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Nielsen, Julius; Hedeholm, Rasmus B; Heinemeier, Jan; Bushnell, Peter G; Christiansen, Jørgen S; Olsen, Jesper; Ramsey, Christopher Bronk; Brill, Richard W; Simon, Malene; Steffensen, Kirstine F; Steffensen, John Fleng

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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.

LIFE HISTORY

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

Julius Nielsen,1,2,3,4 Rasmus B. Hedeholm,2 Jan Heinemeier,5 Peter G. Bushnell,6 Jørgen S. Christiansen,4 Jesper Olsen,4 Christopher Bronk Ramsey,7 Richard W. Brilli,8,9 Malene Simon,10 Kirstine F. Steffensen,1 John F. Steffensen1

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.

T he 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, 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 synthesized 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 SI) collected during scientific surveys in Greenland during 2010–2013 (fig. SI) (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 SI), to evaluate the carbon source (supplementary materials). Depleted 13C and enriched 15N 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...
As the porbeagle (*Lamna nasus*), to those of other marine top predators such as the tope signatures (*Lepisosteus albus*), the bomb pulse (Fig. 1) has been established (Fig. 1). We therefore assign shark no. 3 (total length 220 cm) as the internal agreement between data points and 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, $\Delta R$) differs between regions (26), meaning that the carbon source of the eye lens nucleus reflects food webs of potentially different $\Delta R$ 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 $\Delta R$ 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% (2e) probability in table S2. OxCal also calculated agreement indices for each individual shark ($A_{\text{model}}$) and for the calibration model ($A_{\text{model}}$). 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.
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, 382 cm) (table S2). \( \lambda_{\text{model}} \) 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 \( \delta^{13} \text{C} \) levels (table S1), possibly reflecting the Suess effect, another chemical time marker 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).

**REFERENCES AND NOTES**


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**SUPPLEMENTARY MATERIALS**

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Material and Methods
Supplementary Text
Figs. S1 and S2
Tables S1 and S2
References (39–50)

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Editor's Summary

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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