



Age and growth of Greenland Halibut (*Reinhardtius hippoglossoides*) in the Northwest Atlantic: A changing perception based on bomb radiocarbon analyses



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ARTICLE INFO

Article history:

Received 4 September 2015

Received in revised form 15 January 2016

Accepted 20 January 2016

Available online 15 February 2016

Keywords:

Greenland Halibut
Northwest Atlantic
Bomb radiocarbon dating
Age validation
Stock assessment

ABSTRACT

Greenland Halibut (*Reinhardtius hippoglossoides*) is a large circumpolar, right-eyed flounder that supports several international fisheries. Age estimates for this stock have customarily been obtained by counting annuli on the surface of whole otoliths but a matched pair comparison indicated that ages estimated from whole and thin-sectioned otoliths were the same up until age 9 (~60 cm), after which whole otoliths underestimated the true age of the fish by up to 60% and 18 years. Bomb radiocarbon analyses on otolith cores from thin sections were similar to expectations based on the Greenland Halibut reference chronology, indicating that on average, thin sections gave an accurate age for fish in the 57–108 cm TL range. Growth curves estimated using thin-sectioned otoliths indicated that Greenland Halibut in this region are slower growing and longer lived than was previously thought. A comparison of growth parameters with other populations of Greenland Halibut showed that although the Pacific and Arctic are faster-growing, the stock off the East Coast of Canada is longer lived. This study represents the first age validation study for this stock in the Northwest Atlantic. Since the fishable portion of the population is largely <60 cm, it is possible that these results may not change the current perception of stock status. However, the increased longevity and reduced growth rates will undoubtedly affect other biological parameters and further work should be done to incorporate the new ageing knowledge into the Management Strategy Evaluation for this stock.

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1. Introduction

Greenland Halibut (*Hippoglossoides reinhardtius*) are right-eyed flounders from the family Pleuronectidae. They are relatively large, deepwater flatfish that inhabit the continental shelf and slope down to depths of 2200 m (Boje and Hareide, 1992), and are among the top predators in the Northwest Atlantic. They are an arcto-boreal species and are distributed in both Atlantic and Pacific oceans, where they support large international commercial fisheries off the coasts of Canada, Greenland, Iceland, Faroe Islands, Norway, Russia and the Barents Sea/Aleutian Islands (managed by the United States) (Barbeaux et al., 2012; Godø and Haug, 1989; Healey et al., 2010). The Northwest Atlantic Fisheries Organization (NAFO) manages the stock off the East Coast of Canada in the Northwest Atlantic. Greenland Halibut are known to travel large

distances (Bowering, 1984) and can be considered semi-pelagic in their vertical migrations (Jorgensen, 1997). Though there has been a substantial amount of research on this species, unresolved questions regarding age and growth remain.

Several studies and dedicated age determination workshops have concluded that estimation of age for this species is difficult. The otolith pairs are irregular and asymmetrical, with pronounced finger-like projections that increase in size as the fish ages (Gregg et al., 2006; Treble and Dwyer, 2008). In addition, the oldest individuals are characterized by an uneven deposition of otolith material (Treble et al., 2008), which yields imprecise estimates of age. There have been concerns of low precision in age estimates between readers and potential underageing of the oldest fish in the population for this species in the North Atlantic since 1996 (ICES, 1997, 2011; Treble and Dwyer, 2008). Some laboratories in the various regions have stopped ageing this species altogether (E. Hjørleifsson; Y. Lambert, pers. comm.).

Several studies have been carried out on the age and growth of Greenland Halibut in other regions. Differences in stock dynamics

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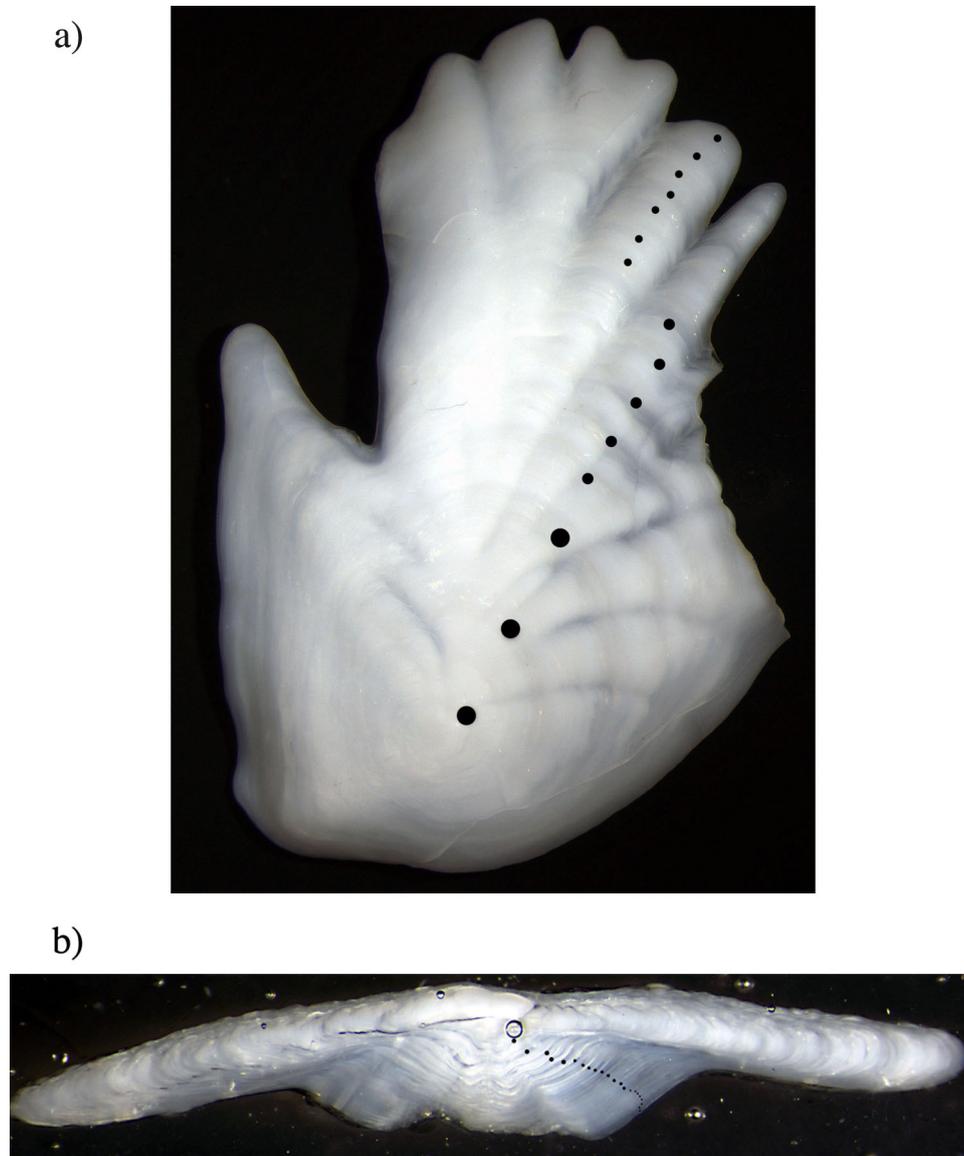


