Growth analysis and age validation of a deepwater Arctic fish, the Greenland halibut (*Reinhardtius hippoglossoides*)

Margaret A. Treble, Steven E. Campana, Rick J. Wastle, Cynthia M. Jones, and Jesper Boje

Abstract: The accuracy of age interpretations on a deep-sea, Arctic fish species, the Greenland halibut (*Reinhardtius hippoglossoides*) was tested using several age validation methods. Consistent annual growth increments were either not formed or not visible in either whole or sectioned otoliths from three fish marked with oxytetracyline and recaptured after 2–4 years at liberty. Bomb radiocarbon assays based on a local reference chronology indicated that both whole and sectioned otoliths underestimated age by 1–15 years, with an average of 6 years. Growth rates estimated using the tag recapture model GROTAG were consistent with growth rates based on the radiocarbon assays and were less than half that of previously reported growth rates. The failure of otolith sections to provide an accurate age is unusual, but may be symptomatic of very slow-growing species with unusually shaped otoliths. Greenland halibut living in the deep-sea, Arctic environment are slower growing and longer lived than previously suspected, suggesting that the age-structured basis for current fisheries management warrants careful examination. Our results highlight the importance of using rigorous tests of ageing accuracy for exploited species and confirm that such age validation methods can be applied successfully in challenging environments such as the deep sea or the Arctic.

Résumé : Nous vérifions, à l'aide de plusieurs méthodes de validation de l'âge, la précision des interprétations de l'âge chez une espèce de poisson marin arctique, habitant les eaux profondes, le flétan du Groenland (*Reinhardtius hippoglossoides*). Chez trois poissons marqués à l'oxytétracycline et recapturés après 2–4 années de liberté, il ne s'était pas formé d'incréments uniformes de croissance annuelle ou alors ces derniers n'étaient pas visibles dans des otolithes entiers ou sectionnés. Des dosages du radiocarbone relié aux essais nucléaires basés sur une chronologie locale de référence montrent que l'utilisation des otolithes entiers ou sectionnés sous-estime l'âge de 1–15 ans, avec une moyenne de 6 ans. Les taux de croissance estimés à l'aide du modèle de récupération des étiquettes GROTAG s'accordent avec les taux de croissance basés sur les analyses de radiocarbone et ils équivalent à moins de la moitié des taux de croissance signalés antérieurement. L'incapacité des coupes d'otolithes à permettre une détermination précise de l'âge est rare, mais elle peut être caractéristique des espèces à croissance très lente qui possèdent des otolithes de forme inhabituelle. Les flétans du Groenland qui vivent dans un environnement arctique en mer profonde ont une croissance plus lente et une longévité plus grande qu'on ne le croyait antérieurement, ce qui indique que la gestion actuelle de la pêche commerciale structurée d'après l'âge devrait être réexaminée avec soin. Nos résultats illustrent bien l'importance d'utiliser des tests rigoureux de l'exactitude des déterminations de l'âge chez les espèces exploitées et ils confirment que de telles méthodes de validation peuvent être utilisées avec succès dans des environnements qui présentent des défis considérables, comme les profondeurs de la mer ou l'Arctique.

[Traduit par la Rédaction]

Introduction

Although our understanding of the population dynamics of marine fishes in the surface layers of the ocean requires improvement, it is immensely better than our understanding of deepwater and Arctic fishes. Deepwater fishes are exceedingly difficult to tag or study in situ, largely because of the difficulties involved in bringing live fishes to the surface without fatal decompression of the swimbladder (Starr et al. 2000). The study of Arctic fishes faces different challenges, often associated with extreme cold environments and ice cover through at least part of the year (Reist 1997). Thus it is not surprising that studies of the population dynamics of deepwater Arctic fishes are few and far between, particularly studies of growth and recruitment (Power 1997).

Our expectation of fish growth in either the Arctic or deep ocean is that of long life and slow growth due to cold temperatures and restricted food supply (e.g., Power 1997;

Received 2 May 2007. Accepted 7 December 2007. Published on the NRC Research Press Web site at cjfas.nrc.ca on 11 April 2008. J19979

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 doi:10.1139/F08-030

Watters et al. 2006). Age and growth studies to date only partially confirm these expectations, with reported growth rates higher than expected. These studies, which were almost invariably based on traditional interpretations of growth increments in calcified structures such as otoliths and scales, have seldom been carried out in conjunction with any tests of ageing accuracy (age validation). Yet many recent studies have demonstrated that scale and otolith surface methods of age determination often grossly underestimate actual age in long-lived and slow-growing fishes (Beamish and McFarlane 1983; Campana 2001). Thus it is possible, if not likely, that many published estimates of growth in Arctic and (or) deepwater fishes are incorrect in reporting relatively rapid growth rates.

Greenland halibut (*Reinhardtius hippoglossoides*) is a deepwater species distributed throughout Arctic and subArctic waters of both the North Atlantic and North Pacific, which support significant national and international fisheries off the coasts of Canada, Greenland, Iceland, Faroe Islands, Norway, Russia, and the state of Alaska in the United States (Alton et al. 1988; Godø and Haug 1989; Bowering and Brodie 1995). In the Northwest Atlantic, Greenland halibut are found down to 2200 m (Boje and Hareide 1993). However, Greenland halibut do not have a swim bladder; therefore, it is possible to use mark and recapture techniques to study them (Boje 2002; Simonsen and Treble 2003). Specific spawning locations have not been identified but they are believed to spawn across a wide range of depths (650 to 1000 m and possibly deeper) (Bowering and Brodie 1995). The eggs and larvae rise near the surface, drift with the prevailing currents, and settle on the shelves of Greenland and Canada at depths of 200–400 m (Stenberg 2007). Greenland halibut migrate to deeper depths as they grow larger (Bowering and Brodie 1995).

Age determination of Greenland halibut has traditionally been carried out using either whole otoliths or scales (Milinsky 1944; Lear and Pitt 1975; Krzykawski 1976), although a more recent study explored the use of stained cross-sections (Gregg et al. 2006). Despite strongly held preferences for one structure or another, tests of ageing accuracy for any of these structures or methods have been limited to Peterson length frequency analyses of the youngest individuals (Smidt 1969; Lear and Pitt 1975; Bowering and Nedreaas 2001). Age validation for adult Greenland halibut has never been reported. Recent workshops held to resolve differences in age readings reported systematic bias and less than 50% agreement among and within labs (Bech 1996; Treble and Dwyer 2006). A conclusion common to these workshops and many previous researchers is that an independent test of ageing accuracy is required before the age and growth of Greenland halibut can be reliably estimated.

Past difficulties in confirming the age of Greenland halibut may be explained by the absence of modern age validation methods, which were not then available. These more recently developed methods include the following: (*i*) detection of bomb radiocarbon (^{14}C released during atmospheric testing of nuclear bombs in the 1960s) incorporated and retained in the otoliths of fish born during that period, thus creating a dated chemical tag (Kalish 1993; Campana 1997); (*ii*) chemically tagged otoliths of fish that are injected with oxytetracycline (OTC) in a tag–recapture program (McFarlane and Beamish 1987); (*iii*) rigorous statistical analysis of the growth of tag–recaptured fish using the maximum likelihood-based GROTAG (growth collected from tagging) model (Francis (1988*a*). The first objective of our study is to test the power of a variety of age validation methods on a fish species inhabiting an environment and depth that is challenging to study. The second objective is to provide one of the first confirmed estimates of growth for a deep-sea, Arctic fish species. We conclude by commenting on the applicability of these methods to other Arctic marine fishes and the outlook for sustainable fishing on these species.

