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Age determination, bomb-radiocarbon validation and growth of Atlantic halibut (*Hippoglossus hippoglossus*) from the Northwest Atlantic

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Abstract Atlantic halibut (*Hippoglossus hippoglossus*) is the largest and one of the most widely-ranging and commercially-valuable groundfish in the Atlantic Ocean. Although presumed to be long-lived, their age and growth has not been validated. Ages were estimated by counting growth increments from approximately 2400 thin-sectioned sagittal otoliths collected from the Scotian Shelf and southern Grand Banks off eastern Canada. The accuracy of age estimates made from otolith thin sections was validated using bomb-radiocarbon assays of 13 otolith cores whose year of formation ranged from 1949 to 1975, encompassing the timeframe of the global radiocarbon pulse. Known-age juvenile halibut from a culture facility were used to identify the approximate location of the first annulus. Growth rate for males and females was similar up to about 70 cm (~5 years), after which point male growth slowed, while female growth continued to an age of up to 38 years and a maximum observed size of 232 cm. Males grew to an observed maximum length of about 175 cm and a maximum age of 50 years. A comparison of age estimates for otoliths collected in a 'historic' time frame (1963 to 1974) with those from recent years (1997 to 2007) shows that growth rate has not changed appreciably between the two time periods. Small but significant growth differences were observed between the Scotian Shelf and southern Grand Banks for both sexes, while large differences in length at age were observed between halibut caught with longline compared to otter trawl due to differences in length-based gear selectivity. Age interpretations based on sectioned otoliths tended to be 10–15% different than those based on break and burn, although the age comparison was confounded by other variables and must be considered provisional. Atlantic halibut is a long-lived fish, living up to at least 50 years, an important consideration for the management of the fishery.

Keywords Age determination · Bomb-radiocarbon validation · Growth · Atlantic halibut

Introduction

Atlantic halibut (*Hippoglossus hippoglossus* L.) is the largest of the flatfish species in the Atlantic Ocean and ranges widely over the North Atlantic, supporting national and international fisheries off the coasts of Canada, Greenland, Iceland, Faroe Islands and Norway. Despite having the highest commercial value per landed weight of all groundfish in the North Atlantic, many of the basic life history characteristics of Atlantic halibut are still unknown. Growth of Atlantic

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halibut is thought to vary somewhat among populations in the North Atlantic (McCracken 1958), with all populations exhibiting sexual dimorphism, and females reaching a substantially larger size than males (Devold 1938; McCracken 1958; Bowering 1986; Trumble et al. 1993; Sigourney et al. 2006). Off the coast of Newfoundland (NAFO divisions 3MNOP), Bowering (1986) reported males growing to 189 cm and females to 229 cm, while halibut from northern Norwegian waters reached lengths of 170 cm in males and >230 cm in females (Devold 1938), and those from the Faroe Islands reached lengths of ~180 cm in males and ~220 cm in females (Jákupsstovu and Haug 1988). Pacific halibut (*Hippoglossus stenolepis*) have been reported to reach maximum sizes of up to 252 cm (IPHC 1998).

In the second half of the 20th century, Atlantic halibut abundance declined markedly in some areas, including U.S. waters in the Gulf of Maine (Kanwit 2007) and in the Gulf of St. Lawrence (DFO 2009), presumably due to over-fishing. Since 1998, the relative abundance of the halibut stock on the Scotian Shelf and southern Grand Banks off of eastern Canada (NAFO Divisions 3NOPs4VWX5Zc; Fig. 1) has been monitored using an industry-based longline survey. Although survey indices track the trajectory of halibut abundance, the age information required to estimate recruitment, growth and mortality rates, age at maturity, and longevity, as well as to develop an age-structured population model for improved management, has not been available to date.

Several studies have reported on the age and growth of Atlantic halibut (Jespersen 1917; Devold 1938; McCracken 1958; Bowering 1986; Neilson et al. 1987; Sigourney et al. 2006). Halibut from the Faroe Islands were reported to live to an age of 50 years (Jákupsstovu and Haug 1988), while halibut from Norwegian waters were aged to a maximum of 41 years for males and 39 for females (Devold 1938). However, none of these studies included an age

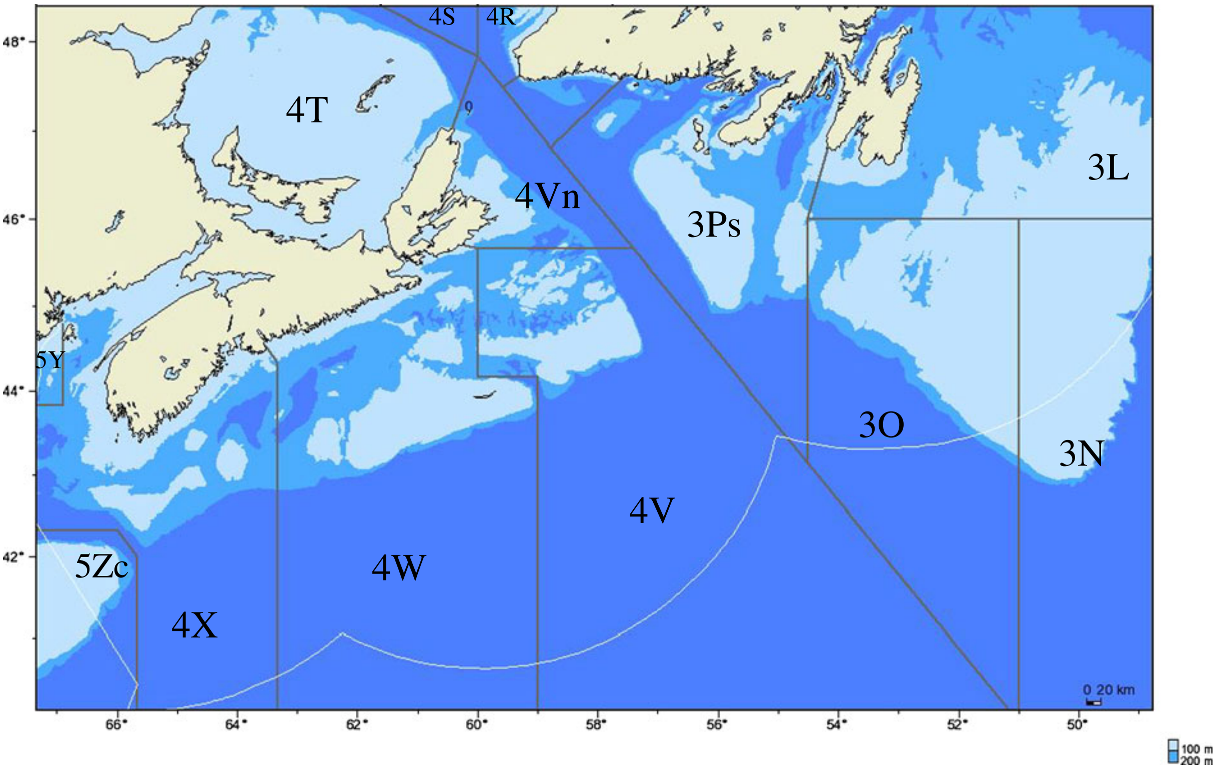

Fig. 1 Map of sampling area showing Northwest Atlantic Fisheries Organization (NAFO) divisions. Atlantic halibut otoliths were collected from within the management unit (NAFO 3NOPs4VWX5Zc). NAFO Divisions 4VWX make up the Scotian Shelf and 3NOPs constitute the southern Grand Banks. The white line indicates Canada's Exclusive Economic Zone (EEZ)

validation study confirming the accuracy of their age estimates. Since errors in age-based assessment of growth and mortality rates can lead to serious errors in the understanding and management of fish populations (Beamish and McFarlane 1983), an independent test of ageing accuracy is critical, especially for long-lived commercially-exploited species (Campana 2001). The age-validation requirement was clearly understood by those studying Pacific halibut, since the longevity estimates of 55 years were validated using bomb radiocarbon (Forsberg 2001; Piner and Wischniowski 2004).