Fig. 1. Comparison of right whole otolith (8X) (left) from an 83 cm female Greenland Halibut and the corresponding left thin-sectioned otolith (16X) (right), assigned a whole otolith age of 15 years and a section age of 22 years.

exist between populations of Greenland Halibut, but few studies exist for the stock in the Northwest Atlantic (NAFO management unit Subarea 2 + Divisions 3KLMNO). Greenland Halibut reach lengths of ~120 cm, making them the second largest flatfish in the North Atlantic, although there have not been many of these large fish captured in recent years. Using surface read whole otoliths (the traditional method of ageing estimation for Greenland Halibut) there is a suggestion of fast, linear growth, with a maximum age of about 18 years old (Bowering, 1983). Except for the validation of the first few years of growth using length frequency modes (Lear and Pitt, 1975; Bowering and Nedreaas, 2001), there has been no age validation of methods across the entire age range of the species. Studies carried out by Treble et al. (2008), using thin sections, indicated that the Arctic stock (including some samples from the Northwest Atlantic) is slow growing, reaching an age of 27 years. The authors used bomb radiocarbon to validate the oldest fish in the population, and concluded that thin sections provided an accurate age (on average), but still underestimated the ages of the oldest fish in the population. Albert et al. (2009) used tag recaptures to validate age in the Northeast Atlantic for the oldest fish in the

population up to 27 years, using a unique method of freezing whole otoliths and then image analysis to enhance the growth rings.

Bomb radiocarbon assays are one of the best techniques currently available to determine the accuracy of an ageing method (Kalish, 1993, 1995; Campana, 2001). This method uses the nearly synchronous increase in the $\Delta^{14}\text{C}$ levels deposited in marine calcareous structures during atmospheric testing of nuclear weapons between the 1950s and 1970s as a dated marker. A reference chronology is created by determining the amount of $\Delta^{14}\text{C}$ in the otoliths of young fish of known age (e.g. ages 1, 2 or 3) born before, during, and after the bomb period. The amount of $\Delta^{14}\text{C}$ in otolith cores of older fish can then be compared to the reference chronology to determine whether an assigned age based on annulus counts is accurate (thus validating an age). If the difference between the true age and the assigned age is significant and cannot be resolved, this suggests the ageing method has failed and should be re-evaluated.

This paper compares the traditional method of surface ageing of whole otoliths to the method of using otolith thin sections. We then employ the bomb radiocarbon method to determine whether

whole or thin-sectioned otoliths provide improved accuracy for estimating ages for Greenland Halibut in the Northwest Atlantic. In addition to providing a maximum longevity value for this stock using new ages, we provide updated growth curves for male and female Greenland Halibut. Growth dynamics from several populations of Greenland Halibut are then compared to that of the NAFO SA 2+3KLMNO stock. The impact of any changes on the current stock assessment will also be discussed.

2. Materials and methods

2.1. Comparison of ageing methods

The traditional method of determining age in Greenland Halibut at the Northwest Atlantic Fisheries Centre (NAFC) is based on surface reading of whole otoliths. When necessary, the surface of the otolith was ground using a rotary grinding wheel, usually for older fish in order to make the annuli more visible. A comparison of this method with the broadly accepted thin-sectioning method (Chilton and Beamish, 1982) was investigated by comparing whole and thin-sectioned otolith age estimates from the same fish. Left and right sagittal otoliths were removed from 266 fish, mainly from 1976 and 1977 annual autumn surveys in NAFO SA 2+3K, as well as some smaller fish (<21 cm) collected in 2007. Whole otoliths were aged by experienced readers at the time of capture, and a portion of these re-read by current age readers to ensure there was no drift. The left otolith is preferred over the right for age determination because it is more symmetrical, with a centric core, resulting in clearer, more evenly spaced annuli.

The left otoliths were sectioned by embedding them in blocks of clear polyester casting resin in a custom-made silicon mould and left to partially cure. Otoliths were arranged in five rows on the resin. The blocks were labelled and coated with another layer of resin and then oven cured for 24 h at 55 °C. Otoliths were sectioned using a Gemmasta lapidary saw fitted with diamond blades. From each row, five sections were taken (~350 µm in thickness), to ensure the core of each otolith was captured. Sections were then cleaned in alcohol and stored in vials. A small amount of resin was poured on each slide and the sections laid on the resin, with the identification label placed at the top of the slide. Once the resin had semi-cured, further resin was added to the section preparations and coverslips applied. The slides were oven-cured again at 30 °C for 3 h.

