Bomb radiocarbon chronologies in the Arctic, with implications for the age validation of lake trout (*Salvelinus namaycush*) and other Arctic species

Steven E. Campana, John M. Casselman, and Cynthia M. Jones

Abstract: Radiocarbon generated by atmospheric testing of nuclear weapons (bomb radiocarbon) produced a strong signal with an abrupt onset in the 1950s, which serves as a dated marker for tracing oceanic circulation and confirming age in animals forming growth bands. Here, we report the first prebomb and postbomb radiocarbon chronologies for marine and freshwater environments in the Canadian Arctic, extend the radiocarbon chronology for the northwest Atlantic Ocean, and use the onset of the bomb signal to validate our age interpretations of lake trout (*Salvelinus namaycush*) in Arctic lakes. Both surface and deepwater Arctic chronologies became detectable on or around 1958, similar to the year of onset elsewhere in the world. In contrast, the freshwater Arctic chronology increased sharply in 1957, with a peak value sixfold higher than the adjacent marine environment. The radiocarbon content of the adult otolith core validated our age interpretation criteria for Arctic lake trout to an age of at least 50 years. Otolith growth in such slow-growing fish was so low as to be unresolvable under conventional examination with a dissecting microscope. With these new radiocarbon reference chronologies, age validation of a large number of Arctic organisms should now be possible.

Résumé : Le radiocarbone généré par les essais atmosphériques d'engins nucléaires (radiocarbone de bombes) produit un fort signal qui apparaît abruptement dans les années 1950 et qui sert de marqueur daté pour suivre la circulation océanique et pour confirmer l'âge chez les animaux qui portent des bandes de croissance. Nous présentons ici des chronologies au radiocarbone avant et après les essais nucléaires pour les environnements marins et d'eau douce de l'Arctique canadien; nous étendons cette chronologie au radiocarbone au nord-ouest de l'Atlantique et nous utilisons l'apparition du signal des bombes pour valider notre interprétation de l'âge de touladis (*Salvelinus namaycush*) dans des lacs arctiques. Les chronologies de l'Arctique, tant en eaux superficielles que profondes, sont devenues décelables en ou vers 1958, comme ailleurs dans le monde. En revanche, la chronologie arctique en eau douce accuse un net accroissement en 1957, avec une valeur du maximum six fois plus élevée que dans l'environnement marin adjacent. La concentration en radiocarbone du noyau des otolithes des adultes valide nos critères d'interprétation de l'âge chez les touladis arctiques jusqu'à l'âge d'au moins 50 ans. La croissance des otolithes chez ces poissons à développement lent est si faible qu'elle ne peut être interprétée par l'examen habituel à la loupe binoculaire. Ces nouvelles chronologies de référence de l'Arctique devraient permettre maintenant de valider la détermination de l'âge chez un grand nombre d'organismes arctiques.

[Traduit par la Rédaction]

Introduction

The atmospheric testing of atomic bombs in the 1950s and 1960s resulted in a rapid and well-documented increase in atmospheric radiocarbon, largely in the form of radioactive carbon dioxide, which first appeared around 1952 and peaked in 1964 (Nydal 1993). The exchange of radiocarbon between the atmosphere and precipitation was rapid and relatively complete, resulting in riverine and shallow freshwater radiocarbon values that peaked shortly after that of the atmosphere, albeit at lower concentrations (Peng and Broecker 1980; Spiker 1980). Peak values of bomb radiocarbon in the world's oceans were delayed until the late 1960s or 1970s as riverine input, precipitation, and atmospheric exchange of CO_2 gradually increased the concentration in surface marine waters (Druffel and Linick 1978). The exact year of peak radiocarbon and its rate of subsequent decline in the ocean was location-specific, because of the strong influence of water residence times, which affect the mixing of radiocarbon-depleted deep waters with bomb-enriched surface waters (Weidman and Jones 1993). However, the period of initial radiocarbon increase around 1958 was almost synchronous around the world and was recorded both directly in the water and measured in marine carbonate structures such as corals (Kalish 1995).

Received 18 May 2007. Accepted 8 December 2007. Published on the NRC Research Press Web site at cjfas.nrc.ca on 15 March 2008.
J20007

S.E. Campana.[1] Bedford Institute of Oceanography, Fisheries and Oceans Canada, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada.
J.M. Casselman. Queen's University, Department of Biology, Kingston, ON K7L 3N6, Canada.
C.M. Jones. Center for Quantitative Fisheries Ecology, Old Dominion University, Norfolk, VA 23508, USA.

[1] Corresponding author (e-mail: campanas@mar.dfo-mpo.gc.ca).

Can. J. Fish. Aquat. Sci. **65**: 733–743 (2008) doi:10.1139/F08-012

Owing to its conservative nature, bomb radiocarbon has proven valuable as a chemical tracer in ocean circulation studies (Follows and Marshall 1996; Peng et al. 1998). Whereas surface marine waters equilibrated with the atmospheric bomb signal years ago, deep water that is upwelled has not been exposed to the bomb signal and therefore is depleted in radiocarbon. However, the tracer properties of bomb radiocarbon are not restricted to the water. Measurements of bomb radiocarbon in marine organisms have been used to trace the flow of carbon through the marine environment, such as the carbon flow from the surface waters to the deep sea (Pearcy and Stuiver 1983). All of these applications take advantage of the well-documented time series of the first appearance of bomb radiocarbon in temperate and tropical environments. This time series is so well understood that the appearance of bomb radiocarbon has proven very useful as a dated marker in any structures that form annual growth bands, such as trees (Worbes and Junk 1989), and in calcified structures such as corals, bivalves, and fish otoliths (Kalish 1993; Weidman and Jones 1993; Campana 1997).

Although the bomb radiocarbon chronology has been well characterized in temperate and tropical regions, it has not been well described in Arctic regions, particularly prior to 1979 (Ostlund et al. 1987). In large part, the absence of Arctic radiocarbon data is due to the absence of trees, corals, and bivalves in the Arctic, organisms that have provided detailed records of the radiocarbon chronology in other parts of the world. Isolated prebomb measurements based on growth bands in marine mammal bones and tusks have been reported (Tauber 1979; Bada et al. 1987), but the only continuous chronology for the Canadian Arctic across the 1950–1980 period is that based on beluga whale (*Delphinapterus leucas*) tooth growth bands (Stewart et al. 2006).

A promising alternative source of a radiocarbon chronology for the Arctic is that of fish otoliths, which have been used extensively for this purpose in other parts of the world (Campana 2001). Otoliths share a number of favourable properties with other radiocarbon proxies such as corals and bivalves: long-term stability, annual growth bands that can be aged and dated, and a radiocarbon content that is representative of the dissolved inorganic carbon (DIC) of the water in which the fish lived (Kalish 1995). In a recent study, Kalish et al. (2001) derived an extensive radiocarbon chronology for the surface waters of the Barents Sea based on annual growth bands isolated from Atlantic cod (*Gadus morhua*) otoliths. A comparable chronology does not yet exist for the terrestrial Arctic or marine waters of the Canadian Arctic, but would be particularly valuable for future studies of the age determination of terrestrial, freshwater, and marine Arctic organisms.