Several different ageing methods have been used for Atlantic halibut, not all of which produce accurate ages. Otolith surface readings are the traditional method for halibut (i.e., Jespersen 1917; Joensen 1954; Perley and Neilson 1985; Bowering 1986; Neilson et al. 1987), but this method is known to underestimate age in other flatfish species (Campana 1984; Sipe and Chittenden 2001; Dwyer et al. 2003), including the closely-related Pacific halibut (Clark and Hare 2006). More recent studies have used ‘break and burn’ or thin sectioning techniques (Chilton and Beamish 1982). After 2001, age estimates for Pacific halibut were made exclusively using the ‘break and burn’ method due to the bias of surface ageing (Clark and Hare 2006). A detailed comparison of Atlantic halibut ages resulting from thin sections and ‘break and burn’ has not yet been reported, in part because it is technically difficult to apply both methods to the same otolith.

In light of the presumed longevity, late maturity, and economic value of Atlantic halibut, the primary goal of this study was to determine the age and growth characteristics of Atlantic halibut from the Scotian Shelf and southern Grand Banks off eastern Canada. In addition to developing an ageing method for the species, we also report the first application of bomb radiocarbon as an age-validation tool for Atlantic halibut otoliths, thus confirming the accuracy of otolith cross-sections as an ageing method. Additional objectives of the study were to: (i) test for a change in growth rate over a period of four decades, (ii) test for differences in growth rate between sexes and major fishing areas, (iii) compare the age estimates resulting from the two major ageing methods (thin-sectioning vs. ‘break and burn’), and (iv) test for size selectivity of halibut by longline and trawl gears.

Materials and methods

Otolith collection

Otoliths from Atlantic halibut were collected from the Scotian Shelf and southern Grand Banks using both otter trawl gear on research vessels (1962 to present) and longline gear on commercial fishing vessels (1998 to present). Of the 65 000 Atlantic halibut otoliths available at the beginning of this study, a total of 2429 otoliths were selected for ageing and comparative growth analyses (Table 1). The selected otoliths were distributed similarly between sexes (997

Table 1 Year, area, and gear information for aged Atlantic halibut otoliths

Year	Area		Gear
	Scotian Shelf	Grand Banks	
1963		1	trawl
1964		32	trawl
1965		18	trawl
1966		3	trawl
1967		24	trawl
1968		12	trawl
1969		3	trawl
1970	13		trawl
1971	32	1	trawl
1973	23		trawl
1974	20		trawl
1977	3		trawl
1978	1		trawl
1982	1		trawl
1997	82	0	trawl
1998	3		longline
1999	157	97	longline
2000	142	156	longline
2001	96	97	longline
2001	75	0	trawl
2002	124	61	longline
2003	177	82	longline
2004	263	196	longline
2005	126	225	longline
2007	83	0	trawl
Total/area	1421	1008	
Grand Total	2429		

males, 1428 females, 4 unknown), across the available size range (17–232 cm fork length (FL) for females and 25–214 cm FL for males), with a target of five fish in each 3-cm length group, and between two geographic areas: the Scotian Shelf (NAFO Divisions 4VWX) and the southern Grand Banks (NAFO 3NOPs). The majority of samples were collected using longline gear (2002 longline; 427 trawl). Otoliths were collected from both a 'recent' time period 1997–2007 ($n=2247$) and a 'historic' time period 1963–1974 ($n=182$) so as to test for long-term changes in growth rate.

Improved sampling in recent years through a multi-stakeholder fishery-independent longline survey for Atlantic halibut resulted in a marked increase in otolith collection effort. Otoliths from the halibut longline survey were collected by commercial longliners using bottom hook-and-line gear (size 14 circle hooks) each year from May to July since 1998 (Armsworthy et al. 2006). Sampling locations were distributed widely over the Scotian Shelf and southern Grand Banks ranging from Georges Bank in the southwest to the eastern portion of the Grand Banks in the northeast. The mean fork length of halibut caught in all years of the survey (1998–2009) was 97 cm. A minimum size regulation of 81-cm FL implemented in 1995 prevented the collection of otoliths from halibut <81 cm caught during the survey.

Otoliths from the DFO Scotian Shelf groundfish research vessel (RV) trawl survey were collected using a Western IIA trawl with a 19-mm mesh liner each July since 1970 (Branton and Black 2004). Sampling locations ranged between the upper Bay of Fundy and the northern tip of Cape Breton and from offshore to the 400-fathom contour (~700 m). Prior to 1982, a Yankee-36 otter trawl with a 19-mm mesh liner was used (Ricard et al. 2010). The average fork length of halibut caught in the Scotian Shelf RV trawl survey was 55 cm from 1970 to 1981 and 59 cm from 1982 to 2008, suggesting that the change in trawl gear did not result in large changes in size-selectivity.

Research vessel trawl samples off Newfoundland and Labrador were collected on the southeastern Grand Bank (NAFO 3N), southwestern Grand Bank (3O), and St. Pierre Bank (3Ps) between 1963 and 1971 to a maximum depth of 530 m using a Yankee-41.5 otter trawl with a 30-mm mesh liner (McCallum and Walsh 1996).

Otolith ageing

From each saggital otolith pair, blind-side otoliths were used exclusively for sectioning and ageing (preferentially selected over eyed-side otoliths). The annuli of blind-side otoliths (the side of the fish facing the seafloor and having no eyes, usually the left side) have been reported to be more distinct and evenly spaced and with fewer checks than the eyed-side in Atlantic halibut (Jespersen 1917; Joensen 1954) and in other flatfish species such as Greenland halibut (*Reinhardtius hippoglossoides*) (Lear and Pitt 1975) and Pacific halibut (Forsberg 2001). Otoliths were embedded in a slow-drying hard epoxy (Araldite epoxy GY502 and hardener HY956 in a 5:1 weight ratio; St. Lawrence Chemicals). A 0.4 mm thick transverse section through the core was prepared with a single cut using two blades separated by spacers on an Isomet low-speed diamond-bladed saw. The sections were lightly polished to improve visibility. While under a binocular microscope at 16–40X magnification using reflected light, the growth-increment sequence was digitally photographed at a resolution of 2048×2048 pixels, and then digitally enhanced for contrast using Adobe Photoshop CS2. Age estimates were made by counting the number of annuli (translucent zones) from the enhanced image of the otolith thin sections. Aging bias and precision of annulus counts were assessed using age-bias plots and the coefficient of variation (Campana et al. 1995; Campana 2001). All errors are reported as one standard deviation about the mean.

Determination of the first annulus

Ideally, the first growth increment is validated by measuring the diameter of 1-yr-old otoliths at the time of first annulus formation and then comparing it to the diameter of the first presumed annulus in sections of adult otoliths (Campana 2001). Since young-of-year halibut were not readily available in early spring (the time of annulus formation), both saggital otoliths were removed from twelve, 16-month-old halibut in mid-August. These juvenile halibut (18.8±0.72 cm) were supplied by the Scotian Halibut culture facility in Clarks Harbour, Nova Scotia. Otolith sections were prepared as described earlier. Since the first annulus was presumed to have been laid down four months prior to extraction, measurements were made of both the diameter (mm) of the whole otolith along the dorso-ventral axis and the dorso-ventral diameter of the first translucent band in the section, presumed to be the first annulus.