Whole otoliths were immersed in 95% alcohol in a black watch-glass and examined at 10× magnification using a stereomicroscope with reflected light. When examining annuli close to the edge for larger fish, higher magnification was used. The preferred age reading zone is within the widest half of the longitudinal axis (although this does vary depending on clarity along that axis) on the distal or convex side. Translucent bands (dark under reflected light) were counted as annuli (Fig. 1).

Thin-sectioned otoliths were examined on slides using magnification of 16–40× with reflected light. Ages were determined by reading along an axis from the core to the proximal edge (thickened “dome”) or toward either the dorsal or ventral edge (Figs. 1 and 2).

Bias of annulus counts between the ageing methods was evaluated using age-bias plots (Campana, 2001).

2.2. Bomb radiocarbon age validation

Twenty four pairs of otoliths, from 22 females and 2 males (Div. 2H $n=4$; Div. 2J $n=11$; Div. 3K $n=7$ and Div. 3L $n=2$), were selected from the archived materials collected by the research surveys carried out in NAFO SA 2+3K between 1971 and 1990. These ranged in length from 57–108 cm. The largest and seemingly oldest fish,

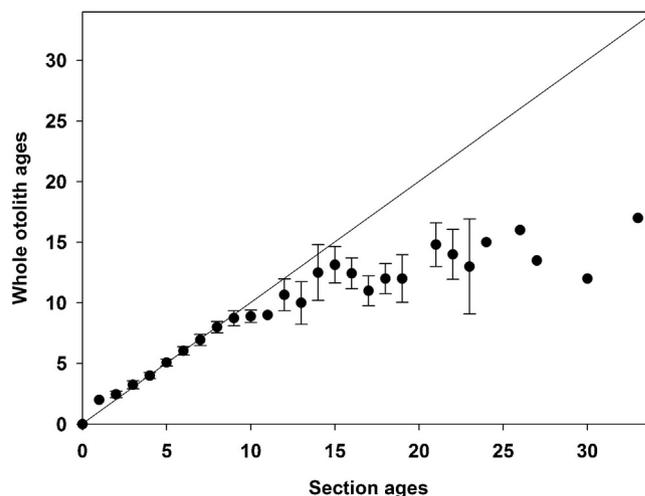


Fig. 2. Age bias plot comparing ages from whole otoliths and thin sections from Greenland Halibut collected from NAFO SA 2+3K. Each error bar represents the 95% confidence interval about the mean age assigned for one otolith for all fish assigned a given age for the second otolith. The 1:1 equivalence (solid line) is also indicated.

which may have hatched in the 1950s and 1960s, were selected as these are the year classes most suited to bomb radiocarbon dating. The left otoliths, where possible, were embedded in epoxy resin and sectioned (1.0–1.5 mm thick) transversely through the core using twin blades separated by a spacer on a low-speed, diamond-bladed saw. After polishing lightly to improve clarity, there was a digital image of each section taken and was enhanced using Adobe Photoshop CS2 (Adobe Systems Incorporated, San Jose, California). No other treatments were applied to the sections.

2.3. Reference chronology

There is a well-established and synchronous chronology of bomb radiocarbon in marine waters worldwide (Campana, 1997, 2001). However, the onset of the radiocarbon increase in the chronology can differ slightly in deep waters, due to delayed penetration of the bomb signal (Piner et al., 2005; Campana et al., 2008; Kestelle and Helser, 2010). Treble et al. (2008) developed a chronology for Greenland Halibut from an area within Davis Strait to the north of the NAFO Subarea 2+3 stock area (but more than half of the otoliths were from fish from SA 2). They found that the Greenland Halibut chronology was delayed and peak levels depleted compared to the Northwest Atlantic otolith chronology (Campana et al., 2008). The $\Delta^{14}\text{C}$ in otolith cores of 6 young Greenland Halibut from the 1960s, 1970s and 1980s collected from NAFO Subarea 2 and 3K fit the pattern of increase of $\Delta^{14}\text{C}$ in the Greenland Halibut reference chronology. Samples of the young fish were less than 21 cm, and effectively of known age (± 1 year) based on the Petersen method of age validation (Bowering and Nedreaas, 2001).

The cores corresponding to the first 3 years of growth of the left and right otoliths were extracted and combined to form a single sample to bring total sample mass used for $\Delta^{14}\text{C}$ analyses to at least 3 mg, as individual core masses were insufficient for assays. The radii for the first three presumed annuli were confirmed through measurements of the dimensions of the otoliths collected from ages 0–3 individuals. Cores were isolated with a Merchantek computer-controlled micromilling machine using 300 µm diameter steel cutting bits and burrs. All otolith material was then decontaminated, stored in acid-washed glass vials and assayed for $\Delta^{14}\text{C}$ using accelerator mass spectrometry (AMS) (Campana, 2001). $\delta^{13}\text{C}$ (‰) values, also provided from AMS assays, were used to correct for isotopic fractionation effects. Radiocarbon values were consequently reported as $\Delta^{14}\text{C}$, which is the per mil (‰) deviation

of the radiocarbon concentration sample of 19th-century wood, adjusted for sample decay prior to 1950 according to procedures given in [Stuiver and Polach \(1977\)](#).

The reference chronology provides a known and dated $\Delta^{14}\text{C}$ series against which the Greenland Halibut core assays can be compared. Samples of otolith cores with prebomb levels of radiocarbon (as indicated by the reference chronology) indicate that the fish was born pre-1958. Postbomb radiocarbon levels are always much higher.

Therefore, comparison of the radiocarbon levels from the validation otolith cores with the reference chronology allowed a $\Delta^{14}\text{C}$ -based age for the fish to be determined.

The $\Delta^{14}\text{C}$ value for a sample analyzed from Div. 2J, collected in 1990, fell well below the other values (-107.7) and was outside the area where it would be possible to predict the year of birth based on ^{14}C assay (aged as 22). Therefore it was removed from the analysis.