Bomb radiocarbon chronologies can also be used to validate the age and growth of many long-lived animals, including fish. The growth rates of fish in the Arctic would be expected to be very low, because of both low temperatures and low nutrient levels (Power 1997). Surprisingly however, there has been no independent confirmation of growth rate or age interpretation in any Arctic fishes other than Arctic grayling (*Thymallus arcticus*) (DeCicco and Brown 2006). This is particularly true for Arctic fishes believed to be long-lived, since traditional length frequency analyses are not effective for fish more than a few years old. In addition, many published age and growth interpretations of Arctic fishes are based on traditional surface readings of scales or otoliths, methods that are now known to underestimate (sometimes grossly) the age of long-lived fishes (Casselman 1987; Campana 2001). Johnson (1976) was the first to report that lake trout (*Salvelinus namaycush*) in the Arctic appear to be long-lived; however, his use of surface otolith readings left open the possibility that they were even longer-lived and slower-growing than he suspected. This possibility was tentatively confirmed by Power (1978), whose use of otolith transverse sections resulted in lake trout age estimates >50 years in some fish. While Power (1978) expressed doubt about the accuracy of previous ageing studies and confidence in his more modern ageing methods, he acknowledged that confirming his age interpretations would prove to be difficult or “impossible”. However, recent technological advancements using bomb radiocarbon now make such age validations possible (Campana 2001).

The first objective of this study is to document the magnitude and timing of the bomb radiocarbon signal in the Canadian Arctic, both in freshwater and ocean environments. We will then contrast these Arctic radiocarbon chronologies with those from more temperate locations. A second objective is to use the bomb radiocarbon chronologies to validate an ageing method for lake trout in Arctic lakes, thus setting a basis for validating the ages of other Arctic organisms, both in fresh water and salt water.

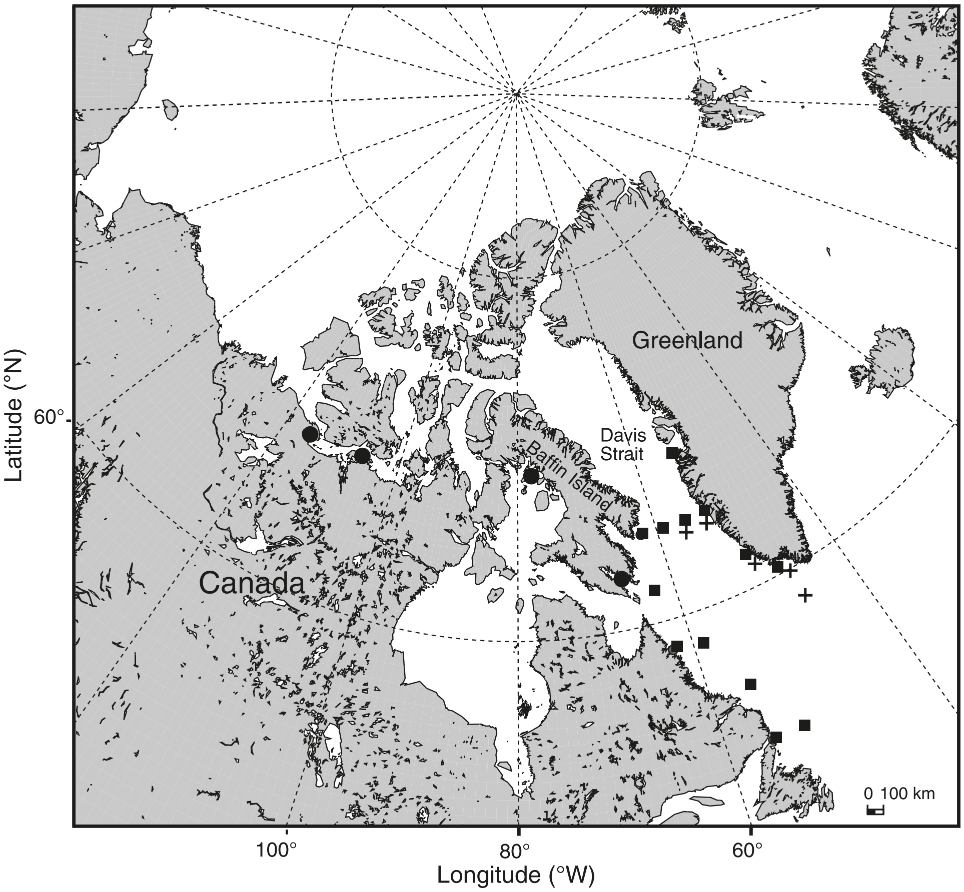
Materials and methods

Reference chronologies

All reference chronologies were based on archived collections of young fish otoliths whose age was either known or could be estimated based on their length. The very distinct length modes in the collections of these young fish suggested that actual age was unlikely to differ from estimated age by more than ±1 year.

The reference $\Delta^{14}C$ carbonate chronology for the Northwest Atlantic (NWA) was derived from 56 sagittal otoliths extracted from haddock (*Melanogrammus aeglefinus*) and redfish (*Sebastes* spp.) of ages 1–3 years from southern Newfoundland (North Atlantic Fisheries Organization (NAFO) Division 3Ps) whose cores were formed between 1949 and 1982 (Campana 1997; Campana et al. 2002). An additional 17 samples of age 1–2 haddock and yellowtail flounder (*Limanda ferruginea*) otoliths were collected from 3Ps between 1980 and 2000 and prepared in a similar manner. Graphically, the $\Delta^{14}C$ chronologies of the three species were indistinguishable, nor was a difference expected given the common depth and environment during the first few years of life. An analysis of variance (ANOVA) of the detrended residuals from a species-combined chronology demonstrated that there were no significant differences among the species; the statistical power of this test to detect an interspecies difference corresponding to about 1 year (a $\Delta^{14}C$ of 11) was 70% for the period of increasing $\Delta^{14}C$ values (1950–1970) and 96% for 1.5 years. Given the absence of interspecies differences, the species were pooled, averaged within years, and used as a single chronology. The prebomb chronology was supplemented by three published $\Delta^{14}C$ values from a bivalve on Georges Bank for the years 1939–

Fig. 1. Map indicating collection sites for bomb radiocarbon reference chronologies of freshwater *Salvelinus alpinus* (●), marine *Gadus ogac* (+), and marine *Reinhardtius hippoglossoides* (■).



1946 (Weidman and Jones 1993). The $\Delta^{14}C$ chronologies of aragonitic fish otoliths and bivalves in the NWA are indistinguishable during the prebomb era (before 1958) and begin to increase at virtually identical times (Campana 1997); thus the NWA chronology is a good proxy for the $\Delta^{14}C$ DIC history of the NWA.

The Greenland cod (*Gadus ogac*) reference chronology represents the surface marine waters of Davis Strait and western Greenland. The chronology was derived from 46 samples of age 0–3 *G. ogac* otoliths collected between 1954 and 2000 from NAFO Divisions 1CDEF (eastern Davis Strait) and stored dry in paper envelopes at the Grønlands Naturinstitut in Greenland (Fig. 1).

The Greenland halibut (*Reinhardtius hippoglossoides*) reference chronology represents the $\Delta^{14}C$ of the deeper waters (200–800 m with an average depth of 300 m) of Davis Strait and western Greenland. The chronology was derived from 38 samples of age 0–3 (<30 cm) *R. hippoglossoides* collected with otter and prawn trawls from NAFO Divisions 0B (western Davis Strait), 1ABCEF (eastern Davis Strait), and 2G and 2J (northern Labrador) on Danish, German, or Canadian surveys (Treble et al. 2008) (Fig. 1). The otoliths were stored dry in paper envelopes at the Grønlands Naturinstitut in Greenland or at the Northwest Atlantic Fisheries Centre in Newfoundland. Otolith cores from an additional three large (66–89 cm) adult Greenland halibut collected from NAFO Divisions 1EF and 2G in 1962–1966 were assayed to characterize the prebomb environment (Treble et al. 2008). Although the exact age of these adult fish was not known, we are confident that they were at least 10 years old, implying that their otolith cores were formed prior to 1958.