Comparison of otolith aging techniques

The standard otolith preparation protocol for this study was embedding and sectioning at the Bedford Institute of Oceanography (BIO; method described above). In order to compare the results of this method with the break and burn method used at the International Pacific Halibut Commission (IPHC; Forsberg 2001), the ideal approach would have been to send one otolith to BIO for sectioning, and the other otolith to IPHC for break and burn, and then for the roles to reverse, and for BIO to undertake break and burn and IPHC undertake sectioning. However, there were three confounding factors. First, BIO was most experienced in sectioning, and IPHC most experienced in break and burn, meaning that it would be difficult to separate method effects from lab effects. Secondly, halibut otolith pairs are asymmetric, implying that annulus appearance or formation in left and right otoliths from a given fish may differ. This implies that it is not possible to split an otolith pair and send an equivalent otolith to each lab. Thirdly, the anterior and posterior regions of the otolith are also asymmetric, implying that it was not possible to section an otolith and send identical halves to each lab. Hence, an ideal experimental design to compare age interpretations from sectioned and break-and-burn otoliths was not possible.

As an alternative to the ideal experimental design, two concurrent experimental designs were applied. First, a matched-pair comparison design was used to test for differences in age interpretations between eyed- and blind-side otoliths. This design used 66 Atlantic halibut saggital otolith pairs (eyed- and blind-sides), extracted from fish ranging in size from 83 to 192 cm (18 males, 39 females). One otolith from each fish was aged at BIO (33 eyed- and 33 blind-side otoliths) and the other aged by IPHC (33 eyed- and 33 blind-side otoliths). The assignment of the eyed- versus blind-side to each lab, within each fish's otolith pair was random. Neither lab read both otoliths from the same fish. Only 57 of the 66 samples could be used in the comparison, usually because one or the other of the labs had a poor-quality otolith.

In the second design, a randomized design was used to test for anterior-posterior differences in age interpretation. This design used 79 blind-side Atlantic halibut otoliths extracted from fish ranging in size from 81 to 175 cm (27 males, 51 females), which were cut in half through the core providing anterior and posterior portions. One portion of each otolith was aged at BIO (45 anterior and 44 posterior) and the other aged by IPHC (44 anterior and 45 posterior). The assignment of anterior and posterior portions to each lab, from each fish's blind side otolith was randomly assigned. Neither lab read both portions from the same fish. One of the 79 otoliths could not be used in the comparison due to poor quality.

To determine if the age interpretations of Atlantic halibut were comparable to those of Pacific halibut, a sample of 104 Pacific halibut were aged by both labs, whereby anterior and posterior regions of blind-side otoliths were prepared using a randomized design similar to the Atlantic halibut otoliths described above, and then evenly distributed between labs. IPHC aged the otoliths by burning their halves (cut at BIO), while BIO aged theirs by preparing a section from the halves.

Comparisons between eyed- and blind-side, and between anterior and posterior regions of the otolith, were made using age bias plots and precision measures, as described earlier. Neither lab was aware of the other lab's results at the time of ageing. Inferences concerning the overall comparison of sectioned versus break and burn otoliths were made after first confirming the absence of bias due to eyed-blind and anterior-posterior differences, and then pooling all age readings by each lab in an overall age bias plot comparing methods. Due to the study design, it was not possible to separate lab effects from method effects.

Radiocarbon age validation

Age validation serves to confirm that an ageing method is accurate (unbiased), not that every single otolith is aged accurately. The onset of atmospheric testing of nuclear weapons in the late 1950s resulted in an abrupt increase in atmospheric and marine ^{14}C, which was rapidly incorporated into calcified structures growing at the time, such as bivalves, corals and fish otoliths (Kalish 1993; Campana et al. 2008). The period 1958–1965 is analogous to a large-scale chemical tagging experiment, wherein all otolith cores of fish born before 1958 (the core = first year of life) contain relatively little ^{14}C, and otolith cores from fish hatched between 1958 and 1968 contain increasingly elevated levels that can be used to validate methods of age estimation. This has proven to be a powerful method for the age validation of long-lived fishes (Campana 2001).

We used bomb-radiocarbon assays to examine the accuracy of growth band counts from otolith cross sections as an annual age indicator. To measure radiocarbon values from before, during, and after the bomb-testing era, sagittal otolith pairs from 13 Atlantic halibut were selected from specimens captured between 1966 and 1999 and having estimated years of core formation ranging from 1949 to 1975. Otolith cores representing what was assumed to be the first two years of growth were isolated from the central section of each otolith pair as a solid piece with a Merchantek computer-controlled micromilling machine using 300-μm-diameter steel cutting bits and burrs. The date of sample formation was calculated as the year of fish collection minus the age span of the fish from the edge of the otolith to the midpoint of the range of growth increments present in the extracted core. After sonification in Super Q water (Millipore) and drying, the sample was weighed to the nearest 0.1 mg in preparation for ^{14}C assay using accelerator mass spectrometry (AMS). AMS assays also provided $\delta^{13}C$ (‰) values, which were used to correct for isotopic fractionation effects and to determine the carbon source. Radiocarbon values were 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 using the methods of Stuiver and Polach (1977).

The year of formation of the halibut otolith cores was estimated by comparing its radiocarbon content with that of a reference radiocarbon chronology based on known-age calcified material deposited between the years 1939 and 2000 in the northwest Atlantic (Campana et al. 2008). Errors in the annular age estimate would result in the core assay value falling off the line defined by the reference chronology.

Growth curve estimates

Von Bertalanffy growth functions (VBGF) were fitted to the length-at-age data by using the following equation (von Bertalanffy 1938):

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

where L_t is predicted length (cm) at age t, L_∞ is mean theoretical maximum fork length, K is a growth rate parameter (year $^{-1}$), and t_0 is the theoretical age (year) at zero length. The VBGFs were calculated by using the nonlinear regression function in SPSS. Locally weighted least squares regression (LOESS) curves were fitted to the length‒at-age data for each sex for each gear type and for each area using SPSS. Differences between VBGFs between areas or gears were tested using likelihood ratio tests (Kimura 1980).

Results

Otolith ageing

Distinct concentric growth zones consisting of alternating opaque and translucent bands and presumed to be annuli were visible in the sectioned otoliths under reflected light (Fig. 2). In males the first eight growth bands were relatively widely spaced; beyond the eighth annulus, spacing between subsequent annuli decreased with increasing age out to the margin. In females, spacing between annuli decreased after the eleventh growth band.

Mean and standard deviations of length at age are shown in Table 2. The oldest fish in our sample was a 50-year-old male measuring 150 cm FL, whereas the oldest female, measuring 187 cm FL, was aged at 38 years.

Ageing precision assessed through replicate age readings was moderate with a CV of 7.7%, slightly higher than the multi-species modal CV of 5.0% reported by Campana (2001), indicating that the halibut otoliths were somewhat more difficult to interpret than in other species.

Determination of the first annulus

The mean diameter of 2.63±0.13 mm along the dorso-ventral axis was determined from 24 whole otoliths taken from twelve, 16-month-old cultured halibut. Thin sections of these otoliths revealed a translucent zone, which was presumed to be the first annulus, measuring 1.64±0.13 mm in diameter along the dorso-ventral axis. The diameter of the presumed first annulus in 30 thin-sectioned otoliths from wild Atlantic halibut was 1.82± 0.22 mm.