2.4. Growth curves

A von Bertalanffy growth curve was fit to the length and age data from the method comparison and bomb radiocarbon studies above. The equation for von Bertalanffy growth is:

$$L_t = L_\infty(1 - e^{-K(t - t_0)})$$

where L_t is the expected length at age t ; L_∞ is the asymptotic maximum length; K is the growth rate coefficient (units are year^{-1}) and t_0 is meant to represent the time or age when the average length was zero. Curves were fitted to the data for each sex using an R script ([Ogle, 2013](#)).

3. Results

3.1. Age structure comparison

The comparison of whole and thin-sectioned otoliths indicated that whole otoliths underestimated section ages by more than 50% in some older fish. An age bias plot indicated that young fish were aged similarly using both methods (± 1 year) but the whole otolith method increasingly underestimated ages compared to the thin sections after age 9 (approximately 60 cm) by up to 18 years ([Fig. 2](#)).

The maximum age determined for whole otoliths was 18, and for thin sections was 33 years. In this study the maximum size was 70 cm total length (TL) for males, and 110 cm TL for females. Since these samples are amongst the largest sizes observed for Greenland Halibut, they may represent near the maximum longevity of the species in this region.

Means and 95% confidence intervals of fish length at age using thin sections to derive age are shown in [Table 1](#). The oldest specimen in the sample was a 17 year old male, measuring 70 cm TL, and a 33 year old female, measuring 109 cm TL.

3.2. Radiocarbon age validation

A comparison of the ^{14}C reference chronology of young Greenland Halibut from NAFO Div. 2+3K in the 1960s, 1970s and 1980s with the commonly used Northwest Atlantic reference chronology ([Campana et al., 2008](#)) and with the Greenland Halibut reference chronology determined by [Treble et al. \(2008\)](#) indicates that the radiocarbon from the cores of the 6 young fish fit this reference chronology and should be used to validate the ages of older Div. 2J3K fish ([Table 2](#); [Fig. 3](#)).

The period of increasing radiocarbon values (1958–1970) in the Greenland Halibut curve results in a relatively narrow range of $\Delta^{14}\text{C}$ values (-10 to -80) that can be used for precise core valida-

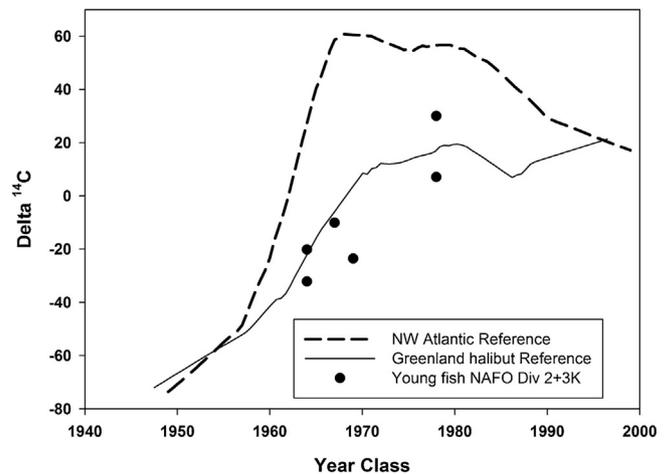


Fig. 3. $\Delta^{14}\text{C}$ reference chronology characteristic for the Northwest Atlantic haddock-redfish ([Campana, 1997](#)) and Greenland Halibut ([Treble et al., 2008](#)) along with the 6 young fish assayed to determine the reference chronology which best fit the pattern of increase of $\Delta^{14}\text{C}$ in the deep water for NAFO Div. 2 + 3 K.

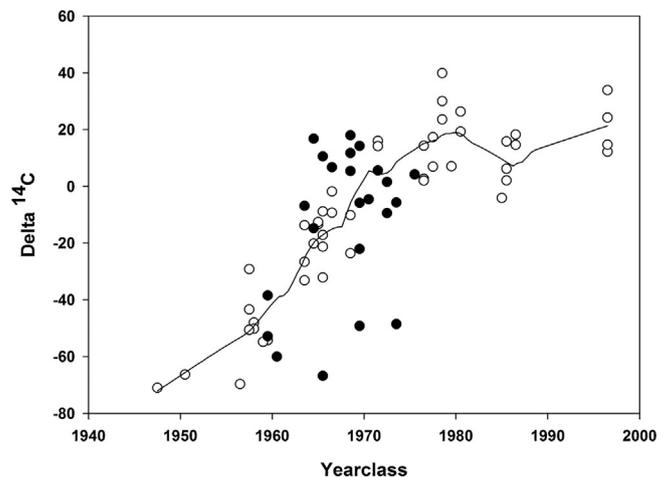


Fig. 4. Greenland Halibut age estimates from thin-sectioned otoliths (solid circles) estimated from 23 otolith cores from older Greenland Halibut (57–108 cm) and $\Delta^{14}\text{C}$ reference chronology for Greenland Halibut (open circles, including young fish added in this study) fitted with a Lowess smoother (solid line; from [Treble et al. \(2008\)](#)).

tion. When the curve has flattened out (both pre- and post-bomb areas), it is harder to get accurate ages during those periods.

The ages from sectioned otoliths indicated that the birthdates for these fish were close to those indicated by the reference chronology ([Table 3](#); [Fig. 4](#)), indicating that ages were, on average, accurate. The age of three fish (aged 18–27 years) exceeded the ^{14}C age by >5 years. The maximum observed age from whole and section ages from this subset of otoliths was 16 and 27 years respectively ([Table 3](#); [Fig. 4](#)).

3.3. Growth curve estimates

The observed length at age was similar up to age 8 (53–54 cm TL) for both males and females, after which growth slowed disproportionately for females ([Fig. 5](#)). The predicted growth from the von Bertalanffy model supports this observation, with similar growth rates until about age 8–9 for both sexes. Females, however, reached a larger asymptotic length (106 cm) and were much older (33 years) than males (90 cm; 17 years) ([Fig. 5](#)). The von Bertalanffy growth curves fit both male and female thin-sectioned age and length data very well ([Fig. 5](#)).