The reference chronology for the freshwater environment in the Arctic was largely based on Arctic char (*Salvelinus alpinus*) collections made in the 1960s by Lionel (Jim) Johnson; these otoliths were stored at the Arctic Institute in Ste-Anne-de-Bellevue, Québec, and subsequently transferred to the Canadian Museum of Nature, where they were accessed. The otoliths used in this study consisted of 58 samples of age 0–5 Arctic char collected between 1957 and 1969 throughout the Canadian Arctic north of latitude 62°50′ (Fig. 1). The mean length of the char was 10 cm (range of 7–21 cm), and the mean age was 2.8 years. Since the otoliths were quite small (0.4–4 mg per pair), otolith pairs were pooled across 1–10 fish of the same age and comparable length for assay. By pooling otoliths across fish, we have implicitly assumed that there is no ageing error for these young fish. Although we have no way to test this assumption, the length modes for these young fish were sufficiently distinct that it appears unlikely that our age estimates were in error by more than ±1 year.

The feature of a bomb radiocarbon chronology that is most stable across locations and environments is the year of initial increase above prebomb levels in response to the period of atmospheric testing of nuclear weapons. In surface marine chronologies in temperate and tropical environments, it is generally accepted that the bomb signal first became visible around 1958 (Druffel and Linick 1978; Kalish 1995). However, there has been little agreement among authors on how the year of first increase is to be determined in a new chronology. Past studies have used graphical interpretation of the Δ^{14}C chronology (Kalish 1993; Campana 1997) or calculation of the year that first exceeds the 95% confidence interval of the Δ^{14}C of the prebomb years after fitting a curvilinear equation to the Δ^{14}C chronology (Kerr et al. 2004; Stewart et al. 2006). Although both approaches are well intentioned, the graphical interpretation is subjective and the years selected for entry into the curvilinear fit are arbitrary. Therefore, we adopted a quantitative but simple approach for defining the year of initial increase, based on bomb input values into the atmosphere. Naegler and Levin (2006) documented bomb radiocarbon inventories for the atmosphere, ocean, and biosphere as part of a global bomb radiocarbon budget. The total cumulative radiocarbon input from nuclear bombs and the nuclear industry increased from about 0 in 1952 to 580 × 10^{26} atoms ^{14}C near its peak in 1963 for an average of 52.7 × 10^{26} atoms ^{14}C annually. This corresponds to an annual increase of 9.1%·year^{-1} and is approximately equal to the annual increase between 1954 and 1955, shortly after atmospheric testing of nuclear weapons began. A comparable pattern exists in both the modelled (Naegler and Levin 2006) and observed (Campana 1997) ocean ^{14}C inventories, with an average increase of 9%–10% per year between prebomb and peak Δ^{14}C levels, although the initial increase in the ocean did not become evident until about 1958. Therefore, it appears that a Δ^{14}C value 10% above the prebomb background is a valid indicator of the year of initial appearance of bomb Δ^{14}C and one that is consistent with atmospheric sources. However, estimation of a suitable prebomb background is not necessarily straightforward. Therefore, we based our calculation on the difference in Δ^{14}C values between the peak and prebomb values, which is easily and unambiguously calculated. Specifically, we estimated the value corresponding to the 10% threshold contribution of Δ^{14}C (C_T) by calculating 90% of the range in Δ^{14}C between its lowest (C_L) and peak (C_P) value and subtracting it from the peak value, as in

$$C_T = C_P - 0.9(C_P - C_L)$$

where C_L is on or after 1952, the year of initial appearance of bomb radiocarbon in the atmosphere. The year of initial appearance of bomb Δ^{14}C (Y_T) is then defined as the year in which the Δ^{14}C chronology first exceeds C_T.

We tested the accuracy of Y_T as a measure of year of initial appearance of bomb Δ^{14}C by applying it to all published marine bomb radiocarbon chronologies. In all cases, the calculated Y_T value lay in the range of 1957–1960, except where sample spacing did not allow more precise estimation (e.g., 1955–1960 for Kalish 1993). The advantage of this measure of Y_T over other methods is that it is relatively insensitive to random variation in prebomb values and is not based on an arbitrary selection of years for estimation. Therefore, it appears suitable for use in bomb radiocarbon studies in general.

Age validation

Otolith cores removed for age validation were collected from subadult and adult lake trout collected from Tasiat Lake (59°10′N, 75°16′W) and Lac Couture (60°08′N, 75°25′W) in the eastern Arctic in 2002 and from Zeta Lake (71°06′N, 106°34′W) in the western Arctic in 2003.

All ages were based on counts of presumed annual growth increments that were visible in transverse sections of the sagittal otolith. Otoliths to be aged were first embedded in a slow-drying hard epoxy (Araldite epoxy GY502 and hardener HY956 in a 5:1 weight ratio). Sections through the core (~450 μm thickness) were prepared with a single cut using twin blades separated by a spacer on an Isomet low-speed, diamond-bladed saw. The sections were subsequently mounted on a standard microscope slide with a thin coat of epoxy, then lightly polished to improve visibility. While under a binocular microscope at 16–40× magnification using reflected light, the growth increment sequence was digitally photographed at a resolution of 1280 × 1024, then digitally enhanced for contrast using Adobe Photoshop CS2. Age interpretation was based on the enhanced images. In the case of lake trout believed to be older than 30 years, a second set of age readings was made under transmitted light using a compound microscope at magnifications of 160× with no imaging. Bias between ageing methods was evaluated with age bias plots, whereas precision was quantified using the coefficient of variation (CV) (Campana 2001).

Otolith cores for bomb radiocarbon age validation were isolated from three adjacent 1.2 mm thick transverse sections of the otolith, polished lightly to view the growth sequence. Otolith cores representing the first 3 years of life were isolated from the central section as a solid piece with a Merchantek computer-controlled micromilling machine using 300 μm diameter steel cutting bits and burrs. Additional core material from the same otolith was isolated from the two adjacent sections, but restricted to the innermost two growth increments so as to allow for the offset of these lateral sections from the primordium. This procedure of obtaining material from multiple sections per otolith was necessary to maximize the amount of sample material available for assay from each otolith. Even then, the mean weight of isolated core material was ~0.5 mg. Therefore, otolith cores from 1–10 additional fish of the same age and similar length were extracted and pooled so as to bring the sample weight up to the minimum of 3 mg necessary for radiocarbon assay. By pooling otolith material across fish, we may have introduced variance into the estimate of year of core formation, but this was unavoidable. The date of sample formation was calculated as the year of fish collection minus the age span of the fish from the edge of the otolith to the midpoint of the range of growth increments present in the extracted core. After sonification in Super Q water and drying, the sample was weighed to the nearest 0.1 mg in preparation for ^{14}C assay with accelerator mass spectrometry (AMS). AMS assays also provided δ^{13}C (‰) values, which were used to correct for isotopic fractionation effects and provide information on the source of the carbon. Radiocarbon values were subsequently reported as Δ^{14}C, which is the per mil (‰) deviation of the sample from the radiocarbon concentration of 19th-century wood, corrected for sample decay prior to 1950 according to methods outlined by Stuiver and Polach (1977).

The mean standard deviation of the individual radiocarbon assays was about 5‰.

Results

Reference chronologies

Despite the broad range of habitats that they represent, the four reference chronologies all showed similar and characteristic bomb radiocarbon patterns: relatively low Δ^{14}C prior to 1957, a sharp increase during the 1960s, and stable or gently declining values after 1970 (Fig. 2; Table 1). Prebomb values (prior to 1957) were virtually identical at a Δ^{14}C of about –70 in the NWA and Arctic deepwater (Greenland halibut) chronologies. In contrast, the prebomb chronology for the surface marine Arctic (*G. ogac*) was markedly less depleted than the other chronologies prior to 1958, a finding that was sufficiently surprising that it prompted a reanalysis of additional samples, but with no change. The prebomb Δ^{14}C value of –114 in the freshwater Arctic chronology (Arctic charr) was markedly more depleted than any of the other chronologies.