Comparison of otolith aging techniques

The age interpretations of the Pacific halibut otoliths were comparable between the two labs, with no bias

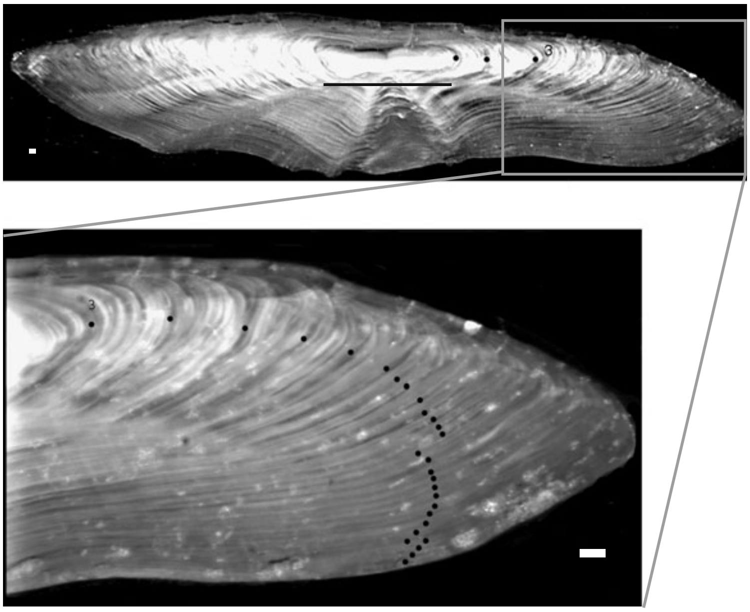

Fig. 2 Atlantic halibut otolith from a 156 cm (fork length) male sectioned transversely through the core showing annual growth increments (translucent zones annotated by black circles). Age estimate is 30 years. Annuli formed before sexual maturation appear wider than those formed after sexual maturation, and can been seen up to age 8 in the lower image panel. The black horizontal line in the upper panel indicates the dorso-ventral diameter of the first annulus. The scale bar in both images is 0.1 mm

evident in the age bias plot and an inter-lab CV of 7.0%. This result suggested that the age interpretations of the two labs were comparable, despite the fact that IPHC used break and burn and BIO used sections. Of course, it does not necessarily follow that the same comparability would apply to a different species, such as Atlantic halibut.

The test for Atlantic halibut age differences between the anterior and posterior halves of the otolith suggested minimal effects due to otolith region, if any. The age bias plot whereby IPHC aged the anterior half and BIO the posterior half showed that IPHC aged an average of 2–3 yr older to Age 14, with the difference disappearing at older ages (n=39 pairs). The CV was 17.5%. However, when BIO aged the anterior half and IPHC the posterior half, IPHC again tended to age older until Age 16, by about 1–2 years (n=39 pairs). The CV was 15.5%. Thus both biases were positive, more consistent with IPHC ageing older than BIO than any difference between anterior and posterior halves.

The test for age differences between eyed- and blind-side otoliths also suggested that there was no effect due to otolith side. The age bias plot whereby IPHC aged the blind side and BIO the eyed side showed that IPHC aged an average of 2 yr older at all ages, with a CV of 14.5% (n=28 pairs). However, when BIO aged the blind side and IPHC the eyed side, IPHC again tended to age older until Age 15, by about 2–3 years (n=29 pairs). The CV was 10.5%. Thus both biases were again positive, more consistent with IPHC ageing older than BIO than any difference between eyed- and blind-side otoliths.

Given that there was no strong evidence of ageing differences due to anterior-posterior or eyed-blind effects, the age comparisons from each study were pooled and assessed as an age bias plot (Fig. 3). Each age bias plot suggested the presence of bias between the two labs/methods, with IPHC ageing 10–15% older than BIO. It could not be determined if BIO was under-ageing or IPHC was over-ageing; nor could it be determined if the age bias was due to the technique (thin-sectioning vs. break-and-burn) or to interpretation differences between the labs. A more rigorous comparison of the methods would require each otolith sample to be aged by both labs.

Radiocarbon age validation

The year of formation of Atlantic halibut otolith cores was estimated in two ways: through annulus counts in thin-sectioned otoliths and through a comparison of otolith core Δ^{14}C values with a reference radiocarbon chronology (Fig. 4). Consistent under-ageing using annulus counts would shift the otolith ^{14}C birth year estimates towards more recent years, while consistent over-ageing would shift them towards earlier years.

Table 2 Mean and standard deviation of the length-at-age estimated from otoliths for male and female Atlantic halibut

Age class	Males			Females		
	Mean FL (cm)	S.D.	*n*	Mean FL (cm)	S.D.	*n*
2	28.7	2.29	9	27.4	5.17	14
3	40.0	6.88	21	43.8	9.85	16
4	49.3	11.76	34	47.8	8.71	34
5	67.3	17.82	43	73.2	18.70	53
6	82.6	22.41	68	92.2	18.96	99
7	90.4	18.69	82	102.7	15.66	142
8	100.3	18.23	94	112.2	18.94	152
9	105.8	20.57	105	117.5	21.43	152
10	104.5	19.31	66	126.0	21.89	124
11	113.0	21.18	66	131.6	24.37	117
12	111.6	17.92	73	137.0	22.11	125
13	115.3	21.93	64	147.7	18.43	67
14	120.0	20.17	48	153.5	16.97	74
15	114.4	15.80	45	156.9	20.97	51
16	122.4	21.56	39	161.8	19.87	38
17	115.8	15.93	17	164.1	15.85	19
18	129.7	17.22	18	164.7	19.54	19
19	126.1	13.13	11	176.4	9.94	8
20	139.6	24.85	10	180.5	15.81	11
21	123.0	14.23	8	178.5	14.63	6
22	135.9	15.17	7	186.9	20.74	16
23	127.0	22.85	5	182.2	17.92	13
24	148.0	23.76	12	188.4	11.80	11
25	138.4	9.74	13	189.4	15.54	10
26	145.6	23.18	5	196.6	10.04	5
27	138.0	10.54	3	196.6	13.81	5
28	139.0	12.73	2	202.0	16.97	8
29	153.0	12.12	3	194.5	8.66	4
30	134.6	14.10	5	206.0	24.25	3
31	157.0		1	200.5	10.61	2
32	153.5	24.75	2	179.5	19.09	2
34				193.0		1
35				211.0		1
37				208.0		1
38				187.0		1
42	148.0		1			
50	150.0		1			

Where the annulus-based and Δ^{14}C-based dates are in agreement, the annulus-based age interpretations must be correct, indicating that the annulus-based ages are unbiased.

Delta carbon 14 values in halibut otolith cores varied between −46 and 92.6, in the range of reported values of other marine carbonates formed in the 1950s and 1960s (Table 3). The mean standard deviation of

