dissociation of this excited state, producing radicals, or by the formation of a diol radical after reaction of an excited-state fatty acid with an adjacent molecule.

Because fatty acid–covered surfaces are ubiquitous, the photochemical production of gas-phase unsaturated and functionalized compounds will affect the local oxidative capacity of the atmosphere and will lead to secondary aerosol formation. This interfacial photochemistry may exert a very large impact, especially if in general the mere presence of a surface layer of a carboxylic acid can trigger this interfacial photochemistry at ocean surfaces, cloud droplets, and the surface of evanescent aerosol particles.

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LIFE HISTORY

Eye lens radiocarbon reveals centuries of longevity in the Greenland shark (*Somniosus microcephalus*)

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The Greenland shark (*Somniosus microcephalus*), an iconic species of the Arctic Seas, grows slowly and reaches >500 centimeters (cm) in total length, suggesting a life span well beyond those of other vertebrates. Radiocarbon dating of eye lens nuclei from 28 female Greenland sharks (81 to 502 cm in total length) revealed a life span of at least 272 years. Only the smallest sharks (220 cm or less) showed signs of the radiocarbon bomb pulse, a time marker of the early 1960s. The age ranges of prebomb sharks (reported as midpoint and extent of the 95.4% probability range) revealed the age at sexual maturity to be at least 156 ± 22 years, and the largest animal (502 cm) to be 392 ± 120 years old. Our results show that the Greenland shark is the longest-lived vertebrate known, and they raise concerns about species conservation.

The Greenland shark (Squaliformes, *Somniosus microcephalus*) is widely distributed in the North Atlantic, with a vertical distribution ranging from the surface to at least 1816-m depth (*1, 2*). Females outgrow males, and adults typically measure 400 to 500 cm, making this shark species the largest fish native to arctic waters. Because reported annual growth is ≤1 cm (*3*), their longevity is likely to be exceptional. In general, the biology of the Greenland shark is poorly understood, and longevity and age at first reproduction are completely unknown. The species is categorized as "Data Deficient" in the Norwegian Red List (*4*).

Conventional growth zone chronologies cannot be used to age Greenland sharks because of their lack of calcified tissues (*5*). To circumvent this problem, we estimated the age from a chronology obtained from eye lens nuclei by applying radiocarbon dating techniques. In vertebrates,

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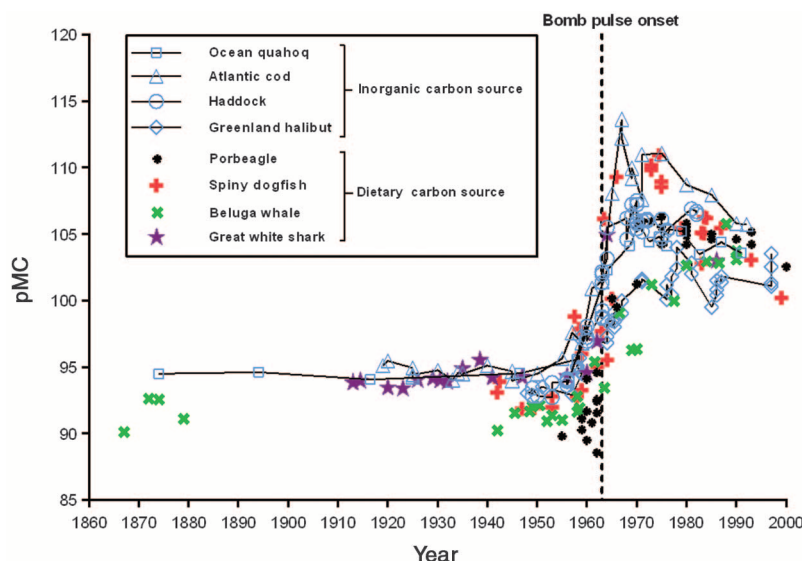*Corresponding author. Email: julius.nielsen@bio.ku.dk

the eye lens nucleus is composed of metabolically inert crystalline proteins, which in the center (i.e., the embryonic nucleus) is formed during prenatal development (*6, 7*). This tissue retains proteins synthetized at approximately age 0: a unique feature of the eye lens that has been exploited for other difficult-to-age vertebrates (*6, 8, 9*).