Δ^{14}C levels after 1970 differed substantially among all of the chronologies. Peak Δ^{14}C levels were reached around 1966 in the case of the Arctic freshwater chronology, around 1969 for the NWA, and in the late 1970s for the two Arctic marine chronologies (Table 1).

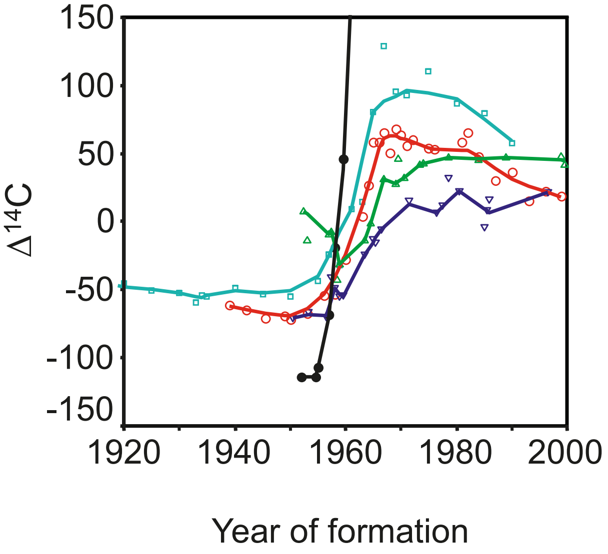
The feature of a bomb radiocarbon chronology that best serves as a dated reference mark is the year of initial increase above prebomb levels in response to the period of atmospheric testing of nuclear weapons. In the three marine reference chronologies reported here, this period of initial increase was calculated to lie between 1957 and 1959 in all cases. The NWA and deepwater Arctic marine chronologies began to increase in 1957, while the surface marine chronology began 2 years later in 1959 (Fig. 2; Table 1). In contrast, the freshwater Arctic chronology increased sharply in 1957, much more abruptly than the others.

The Arctic freshwater radiocarbon chronology clearly differed from that of the other habitats, both with respect to period of increase, prebomb Δ^{14}C, and peak Δ^{14}C (Fig. 2). Comparison of the freshwater pattern with the atmospheric Δ^{14}C chronology documented by Nydal (1993) indicates that the freshwater Δ^{14}C signal closely resembled an attenuated version of the atmospheric chronology. Both time series began to increase in earlier years and reached much greater peak values than did the NWA or other marine chronologies (Fig. 3). Indeed, the peak Δ^{14}C values in the freshwater environment were so much greater than those of the marine environment that environment type was easily identifiable in otolith samples collected in the mid-1960s.

Otolith growth patterns of lake trout

Growth increments, presumed to be formed annually, were clearly visible under reflected light in at least some regions of all of the otolith sections examined. In most otoliths up to an apparent age of about 20 years, one or several growth axes appeared to contain complete growth sequences, particularly those leading from the core to the dorso-proximal or ventro-proximal surfaces (Fig. 4). In older fishes, however, the number of increments visible along the growth axis often differed with the transect selected for ageing. In general, the clarity and spacing of the growth increment sequence was optimized in the thickened dorsal lobe (proximal surface) immediately adjacent to the sulcus (Fig. 4). Growth increments were also often interpretable in the ventral lobe (proximal surface) immediately adjacent to the sulcus, but sometimes produced an increment count 1–2 years less than that of the dorsal lobe. Growth increments did not appear to form consistently after an age of 20–30 years towards the ventral or dorsal tips, despite the fact that these axes were often the longest in the section.

Fig. 2. Bomb radiocarbon reference chronologies for Arctic fishes based on Δ^{14}C incorporated during the first few years of growth into young, known-age fish otoliths. While the prebomb (before 1958) and postbomb (after 1970) Δ^{14}C values differ among species, the period of increasing values is very similar in all of the marine time series and thus can be used as a dated marker. Fitted lines are locally weighted least square (LOESS) regressions. Freshwater *Salvelinus alpinus*, black solid circles; marine *Gadus ogac*, green open triangles; marine *Reinhardtius hippoglossoides*, blue inverted open triangles; marine Northwest Atlantic reference chronology, red open circles; marine *Gadus morhua* (Kalish et al. 2001), light blue open squares.



Difficulties in resolving growth increments first became apparent at an age of 40–45 years towards the edge of the otolith (Fig. 5*a*). This region of the otolith was often characterized by a regular sequence of increments of gradually decreasing width that eventually became almost featureless, even after aggressive image enhancement at a magnification of 40×. Visibility was not improved appreciably under transmitted light using the same microscope. However, after the section was polished to a smooth surface, the growth increments became very clear when examined with transmitted light under a compound microscope at 160× (Fig. 5*b*). Increment width near the proximal surface of old fish could be as narrow as 20 µm, which probably explains the difficulty in viewing the individual increments under a binocular microscope.

To insure that the increments visible using transmitted light under the compound microscope were comparable to those visible using reflected light under the binocular microscope after image enhancement, a series of 107 otoliths were

Table 1. Summary of $\delta^{13}C$ (‰) and $\Delta^{14}C$ assay results for young Arctic fish otoliths used in the preparation of reference chronologies.

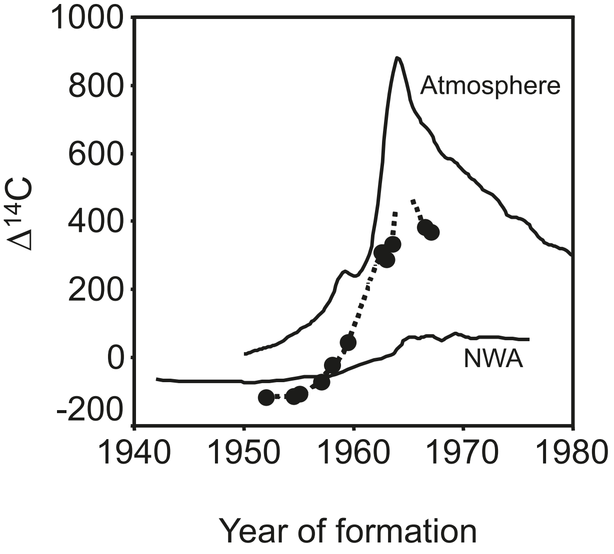
	Salvelinus alpinus		*Gadus ogac*		*Reinhardtius hippoglossoides*		NWA reference	
Year of formation	$\delta^{13}C$	$\Delta^{14}C$	$\delta^{13}C$	$\Delta^{14}C$	$\delta^{13}C$	$\Delta^{14}C$	$\delta^{13}C$	$\Delta^{14}C$
1939.0								–61.3
1942.0								–64.4
1945.5								–70.6
1947.5					–1.1	–71.0		
1949.0							–2.7	–68.8
1950.0							–3.6	–71.8
1950.5					–1.9	–66.3		
1952.0	–2.3	–114.0						
1952.5			–1.2	7.7				
1953.0			–2.1	–13.6			–1.8	–67.3
1954.5	–7.6	–113.7						
1955.0	–7.5	–106.6						
1956.0							–3.0	–54.5
1956.5					–2.2	–69.7		
1957.0	–11.6	–68.3	–2.3	–8.9				
1957.5			–2.0	–7.3	–2.8	–41.1		
1958.0	–10.0	–19.0			–3.1	–49.1	–3.4	–53.0
1958.5			–1.2	–42.4				
1959.0			–2.0	–31.2	–2.9	–54.8		
1959.5	–8.8	45.9			–3.1	–54.2		
1960.0							–2.1	–27.8
1962.5	–6.9	309.7						
1963.0	–7.0	287.7					–1.1	3.6
1963.5	–6.9	335.5	–2.2	–13.5	–3.5	–24.5		
1964.0							–3.4	26.4
1964.5			–1.9	–1.4				
1965.0					–3.0	–13.0	–3.8	58.9
1965.5					–2.6	–15.7		
1966.0							–4.3	58.2
1966.5	–7.6	383.4			–2.8	–5.6		
1967.0	–6.8	369.4	–1.8	31.0			–3.9	65.5
1968.0							–2.6	50.6
1969.0			–2.5	27.9			–1.9	68.0
1969.5			–3.6	46.2				
1970.0							–1.4	63.7
1970.5			–1.8	31.7				
1971.0							–2.2	55.9
1971.5					–2.6	15.1		
1972.0							–1.3	60.4
1973.5			–2.0	41.8				
1974.0			–2.7	42.7				
1975.0							–0.5	53.9
1976.0							–1.5	52.8
1976.5					–2.8	6.3		
1977.5					–2.9	12.1		
1978.5			–1.7	46.8	–2.5	31.8		
1980.5					–2.9	22.8		
1981.0							–1.6	58.2
1982.0							–0.7	65.9
1984.0			–2.7	45.0			–2.4	47.6
1985.0					–2.3	–4.1		
1985.5					–3.3	8.0		
1986.5					–2.8	16.4		
1987.0							–1.1	30.3
1989.0			–2.0	47.5				