Table 1
Means and confidence intervals of length at age for male and female Greenland Halibut from thin-sectioned otoliths.

| Age | Male | | | Female | | |
|-----|------------------|-----|----|------------------|------|----|
| | Mean length (cm) | CI | n | Mean length (cm) | CI | n |
| 0 | 9.0 | – | 1 | 9.2 | 0.7 | 5 |
| 1 | – | – | 0 | 13.5 | 0.6 | 4 |
| 2 | 16.4 | 1.9 | 10 | 17.1 | 1.7 | 10 |
| 3 | 22.9 | 2.5 | 14 | 22.5 | 2.7 | 11 |
| 4 | 28.6 | 2.5 | 9 | 27.4 | 1.6 | 18 |
| 5 | 35.4 | 2.3 | 17 | 34.7 | 4 | 11 |
| 6 | 40 | 3.3 | 13 | 42.2 | 3.4 | 14 |
| 7 | 45.2 | 4.3 | 10 | 48.4 | 1.7 | 8 |
| 8 | 52.6 | 5.7 | 8 | 54 | 6.1 | 6 |
| 9 | 58.1 | 4.5 | 8 | 64.5 | 4.1 | 6 |
| 10 | 59.3 | 6.5 | 4 | 60.8 | 5.4 | 5 |
| 11 | 60 | – | 1 | 62 | – | 1 |
| 12 | – | – | – | 71 | 8.5 | 6 |
| 13 | 50 | – | 1 | 74.2 | 10.4 | 6 |
| 14 | 55 | – | 1 | 86.2 | 6.7 | 6 |
| 15 | – | – | – | 86.4 | 10.4 | 7 |
| 16 | – | – | – | 81.6 | 6.8 | 7 |
| 17 | 68 | 3.9 | 2 | 77 | 5.5 | 6 |
| 18 | – | – | – | 78 | 6.9 | 6 |
| 19 | – | – | – | 78 | 10.8 | 3 |
| 20 | – | – | – | – | – | – |
| 21 | – | – | – | 92 | 10.1 | 5 |
| 22 | – | – | – | 89 | 10.3 | 7 |
| 23 | – | – | – | 85 | – | 2 |
| 24 | – | – | – | 85 | – | 1 |
| 25 | – | – | – | – | – | – |
| 26 | – | – | – | 104 | 2.0 | 2 |
| 27 | – | – | – | 84.5 | 32.3 | 2 |
| 28 | – | – | – | – | – | – |
| 29 | – | – | – | – | – | – |
| 30 | – | – | – | 88 | – | 1 |
| 31 | – | – | – | – | – | – |
| 32 | – | – | – | – | – | – |
| 33 | – | – | – | 109 | – | 1 |

Table 2
Results of $\Delta^{14}\text{C}$ assays for young Greenland Halibut selected for validation (of reference chronology).

| NAFO | Year sampled | Length (cm) | Sex | Whole age | Section age | $\Delta^{14}\text{C}$ |
|---------|--------------|-------------|-----|-----------|-------------|-----------------------|
| Div. 2G | 1966 | 14 | F | 1 | 2 | –32.2 |
| Div. 2G | 1966 | 17 | M | 2 | 3 | –20.2 |
| Div. 3K | 1970 | 21 | F | 3 | 3 | –10.1 |
| Div. 3K | 1970 | 16 | F | 2 | 3 | –23.6 |
| Div. 2J | 1980 | 16 | F | 2 | 2 | 7.1 |
| Div. 2J | 1980 | 21 | F | 3 | 3 | 30.0 |

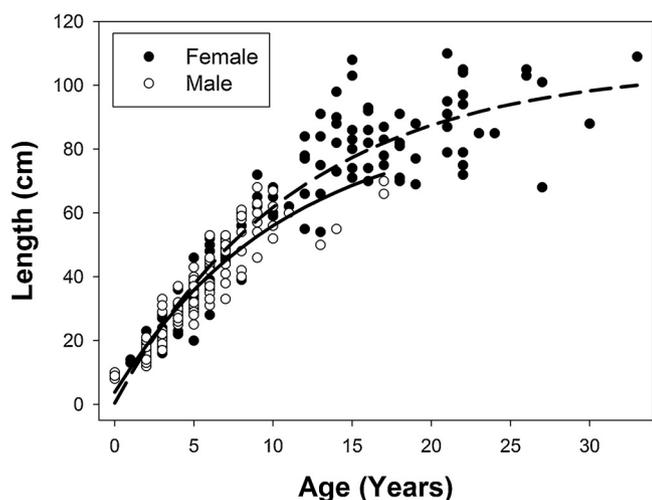


Fig. 5. Length at age for male (open circles; $L_{\infty} = 90$; $K = 0.09$; $t_0 = -0.05$) and female (solid circles; $L_{\infty} = 109$; $K = 0.09$; $t_0 = -0.05$) Greenland Halibut. The lines are the fitted von Bertalanffy growth curves (dashed line: female; solid line: male) for the data.

A comparison of growth rates from this study with those of previous studies indicates a major difference in growth rates estimated from whole otoliths and those estimated from thin sections, as expected (Fig. 6). The growth estimates from Bowering and Nedreaas (2001), using whole otoliths, show little if any slowing of growth as the fish aged, reaching a L_{∞} of 260 cm (male) and 269 cm (female). All of the studies that used thin sections for age determination showed fast growth for ages up to age 10, with slowing thereafter.