Materials and methods

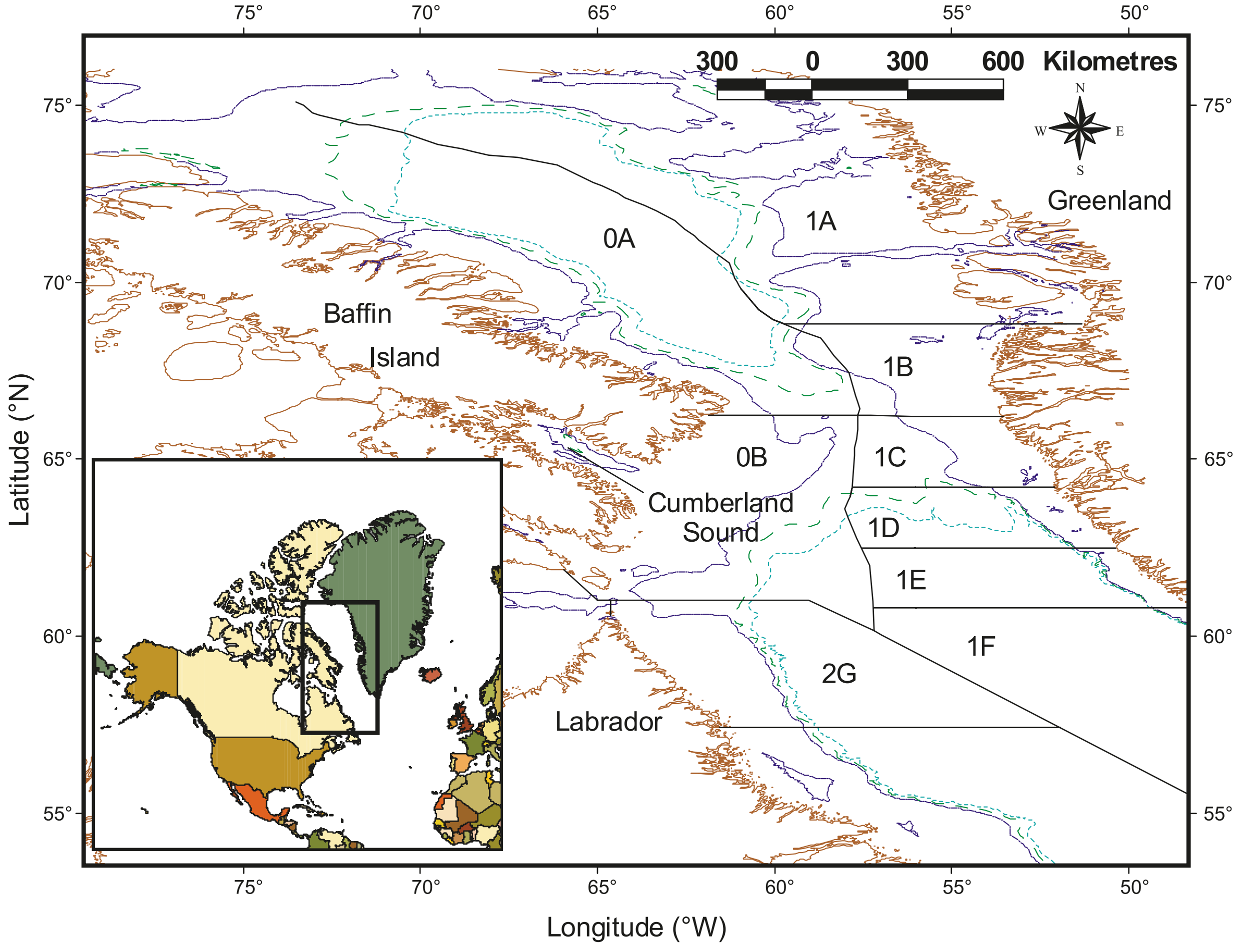
Age structure comparison

Scales and otoliths were collected from Greenland halibut during a research survey in northern Baffin Bay (NAFO Division 0A) (Fig. 1) during September 2004. The scales were taken from the dorsal side in an area just anterior of the midline of the body between the dorsal fin and the lateral line (Igashov 2004). Left otoliths were selected because they are the structure preferred by most researchers. Lear and Pitt (1975) noted that the annuli (a pair of opaque and translucent bands) are spaced more evenly and are more distinct on the left otolith compared with the right. Eighty-one samples were selected for comparative analysis. They were evenly distributed between sexes (40 males, 41 females) and across the available size range (20–82 cm for females and 24–66 cm for males), with a target of two samples per 3 cm length group.

A single age reader conducted age determinations on each of three different aging structures: left whole otoliths, scales, and left otolith cross-sections. The left whole otolith was viewed in water under reflected light using a dissecting microscope under 10× magnification. The otolith core was identified, and subsequent annuli were counted to determine the fish's age. For thicker (older) otoliths, reflected light was used initially but transmitted light was used subsequently to help determine outer annuli. Once the three whole age readings were completed, the otoliths were then embedded in Cold Cure epoxy resin, and a single, transverse cut was made through the core using an Isomet low-speed saw (Buehler Ltd.). The two halves were polished by hand using wet 30 μm lapping film followed by wet 9 μm film and finally dry 0.3 μm film. The sections were then viewed in water using a dissecting microscope (30×–40× magnification; reflected light). Annuli were usually read on the left slope of the central dome (Fig. 2).

A single scale was selected from the sample of scales taken from each fish. This scale was used for each of the three subsequent age readings. A dissecting microscope outfitted with circular polarizing filters (20×–30× magnification; transmitted light) was used. The scale was placed in water and turned until a pattern of alternating dark and light bands became visible. The scale was also turned back and forth during the age reading to aid in annulus identification. The typical compression of circuli to form annuli is not distinct in Greenland halibut scales viewed using transmitted light, but when viewed under polarized light, pairs of dark

Fig. 1. Sampling area with Northwest Atlantic Fisheries Organization (NAFO) divisions indicated.



and light bands are present. A single pair was considered an annulus (Fig. 2).

Bias due to the ageing method was evaluated using age bias plots (Campana 2001). Length-at-age linear regression analysis was used to calculate an approximate growth rate for each of the age determination methods. A single regression covering the entire length range was calculated as well as two separate regressions covering lengths less than or equal to 50 cm and lengths greater than 50 cm.

Annulus validation in OTC-marked fish

A Greenland halibut tagging project was conducted by Fisheries and Oceans Canada (DFO) in Cumberland Sound from 1997 to 2000. Fish were caught in the spring (March–April) using long-lines, set through the land-fast sea ice. Following capture and prior to release after measuring for fork length (cm) and tagging (Floy tag, model FD-94), the fish were kept in a tank of sea water maintained at a temperature between 1 and 5 °C (Simonsen and Treble 2003). The antibiotic OTC was added to the tagging protocol in 1998 to introduce a chemical mark in 1119 of the 1674 fish tagged. OTC is known to be taken up and bound to calcified structures shortly after injection and is visible under ultraviolet light (McFarlane and Beamish 1987). The number of growth increments distal to the OTC mark in recaptured fish is then compared with the number of years at liberty to determine if the growth increments are formed annually and thus if they are valid age indicators.

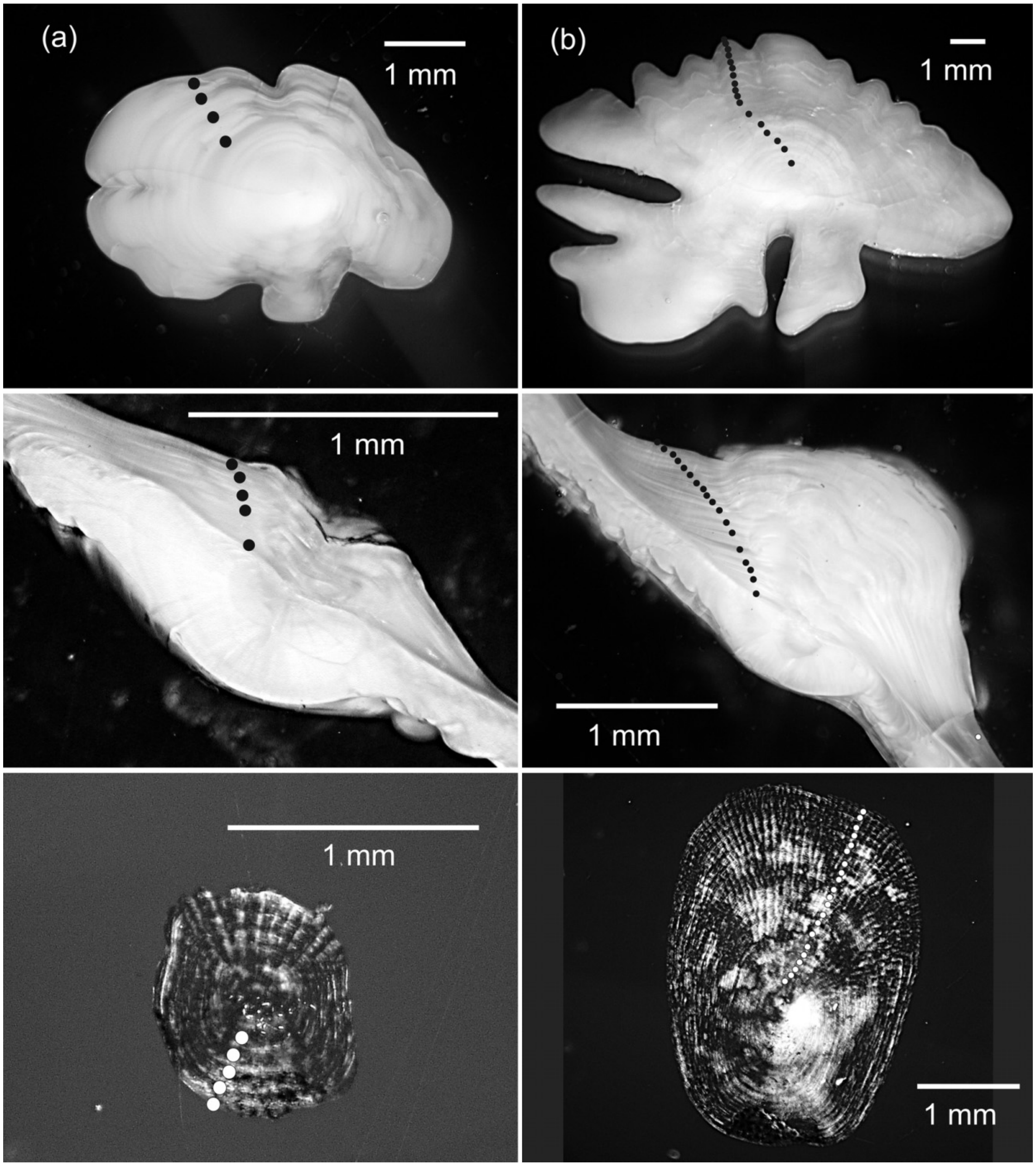
A 200 $mg \cdot mL^{-1}$ solution of Oxyvet 200 LA (commercial OTC solution) was injected into the intraperitoneal cavity or muscle tissue immediately after the fish was measured and tagged with a plastic Floy tag. A dosage rate of 50 mg $OTC \cdot kg^{-1}$ was chosen based on information provided by McFarlane and Beamish (1987) and Babaluk and Craig (1990); fish weight was approximated using a weight–length relationship for Greenland halibut previously determined from the Cumberland Sound fishery.