Table 1 (*concluded*).

	Salvelinus alpinus		*Gadus ogac*		*Reinhardtius hippoglossoides*		NWA reference	
Year of formation	$\delta^{13}C$	$\Delta^{14}C$	$\delta^{13}C$	$\Delta^{14}C$	$\delta^{13}C$	$\Delta^{14}C$	$\delta^{13}C$	$\Delta^{14}C$
1990.0							–2.5	36.5
1993.0							–2.2	15.4
1996.0							–3.2	22.6
1996.5					–3.2	21.3		
1999.0			–2.3	48.1			–2.6	19.3
1999.5			–3.2	41.9				
2000.5							–2.8	33.7

Note: The Northwest Atlantic (NWA) reference chronology is composed of three fish species from the eastern coast of Canada; samples prior to 1946 are values reported by Weidman and Jones (1993) for east coast bivalves.

Fig. 3. The $\Delta^{14}C$ reference chronology for a freshwater Arctic species (●) more closely resembles the atmospheric time series (adapted from Nydal 1993) than the marine Northwest Atlantic (NWA) time series, with an earlier period of increase and higher peak values than the marine reference chronology. Fitted solid lines are locally weighted least square (LOESS) regressions, while the broken line is an interpolated fit.

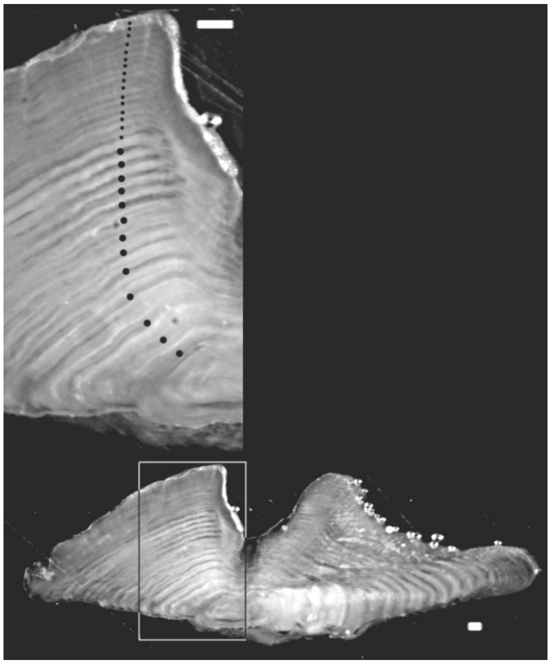


independently aged under both microscopes. An age bias plot indicated that there was no bias between the two viewing procedures until an age of about 45 years (Fig. 6). The precision (CV) between the ageing methods for these unbiased ages was 4.6%. At ages greater than 45 years, more increments were consistently seen under the compound microscope (Fig. 6). There were 63 otoliths aged as being over 45 years of age using the compound microscope for which reflected light increment counts were not possible because of poor visibility of the most recently formed growth increments.

Age validation of lake trout

The date of formation of the lake trout otolith cores was estimated in two ways: through age determination of the fish based on otolith growth increment counts and through comparison of otolith core $\Delta^{14}C$ values with the values known to be present in the Arctic freshwater environment at the time (the Arctic freshwater reference chronology). Where the increment-based and $\Delta^{14}C$-based dates are in agreement, the increment-based age interpretations must be (on average) correct.

Fig. 4. Annual growth increments in a transverse otolith section of a 56 cm, 29-year-old lake trout (*Salvelinus namaycush*) from Tasiat Lake. Inset shows the axis used for age determination and annotated growth increments. The image has been contrast-enhanced. Scale bar = 100 µm.



The correspondence between the Arctic freshwater reference chronology and the chronology derived from the lake trout otolith cores was very close (Fig. 7). Both chronologies describe a curve that closely resembles an attenuated version of the atmospheric chronology (Fig. 3), with a rapid increase between 1957 and the late 1960s, followed by a gradual decline through to 1995. The key samples for comparison were the cores formed before 1962 (Table 2), since they were formed during the period when environmental ^{14}C levels changed most rapidly. The core that was formed during the 1940s, and that was 62 years old based on increment counts, was clearly a prebomb value based on $\Delta^{14}C$ and thus must

Fig. 5. Growth increments near the otolith margin in a transverse section of a 46-year-old lake trout (*Salvelinus namaycush*) otolith are less visible in a reflected light image (*a*) than in a transmitted light image (*b*), largely because of the narrow width of the growth increments. Both images have been digitally enhanced to the same extent. Scale bar = 100 µm.

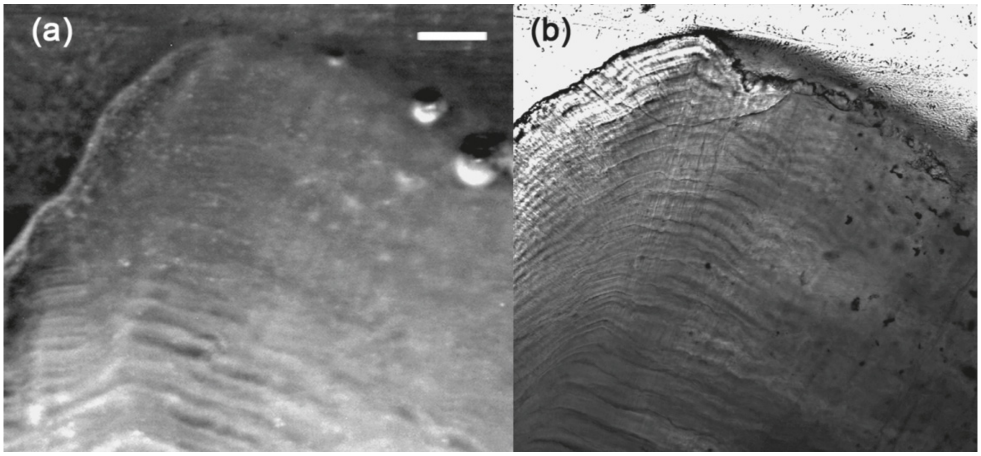


Fig. 6. Age bias plot comparing lake trout (*Salvelinus namaycush*) age estimates using a compound microscope and transmitted light with a stereomicroscope and reflected light. Deviation of mean ± 95% confidence interval bars from 1:1 line at older ages indicates that reflected light increment counts increasingly underestimate ages of trout older than about 45 years. An additional 63 otoliths (Δ) from fish over 45 years of age (using the compound microscope and transmitted light) could not be aged under reflected light, because of poor visibility of the most recently formed growth increments.