4. Discussion

This is the first comprehensive age validation study that has been carried out across all ages for Greenland Halibut off Newfoundland and Labrador in the Northwest Atlantic. The results of the bomb radiocarbon assays show that Greenland Halibut can be aged accurately, on average, up to at least 27 years using thin-sectioned otoliths. As reported throughout the literature, bomb radiocarbon assays derived from nuclear testing in the 1950s and 1960s provide one of the best validation techniques for old fish (Kalish, 1993; Campana, 1999; Campana et al., 2008). The assays of

Table 3Results of $\Delta^{14}\text{C}$ assays for larger Greenland halibut otoliths selected for validation from fish 57–108 cm. Shaded not used in analysis.

| NAFO | Year sampled | Length (cm) | Sex | Whole age | Section age | Year of formation (Section) | $\Delta^{14}\text{C}$ |
|---------|--------------|-------------|-----|-----------|-------------|-----------------------------|-----------------------|
| Div. 2J | 1990 | 79 | F | 13 | 22 | 1969.5 | -107.7 |
| Div. 2J | 1976 | 84 | F | 12 | 12 | 1965.5 | -66.8 |
| Div. 3L | 1971 | 57 | F | 9 | 12 | 1960.5 | -60.0 |
| Div. 3L | 1971 | 62 | F | 9 | 13 | 1959.5 | -52.9 |
| Div. 2J | 1983 | 108 | F | 16 | 15 | 1969.5 | -49.2 |
| Div. 3K | 1990 | 70 | F | 10 | 18 | 1973.5 | -48.5 |
| Div. 2J | 1976 | 71 | F | 11 | 18 | 1959.5 | -38.5 |
| Div. 2H | 1984 | 82 | F | 13 | 16 | 1969.5 | -22.1 |
| Div. 2J | 1990 | 68 | F | 11 | 27 | 1964.5 | -14.8 |
| Div. 3K | 1980 | 72 | F | 8 | 9 | 1972.5 | -9.4 |
| Div. 2H | 1984 | 75 | F | 12 | 22 | 1963.5 | -6.9 |
| Div. 2H | 1979 | 64 | F | 10 | 11 | 1969.5 | -5.8 |
| Div. 2J | 1990 | 70 | F | 11 | 18 | 1973.5 | -5.6 |
| Div. 2J | 1990 | 79 | F | 13 | 21 | 1970.5 | -4.5 |
| Div. 2J | 1990 | 69 | F | 11 | 19 | 1972.5 | 1.6 |
| Div. 3K | 1990 | 70 | F | 11 | 16 | 1975.5 | 4.2 |
| Div. 3K | 1979 | 69 | F | 9 | 12 | 1968.5 | 5.4 |
| Div. 3K | 1990 | 70 | F | 11 | 20 | 1971.5 | 5.6 |
| Div. 3K | 1977 | 62 | F | 10 | 12 | 1966.5 | 6.7 |
| Div. 2J | 1976 | 57 | M | 9 | 12 | 1965.5 | 10.5 |
| Div. 2J | 1976 | 57 | M | 8 | 9 | 1968.5 | 11.8 |
| Div. 2H | 1979 | 64 | F | 9 | 11 | 1969.5 | 14.2 |
| Div. 2J | 1976 | 59 | F | 8 | 13 | 1964.5 | 16.8 |
| Div. 3K | 1977 | 61 | F | 10 | 10 | 1968.5 | 18.0 |

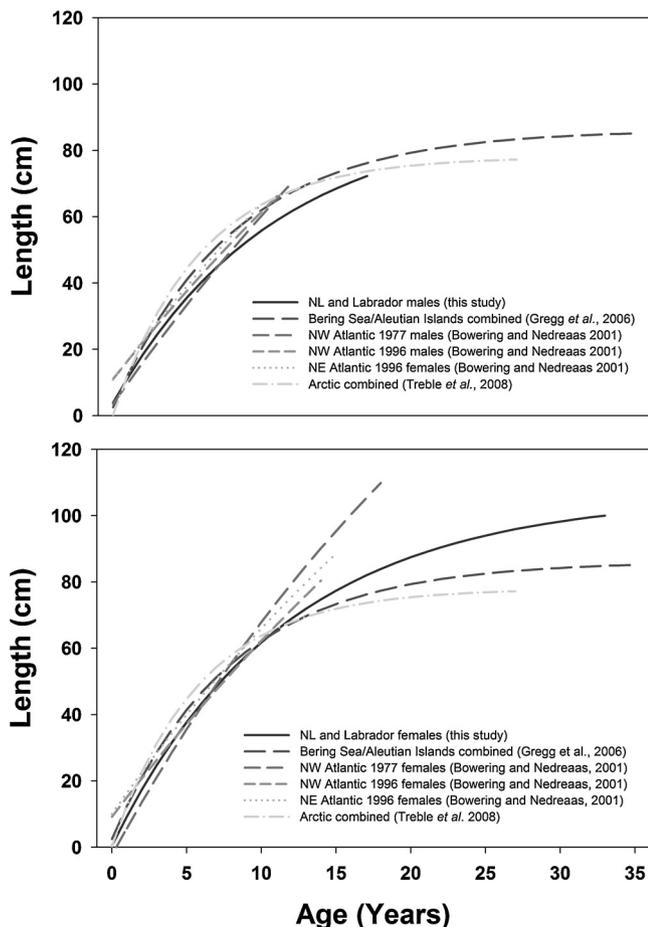


Fig. 6. Comparison of fitted von Bertalanffy growth curves for Greenland Halibut from this study and published growth information. Top panel shows male growth curves (plus combined sexes growth curves) and bottom panel shows female growth curves (plus combined sexes growth curves).

Greenland Halibut otolith cores showed levels of $\Delta^{14}\text{C}$ that fit well within the reference chronology curve, indicating that for these old fish, on average, thin sections can provide an accurate age. This method has been used to validate age in other flatfish species such as Atlantic Halibut (*Hippoglossus hippoglossus*, Armsworthy and Campana, 2010), Petrale Sole (*Eopsetta jordani*, Haltuch et al., 2012), Pacific Halibut (*Hippoglossus spinolepis*, Piner and Wischniowski, 2004) and Yellowtail Flounder (Dwyer et al., 2003).

