C chronology could be used to calibrate the age of older cod because the reference is largely established by the same species.

The ^{14}C patterns revealed from just a few otoliths of three Baltic species present opportunities for larger studies of these and other regional fishes that would provide valuable insights into age and growth. Use of more otoliths from these species through time and across size and age classes would provide baselines that place constraints on age estimates. While further investigations on inland vs nearshore Baltic locations in terms of bomb-produced ^{14}C levels is warranted, the archives

that were canvassed for the specimens used in this study cover numerous opportunities dating back several decades. Further study in this regard would provide evidence to either support or refute age estimation methods that may be outdated, especially in terms of establishing longevity for better estimates of reproductive potential and natural mortality.

Variations of ^{14}C in the Baltic Sea

Inflow events to the Baltic Sea from the North Sea may account for the reduced sprat and herring ^{14}C values relative to the reference chronology (e.g. Morholz 2018). Specifically, a strong inflow event was recorded for 2003 that correlates with low ^{14}C values from two sprat with hatch years from the same year. However, the lowest ^{14}C value for sprat was from a very small subsample with low AMS counts and may be unreliable (S30-006, Table SM3). In contrast, the herring specimens with the lowest ^{14}C value (with adequate AMS counts and considered reliable) for hatch year 2000 shows no correlated inflow event for a few years on either side. Hence, the alignment of ^{14}C values in otoliths of fishes to inflow events will require further investigation, as well as consideration for ^{14}C -deficient freshwater sources (e.g. Philippsen 2013).

The Chernobyl NPP incident was not evident in any of the otolith ^{14}C values that had a period of formation through the date of the accident (26 April 1986). Four YOY sprat collected from the northern Baltic Sea (ICES SD29) in October 1986 did not show ^{14}C levels that were above what is likely to be an already elevated ^{14}C level due to the other anthropogenic ^{14}C sources mentioned earlier. While other radioisotopes measured in brown algae (*Fucus vesiculosus*) could be clearly linked to fallout from the incident to the Baltic Sea basin (Carlson and Holm 1992), the few atmospheric ^{14}C measurements and proxies that were available revealed low level emissions that were unlikely to cause a measurable increase in aquatic environments (Florkowski et al. 1988, Olsson 1989, Nydal and Gislefoss 1996).

Conclusions

The development of an 80-year otolith-based bomb ^{14}C chronology, and its application as a temporal reference to validate age estimates, has set a baseline for fisheries science studies in the Baltic Sea. The use of this tool on Baltic sprat and herring to confirm both the accuracy of age estimates and the reliability of age reading protocols used to determine ages beyond 20 years is the first of its kind for the region. Despite the caveats on use of the post-peak decline as an age validation tool, temporal constraints remain that provide valuable age, growth and longevity information. This is especially useful for fishes with untested life-history characteristics that may rely on outdated and possibly invalid age estimation methods, such as continued reliance on scales, fin rays, or bones that are not conserved structures over time and have been shown to underestimate age (Campana 2001). The initial results for older Baltic cod — coupled with the new bomb ^{14}C reference chronology as established with young Baltic cod otoliths — show promise for a comprehensive age validation study for the species, as was specifically suggested in a recent review (Hüssey et al. 2016). The applicability of bomb ^{14}C dating to other species, like Baltic pike and pikeperch, is particularly useful, considering the extensive otolith archives that are available for some species in Sweden and other Baltic coun-

tries, and the increased need to establish stock assessments for these non-commercial fishes due to their socio-economic importance (Bergström et al. 2016, Arlinghaus et al. 2023). In addition, the method remains effective in discovering unexpectedly long lifespans. Some long-lived freshwater fishes were shown to have lived prior to nuclear testing to ages exceeding 100 years in North America (Andrews et al. 2024a, Lackmann et al. 2019). Similar candidates exist in Europe, like Wels catfish (*Silurus glanis*; Bergström et al. 2022) and European eel (Andrews et al. 2025), that may have an entire bomb ^{14}C signal recorded in their otoliths. Bomb ^{14}C dating is also now widely applicable to other animals of the Baltic Sea that grow conserved skeletal and non-skeletal structures (both organic and inorganic) that may have recorded the bomb-produced ^{14}C signal through their lifespans. For example, marine mammals, of which the teeth of beluga (*Delphinapterus leucas*) revealed a 60-year lifespan over erroneous estimates up to just 30 years (Stewart et al. 2006), and shellfish, where shells of various mollusks were confirmed to live decades to over a century in the absence of well-defined annual growth zone structure (Andrews et al. 2013b, Kilada et al. 2007, 2009, Scourse et al. 2012). As illustrated by the results presented here for fishes of the Baltic Sea basin, and in reference to numerous studies of this kind around the world, bomb ^{14}C dating is poised to make further revelations on the life histories of marine and freshwater organisms of this unique ecosystem.

Conflict of interest

The authors declare there are no competing interests.

Acknowledgements

Thank you to Lukas Wacker, Marcus Christl, and Hans-Arno Synal for project support at the Laboratory of Ion Beam Physics at ETH Zürich. Joakim Hjelm and Noël Holmgren of the Swedish University of Agricultural Sciences, Department of Aquatic Resources provided project support and funding. Thanks to the fishers, angling guides, and laboratory assistants that helped with specimen acquisition and sample handling. Thanks to the editors and an anonymous reviewer for comments and suggestions that improved the manuscript.

Author contributions

Comprehensive to specific conceptualizations (A.H.A., F.V., C.W., N.H., B.C.L., Y.H., Ö.Ö., T.R.), data curation (A.H.A., F.V., C.W., N.H.), formal analysis (A.H.A., F.V., C.W., N.H., B.C.L., T.R.), investigation (A.H.A., F.V., B.C.L., T.R.), methodology (A.H.A., F.V., C.W., N.H., B.C.L., T.R.), visualization (A.H.A., F.V., B.C.L.), writing original draft (A.H.A., C.W., F.V., B.C.L.), writing review and editing (A.H.A., F.V., C.W., N.H., B.C.L., Y.H., Ö.Ö., T.R.).

Supplementary material

Supplementary data is available at *ICES Journal of Marine Science* online.

Funding

This work was supported in part by the August T Larsson Guest Researcher Programme at the SLU for AH Andrews

(2020–2022) with significant project funding provided by the Baltic Waters Foundation (www.balticwaters.org; Grant #2121 to F Vitale at SLU).

Data availability

The data underlying this article are available in the article and in its online supplementary material.

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Handling Editor: Francis Juanes