The whole otoliths of the fish tagged and recaptured during sampling were photographed under reflected light, transmitted light, and ultraviolet reflected light (UV). A whole age was determined using the method described above. The left otolith was then embedded in epoxy resin, and a series of thin sections (0.35 mm) were cut through the thickest portion of the otolith. These sections were placed on microscope slides and viewed under UV light using a compound microscope. Photos were taken under UV light as well as reflected and transmitted light.

Growth analysis using tag–recapture length data

The Greenland Institute of Natural Resources conducted a Greenland halibut tagging program from 1986 to 1998 (Boje 2002). A total of 7244 Greenland halibut were tagged within

Fig. 2. Age determination structures for (*a*) a 20 cm female (median whole age = 4; scale age = 5; and section age = 5) and (*b*) a 61 cm female (median whole age = 17; section age = 17; and scale age = 22).



the fjords along the west and east Greenland coast and offshore areas of Baffin Bay and Davis Strait. Of the 517 individuals that were recaptured, 137 had associated length data and date of recapture information suitable for growth analysis. Information on the sex of recaptured fish was not available, so a comparison of female and male growth rates was not possible. We also included six samples from a tagging study conducted by DFO in Cumberland Sound (Treble 2003) for a total of 143 fish.

Francis (1988*a*) developed a model using maximum likelihood estimation that analyzes changes in length over time (growth) collected from tagging data (GROTAG). An Excel-based application of Francis' GROTAG model developed by Simpfendorfer (2000) was used to analyze our data.

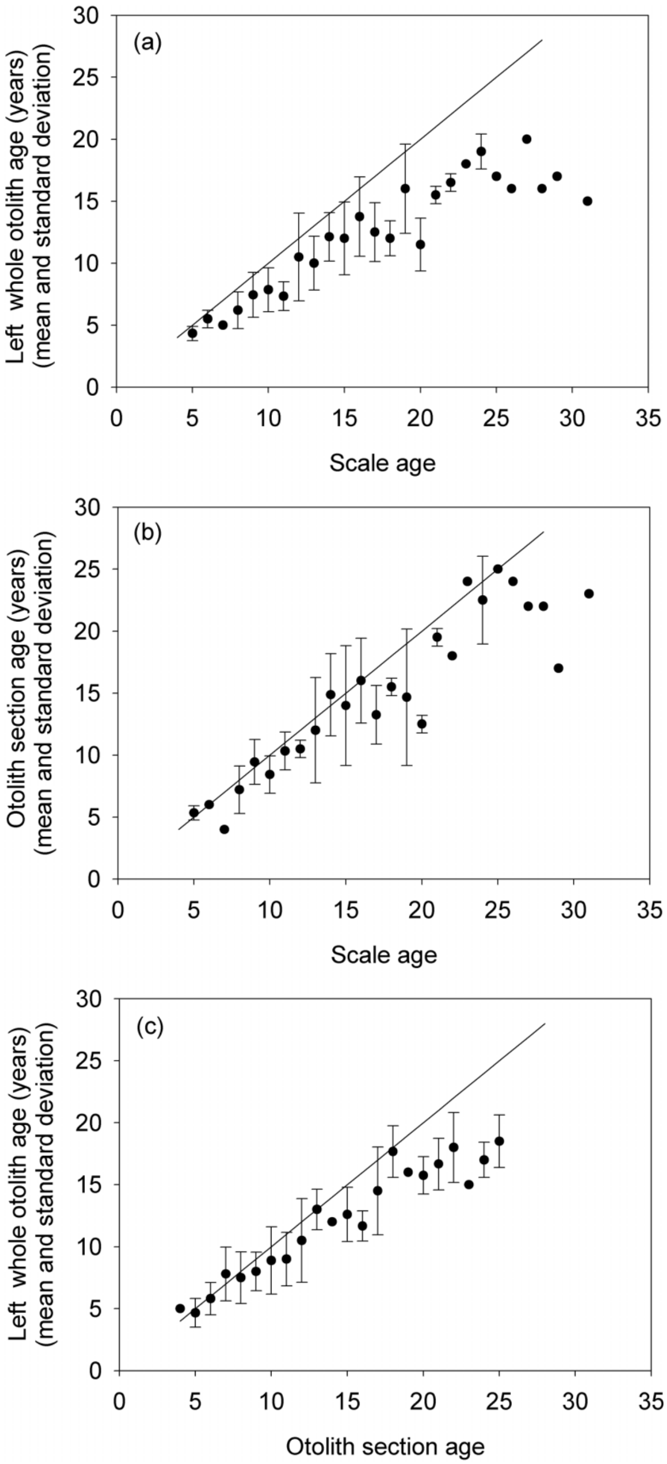
A Gulland and Holt (1959) model, with annual growth rates plotted against average length ((length at tagging + length at recapture)/2) was applied to the full data set. A subset of the data was also analyzed in which time at liberty was greater than 0.9 years, and three outliers, with average growth per year of –13, –16, and 23 cm, were removed.

Radiocarbon age validation

Reference curve

Although the timing of the appearance of bomb radiocarbon in surface marine waters around the world is well established (Campana 2001), Greenland halibut may live at depths where the appearance of the bomb signal is delayed.

Fig. 3. Age bias plots comparing three structures (left whole otoliths, left otolith sections, and scales) from Greenland halibut (*Reinhardtius hippoglossoides*) collected from NAFO Division 0A.



Therefore, a ^{14}C reference chronology unique to Greenland halibut was developed using 39 otolith pairs of young (age 0–3) Greenland halibut born between 1955 and 1997 selected from collections archived at DFO's Northwest Atlantic Fisheries Centre in St. John's, Newfoundland, Canada (Divisions 0A, 0B, 2G, and 1C) and at the Greenland Institute of Natural Resources in Nuuk, Greenland (1A inshore, 1E, 1F, and 2J). These samples were effectively known-age (±1 year), because the lengths of such young fish are relatively accurate indicators of age. The left and right otoliths were combined to form a single sample to bring total sample weight used for ^{14}C analyses to at least 3 mg. All otolith material was then decontaminated, stored in acid-washed glass vials, and assayed for ^{14}C using accelerator mass spectrometry (AMS) (described in Campana 2001). AMS assays also provided $\delta^{13}C$ (‰) values, which were used to correct for isotopic fractionation effects. Radiocarbon values were subsequently reported as $\Delta^{14}C$, 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).

To extend the reference chronology to the years before 1959, otolith cores from Greenland halibut aged 10 years or older captured in the early 1960s in Division 1F were also assayed for ^{14}C. Although these samples were not extracted from fish of known age, the fact that prebomb (before 1958) radiocarbon levels are relatively low and stable within a given region indicates that these samples should provide reliable prebomb radiocarbon values even if the age assignments of the fish were incorrect. The methods used for core extraction are described below.

^{14}C values for two samples analyzed from Division 0A, collected in 1978, fell well below the other values. We had only a single survey in this area during the period of interest. Therefore, we chose not to include them in the reference curve.

Age validation

Twenty pairs of otoliths from 5 males, 11 females, and 4 of unknown sex were selected for bomb radiocarbon age validation from archived material collected from research surveys carried out in Davis Strait (0B, 1C), Northern Labrador (2G), and West Greenland (1E) between 1967 and 1989. These were in addition to samples of mature fish that had been analyzed previously as part of our assessment of the suitability of the ^{14}C technique for Greenland halibut and the development of the reference curve (four from Cumberland Sound, sex unknown; and four females from 2G). Fish presumed to be 13–20 years old, which may have hatched in the 1950s and 1960s, were selected because these are the year classes most suited to bomb radiocarbon dating. Otolith cores with prebomb levels of radiocarbon (as indicated by the reference chronology) must have been born before 1958, because postbomb radiocarbon levels are always much higher. Therefore, comparison of the radiocarbon levels of the validation otolith cores with the reference chronology allowed a ^{14}C-based age for the fish to be determined.