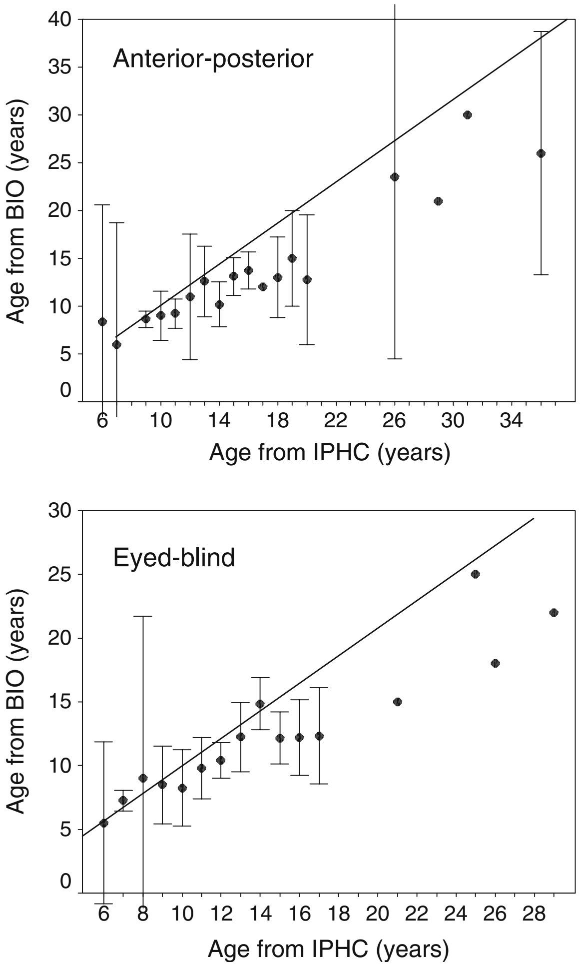

Fig. 3 Age bias plots showing systematic differences between age estimates from break and burn (IPHC) and sectioned (BIO) otoliths. Upper panel shows the pooled results from the anterior-posterior study (each lab aged one half of the blind-side otolith), while the lower panel shows the pooled results from the eyed-blind study (each lab aged one otolith from the same fish). Extent of deviation of 95% confidence interval bars from 1:1 (—) line indicates extent of ageing bias. Some bias is evident in both plots, but could not be disentangled from laboratory reader effects (BIO vs IPHC)

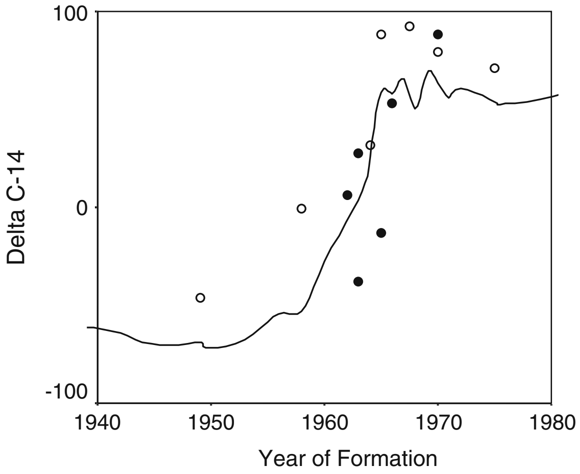

Fig. 4 Atlantic halibut age estimates from thin-sectioned otoliths (circles) and $\Delta^{14}C$ reference chronology for the Northwest Atlantic (line representing a LOESS fit to reference data, Campana et al. 2008). Open circles represent older halibut (≥12 yr); solid circles represent young fish (≤8 yr). No fish between 8 and 12 years were assayed

the individual radiocarbon assays was about 7‰. The correspondence between the core $\Delta^{14}C$ values of the young halibut (≤8 years; whose age is presumably reasonably exact based on size) and the reference chronology indicated that the reference chronology is a good proxy for the radiocarbon history of halibut otoliths (e.g., the underlying assumptions are satisfied). A comparison of the core $\Delta^{14}C$ values from old halibut with the reference chronology was less precise, but without evidence of strong bias, suggesting that the older fish had been aged correctly using annulus counts, at least on average. The two $\Delta^{14}C$ values lying between −2 and 32 were particularly instructive for assessing ageing error (Table 3), since they lay on the increasing portion of the reference chronology, and therefore were most sensitive to annulus-based ageing error. Those two values suggest that a 19-yr-old fish was aged accurately, while a 21-yr old fish may have been over-aged by about 5 yr. In contrast, 3 fish with cores formed after 1965 and aged between 24 and 35 yr may have been aged accurately, but also could have been over-aged by up to (but no more than) 5 yr, since their high $\Delta^{14}C$ values were inconsistent with an older age. Conversely, a 50-yr-old fish with a presumed core formation in 1949 could not have been over-aged by more than 10 yr, given its pre-bomb $\Delta^{14}C$ value. These constraints on possible ages indicate that individual annulus-based ages could be in error, but that there was no evidence that this ageing error was consistently too old or young (e.g., no evidence of ageing bias). Additional samples from the period of the increasing portion of the reference chronology would be required to be more definitive about the absence of ageing bias.

There was no significant relationship between $\delta^{13}C$ and either presumed age or hatch date (linear

Table 3 Summary of $\delta^{13}C$ and $\Delta^{14}C$ assay results for otolith cores sampled from Atlantic halibut (n=13) from the Scotian Shelf (4VWX) and southern Grand Banks (3NOPs) from 1966 through to 1999. m = male and f = female

Otolith Sample	Stock Area	Collection Year	Gear	Fork Length (cm)	Sex	Core Weight (mg)	Year of Core Formation	Core Age (yrs)	Age, annulus-based	$\delta^{13}C$ ($^0/_{00}$) of core	^{14}C ($^0/_{00}$) of core±S.D.
ATC-126-2	3NOPs	1966	trawl	45	m	7.70	1963	1.5	4	[a]	−37.7±10.6
ATC-141-6	3NOPs	1968	trawl	44	m	10.30	1963	2.0	6	[a]	27.9±10.1
ATC-141-2	3NOPs	1968	trawl	46	m	14.90	1965	2.0	4	[a]	−12.8±11.4
ATC-181-5	3NOPs	1971	trawl	46	m	8.80	1966	2.0	6	[a]	52.9±11.8
ATC-131-3	3NOPs	1967	trawl	63	f	10.79	1962	2.0	6	−2.50	6.5±5.0
ATC-265-44	4VWX	1977	trawl	100	f	11.27	1970	2.0	8	−1.80	88.6±5.5
ATC-280-16	4VWX	1978	trawl	122	m	11.66	1958	2.0	21	−2.10	−1.0±5.0
CK-45	4VWX	1999	longline	156	m	7.78	1970	2.0	30	−2.00	79.1±5.4
GM-7	4VWX	1998	longline	190	f	12.80	1975	2.0	24	−3.10	71.1±5.4
HAM-071-42	4VWX	1982	trawl	158	f	13.45	1964	2.0	19	−2.10	31.8±6.5
KY-290	4VWX	1998	longline	150	m	11.52	1949	2.0	50	−2.90	−46.0±4.8
KY-293	4VWX	1998	longline	171	m	10.50	1968	2.0	32	−2.50	92.6±5.5
VP-224	4VWX	1999	longline	211	f	9.73	1965	2.0	35	−2.10	88.6±5.5

[a] Data not available

regression: n=9; p>0.1). Halibut $\delta^{13}C$ values were relatively constant, with a mean of −2.3±0.40‰ (Table 3).

Growth curve estimates

The observed length at age of male and female Atlantic halibut was similar up to about 5 years (~70 cm), after which point male and female growth increasingly diverged. The predicted growth from the model showed a similar divergence between sexes, with females reaching a larger asymptotic length (~232 cm) than males (~175 cm) (Fig. 5). In our samples, males reached a maximum age of 50 years and a maximum size of 214 cm and females reached a maximum age of 38 years and a maximum size of 232 cm.

Von Bertalanffy growth curves fit the female Atlantic halibut annulus-based length-at-age data reasonably well, but appeared to underestimate the observed lengths of large males (Fig. 5). It is possible that the combined use of trawl and longline samples produced a steep artifactual initial growth rate (K), and thus a lower asymptotic length (L_∞). To test this possibility, von Bertalanffy growth curves were fit to longline data alone, broken out by area (Table 4). In all cases, the resulting L_∞ for males was considerably larger than when the data were pooled across gears, supporting the view that L_∞ is greater than 150 cm in males. However, the absence of small fish in longline-only samples implies that the resulting growth curve fit to young ages would be poor.