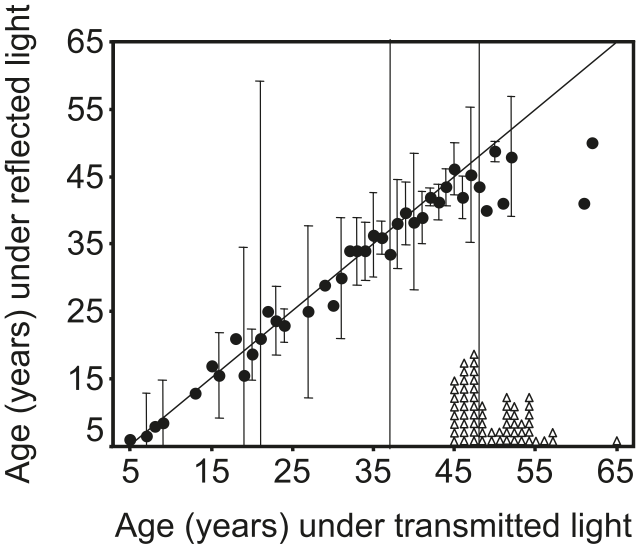
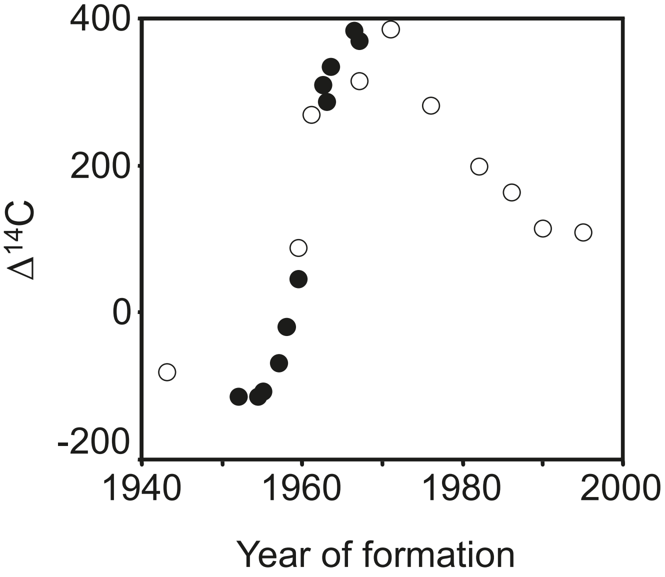


Fig. 7. Δ^{14}C in otoliths of young known-age Arctic char (*Salvelinus alpinus*) (●) and cores of old lake trout (*Salvelinus namaycush*) (○) versus year of formation inferred from counts of the growth increments. The correspondence between the two radiocarbon chronologies indicates that the ages of the older lake trout were relatively accurately interpreted based on the growth increment counts.



have been at least 50 years old (Table 2). Two other core samples, dated as having formed between 1960 and 1961 based on increment counts of 42–45 years, were dated by Δ^{14}C as having formed between 1960 and 1961, with a maximum uncertainty of about 2 years. Therefore, these results clearly validate the interpretation of the lake trout otolith increments as accurate age indicators to an age of at least 45 years and longevity of at least 50 years.

The core samples dated as forming between 1970 and 1995 closely resemble the declining bomb radiocarbon levels in the atmosphere during those years, but lagged by several years compared with the period of increase (Table 2; Fig. 7). The lagged pattern is that expected of recycled carbon in a living aquatic system and underlines the importance of using the period of increasing radiocarbon levels as a dated marker rather than the subsequent decline.

Discussion

The Arctic radiocarbon chronologies all showed the generic bomb signal characteristic of other regions around the world: relatively low Δ^{14}C prior to 1957, a sharp increase during the 1960s, and stable or gently declining values after 1970. However, there were subtle differences among the marine chronologies and more prominent differences be-

Table 2. Summary of $\delta^{13}C$ (‰) and $\Delta^{14}C$ assay results for otolith cores (3 years of growth) microsampled from Arctic lake trout (*Salvelinus namaycush*) for age validation.

Sampling site	Year collected	Age (years)	Year of core formation	No. of cores	$\delta^{13}C$	$\Delta^{14}C$
Tasiat–Couture	2002	8	1995	11	–11.9	110.4
	2002	13–14	1989–1990	11	–10.9	115.7
	2002	17–18	1985–1986	12	–10.3	163.4
	2002	21–23	1980–1982	10	–10.1	198.6
	2002	27–28	1975–1976	9	–9.8	282.4
	2002	32–34	1969–1971	13	–9.4	385.1
	2002	36	1967	4	–10.4	314.7
	2002	42	1961	3	–9.8	270.0
Zeta	2003	44–45	1960–1961	5	–4.5	88.6
	2003	62	1942–1946	1	–4.3	–80.7

Note: Year of core formation is that based on the number of growth increments.

tween the freshwater and marine chronologies. Compared with the marine chronologies, the two freshwater chronologies were more depleted (by a $\Delta^{14}C$ of about –44) during prebomb years, first showed evidence of a strong bomb signal somewhat earlier, and reached a peak $\Delta^{14}C$ at least sixfold higher. These freshwater characteristics reflect a slightly muted atmospheric radiocarbon signal, thus emphasizing the strong influence of atmospheric input of radiocarbon into terrestrial (including freshwater) systems. The contrast in prebomb and peak radiocarbon values between the freshwater and marine systems was so strong that it was easy to distinguish the habitat type of the target species based only on the radiocarbon chronology of the otolith; this was even more evident when done in concert with the more depleted $\delta^{13}C$ values that were characteristic of the freshwater fish otoliths. There are no other published freshwater radiocarbon chronologies for comparison. However, the estuarine radiocarbon signal derived from otolith cores of black drum (*Pogonias cromis*) was very similar to the freshwater Arctic chronology, both in terms of timing and peak values (Campana and Jones 1998).