Whole ages were determined for both the left and right otoliths (if both otoliths were in good condition) prior to embedding them in epoxy resin. The method used to age the whole otoliths was the same as that described above (under Age structure comparison).

Thin sections (1.0–1.5 mm thick) of each otolith were prepared with a low-speed, diamond-bladed saw by sectioning transversely through the core. After polishing lightly to improve clarity, digital images of each section were taken and enhanced using Adobe Photoshop (Adobe Systems Incorporated, San Jose, California). No other treatments were

Table 1. Length-at-age linear regression statistics for Greenland halibut (*Reinhardtius hippoglossoides*) age structure comparison.

Independent variable	Length range (cm)	Sample no. (n)*	Slope	Intercept	F	P	R^2
Cross-section age	20–82	81	2.26	15.2	230	<0.01	0.74
Whole otolith age	20–82	81	2.96	11.9	311	<0.01	0.79
Scale age	20–82	80	2.25	12.0	620	<0.01	0.94
Cross-section age	20–50	55	1.65	19.2	84	<0.01	0.60
	51–82	26	1.27	38.2	22	<0.01	0.69
Whole otolith age	20–50	55	2.14	17.3	133	<0.01	0.71
	51–82	26	1.96	31.2	16	<0.01	0.64
Scale age	20–50	54	2.25	11.1	278	<0.01	0.91
	51–82	26	1.37	32.4	38	<0.01	0.78

*Both sexes combined.

applied to the sections. Ages were determined from the section prior to isolating the core material for the ^{14}C assay. The radii of the first three presumed annuli were confirmed through measurements of the dimensions of intact sagittae collected from ages 0–3 individuals.

To isolate otolith material for bomb radiocarbon assay, otolith cores corresponding to the first 3 years of growth were extracted from each thin section. Cores were isolated with a Merchantek computer-controlled micromilling machine using 300 μm diameter steel cutting bits and burrs. Because individual core weights were insufficient for assay (3 mg minimum), cores were isolated from each otolith of the pair and pooled. All core material was then decontaminated and assayed for ^{14}C assay using AMS as described earlier.

To assign a fish age to the validation sample, the ^{14}C value for each core sample was compared with the ^{14}C values in the reference chronology to determine the most plausible range of years for core formation, defined by the uncertainty observed in samples surrounding the LOESS curve fit with a smoothing value of 0.35 to the Greenland halibut reference chronology. Where a range of potential years of core formation existed, the most recent year was used in the calculation of ^{14}C age. In cases where the ^{14}C-based age placed it in a prebomb year class, the ^{14}C-based age represents a minimum age for the fish.

Results

Age structure comparison

Annuli were clearly visible on all three structures, although the number of annuli was not necessarily the same (Fig. 2). Age bias plots demonstrated that otolith cross-section age and scale age tended to be similar across most ages, with the cross-section age underestimating scale ages for the few fish older than age 25. The whole otolith preparation underestimated both scale ages and cross-section ages for fish older than age 15 (Fig. 3).

The maximum age determined for whole otoliths, otolith cross-sections, and scales was 20, 25, and 31, respectively (Fig. 3). Given that the ageing samples included relatively large Greenland halibut (Table 1), these ages may represent something close to the longevity of the species in Division 0A (assuming that the ageing method is accurate). The slope parameter for length-at-age linear regression analysis indicated approximate growth rates over all ages of 2.3 cm·year^{-1} for otolith cross-sections and scales and 3.0 cm·year^{-1} for whole otoliths (Table 1). Growth rates for fish greater than 50 cm were less: 1.3 and 1.4 cm·year^{-1} for cross-sections and scales, respectively, and 2.0 cm·year^{-1} for whole otoliths (Table 1).

Growth in OTC-marked fish

To date, 14 of the 1674 Greenland halibut tagged (1417 also marked with OTC) and released have been recaptured. Otoliths were collected from three fish that had been marked with OTC in April 1999 and recaptured during the winter fishery in March 2001, April 2002, and March 2003 (Table 2). The recaptured fish were all greater than 50 cm at time of tagging. Two of these fish had grown very little, less than 1 cm in 2–3 years. The other had grown 6 cm in almost 4 years for an annual growth rate of approximately 1.5 cm·year^{-1}. Whole and section ages for these fish varied between 18 and 22 years (Table 2).

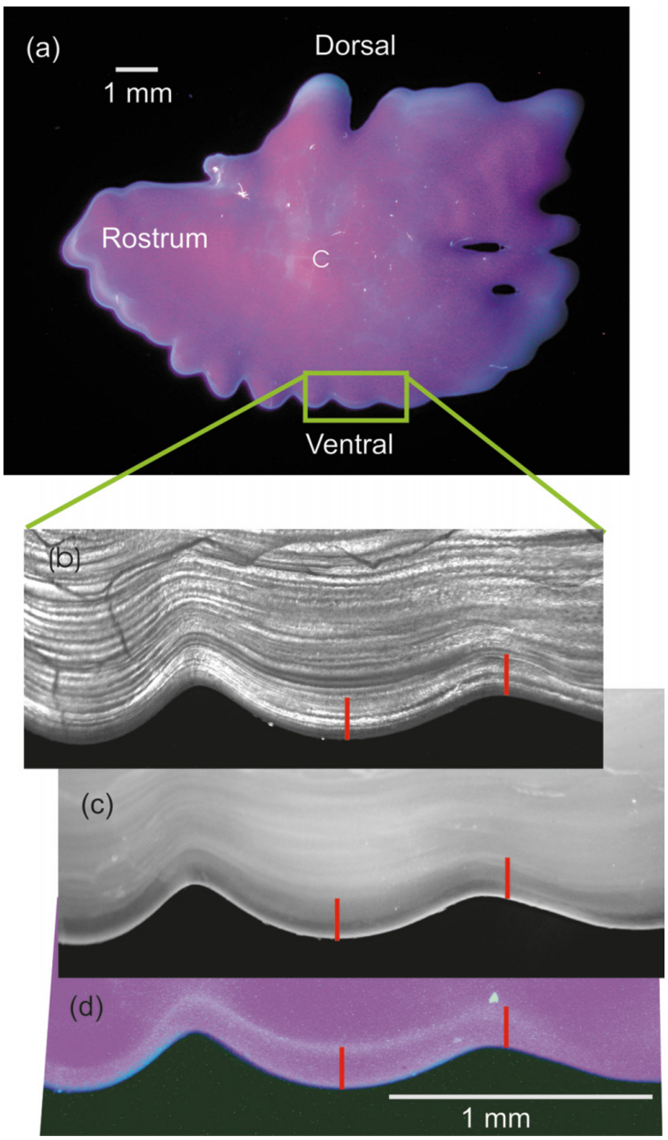
It was not possible to see any mark along the outer edge of the whole otoliths from the fish recaptured in 2001 or 2002, and the OTC was still visible as fluorescent green patches on large parts of the surface of these otoliths. However, otoliths from the fish recaptured in 2003 had been almost completely covered by new growth, and we could see the OTC-marked material as a band along the outer edge of the left (Fig. 4). While bands could be seen when the left whole otolith was viewed under reflected light, the material at the edge was translucent and the expected three annuli were not visible, even when examined under increased magnification (Fig. 4). Using transmitted light, more light and dark banding could be seen, but again three annuli were not visible within the area of new growth at the edge of the left otolith.

The OTC mark could be seen on cross-sections taken through the left otolith of all three recaptured Greenland halibut. However, only the fish recaptured in 2003 had sufficient growth to make out presumed annuli in numbers that correspond to the number of years since marking (Fig. 5). However, in some areas of the section the growth bands were not as distinct as in others, and additional bands (that might be interpreted as annuli) could be observed under different focal lengths. The determination of annuli prior to the

Table 2. Data for three fish marked with oxytetracycline during the Cumberland Sound tagging project.

Date tagged	Length at tagging (mm)	Date recaptured	Length at recapture (cm)	Round weight (g)	Sex	Whole age	Section age	Time since tagging
20 April 1999	550	15 March 2001	55	1550	M	18	20	1 year, 10+ months
15 April 1999	635	4–7 April 2002	64	2340	F	20	21	2 years, 11+ months
20 April 1999	600	4 March 2003	66	2730	F	20	22	3 years, 10+ months

Fig. 4. The distal view of the left otolith from a Greenland halibut (*Reinhardtius hippoglossoides*) recovered 3 years, 10 months after tagging is shown under ultraviolet light (*a*). The oxytetracycline (OTC) mark is visible near the rostrum in this view. Magnified views of the ventral edge are also shown using transmitted light (*b*), reflected light (*c*), and ultraviolet light (*d*). The OTC mark is clearly visible under ultraviolet light, and its distance from the edge is marked by a red vertical line. The position of the OTC mark under transmitted and reflected light is indicated using similarly sized red lines.



mark was also uncertain because of the complex structure of these growth bands. We noted uneven accrual of otolith material on the outer edges of the otolith, which could affect our ability to distinguish annuli throughout the otolith.