A comparison of our fitted growth curve with previous studies of Atlantic halibut showed variable levels of agreement (Fig. 5). All studies reported a relatively rapid growth rate in young halibut, declining after the presumed onset of sexual maturity. Some studies displayed an age distribution which was truncated at young ages, despite the presence of large fish; this effect is often characteristic of the large, old fish being mistakenly under-aged, while the younger smaller fish are not. In general, Pacific halibut appeared to grow more slowly than Atlantic halibut.

A comparison of halibut longline survey and RV trawl survey samples indicates that there is a substantial difference in length at young ages between the two gears for both males (Fig. 6a) and females (Fig. 6b). Halibut

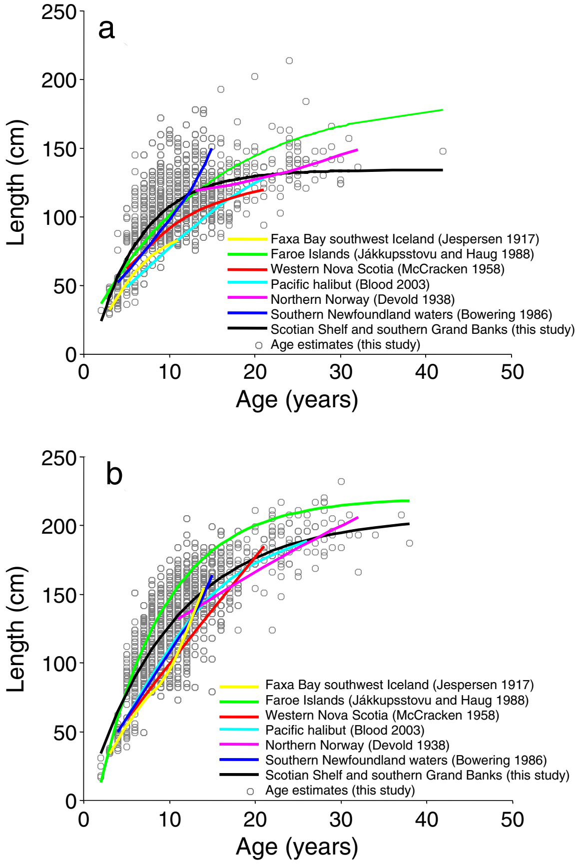

Fig. 5 Length at age for male (A; L_∞=134, K=0.18, t_0=0.88, R^2=0.49, n=995) and female (B: L_∞=205, K=0.10, t_0=0.49, R^2=0.69, n=1428) Atlantic halibut caught by longline and trawl gear. The black line indicates the fitted von Bertalanffy growth curve for our data. Published growth information is overlaid

caught using longline gear reached greater lengths at age than those caught by trawl. Gear selectivity appears to be more pronounced in younger fish and males (up to at least age 18) than for females (up to at least age 7). The greatest length differences at age were observed in 5 year old halibut, where the mean length at age was 61 cm in the trawl and 91 cm in the longline for both sexes. Similar large differences in mean length at age were observed in both areas (3NOPs and 4VWX).

The mean length at age of trawl-caught male and female halibut sampled during the historic time period was not appreciably different from those collected with otter trawls during recent years, suggesting that growth has not changed between the two time periods (Fig. 7). Male length at age differed significantly at Age 4 (t-test; df=30; p<0.001), but there were no significant differences at other ages (p>0.1). Female length at age differed significantly at Age 2 (t-test; df=12; p<0.05), Age 3 (df=16; p<0.01), Age 7 (df=15; p<0.05), Age 8 (df=10; p<0.05) and Age 9 (df=12; p<0.05), but the direction of the differences was not consistent across ages.

The observed length at age of female halibut caught with longline gear appeared to be similar between the Scotian Shelf (NAFO 4VWX) and the southern Grand Banks (NAFO 3NOPs) (Fig. 8); however, length at age plots indicate that longline-caught male halibut appear to grow to both larger sizes and greater ages on the Scotian Shelf. Although the L_∞ values in Table 4 suggest large differences in asymptotic length between areas, the length at age plots by area show that the larger Grand Banks L_∞ values are artifactual due to the relative scarcity of samples of large fish from the Grand Banks, which leaves the L_∞ values unconstrained compared to the Scotian Shelf L_∞ values. As a result, the asymptotic lengths are not well defined by the growth model. Based on LOESS fits to the data, there was no obvious difference in size at age between areas within gear and sex. Nevertheless, likelihood ratio tests confirmed the presence of significant differences in K and L_∞ between areas for both sexes (chi-square from likelihood ratio tests; n=759 for males and n=1228 for females; p<0.05).

Discussion

The results of the bomb-radiocarbon assays indicate that Atlantic halibut can be aged without strong bias to at least 40 years using transverse otolith sections. The correspondence between the otolith core $\Delta^{14}C$ values and the reference radiocarbon chronology indicates that growth increments must be formed annually in this species; consistent under- or over-ageing would have resulted in core $\Delta^{14}C$ values which were phase-shifted in relation to the reference chronology. However, given the low number of radiocarbon assays that were completed, it would have been difficult to detect under- or over-ageing of less than about 5 years, such as has been detected in other species (e.g., Piner et al. 2005). Validation of transverse otolith sections as an unbiased ageing method presumably extends to the 'break and polish' method first reported by Devold (1938), which is

Table 4 von Bertalanffy growth parameters of Atlantic halibut by sex, location and gear type. Scotian Shelf = NAFO 4VWX; Grand Banks = NAFO 3NOPs; All = NAFO 3NOPs4VWX; LL = longline, OT = otter trawl

Location (gear)	Sex	Ages fitted (yrs) (n)	L_∞	K	t_o
All (LL & OT)	Male	2 to 32 (995)	134.2	0.18	0.88
All (LL & OT)	Female	2 to 38 (1428)	205.1	0.10	0.49
Grand Banks (LL & OT)	Male	4 to 30 (418)	127.3	0.14	−1.29
Grand Banks (LL & OT)	Female	4 to 37 (589)	243.1	0.05	−2.59
Scotian Shelf (LL & OT)	Male	2 to 32 (577)	140.9	0.18	1.16
Scotian Shelf (LL & OT)	Female	2 to 38 (839)	200.9	0.12	1.08
Grand Banks (LL)	Male	5 to 30 (363)	169.0	0.03	−18.4
Grand Banks (LL)	Female	5 to 37 (551)	287.9	0.03	−5.40
Scotian Shelf (LL)	Male	4 to 32 (401)	150.2	0.10	−5.46
Scotian Shelf (LL)	Female	5 to 38 (685)	210.8	0.09	−0.76

functionally analogous to sectioning. Nevertheless, despite the validation of the ageing method, the low ageing precision (high CV) indicated that the halibut otoliths were not necessarily easy to read, and that individual ages could still be in error, albeit without bias.

The underlying assumptions of bomb radiocarbon as a dated marker must be met if the method is to be applied with confidence (Kalish 1995; Campana 2001). The principle assumption is that the period of otolith growth corresponding to core formation takes place in waters exposed to the surface marine bomb-radiocarbon signal. The close correspondence between the $\Delta^{14}C$ of the young halibut cores and that of the reference radiocarbon chronology confirmed this assumption. The second assumption is that the water masses representing the reference and halibut chronologies show similar radiocarbon chronologies (Andrews et al. 2007; Hamel et al. 2008). This assumption is less stringent than the first, since surface marine waters in different regions tend to differ only in the post-bomb radiocarbon content, not in their timing. Nevertheless, halibut live in the same environment as that used to develop the reference chronology for the northwest Atlantic (Campana et al. 2008), and thus are well-matched signals. Bomb radiocarbon has also proven effective in validating the accuracy of ageing methods for other flatfish species, including Pacific halibut (Piner and Wischniowski 2004), yellowtail flounder (*Limanda ferruginea*; Dwyer et al. 2003), and Greenland halibut (Treble et al. 2008).