The differences among the various Arctic marine chronologies were more subtle, apparently reflecting their environments. The prebomb $\Delta^{14}C$ value of about –70 in the Arctic deepwater (Greenland halibut) chronology was only marginally different than the prebomb value of –54 reported by Kalish et al. (2001) for Arcto-Norwegian Atlantic cod (*G. morhua*) off of east Greenland. Ostlund et al. (1987) reported $\Delta^{14}C$ values of about –46 for the surface waters of the East Greenland Current in 1957, but noted that there was no radiocarbon data available for the Arctic Ocean prior to 1979. The only other prebomb values available for the Arctic are those based on marine mammal hard parts: $\Delta^{14}C$ of –58 to –71 from marine mammal bones (Tauber 1979) and a $\Delta^{14}C$ of about –80 from beluga whale teeth (Stewart et al. 2006). In contrast, the prebomb $\Delta^{14}C$ values of around zero from our surface marine Arctic chronology (Greenland cod) were markedly less depleted than the other chronologies. Although we are satisfied (through repeat assays) that the relatively high prebomb values in the Greenland cod assays are not due to analytical error, we are at a loss to explain $\Delta^{14}C$ values that apparently declined substantially in the 6 years predating the appearance of the bomb signal in 1959. Natural variability in the background $\Delta^{14}C$ signal has been documented in tree ring chronologies (Levin and Hesshaimer 2000), but the magnitude of this variability is somewhat less than what was observed in the prebomb surface marine Arctic chronology. Nevertheless, the initial appearance of the bomb signal between 1957 and 1959 in the two Arctic marine chronologies was relatively similar, despite the fact that the deep-sea chronology would have been expected to be delayed relative to that in surface waters. No such delay was evident, perhaps because of rapid transport of dissolved organic carbon and particulate organic carbon from the surface to the depths at which the Greenland halibut lived (Pearcy and Stuiver 1983; Williams et al. 1987). Indeed, many of the postbomb values in the deep-sea chronology were only slightly above zero, a $\Delta^{14}C$ reference level that often distinguishes clearly between prebomb and postbomb dates in other environments. Since a postbomb $\Delta^{14}C$ value of zero is more characteristic of depths of 500–1000 m in Arctic waters (Schlosser et al. 1994), the young Greenland halibut used to develop the deep-sea chronology may have lived at greater depths than indicated by their 300 m mean depth of capture. Differences in $\Delta^{14}C$ values after 1970 among the chronologies was expected given the very different water mixing times of the various habitats (Kalish 1995) and a latitudinal gradient in surface water $\Delta^{14}C$ of about 100 between the maximum at 30°N and a minimum at about 60°N (Levin and Hesshaimer 2000).

The radiocarbon assays reported in this study, that of cod by Kalish et al. (2001), and that of Greenland halibut by Treble et al. (2008) form the only available reconstructions of the bomb radiocarbon chronology for the Arctic. Presumably, the prior absence of these chronologies in the Arctic is due to the absence of recent trees and corals, upon which most chronologies are based. Licht et al. (1998) studied bomb radiocarbon in Arctic marine sediments, but no link to water-borne values was made. Bada et al. (1987) presented what they believed to be a prebomb and postbomb radiocarbon chronology based on narwhal (*Monodon monoceros*) growth bands, but the bomb signal was weak, never exceeding a $\Delta^{14}C$ of –50. Similarly, Tauber (1979) reported some prebomb radiocarbon values based on marine mammal bones, but no chronology. A bomb chronology based on growth bands in beluga whales was much clearer, but the discovery that the teeth incorporated metabolic carbon rather than DIC suggested that mammalian chronologies in general would be expected to reflect their diet rather than the water in which they lived (Stewart et al. 2006).

Despite the unique environment of the Arctic, the 1957–1959 appearance of the bomb signal in the Arctic surface and deepwater marine radiocarbon chronologies was very similar to that of the reference chronology from the NWA, Northeast Pacific, and tropical regions around the world. The NWA chronology reported here represents an extension to that initially reported by Campana (1997), which was previously shown to have a virtually identical year of initial bomb radiocarbon increase to NWA chronologies based on bivalves (Weidman and Jones 1993) and corals (Druffel and Linick 1978). Otolith reference chronologies from the Northeast Pacific based on yelloweye rockfish (*Sebastes ruberrimus*) (Kerr et al. 2004) and Pacific halibut (*Hippoglossus stenolepis*) (Piner and Wischniowski 2004), an NWA chronology based on Atlantic cod (*G. morhua*) (Kalish et al. 2001), and a South Pacific chronology based on *Pagrus auratus* (Kalish 1993) all reported the initial appearance of bomb radiocarbon between 1957 and 1960, consistent with reports based on corals in the Central and South Pacific (Toggweiler et al. 1991; Guilderson and Schrag 1998). Clearly the appearance of the bomb signal is expected to be nearly synchronous in surface marine waters around the world, including the Arctic. An Antarctic reference chronology remains to be developed, but Peck and Brey (1996) reported the presence of a bomb signal in an Antarctic bivalve.

The close correspondence of otolith section age and the age indicated by the radiocarbon content of the adult otolith core indicates that our age estimates are realistic and validates our age interpretation criteria for lake trout. These results demonstrate that lake trout is a very long-lived species — at least 50 years — in the Arctic. Otolith transverse sections are now routinely applied to determine the age of many fishes, but such was not the case as recently as 20 years ago (Beamish and McFarlane 1987). With the realization that surface readings of otoliths often led to severe age underestimation in long-lived fishes (Beamish 1979), modern ageing methods often strive to prepare transverse sections or their functional equivalent, charred otolith halves. This development in ageing methodology explains why some early reports of lake trout growth and longevity appear to underestimate actual age (Johnson 1976). Power's (1978) insightful examination of otoliths broken through the core resulted in much greater ages, which were presumably more in keeping with the age interpretations reported here. However, the extremely narrow growth increments noted in the current study may indicate that even Power's (1978) age estimates were artifactually truncated at around age 45–50 years. We are not aware of any other published studies reporting annual otolith growth increments as narrow as 20 µm and thus below the resolution limit of a typical dissecting microscope. However, there are some reports of apparently "missing" annual increments in fish of known age (Beamish and McFarlane 2000; Dwyer et al. 2003). Conceivably, inadequate resolution could limit age determination accuracy in fish species where otolith growth is very slow.

The implications of having radiocarbon chronologies in the Arctic extend not only to ocean mixing models, but also to age determinations of Arctic organisms. Our age validation focused on lake trout in Arctic lakes, but the reference chronologies provided are applicable to the age validation of many terrestrial, freshwater, and marine organisms, as long as they contain calcified hard parts. Clearly, however, the difference in onset timing of the bomb signal between the freshwater and marine systems highlights the need to apply a reference chronology from a comparable environment to the animal being aged; for example, if the marine chronology was used to validate the age interpretation of a freshwater organism, an age underestimate on the order of 3–4 years could be expected, because of the earlier onset of the freshwater bomb signal.

With these new radiocarbon reference chronologies, age validation of a large number of Arctic organisms, both marine and freshwater, should now be possible. The age validation of Greenland halibut (Treble et al. 2008) and beluga whale (Stewart et al. 2006) has already been completed. Obvious candidates for future work include whitefish (*Coregonus* spp.) in Arctic lakes and Greenland cod, Arctic cod (*Boreogadus saida*), and bivalves in Arctic and subArctic oceans. As was the case with belugas, age validations need not be limited to fish or bivalves, suggesting that walruses, seals, and polar bears (*Ursus maritimus*) may also possess the bomb radiocarbon dated marker in their teeth. Such work will be critical to determine if slow growth and extended longevity are ubiquitous characteristics of Arctic organisms.

Acknowledgements

We sincerely thank Marie-Storr Paulsen of the Grønlands Naturinstitut in Greenland for providing the Greenland cod otoliths. We also thank the Canadian Museum of Nature for providing archived Arctic char otoliths. Linda Marks, Jill Moore, and Warren Joyce provided expert technical assistance. Thanks go to the staff of National Ocean Sciences Accelerator Mass Spectrometry Facility (NOSAMS) at Woods Hole Oceanographic Institution for their expertise in carrying out the radiocarbon assays. Funding was provided by Fisheries and Oceans Canada and US National Science Foundation grant OCE-9985884.

References

Bada, J.L., Vrolijk, C.D., Brown, S., Druffel, E.R.M., and Hedges, R.E.M. 1987. Bomb radiocarbon in metabolically inert tissues from terrestrial and marine mammals. Geophys. Res. Lett. **14**: 1065–1067.

Beamish, R.J. 1979. New information on the longevity of Pacific ocean perch (*Sebastes alutus*). J. Fish. Res. Board Can. **36**: 1395–1400.