Our shark chronology was constructed from measurements of isotopes in the eye lens nuclei from 28 female specimens (81 to 502 cm total length, table S1) collected during scientific surveys in Greenland during 2010–2013 (fig. S1) (see supplementary materials). We used radiocarbon (¹⁴C) levels [reported as percent of modern carbon (pMC)] to estimate ages and stable isotopes, ¹³C and ¹⁵N (table S1), to evaluate the carbon source (supplementary materials). Depleted $\delta^{13}C$ and enriched $\delta^{15}N$ levels established that the embryonic nucleus radiocarbon source was of dietary origin and represents a high trophic level. In other words, isotope signatures are dictated by the diet of the shark's mother, not the sampled animals. We set the terminal date for our analyses to 2012, because samples were collected over a 3-year period. The chronology presumes that size and age are positively correlated.

Since the mid-1950s, bomb–produced radiocarbon from atmospheric tests of thermonuclear weapons has been assimilated in the marine environment, creating a distinct "bomb pulse" in carbon-based chronologies (*10*). The period of rapid radiocarbon increase is a well-established time stamp for age validation of marine animals (*11–14*). Radiocarbon chronologies of dietary origin (reflecting the food web) and chronologies reflecting dissolved inorganic radiocarbon of surface mixed and deeper waters, have shown that the timing of the bomb pulse onset (i.e., when

Fig. 1. Radiocarbon chronologies of the North Atlantic Ocean. Radiocarbon levels (pMC) of different origin (inorganic and dietary) over the past 150 years are shown. Open symbols (connected) reflect radiocarbon in marine carbonates (inorganic carbon source) of surface mixed and deeper waters (*26, 36–38*). Solid symbols reflect radiocarbon in biogenic archives of dietary origin (*11, 14, 22, 24*). The dashed vertical line indicates the bomb pulse onset in the marine food web in the early 1960s.
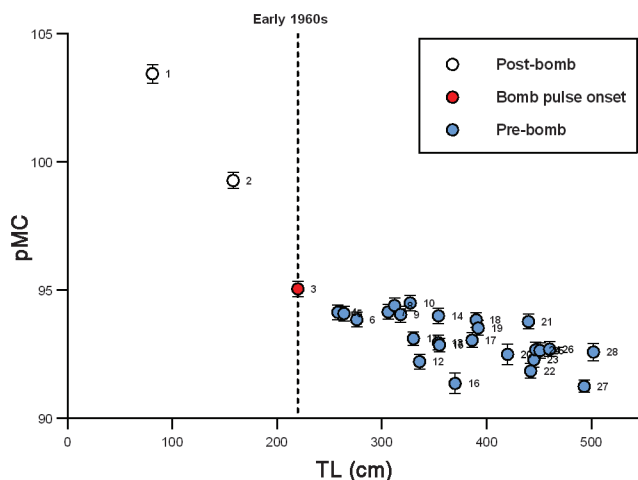

Fig. 2. Radiocarbon in eye lens nuclei of Greenland sharks. Radiocarbon levels (pMC ± SD, table S1) from 28 females plotted against total length (TL) are shown. Individual animals are identified by the numbers next to the symbols. Nos. 1 and 2 are of postbomb origin, and nos. 4 to 28 are of prebomb origin. We consider shark no. 3 to be from the early 1960s, which is the latest timing of the bomb pulse onset (dashed vertical line).

bomb-produced radiocarbon becomes detectable in a chronology) is synchronous within a few years and no later than early 1960s across the northern North Atlantic (Fig. 1).