Given its longevity and depth of occurrence, it is unlikely that alternative methods of age validation or corroboration would have been effective with Atlantic halibut. Clear length-frequency modes could not be distinguished in the RV length-frequency data (Armsworthy, unpublished data), and annulus width after sexual maturity was too narrow for application of marginal-increment analysis (Campana 2001). Chemical mark-recapture studies are an effective means of age validation, but only if tagged fish can be recaptured after several years at liberty. In recent conventional tag-recapture studies, very few of the 1898 tagged halibut had been reported to be at liberty more than 5 yr (Kanwit 2007; DFO 2009), suggesting that the method would be challenging as a source of chemically-marked tags. Blood (2003) reported that two decades were spent unsuccessfully attempting age validation of Pacific halibut using a chemical tag-recapture technique.

Although our determination of the first annulus in Atlantic halibut is presumed to be (but is not necessarily) correct, it is unlikely that its identification could be in error by more than one year. The diameter of the first annulus in a 12-month-old halibut must logically be less than 2.6 mm, the mean diameter of the 16-month whole otoliths as measured along the axis used for ageing. The mean diameter of the first annulus in the captive-reared halibut was 1.64 mm and in wild halibut was 1.82 mm, indicating a likely range of diameters for first annulus deposition, and suggesting a slower growth rate for cultured halibut compared to wild halibut during the first year of life. The mean diameter of the first annulus in both cultured and wild Atlantic halibut is slightly larger than that of similarly-aged Pacific halibut, which ranges from 1.29 mm (Piner and Wischniowski 2004) to 1.49 mm (Forsberg 2001). This size difference is consistent with the fact that otoliths from Atlantic

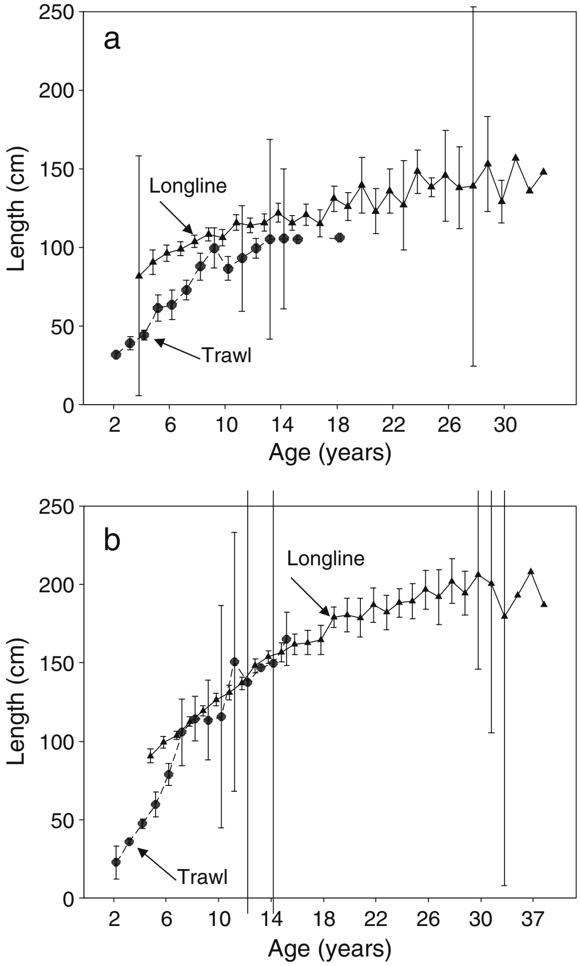

Fig. 6 Mean length at age ±95% confidence interval for male (**a**) and female (**b**) Atlantic halibut caught using longline and trawl gear

halibut tend to be larger than those of Pacific halibut (Trumble et al. 1993).

The results of this study indicate that growth increments visible in Atlantic halibut otolith sections provide an accurate but somewhat imprecise age to at least 40 years. Earlier studies of Atlantic halibut growth used surface-ageing techniques which almost certainly underestimated the age of older fish. A study of halibut from southern Newfoundland (Bowering 1986) reported a larger size at age for 12 to 16 year old male fish when compared to fish lengths of the same age in our study. Even allowing for their use of trawl collections (which select for smaller fish), the ages of their largest male halibut were less than one half of those aged in this study, despite a comparable range of fish lengths.

The results of other early halibut growth studies suggest that surface ageing of otoliths may produce relatively accurate ages for young halibut. Jespersen (1917) reported lengths at age of halibut from Faxa Bay, Iceland based on surface otolith readings that were consistent with those of the current study; however, the length-range of fish examined only extended to 83 cm for males and 155 cm for females, thereby not encompassing the larger length groups generally associated with age underestimation. On the other hand, McCracken (1958) used surface ageing of male and female halibut from western Nova Scotia to estimate growth rates that were slightly lower than those reported here, suggesting accurate age determi-

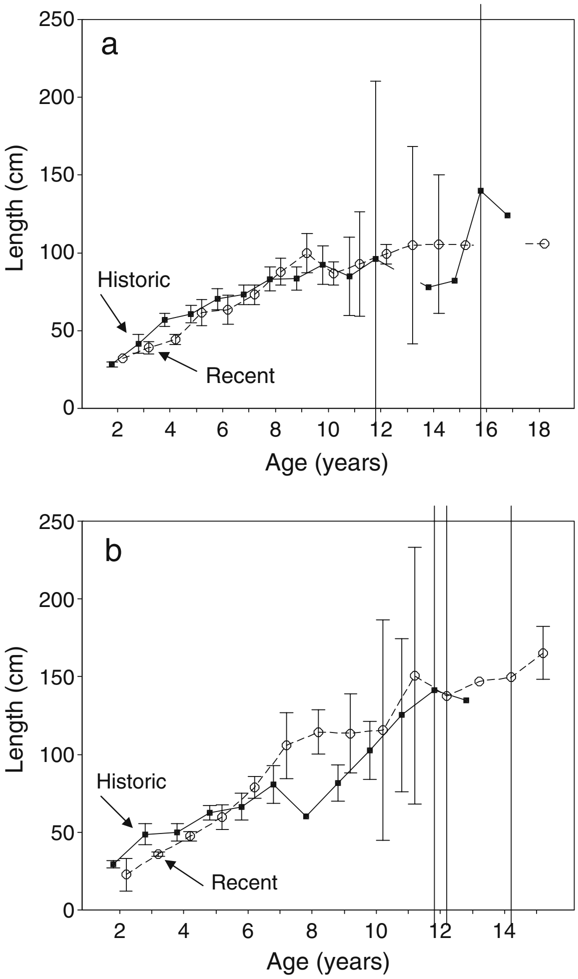

Fig. 7 Mean length at age ±95% confidence intervals for male (**a**) and female (**b**) trawl-caught Atlantic halibut collected during historic (1964–1974) and recent (1997–2005) time periods