Whole otoliths have provided underestimates of age in many studies and are not accurate for most fish at the oldest ages (Campana, 2001), with a few exceptions (American Plaice, *Hippoglossoides platessoides*; Morin et al., 2013). In this study for Greenland Halibut, whole otoliths gave the same age as thin sections up to 9 years of age (~ 60 cm from length-at-age values) after which estimates from whole otoliths underestimated by greater than 50% the true age of Greenland Halibut for the oldest fish (18 years) in some cases. This bias increased with fish size. As with other species, the new material in whole otoliths is laid down over the old growth (Chilton and Beamish, 1982). This lack of relationship between fish length and age has been called uncoupling (Wright et al., 1990). The Greenland Halibut otolith, which is quite thin compared to other flatfish species, with its unusual finger-like protrusions and thickened “peri-sulcular” region on the left otolith, is exceptionally difficult to age (for both whole and thin-sectioned otoliths). This dome on the left otolith is unique to Greenland Halibut (J. Casselman, pers. comm.) and may be the best area along which to count annuli in cross-section.

Other ageing studies for Greenland Halibut in this region have corroborated the use of whole otoliths for the earliest ages; Lear and Pitt (1975) used length frequency modes (Petersen method) to conclude that there was an annual formation of opaque and translucent zones on the whole otoliths of Greenland Halibut up to the age of 3 years. Bowering and Nedreaas (2001) used the same method to provide length at age up to the age of 4 years, with an average growth of 6–8 cm per year. There were some differences in length at age even between these two studies. For example, Lear and Pitt (1975) determined that an average three year old was 16 cm in length, while Bowering and Nedreaas (2001) concluded that three year old fish averaged 21 cm. This is likely due to the presumed occurrence of a protracted spawning season, and therefore large variation in size for the youngest year classes (Bowering and Nedreaas, 2001).

It also may be due to confusion on selection of the first annulus as the settling mark (i.e. mark on the otolith that forms during metamorphosis) appears strongly in this species.

Although the bomb radiocarbon signal is almost synchronous worldwide, there are some differences in the onset of timing of the increase in ^{14}C values and magnitude of levels depending on a number of oceanographic factors. Water depth, currents and other factors are among the factors known to influence bomb radiocarbon levels in different habitats (Piner and Wischniowski, 2004; Campana et al., 2008; Passerotti et al., 2010). The known-age reference chronology used here for Arctic Greenland Halibut provided a good fit to the fish in the NAFO SA 2+ 3K management unit, as seen by the addition of a subsample of six known-age fish from this area. The ^{14}C from the cores of these young fish fit well with the known age Arctic fish bomb radiocarbon reference chronology (about 50% of the fish that make up the curve are in fact, from Sub-area 2) (Treble et al., 2008). As seen with the Arctic stock, there is a slight delay in the timing of the initial bomb radiocarbon increase compared to the Northwest Atlantic otolith chronology (Campana et al., 2008) as well as lower levels of bomb radiocarbon after 1970, probably due to radiocarbon flux to deep water where most of the large Greenland Halibut reside (Treble et al., 2008).

There were three thin-sectioned otoliths that did not fit well with the reference chronology. Kalish et al. (1997) indicated that differences seen in the timing and magnitude of peak values might be due to the penetration and dilution of radiocarbon in deeper water, as well as various water mixing characteristics. Greenland Halibut inhabit the Continental shelf and deep slopes to depths of greater than 1500 m, although the fish is generally found between 300–500 m off the Grand Bank and into the Flemish Pass. As such the habitat is affected by major water currents, such as the Labrador Current and Gulf streams. It is thought that large mature females prefer deeper waters (Bowering, 1978). However, there was no correlation with depth and the amount of ^{14}C in the three otolith cores that did not fit the reference curve, so clearly these fish were underaged. Thin-sections can sometimes fail to provide an accurate age for other species, such as Sablefish, *Anaoploma fimbria* (Beamish and McFarlane, 2000), and Yellowtail Flounder, *Limanda ferruginea* (Dwyer et al., 2003) but in most cases this has just been by a few years at most. Treble et al. (2008) reported this for Arctic Greenland Halibut on a larger scale, by up to 15 years in some cases.

Maximum age from ^{14}C indicates that the Arctic (Treble et al., 2008; ICES, 2011), Pacific (ICES, 2011) and Northwest Atlantic stocks have a lifespan of about 35 years and, since the bomb radiocarbon sample here included fish lengths close to the known maximum species' size, it seems likely that this approximates the actual longevity of the species. Greenland Halibut is considered a moderately lived flatfish; other flatfish, such as Atlantic Halibut (40–50 years; Armsworthy and Campana, 2010), Pacific Halibut (55 years; Piner and Wischniowski, 2004), and Dover Sole (*Microstomus pacificus*, 60 years; Munk, 2001), are considered long lived; others less so, but with longevity greater than age estimates from traditional whole otoliths would have indicated (Yellowtail Flounder (25 years; Dwyer et al., 2003) and Starry Flounder (*Platichthys stellatus*, 24 years; Campana, 1984).

Growth varies among populations of Greenland Halibut from the Pacific region, Arctic region and the Northwest Atlantic. In general, growth curves as estimated from thin sections indicate faster growth for the first years of life and slower growth after (compared to those estimated from whole otoliths). Although the Pacific and Arctic stocks reach maximum length faster than the stock in the Northwest Atlantic, ultimately both those populations reach a lower maximum length. Maximum age reached by the Pacific Greenland Halibut stocks is 35 years (Gregg et al., 2006) and 27 years for the Northeast Atlantic stock (Albert et al., 2009). Maxi-

mum age from thin-sectioned otoliths was 25 years for the Arctic stock (NAFO Division 0B) (Treble et al., 2008).