We found it difficult to see the OTC mark on the whole otolith, particularly in the traditional age reading zone of the left otolith (marked by the grid applied to the image in Fig. 4) without increased magnification, although the OTC mark was visible in certain fast-growing areas of the whole otolith and throughout the cross-section. As a result, we believe that it is very likely that the Greenland halibut recaptured in 2003 (66 cm female) would have been under-aged by at least 4 years using the left whole otolith age determination method.

Growth analysis using tag–recapture length data

Time at large for tag–recaptured fish varied from 0.08 to 7.17 years, with length at recapture ranging from 44 to 87 cm. The Gulland and Holt (1959) analysis of average growth rate plotted against average length for the subset for those fish at large longer than 0.9 years showed a growth rate of approximately 2.0 cm·year^{-1} (Fig. 6). The relationship between annual growth rate and mean length has a slight positive slope, so the Gulland and Holt (1959) model estimates for K and L_∞ could not be calculated using these data.

The GROTAG model is designed to partition uncertainty in the data into three components: measurement error (*m* and *s*), growth variability (*v*), and general variability or outliers (*p*). Reference lengths of 50 and 75 cm were chosen for estimation as the majority of the data fell between these lengths. The full model (model 3, Table 3) was determined to be the best fit for the data, because λ decreased by more than 3.00 with the addition of the two additional parameters (*m* and *p*) (Francis 1988*a*).

The estimated growth rate of 3.22 cm·year^{-1} for 75 cm fish was very similar to the 3.26 cm·year^{-1} estimated for 50 cm fish. Both estimates of growth rate were consistent with the empirical analysis suggested by the regression of growth rate on average length (Fig. 6), but were greater than the growth in length observed in the three fish marked with OTC (Table 2). Growth variability (*v*) was low (0.39) but not close to 0, indicating there was sufficient information for GROTAG to differentiate growth variability from measurement variability (Francis and Mulligan 1998). However, the measurement bias (m = –1.98 cm) and standard error for measurement bias (s = 3.27 cm) were large relative to the estimates of growth, indicating that there is considerable uncertainty in our growth estimates using this model.

^{14}C validation

The Δ^{14}C reference chronology for otoliths of known ages 0- to 3-year-old Greenland halibut is shown (Fig. 7*a*). The period of increasing radiocarbon values (1958–1970) in the Greenland halibut reference curve results in a relatively narrow range of Δ^{14}C values (–10 to –80) that can be used for validation purposes. Within this time period, otolith

Fig. 5. Transverse section of the otolith shown in Fig. 3: (*a*) the oxyetracycline (OTC) mark is visible under ultraviolet light; and (*b*) the position of the mark (large white circle) in relation to the annuli (three smaller circles subsequent to the mark) is shown on the reflected light image.

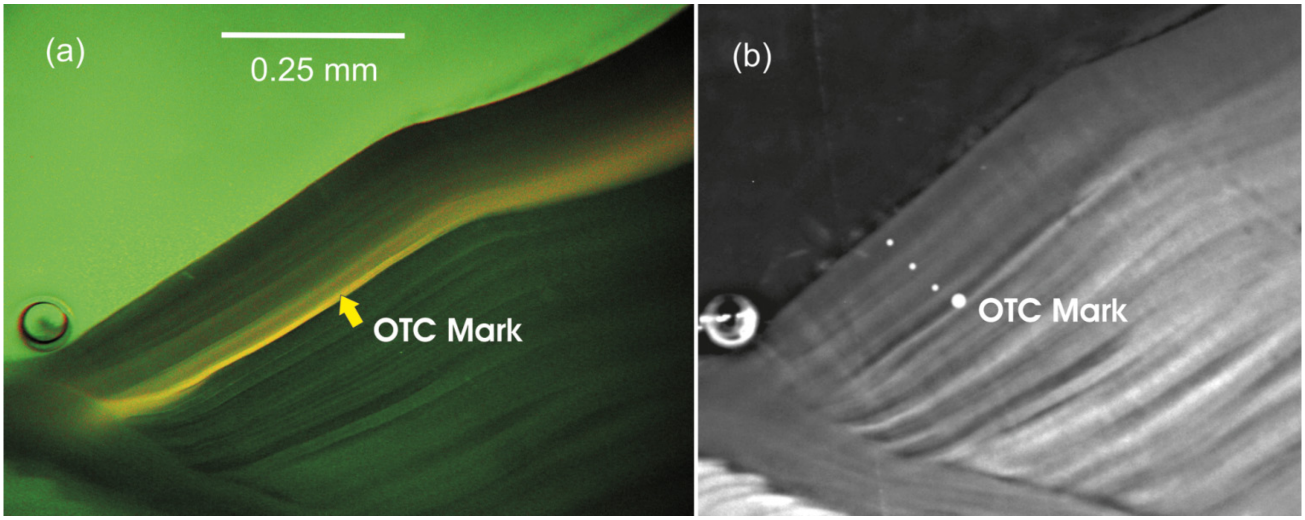
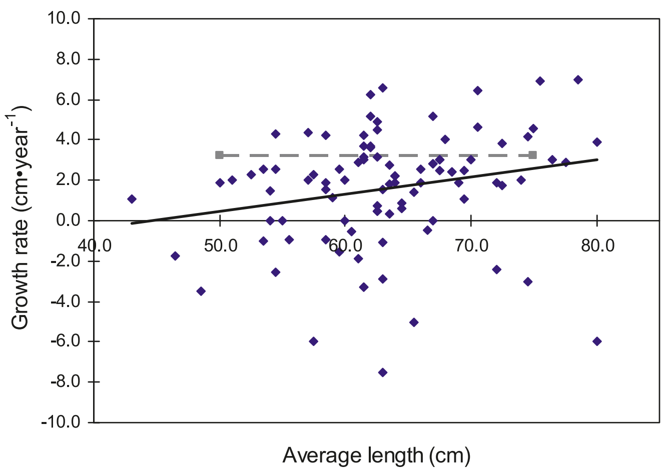


Fig. 6. Growth rate (cm·year^{-1}) and average length ((length at tagging + length at recapture)/2) for data used in the GROTAG (Francis (1988*a*) and Gulland and Holt (1959) analysis of growth for those fish at liberty longer than 0.9 years. The GROTAG model estimates are also shown (broken line).



cores from adult fish could be assigned a year of formation relatively accurately only for fish with core values between about –10 and –40, because $\Delta^{14}C$ values within this range could only be found in the 1960s. Otolith cores with values less than –40 were clearly prebomb, but their year of formation was unknown other than being before 1958. Therefore, the ^{14}C-based age for these latter fish represented a minimum age. Based on this range of suitable $\Delta^{14}C$ values, a year of core formation could be determined for six and a minimum age determined for four of the mature Greenland halibut samples tested for age validation (Table 4, Fig. 7*b*). Of the ten samples used for validation, six had been assigned a whole age (five for the left otolith and six for the right) and a section age, while four had only a section age.

The ^{14}C age exceeded the whole otolith age by a range of 3–11 years (Table 4) and the section age by a range of 1–15 years, with an average difference of 6 years for both methods (Table 4). Because ^{14}C ages represent the minimum possible ages consistent with the radiocarbon data, these results indicate that the age readings from the whole otolith and otolith sections underestimated the actual age of these fish. Age underestimation was most pronounced in the oldest fish. The maximum observed age from whole and section ages of this subset of otoliths was 22 and 20 years, respectively, while the maximum ^{14}C age was 27 years (Table 4).

A plot of length versus ^{14}C age is illustrated (Fig. 8). It shows a sharp increase in length in the first 3 years continuing to an asymptote, varying between 70 and 80 cm beyond approximately age 10–15 years. Since this figure is based on minimum possible age, it is possible that growth rate is slower than depicted here.