Beamish, R.J., and McFarlane, G.A. 1987. Current trends in age determination methodology. *In* Age and growth of fish. *Edited by* R.C. Summerfelt and G.E. Hall. Iowa State University Press, Ames, Iowa. pp. 15–42.

Beamish, R.J., and McFarlane, G.A. 2000. Reevaluation of the interpretation of annuli from otoliths of a long-lived fish, *Anoplopoma fimbria*. Fish. Res. **46**: 105–111.

Campana, S.E. 1997. Use of radiocarbon from nuclear fallout as a dated marker in the otoliths of haddock, *Melanogrammus aeglefinus*. Mar. Ecol. Prog. Ser. **150**: 49–56.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. **59**: 197–242.

Campana, S.E., and Jones, C.M. 1998. Radiocarbon from nuclear testing applied to age validation of black drum, *Pogonias cromis*. Fish. Bull. **96**: 185–192.

Campana, S.E., Natanson, L.J., and Myklevoll, S. 2002. Bomb dating and age determination of large pelagic sharks. Can. J. Fish. Aquat. Sci. **59**: 450–455.

Casselman, J.M. 1987. Determination of age and growth. *In* The biology of fish growth. *Edited by* A.H. Weatherley and H.S. Gill. Academic Press, London, UK. pp. 209–242.

DeCicco, A.L., and Brown, R.J. 2006. Direct validation of annual growth increments on sectioned otoliths from adult Arctic grayling and a comparison of otolith and scale ages. N. Am. J. Fish. Manag. **26**: 580–586.

Druffel, E.M., and Linick, T.W. 1978. Radiocarbon in annual coral rings of Florida. Geophys. Res. Lett. **5**: 913–916.

Dwyer, K.S., Walsh, S.J., and Campana, S.E. 2003. Age determination, validation and growth of Grand Bank yellowtail flounder (*Limanda ferruginea*). ICES J. Mar. Sci. **60**: 1123–1138.

Follows, M.J., and Marshall, J.C. 1996. On models of bomb ^{14}C in the North Atlantic. J. Geophys. Res. **101**: 22577–22582.

Guilderson, T.P., and Schrag, D.P. 1998. Radiocarbon variability in the western equatorial Pacific inferred from a high-resolution coral record from Naura Island. J. Geophys. Res. **103**: 24641–24650.

Johnson, L. 1976. Ecology of Arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic char, *S. alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. J. Fish. Res. Board Can. **33**: 2459–2488.

Kalish, J.M. 1993. Pre- and post-bomb radiocarbon in fish otoliths. Earth Planet. Sci. Lett. **114**: 549–554.

Kalish, J.M. 1995. Radiocarbon and fish biology. *In* Recent developments in fish otolith research. *Edited by* D.H. Secor, J.M. Dean, and S.E. Campana. University of South Carolina Press, Columbia, S.C. pp. 637–653.

Kalish, J.M., Nydal, R., Nedreaas, K.H., Burr, G.S., and Eine, G.L. 2001. A time history of pre- and post-bomb radiocarbon in the Barents Sea derived from Arcto-Norwegian cod otoliths. Radiocarbon, **43**: 843–855.

Kerr, L.A., Andrews, A.H., Frantz, B.R., Coale, K.H., Brown, T.A., and Cailliet, G.M. 2004. Radiocarbon in otoliths of yelloweye rockfish (*Sebastes ruberrimus*): a reference time series for the coastal waters of southeast Alaska. Can. J. Fish. Aquat. Sci. **61**: 443–451.

Levin, I., and Hesshaimer, V. 2000. Radiocarbon — a unique tracer of global carbon cycle dynamics. Radiocarbon, **42**: 69–80.

Licht, K.J., Cunningham, W.L., Andrews, J.T., Domack, E.W., and Jennings, A.E. 1998. Establishing chronologies from acid-insoluble organic C-14 dates on Antarctic (Ross Sea) and Arctic (North Atlantic) marine sediments. Polar Res. **17**: 203–216.

Naegler, T., and Levin, I. 2006. Closing the global radiocarbon budget 1945–2005. J. Geophys. Res. **111**: D12311.

Nydal, R. 1993. Application of bomb C-14 as a tracer in the global carbon cycle. Trends Geophys. Res. **2**: 355–364.

Ostlund, H.G., Possnert, G., and Swift, J.H. 1987. Ventilation rate of the deep Arctic Ocean from carbon-14 data. J. Geophys. Res. **92**: 3769–3777.

Pearcy, W.G., and Stuiver, M. 1983. Vertical transport of carbon-14 into deep-sea food webs. Deep-Sea Res. **30**: 427–440.

Peck, L.S., and Brey, T. 1996. Bomb signals in old Antarctic brachiopods. Nature (London), **380**: 207–208.

Peng, T.H., and Broecker, W. 1980. Gas exchange rates for three closed-basin lakes. Limnol. Oceanogr. **25**: 789–796.

Peng, T.H., Key, R.M., and Ostlund, H.G. 1998. Temporal variations of bomb radiocarbon inventory in the Pacific Ocean. Mar. Chem. **60**: 3–13.

Piner, K.R., and Wischniowski, S.G. 2004. Pacific halibut chronology of bomb radiocarbon in otoliths from 1944 to 1981 and a validation of ageing methods. J. Fish Biol. **64**: 1060–1071.

Power, G. 1978. Fish population structure in Arctic lakes. J. Fish. Res. Board Can. **35**: 53–59.

Power, G. 1997. A review of fish ecology in Arctic North America. Am. Fish. Soc. Symp. **19**: 13–39.

Schlosser, P., Kromer, B., Ostlund, G., Ekwurzel, B., Bonisch, G., Loosli, H.H., and Purtschert, R. 1994. On the ^{14}C and ^{39}Ar distribution in the central Arctic Ocean: implications for deep water formation. Radiocarbon, **36**: 327–343.

Spiker, E.C. 1980. The behavior of C-14 and C-13 in estuarine water: effects of in situ CO_2 production and atmospheric exchange. Radiocarbon, **22**: 647–654.

Stewart, R.E.A., Campana, S.E., Jones, C.M., and Stewart, B.E. 2006. Bomb radiocarbon dating calibrates beluga (*Delphinapterus leucas*) age estimates. Can. J. Zool. **84**: 1840–1852.

Stuiver, M., and Polach, H.A. 1977. Reporting of C-14 data. Radiocarbon, **19**: 355–363.

Tauber, H. 1979. ^{14}C activity of Arctic marine mammals. *In* Radiocarbon dating. *Edited by* R. Berger and H.E. Suess. University of California Press, Los Angeles, Calif. pp. 447–452.

Toggweiler, J.R., Dixon, K., and Broecker, W.S. 1991. The Peru upwelling and the ventilation of the South Pacific thermocline. J. Geophys. Res. **96**: 20467–20497.

Treble, M.A., Campana, S.E., Wastle, R.J., Jones, C.M., and Boje, J. 2008. Growth analysis and age validation of a deepwater Arctic fish, the Greenland halibut (*Reinhardtius hippoglossoides*). Can. J. Fish. Aquat. Sci. **65**. In press.

Weidman, C.R., and Jones, G.A. 1993. A shell-derived time history of bomb C-14 on Georges Bank and its Labrador Sea implications. J. Geophys. Res. **98**: 14577–14588.

Williams, P.M., Druffel, E.R.M., and Smith, K.L., Jr. 1987. Dietary carbon sources for deep-sea organisms as inferred from their organic radiocarbon activities. Deep-Sea Res. **34**: 253–266.

Worbes, M., and W.J. Junk. 1989. Dating tropical trees by means of C-14 from bomb tests. Ecology, **70**: 503–507.