Sexually mature females >400 cm have been caught across the Greenland continental shelf at depths between 132 and ~1200 m [(*15, 16*) and table S1]. Their diet (*15–17*) and stable isotope signatures (*18*) (table S1) are comparable to those of other marine top predators such as the porbeagle (*Lamna nasus*), white shark

(*Carcharodon carcharias*), spiny dogfish (*Squalus acanthias*), and beluga whale (*Delphinapterus leucas*) (*11, 14, 19–24*), for which the bomb pulse onset has been established (Fig. 1). We therefore consider the early 1960s as appropriate for the timing of the bomb pulse onset for the Greenland shark chronology as well.

The two smallest animals (nos. 1 and 2) had the highest radiocarbon levels (>99 pMC), implying that they were indeed affected by the bomb pulse (Fig. 2). However, given the variabi-

lity of bomb pulse curves (Fig. 1), no exact age can be assigned to these animals other than that they were born later than the early 1960s. The third animal in the chronology (no. 3, 95.06 pMC), on the other hand, had a radiocarbon level slightly above those of the remaining sharks (nos. 4 to 28, pMC <95), placing its birth year close to the same time as the bomb pulse onset (i.e., early 1960s, Fig. 2). We therefore assign shark no. 3 (total length 220 cm) an age of ~50 years in 2012 and consider the remaining 25 larger animals to be of prebomb origin.

We estimated the age of prebomb sharks based on the Marine13 radiocarbon calibration curve (*25*), which evaluates carbon-based matter predating the bomb pulse that originates from surface mixed waters. The observed synchronicity of the bomb pulse onset (Fig. 1) supports the presumption that natural temporal changes of prebomb radiocarbon are imprinted in the marine food webs with negligible delay. We contend that the Marine13 curve can contribute to the assessment of the age of prebomb sharks despite the difficulties associated with (i) the low variation in the radiocarbon curve over the past 400 years (*25*); and (ii) that the degree of radiocarbon depletion in contemporaneous surface mixed waters (local reservoir age deviations, ΔR) differs between regions (*26*), meaning that the carbon source of the eye lens nucleus reflects food webs of potentially different ΔR levels. Consequently, radiocarbon levels of prebomb animals must be calibrated as a time series under a set of biological and environmental constraints.

We used OxCal (version 4.2) to do this calibration (*27*). The program uses Bayesian statistics to combine prior knowledge with calibrated age probability distributions to provide posterior age information (*28, 29*). We constrained age ranges with presumptions about von Bertalanffy growth, size at birth, the age of animal no. 3 deduced from the bomb pulse onset (biological constraints), and plausible ΔR levels from the recent past (environmental constraint). This makes up a Bayesian model that is detailed in the supplementary materials.