Discussion

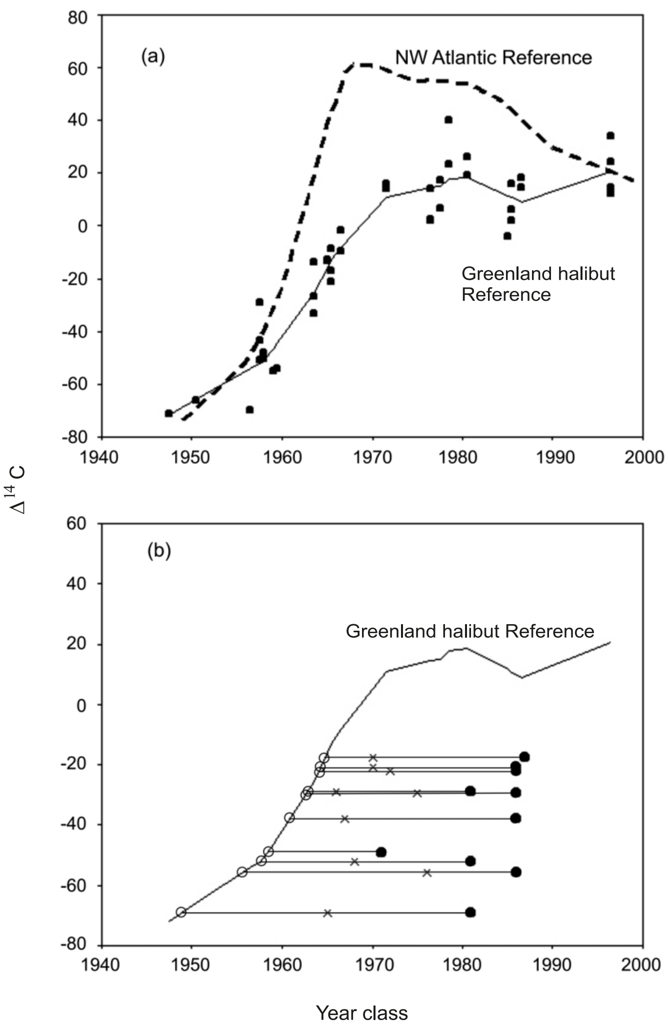
A method for routine, accurate age determinations of Greenland halibut is a challenge that has not yet been solved. Despite the prevalence and proven track record of otolith crosssections as an ageing method for most fishes (Beamish and McFarlane 1987), this method performed poorly in Greenland halibut otoliths when measured against two independent and rigorous age validation methods. Both the bomb radiocarbon assays and the OTC recaptures indicated that otolith cross-sections underestimated age in sexually mature Greenland halibut. Alternative ageing methods did not perform any better. Whole otolith ages tended to be lower than section ages and thus underestimated age even more than section ages. Similar findings have been reported for other species (Campana 1984; Dwyer et al. 2003). A somewhat surprising result was the possible value of scale ages read under polarized light, despite the fact that scale ages tend to be exceedingly poor age indicators in other slow-growing fishes (Casselman 1983). The accuracy of the scale ages was not tested in this study and therefore needs to be further evaluated. However, unless a new method of otolith examination is developed, routine age determination of Greenland halibut would only appear to be possible using al-

Table 3. GROTAG model results.

Parameter	Model 1	Model 2	Model 3
Loglikelihood: λ	–460.9	–456.26	–445.73
Mean growth rate, 50 cm fish: g (cm·year^{-1})	2.77	4.58	3.26
Mean growth rate, 75 cm fish: g (cm·year^{-1})	0.42	1.85	3.22
Growth variable: v	0.95	0.59	0.39
Standard deviation of measurement bias: s (cm)	5.42	5.04	3.27
Measurement bias: m (cm)	0*	–2.65	–1.98
Outlier contamination: p	0*	0*	0.14

*Indicates a fixed parameter.

Fig. 7. (*a*) Plot of $\Delta^{14}C$ values for Greenland halibut (*Reinhardtius hippoglossoides*) with line fitted using a LOESS regression. The reference chronology characteristic of the Northwest Atlantic (Campana et al. 2002) is also shown. (*b*) Radiocarbon reference chronology for Greenland halibut in relation to 10 validation samples showing the year of collection (solid circle), the section age year class (×), and the otolith core year class (open circle).



ternate ageing structures, such as scales, vertebrae, or bones, if at all.

The failure of otolith-based ageing methods is unusual, but has been previously reported. Stevens et al. (2004) noted regions in the older growth zones of blackgill rockfish (*Sebastes melanostomus*) otolith sections that were "beyond optical resolution". Annuli were reported missing in several sablefish (*Anoplopoma fimbria*) recaptured a known number of years after tagging and injection with OTC (Beamish and McFarlane 2000). Dwyer et al. (2003) also reported unexplained otolith section age underestimation in wild, known-age, old yellowtail flounder (*Limanda ferrugenea*). No satisfactory explanation is available for the poor performance of the otolith section method in these unusual cases, although it can likely be attributed to the uneven deposition of otolith material in particularly slow-growing otoliths. Uneven deposition was clearly evident from the distribution of OTC in the Greenland halibut recaptured after tagging, and in some regions of the otolith, OTC appeared to be absent. An additional factor may be the unusual shape and growth of the Greenland halibut otolith, with its multiple crystal fields reminiscent of the problematic orange roughy (*Hoplostethus atlanticus*) otolith (Tracey and Horn 1999).

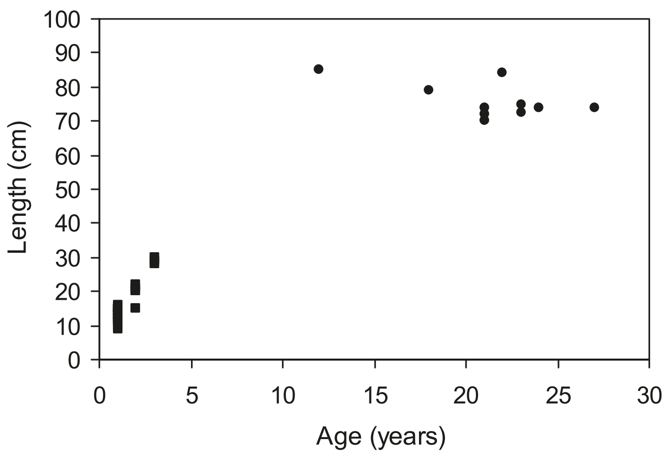
Despite the difficulties in establishing a routine method of age determination for Greenland halibut, the results of this study provided several reliable, independent estimates of growth rate and longevity and one of the first confirmed estimates for a deep-sea Arctic fish species. Growth rates for adult Greenland halibut derived from the ^{14}C ages of the radiocarbon-dated fish were less than 2 cm·year^{-1}, while growth based on section ages from our method comparison was 1–2 cm·year^{-1}. These growth rates would be overestimates if age were underestimated. Although growth rates calculated from tagging data are not directly comparable with those calculated from age–length data (Francis 1988*b*), the Gulland and Holt and GROTAG analyses indicated that growth of moderate-sized adults was fairly uniform at 3 cm·year^{-1}, albeit with considerable variability around the estimates. Sex-specific growth rates, whereby females grow faster than males to a larger maximum size, would be expected but could not be evaluated in this study. These growth rates are considerably lower than the constant growth rate of approximately 5 cm·year^{-1} based on otolith surface ages that have previously been reported for male and female Greenland halibut from the Northwest Atlantic (Bowering 1978; Boje and Jørgensen 1991; Bowering and Nedreaas 2001), but were more comparable with growth rates reported by Nizovtsev (1991) for the Barents Sea and Iceland, where growth rates based on scale ages differed between the sexes and gradually declined with age to approximately 3 cm·year^{-1} for adult fish. It is difficult to determine if the growth differences between these studies and our own reflect biases due to use of whole otoliths and scales (resulting in overestimation of growth) or regional variations in growth rate. Most likely, both factors

Table 4. Results of ^{14}C assays for mature Greenland halibut (*Reinhardtius hippoglossoides*) otoliths selected for validation.

NAFO Division	Year sampled	Length	Sex	Whole age, left	Whole age, right	Section age, dome	Year of core formation	Age, ^{14}C-based	$\delta^{13}C$	$\Delta^{14}C$
0B	1986	70		16	16	17	1966	21	–3.5	–20.7
		74		17	18	15	1966	21	–5.6	–21.9
		72		20	20	20	1964	23	–3.4	–37.6
		72		14	16	12	1966	21	–3.0	–29.2
2G*	1987	84	F	—	—	19	1966	22	–2.4	–17.4
	1981	74	F	—	—	18	1958	24	–1.2	–69.1
		75	F	—	—	15	1959	23	–2.1	–51.8
		79	F	—	—	17	1964	18	–1.0	–28.8
1C	1986	74	F	16	22	12	1960	27	–2.5	–55.8
	1971	85		—	19	—	1960	12	–2.3	–49.0

*Otolith core samples of mature fish originally analyzed in the development of the reference curve.

Fig. 8. Length and ^{14}C age for samples used in the reference chronology (squares) and age validation (circles). The reference sample ages (all juvenile fish) are based on the whole otolith method, while the ages for the validation samples are based on the ^{14}C assay.



were present, since the transition from ages based on whole otoliths to otolith sections in yellowtail flounder resulted in a substantial decrease in estimated growth rate (Dwyer et al. 2003), while reduced growth would be expected in colder, more northerly waters.