Regardless of difficulties associated with estimating age for the Arctic stock using thin sections, it would seem that the Arctic stock of Greenland Halibut ultimately grows more slowly than the Northwest Atlantic stock. However, recent tagging results indicate that some degree of mixing between stocks occurs; at least 10 fish (out of 240 returns; approximately 4.2%) tagged in either the Arctic or off Greenland have been recaptured off Labrador and Newfoundland (M. Treble, pers. comm.). Thus a direct comparison of growth between these two populations is confounded by gene flow between populations, and the fact that the authors were unable to provide sex-specific growth rates (Treble et al., 2008). In fact, it is noted by Roy et al. (2014) that there is a common gene pool of seven stocks of Greenland Halibut in the North Atlantic, but the authors do note that there is local differentiation of recruits in areas where larvae settle from drift. This local differentiation may explain why there are different growth rates in different areas. Prior tagging from Treble et al. (2008) indicated slow growth for these fish, demonstrated (from OTC/SrCl marking) that new growth on the whole otolith masks old growth, and revealed that the expected number of annuli based on time at liberty were not visible in this structure. Even OTC marking examined from the thin section indicated that otolith growth was uneven and that annuli could not always be seen (Treble et al., 2008). Treble et al. (2008) concluded that growth estimated from bomb radiocarbon ages and section ages from a method comparison was about 1–2 cm/year for adult Greenland Halibut. From our study, the growth rate for 50–70 cm fish was about 2.4 cm/year, and for >70 cm fish was 1.4 cm/year. Both studies concluded that growth was far slower than the 5 cm/year estimated from whole otoliths previously reported in the literature (Bowering, 1978; Boje and Jorgensen, 1991; Bowering and Nedreaas, 2001).

Growth curves from our study were comparable to other studies of Greenland Halibut growth that used thin sections for ageing (Gregg et al., 2006; Treble et al., 2008) (even though age data from males and females were combined in these earlier studies, thus lowering the overall L_{∞}). However, growth curves were very different than those using whole otoliths for age estimation. Bowering and Nedreaas (2001) showed growth curves from the Northwest and Northeast Atlantic that were almost linear, showing little or any slowing of growth as the fish aged, reaching biologically unlikely high L_{∞} values. This pattern of shortened age composition may also be indicative of the larger, old fish being underaged while the younger fish are not. In addition, their growth curves from 1996 were truncated in age compared to 1977, suggesting a loss of size range over time. Since our study examined historical samples that mostly came from the 1970s, we cannot comment whether growth has changed over time. This should be investigated further.

As with other marine flatfish (Beverton, 1964; Pitt, 1974; Dwyer et al., 2003), Greenland Halibut exhibit pronounced sexual dimorphism with respect to size, with males reaching a lower maximum length (L_{∞}) than females. The difference between sexes is thought to be due to the manner in which males and females direct excess energy into growth and reproduction. Growth rate is similar between males and females up to about age 10 years, but females live much longer than males. Greenland Halibut appear to mature considerably later, and at larger sizes, in the Northwest Atlantic (Div. 2+3 K) than in other stocks (Morgan and Bowering, 1997). Our study indicates that this late maturation would occur even later, based on ages estimated from thin-sectioned otoliths. The most recent cohort of Greenland Halibut males have an L_{50} of 70 cm, corresponding to an A_{50} of 10 years using whole otoliths and females have an L_{50} of ~72 cm, which corresponds to an A_{50} of 12–13 years using whole otolith-estimated ages (Healey et al., 2010), thus requiring further exploration.

This stock is presently managed using a harvest control rule, which was tested using Management Strategy Evaluation (MSE) (Miller and Shelton, 2010). Prior to this, XSA was the basis of management advice for many years and the last XSA was conducted in 2010 and is one of two population models that form the basis of the MSE. The proportion of larger fish in the population is very small; in the RV survey, the number of fish >60 cm is less than 2% for the past 5 years and for the Canadian commercial catch this value depends on gear and fleet but is generally less than 15%. Though there are relatively few fish in the assessment at the length where ageing becomes a problem in recent years, this issue has to be investigated further and should not be taken as the solution to the ageing issue.

Underageing the oldest fish in the population can have significant impacts on assessments. Several studies indicated that natural mortality (M) for fish populations may be underestimated using whole otoliths to determine age. Using $M = 4.22/t_{\max}$ (maximum age in years) as a rule of thumb (Hewitt and Hoenig, 2005), and assuming a maximum age of 33 years, yields an estimate of 0.13 for M , which is comparable to the 0.15 from Gregg et al. (2006) using thin-sectioned otoliths stained with aniline blue, and the 0.12 from Treble et al. (2008). Cooper et al. (2007) independently concluded that M was about 0.12 for the same stock of Greenland Halibut using the relationship with gonadosomatic index (GSI). Fortunately, an M of 0.1 was tested in the MSE for this stock.

This paper focused on improving age estimation for Greenland Halibut, a commercially and ecologically important fish species in the Northwest Atlantic. In addition to supporting major international fisheries in this region, it is also one of the top predators in this system (Dwyer et al., 2010). Hence, reliable knowledge of age and growth is vital in accurately assessing this resource and determining biological parameters for the population. Greenland Halibut in this region is slower growing and longer lived than was previously believed based on ages from whole otoliths. They reach a maximum age of more than 30 years, and growth slows after age 9 (based on newly validated ages) in both males and females, with females reaching a larger maximum size than males. Age-disaggregated results for fish older than 9 years are likely to be biased, and several cohorts may be within the assigned ages. Therefore, thin sectioning of otoliths is recommended for ageing all or a subsample of fish older than 9 years (~60 cm total length). Conversion factors (using an adjustment from whole ages to thin-sectioned ages) have not been the answer to most ageing problems (herring (*Clupea harengus*, Melvin and Campana, 2010), Haddock (Campana, 1995), Yellowtail Flounder (Koen-Alonso et al., 2006)) because of somatic and otolith growth uncoupling. Future work should focus on how to incorporate this new knowledge into the assessment and/or any review of the management strategy that currently exists for this stock.

Acknowledgements

The authors would like to acknowledge Fisheries and Oceans Canada's International Governance Strategy for funding to complete radiocarbon assays. In addition, this manuscript benefited from comments by several people, including Brian Healey and Joanne Morgan at Fisheries and Oceans Canada. Thanks also to Peter Upward for sectioning of otoliths and Brian Greene for locating archived samples.

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