Calibrations of single pMC measurements without biological constraints are shown as probability distributions of age with very wide ranges (light blue distributions, Fig. 3). When imposing the model, constrained and narrower age estimates are produced for each prebomb individual, shown as posterior probability distributions of age (dark blue distributions) in Fig. 3 and posterior calibrated age ranges at 95.4% (2σ) probability in table S2. OxCal also calculated agreement indices for each individual shark (A index) and for the calibration model (A_{model}). This allowed us to evaluate the consistency between modeled age ranges and Marine13, as well as the internal agreement between data points of the model (table S2) (*30*). To test the effect of the fixed age parameter (shark no. 3), a sensitivity analysis was made (supplementary materials and fig. S2), showing that the overall finding of extreme Greenland shark longevity is robust
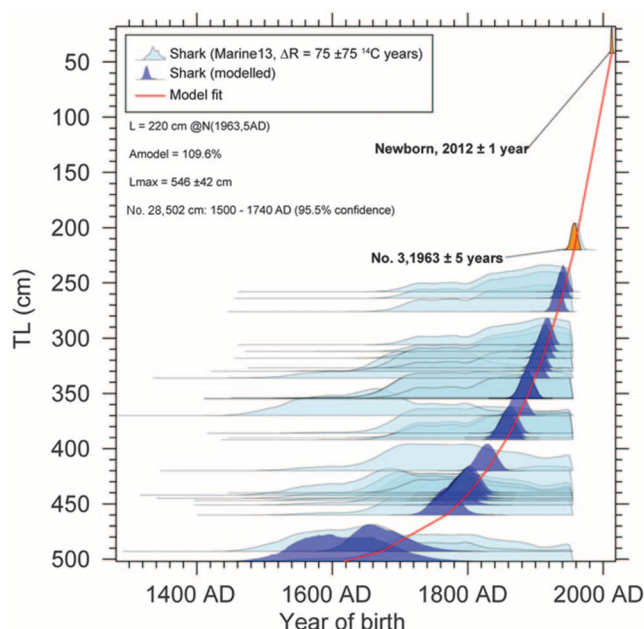
Fig. 3. Bayesian age ranges of prebomb sharks. The estimated year of birth against total length (TL) for prebomb sharks (nos. 4 to 28) is shown. Light blue shows the individual age probability distributions for each shark, and modeled posterior age probability distributions are shown in dark blue. Fixed date distributions (model input) of one newborn shark (42 cm, 2012 ± 1) and of shark no. 3 (220 cm, born in 1963 ± 5) are shown in orange. The red line is the model fit connecting the geometric mean for each posterior age probability distribution. (**Inset**) The model output; i.e., A_{model}, L_{max}, and range of birth year for shark no. 28. Also see the supplementary materials.

regardless of the exact timing of the bomb pulse onset (1958–1980).

The model estimated asymptotical total length to be 546 ± 42 cm (mean ± SD), a size matching the largest records for Greenland sharks (2), and the age estimates (reported as midpoint and extent of the 95.4% probability range) of the two largest Greenland sharks to be 335 ± 75 years (no. 27, 493 cm) and 392 ± 120 years (no. 28, 502 cm). Moreover, because females are reported to reach sexual maturity at lengths >400 cm (15), the corresponding age would be at least 156 ± 22 years (no. 19, 392 cm) (table S2). A_{model} was 109.6%, demonstrating that samples are in good internal agreement, implying that the age estimates are reliable.

The validity of our Greenland shark age estimates is supported by other lines of evidence. For instance, we found sharks <300 cm to be younger than 100 years (table S2). Such age estimates are indirectly corroborated by their depleted $\delta^{13}C$ levels (table S1), possibly reflecting the Suess effect, another chemical time mark triggered by emissions of fossil fuels, imprinted in marine food webs since the early 20th century (31, 32). In addition, high levels of accumulated anthropogenic contaminants may suggest that ~300-cm females are older than 50 years (33). Taken together, these findings seem to corroborate an estimated life span of at least 272 years for Greenland sharks attaining more than 500 cm in length.

Our results demonstrate that the Greenland shark is among the longest-lived vertebrate species, surpassing even the bowhead whale (*Balaena mysticetus*, estimated longevity of 211 years) (9). The life expectancy of the Greenland shark is exceeded only by that of the ocean quahog (*Arctica islandica*, 507 years) (34). Our estimates strongly suggest a precautionary approach to the conservation of the Greenland shark, because they are common bycatch in arctic and subarctic groundfish fisheries and have been subjected to several recent commercial exploitation initiatives (35).

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Science

Eye lens radiocarbon reveals centuries of longevity in the Greenland shark (*Somniosus microcephalus*)

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Deep living for centuries

We tend to think of vertebrates as living about as long as we do, give or take 50 to 100 years. Marine species are likely to be very long-lived, but determining their age is particularly difficult. Nielsen *et al.* used the pulse of carbon-14 produced by nuclear tests in the 1950s—specifically, its incorporation into the eye during development—to determine the age of Greenland sharks. This species is large yet slow-growing. The oldest of the animals that they sampled had lived for nearly 400 years, and they conclude that the species reaches maturity at about 150 years of age.

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