The period of initial bomb radiocarbon increase in the ^{14}C reference chronology is similar for Greenland halibut from Davis Strait and the Northwest Atlantic haddock–redfish previously published in Campana et al. (2002), albeit with a possible slight delay in the Greenland halibut chronology. However, for Greenland halibut, the peak levels after 1970 are somewhat depleted consistent with the latitudinal decrease associated with high latitudes (Levin and Hesshaimer 2000). Kalish et al. (1997) found that the onset of the increase in the ^{14}C chronology between three species of fish from the Southern Hemisphere was similar, but there were slight differences in the timing and magnitude of peak values. It was suggested that these differences might be explained by a delay in the flux of radiocarbon to deeper water and the influence of currents on water mixing. Campana and Jones (1998) found that the black drum (*Pogonias cromis*), an estuarine species, had a ^{14}C chronology that resembled the atmospheric signal and was significantly higher than that for haddock, a relatively shallow marine species, while we found the haddock–redfish ^{14}C chronology to be higher than that for Greenland halibut that occupy relatively deep marine waters.

Longevity estimates of at least 27 years were indicated by the radiocarbon results for this deepwater Arctic species. These estimates were considerably greater than has been previously reported for Greenland halibut, but not nearly as old as has been reported for deepwater fishes such as *Sebastes* (75+ years) (Beamish 1979) or orange roughy (100+ years) (Tracey and Horn 1999) or for Antarctic fishes such as the Patagonian toothfish (*Dissostichus eleginoides*) (50 years) (Horn 2002). In contrast, few ages beyond 18 years have previously been reported for Greenland halibut, even for much larger specimens (Bowering 1983; Boje and Jørgensen 1991; Bowering and Nedreaas 2001). Presumably, age underestimation due to use of whole otoliths is the cause of the discrepancy between previous and current longevity estimates (Gregg et al. 2006).

Our results highlight the importance of using rigorous tests of ageing accuracy rather than assuming that traditional ageing methods are accurate and confirm that such age validation methods can be applied successfully in challenging environments such as the deep sea or the Arctic. All three of the age validation methods applied in this study confirmed that whole otolith and section ages underestimated actual age in adult Greenland halibut that were greater than 50 cm in length. The estimates of minimum fish age from the radiocarbon assays were unambiguous in that no known mechanism can account for the presence of prebomb radiocarbon values in otolith material formed after about 1958 in the surface oceans of the world (Kalish 1993; Campana 2001). The radiocarbon reference chronology based on young Greenland halibut otoliths confirmed that the young juveniles were indeed exposed to the surface ocean bomb signal. These radiocarbon-based age validation results were completely consistent with the examination of the OTC-marked otoliths, which confirmed that annual growth increments did not always form (or at least were not always visible) in the otolith. Both validation methods were also consistent with the growth rate estimates from the GROTAG tag recapture model. Both the radiocarbon assays and the OTC-marked recaptures represent two of the most rigorous, objective methods of age validation that are available, while the GROTAG model is considered the most statistically rigorous of the age corroboration methods (Campana 2001). Despite the fact that this powerful suite of age validation methods performed well in this study, the paradoxical result is that the overall goal of the study was not met. The reason for this is that age validation methods were never intended as routine ageing tools; they are too expensive and logistically complicated for this purpose. Rather, they were intended as objective, reliable tools to test the accuracy of more routine ageing methods. Although the validation methods successfully met their objective with Greenland halibut, there is still no reliable routine method for ageing the species.

Notwithstanding the failure to develop a routine and accurate ageing method for Greenland halibut, the suite of age validation methods applied in this study appear to be well suited for the age validation of other Arctic species. The reference chronology developed for Greenland halibut is equally applicable to any other Arctic fish species whose juvenile stage is spent in waters between about 200 and 400 m. Similar reference chronologies have also been developed for surface marine Arctic species and freshwater Arctic species (S.E. Campana, J.M. Casselman, and C.M. Jones, unpublished data). As with all bomb radiocarbon studies, the constraint is that at least some of the individuals whose age is to be validated must have been born before the year of peak radiocarbon exposure: around 1968. Similar constraints do not apply to recaptures of OTC-tagged individuals, where the number of growth increments formed distal to the OTC mark can be compared with the number expected based on time at liberty. However, with the probability of recapture being proportional to sampling effort, OTC recapture studies are often limited to commercially exploited species. Therefore, there will inevitably be a suite of short-lived, noncommercial species for which neither of these validation methods will apply and for which alternate methods of age validation must be sought.

Given that previous studies of Greenland halibut have been based on ageing methods that are now known to underestimate true age and growth rate in the Arctic population (Bowering and Nedreaas 2001; Høines and Korsbrekke 2003; Morgan et al. 2003), there may be serious implications for stock assessments of the species. Ageing error propagates through estimates of age at maturity, lifespan, natural mortality rate, population size, and other vital rates and thus has a pervasive effect on the understanding of the population dynamics (Lai and Gunderson 1987; Tyler et al. 1989; Bradford 1991). Assumptions of a fast growth rate and lower life expectancy will introduce errors into both stock assessment models and sustainable catch quotas, often producing overly optimistic estimates of stock production (Bradford 1991; Reeves 2003). Although Greenland halibut are now assessed and managed in several areas of the world, it does not necessarily follow that the assessments and advice are flawed; the ageing errors documented in this study of an Arctic population will not necessarily apply to a more southerly or faster-growing population. However, our results do suggest that the age-structured basis for advice in these other populations warrants careful examination.

Acknowledgements

John Babaluk at Fisheries and Oceans Canada, Winnipeg, encouraged us to initiate an age validation project for Greenland halibut and provided advice for the use of the chemical marker OTC. We relied on the expert fishing skills of Davidee Evic and field technicians Jean-Guy Duchesne, Linda Porter, Pierre Landry, and Aaron Fisk. Ray Bowering and Randy Burry at Fisheries and Oceans Canada, St. John's, and Ole Jørgensen and Claus Simonsen at the Greenland Institute of Natural Resources provided the historic samples necessary to carry out ^{14}C validation. We thank Linda Marks, Jill Moore, and Warren Joyce for their expert technical assistance. Radiocarbon assays were carried out by the National Ocean Sciences Accelerator Mass Spectrometer Facility at Woods Hole Oceanographic Institution under National Science Foundation (NSF) Cooperative Agreement OCE-9807266 and by Beta Analytic Inc. Funding was provided by the Nunavut Wildlife Management Board and Fisheries and Oceans Canada – Nunavut Implementation Fund to MAT, with additional funding provided by NSF OPP-9985884 to SEC and CMJ.

References

Alton, M.S., Bakkala, R.G., Walters, G.E., and Munro, P.T. 1988. Greenland halibut *Reinhardtius hippoglossoides* of the eastern Bering Sea and Aleutian Islands region. NOAA Tech. Rep. NMFS 71.

Babaluk, J.A., and Craig, J.F. 1990. Tetracycline marking studies with pike, *Esox lucius* L. Aquac. Fish. Manag. **21**: 307–315.

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. 1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. **112**: 735–743. doi:10.1577/1548-8659(1983)112<735:TFRFAV>2.0.CO;2.

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. doi:10.1016/S0165-7836(00)00137-5.

Bech, G. 1996. An exchange program of Greenland halibut otoliths. Vol. 4. Available from the Greenland Institute of Natural Resources. P.O. Box 570, 3900 Nuuk, Greenland.

Boje, J. 2002. Intermingling and seasonal migrations of Greenland halibut (*Reinhardtius hippoglossoides*) populations determined from tagging studies. Fish. Bull. (Wash., D.C.), **100**: 414–422.

Boje, J., and Hareide, N.R. 1993. Trial deepwater longline fishery in the Davis Strait, May–June 1992. Northwest Atlantic Fisheries Organization, Dartmouth, N.S. SCR Doc. 93/53, Ser. No. N2236.

Boje, J., and Jørgensen, O.A. 1991. Growth of Greenland halibut in the Northwest Atlantic. ICES Demersal Fish Committee, Copenhagen, Denmark. C.M. 1991/G:40.

Bowering, W.R. 1978. Age and growth of the Greenland halibut *Reinhardtius hippoglossoides* (Walbaum), in ICNAF Subareas 2–4. Int. Comm. Northwest Atl. Fish. Res. Bull. **13**: 5–10.

Bowering, W.R. 1983. Age, growth, and sexual maturity of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Canadian Northwest Atlantic. Fish. Bull. (Wash., D.C.), **81**: 599–611.

Bowering, W.R., and Brodie, W.B. 1995. Greenland halibut (*Reinhardtius hippoglossoides*). A review of the dynamics of its distribution and fisheries off eastern Canada and Greenland. *In* Deep-water fisheries of the North Atlantic oceanic slope. *Edited by* A.G. Hopper. Kluwer Academic Publishers, Netherlands. pp. 113–160.