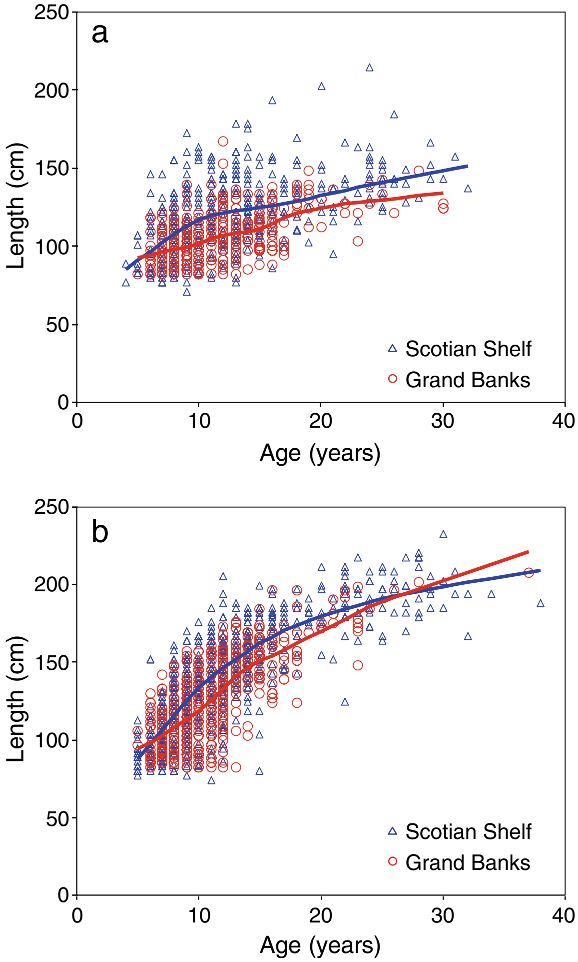

Fig 8 Length at age for male (**a**) and female (**b**) longline-caught Atlantic halibut from the Scotian Shelf (*blue triangles*) and southern Grand Banks (*red circles*). Fitted lines are locally weighted least squares (LOESS) regressions

nations up to 26 years for both sexes. While there may be variations of the surface-ageing technique that can increase the range of fish sizes which can be aged accurately, surface ageing of otoliths is generally considered to become less reliable at older ages (Campana 2001).

Thin-sectioning and break-and-burn ageing techniques have been demonstrated to produce more accurate age readings compared to surface ageing in numerous fish species. Otolith sections and whole otoliths produced comparable ages in yellowtail flounder up to an age of 7 years, after which surface readings underestimated the actual age by as much as 50% in the oldest fish (Dwyer et al. 2003). Summer flounder (*Paralichthys dentatus*) sectioned otoliths had the shortest reading times, the highest confidence scores, the highest within- and between-reader agreement, and were consistently clearer and easier to read than whole otoliths (Sipe and Chittenden 2001). The IPHC has greater confidence in age readings of Pacific halibut prepared with break and burn compared to those aged whole (Forsberg 2001); only the former has been validated as producing accurate ages (Piner and Wischniowski 2004). In general, thin-sectioning and break-and-burn ageing techniques would be expected to provide more accurate age estimates than surface readings because of the asymmetric growth of old otoliths (Chilton and Beamish 1982; Treble et al. 2008).

A rigorous comparison of ageing precision and accuracy between the break-and-burn and thin-sectioning methods would have been useful, but was not possible in this study. The break-and-burn method has often been used with flatfish otoliths (Chilton and Beamish 1982; Forsberg 2001), while otolith transverse sections have been used most often in other species (Casselman 1983). In fish species where the otolith pair is symmetric, one otolith could have been used for one ageing method, and the other otolith used in the second method. However, flatfish otoliths are unusual in that they are asymmetric, with the blind-side otolith preferred for ageing (Jespersen 1917; Lear and Pitt 1975; Forsberg 2001). Thus an exact comparison of the two methods would have required a logistically challenging comparison of a single otolith, aged both through sectioning and break and burn. Our comparison of the two ageing methods was not able to disentangle inter-laboratory effects, and found about a 10–15% bias between methods. Nevertheless, given that both methods take advantage of a transverse view through the centre of the otolith, there is no reason to expect a systematic difference between them, although ageing precision may well vary.

Our growth curve compares well with published growth information for Atlantic halibut from other areas of the north Atlantic. Sexual dimorphism in Atlantic and Pacific halibut size and growth has been well documented (Jespersen 1917; Devold 1938; Joensen 1954; McCracken 1958; Bowering 1986; Jákupsstovu and Haug 1988; Trumble et al. 1993; Sigourney et al. 2006). In most studies, juvenile growth was reported to be rapid and similar between sexes until sexual maturity, which ranges from 55 to 80 cm in length (4 or 5 to 12 years) in males and 103–125 cm in length (7–13 years) in females, depending upon the area under consideration. After the presumed onset of maturity, we found that females had a faster growth rate than males, and reached a substantially larger size. Based on otolith sections, male and female halibut from the Faroe Islands were reported to grow faster than in any other location where Atlantic halibut have been studied (Jákupsstovu and Haug 1988), an observation made previously by both Joensen (1954) and McCracken (1958). On the other hand, Pacific halibut appear to grow slower than Atlantic halibut (Blood 2003).

Our results confirm that Atlantic halibut is a long-lived species, living up to 40–50 years in the northwest Atlantic. Longevity estimates of 50 and 41 years have also been reported from the Faroe Islands (Jákupsstovu and Haug 1988) and Norway (Devold 1938), respectively; both estimates are assumed to be correct given their use of thin-sectioning and break-and-polish methods. Based on a validated ageing method (Piner and Wischniowski 2004), both sexes of Pacific halibut have been reported to live to an age of at least 55 years (Forsberg 2001). Similarly, Dover sole (*Microstomus pacificus*) have been aged as old as 60 years (Munk 2001). Longevities of other flatfish species appear to be less than that of Atlantic halibut. Maximum ages based on otolith sections have been reported to range between 24–25 yr for yellowtail flounder (Dwyer et al. 2003), starry flounder (*Platichthys stellatus*; Campana 1984), and witch flounder (*Glyptocephalus cynaglossus; Burnett et al. 1992).*

Our results indicate that gear selectivity can produce marked effects on estimates of length at age, with longline gear selecting for larger, faster-growing halibut than trawl gear, especially at small sizes. The extent of the gear selectivity was sufficiently large so as to provide very different estimates of length at age depending on the gear used for collection, suggesting that incorrect assumptions about growth could result if this effect were ignored. Similar size-dependent gear selectivity has been reported for Atlantic halibut in US waters (Sigourney et al. 2006) and for Pacific halibut (Kaimmer 1999).

Over a period of four decades we observed no appreciable change in the growth rate of Atlantic halibut caught with trawl gear. The possibility that a change in length at age might have occurred among older/larger fish could not be rejected, since historic longline samples were not available for examination. Nevertheless, there does not appear to be any reduction in growth rate of the scale documented for other groundfish species on the Scotian Shelf since the 1980s (Zwanenburg et al. 2002). In contrast, Pacific halibut weight at age has declined markedly over the last century (Clark and Hare 2002).

There was no strong evidence of spatial structure in size at age across the Atlantic halibut stock area, although males caught with longlines tended to be larger at age on the Scotian Shelf than on the Grand Banks. Neilson et al. (1987) suggested that both male and female halibut were larger at age on the Scotian Shelf, but those inferences were based on less accurate otolith surface ageing. If real differences in size at age do exist between the Scotian Shelf and the Grand Banks, they are difficult to rationalize with existing information on halibut stock structure. Tagging studies indicate that Atlantic halibut move extensively throughout the Northwest Atlantic (McCracken 1958; Stobo et al. 1988; Kanwit 2007), often well outside Canada's 200-mile exclusive economic zone (McCracken 1958; Jensen and Wise 1961; Trzcinski et al. 2009). Movements of fish between areas would be expected to homogenize any spatial differences in growth rate. A tendency for small halibut (<75 cm) to move further than large halibut could produce a gradient in size at age (Stobo et al. 1988), although Bowering (1986) reported that both small (<57 cm) and large (120 cm) halibut could travel long distances. Further research on halibut movements within the stock area will be required before this issue can be fully resolved.

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