Bowering, W.R., and Nedreaas, K.H. 2001. Age validation and growth of Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)): a comparison of populations in the Northwest and Northeast Atlantic. Sarsia, **86**: 53–68.

Bradford, M.J. 1991. Effects of ageing errors on recruitment time series estimated from sequential population analysis. Can. J. Fish. Aquat. Sci. **48**: 555–558.

Campana, S.E. 1984. Comparison of age determination methods for the starry flounder. Trans. Am. Fish. Soc. **113**: 365–369. doi:10.1577/1548-8659(1984)113<365:COADMF>2.0.CO;2.

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. doi:10.3354/meps150049.

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. doi:10.1111/j.1095-8649.2001.tb00127.x.

Campana, S.E., and Jones, C.M. 1998. Radiocarbon from nuclear testing applied to age validation of black drum, *Pogonias cromis*. Fish. Bull. (Wash., D.C.), **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. doi:10.1139/f02-027.

Casselman, J.M. 1983. Age and growth assessment of fish from their calcified structures — techniques and tools. NOAA Tech. Rep. NMFS No. 8. pp. 1–17.

Dwyer, K.S., Walsh, S.J., and Campana, S.E. 2003. Age determination, validation and growth of Grand Bank yellowtail flounder (*Limanda ferrugenea*). ICES J. Mar. Sci. **60**: 1123–1138. doi:10.1016/S1054-3139(03)00125-5.

Francis, R.I.C.C. 1988*a*. Maximum likelihood estimation of growth and growth variability from tagging data. N.Z. J. Mar. Freshw. Res. **22**: 42–51.

Francis, R.I.C.C. 1988*b*. Recalculated growth rates for sand flounder, *Rhombosolea plebeia*, from tagging experiments in Canterbury, New Zealand, 1964–66. N.Z. J. Mar. Freshw. Res. **22**: 53–56.

Francis, M.P., and Mulligan, K.P. 1998. Age and growth of New Zealand school shark, *Galeorhinus galeus.* N.Z. J. Mar. Freshw. Res. **32**: 427–440.

Godø, O.R., and Haug, T. 1989. A review of the natural history, fisheries, and management of Greenland halibut (*Reinhardtius hippoglossoides*) in the Eastern Norwegian and Barents Seas. ICES J. Mar. Sci. **46**: 62–75. doi:10.1093/icesjms/46.1.62.

Gregg, J.L., Anderl, D.M., and Kimura, D.K. 2006. Improving the precision of otolith-based age estimates for Greenland halibut (*Reinhardtius hippoglossoides*) with preparation methods adapted for fragile sagittae. Fish. Bull. (Wash., D.C.), **104**: 643–648.

Gulland, J.A., and Holt, S.J. 1959. Estimation of growth parameters for data at unequal time intervals. ICES J. Mar. Sci. **25**: 47–49. doi:10.1093/icesjms/25.1.47.

Horn, P.L. 2002. Age and growth of Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*D. mawsoni*) in waters from the New Zealand subantarctic to the Ross Sea, Antarctica. Fish. Res. **56**: 275–287. doi:10.1016/S0165-7836(01)00325-3.

Høines, Å., and Korsbrekke, K. 2003. Population structure of Greenland halibut (*Reinhardtius hippoglossoides*) in the Northeast Arctic, 1992–2000. J. Northwest Atl. Fish. Sci. **31**: 85–98.

Igashov, T.M. 2004. Results of comparative age reading of Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum) by scales and otoliths. Northwest Atlantic Fisheries Organization, Dartmouth, N.S. SCR Doc. 04/7.

Kalish, J.M. 1993. Pre- and post-bomb radiocarbon in fish otoliths. Earth Planet. Sci. Lett. **114**: 549–554. doi:10.1016/0012-821X(93)90082-K.

Kalish, J.M., Johnston, M.M., Smith, D.C., Morison, A.K., and Robertson, S.G. 1997. Use of the bomb radiocarbon chronometer for age validation in the blue grenadier *Macruronus novaezelandiae.* Mar. Biol. (Berl.), **128**: 557–563. doi:10.1007/s002270050121.

Krzykawski, S. 1976. Comparative analysis of some anatomical elements with regard to their relevance to the age and growth rate determination in Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum). Acta Ichthyologica et Piscatoria Vol. VI. Fasc. 2. Pap. No. 6.

Lai, H.L., and Gunderson, D.R. 1987. Effects of ageing errors on estimates of growth, mortality and yield per recruit for walleye pollock (*Theragra chalcogramma*). Fish. Res. **5**: 287–302. doi:10.1016/0165-7836(87)90048-8.

Lear, W.H., and Pitt, T.K. 1975. Otolith age validation of Greenland halibut (*Reinhardtius hippoglossoides*). J. Fish. Res. Board Can. **32**: 289–292.

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

McFarlane, G.A., and Beamish, R.J. 1987. Selection of dosages of oxytetracycline for age validation studies. Can. J. Fish. Aquat. Sci. **44**: 905–909.

Milinsky, G.I. 1944. Materials on biology and fishery for Greenland halibut of the Barents Sea. Trudy PINRO. **8**: 375–387. [In Russian.]

Morgan, M.J., Bowering, W.R., Gundersen, A.C., Høines, Å., Morin, B., Smirnov, O., and Hjöleifsson, E. 2003. A comparison of the maturation of Greenland halibut (*Reinhardtius hippoglossoides*) from populations throughout the North Atlantic. J. Northwest Atl. Fish. Sci. **31**: 99–112.

Nizovtsev, G.P. 1991. Growth patterns of Greenland halibut (*Reinhardtius hippoglossoides*) in the Northeast Atlantic. Northwest Atlantic Fisheries Organization Sci. Coun. Studies, **15**: 35–41.

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

Reeves, S.A. 2003. A simulation study of the implications of age-reading errors for stock assessment and management advice. ICES J. Mar. Sci. **60**: 314–328. doi:10.1016/S1054-3139(03)00011-0.

Reist, J.D. 1997. The Canadian perspective on issues in Arctic fisheries management and research. Am. Fish. Soc. Symp. **19**: 13–39.

Simonsen, C.S., and Treble, M.A. 2003. Tagging mortality of Greenland halibut *Reinhardtius hippoglossoides* (Walbaum). J. Northwest Atl. Fish. Sci. **31**: 373–385.

Simpfendorfer, C.A. 2000. Growth rates of juvenile dusky sharks, *Carcharhinus obscurus* (Lesueur, 1818), from southwestern Australia estimated from tag–recapture data. Fish. Bull. (Wash., D.C.), **98**: 811–822.

Smidt, E.L.B. 1969. The Greenland halibut, *Reinhardtius hippoglossoides* (Walb.), biology and exploitation in Greenland waters. Medd. Dan. Fisk.- Havunders. **6**: 79–148.

Starr, R.M., Heine, J.N., and Johnson, K.A. 2000. Techniques for tagging and tracking deepwater rockfishes. N. Am. J. Fish. Manag. **20**: 597–609. doi:10.1577/1548-8675(2000)020<0597:TFTATD>2.3.CO;2.

Stenberg, C. 2007. Recruitment processes in West Greenland waters. With special focus on Greenland halibut (*Reinhardtius hippoglossoides*, W.). Ph.D. thesis, University of Bergen, Norway.

Stevens, M.M., Andrews, A.H., Cailliet, G.M., and Coale, K.H. 2004. Radiometric validation of age, growth, and longevity for the blackgill rockfish (*Sebastes melanostomus*). Fish. Bull. (Wash., D. C.), **102**: 711–722.

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

Tracey, D.M., and Horn, P.L. 1999. Background and review of ageing orange roughy (*Hoplostethus atlanticus*, Trachichthyidae) from New Zealand and elsewhere. N.Z. J. Mar. Freshw. Res. **33**: 67–86.

Treble, M.A. 2003. Results of a Greenland halibut (*Reinhardtius hippoglossoides*) tagging project in Cumberland Sound, NAFO Division 0B, 1997–2000. Northwest Atlantic Fisheries Organization, Dartmouth, N.S. SCR Doc. 03/41.

Treble, M.A., and Dwyer, K.S. 2006. Report of the Greenland halibut (*Reinhardtius hippoglossoides*) age determination workshop. Northwest Atlantic Fisheries Organization, Dartmouth, N.S. SCR 06/49.

Tyler, A.V., Beamish, R.J., and McFarlane, G.A. 1989. Implications of age determination errors to yield estimates. Can. Spec. Publ. Fish. Aquat. Sci. **108**: 27–35.

Watters, D.L., Kline, D.E., Coale, K.H., and Cailliet, G.M. 2006. Radiometric age confirmation and growth of a deep-water marine fish species: the bank rockfish, *Sebastes rufus*. Fish. Res. **81**: 251–257. doi:10.1016/j.fishres.2006.06.019.