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Original research article

Can back-calculated lengths based on otoliths measurements provide reliable estimates of Atlantic halibut (*Hippoglossus hippoglossus*) growth in the Gulf of Maine (U.S.A.)?

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ABSTRACT

Atlantic halibut (*Hippoglossus hippoglossus*, Linnaeus, 1758) are a data-poor stock within the waters of the United States. This study evaluated the use of otolith measurements to back-calculate lengths of Atlantic halibut at previous ages. Back-calculations have proven useful for estimating length at age and growth rates of other species. To the best knowledge of the authors, this study is the first to document the use of this method for Atlantic halibut. Otolith back-calculations rely on a few key assumptions, such as proportionality of fish length and otolith length, which are not always met. This study shows that back-calculations using the Fraser-Lee method can provide reasonable estimates of Atlantic halibut length at previous ages, especially when samples from young halibut are included to improve estimates of the intercept of the linear regressions. Based on back-calculated estimates, female and male halibut in the Gulf of Maine showed different growth rates after age five. There was no evidence of changes in growth rates over an approximately 15 year time period. Halibut caught in the Gulf of Maine and on the neighboring Scotian Shelf showed some differences in growth rates; however, the results did not support strong conclusions about differences between the two regions as the direction of the differences was not consistent between the sexes and previous tagging studies have shown extensive movement between the two areas. The finding of reasonably accurate back-calculated lengths at previous ages is important for this data-poor species, as back-calculations increase the amount of information that can be obtained from otoliths.

1. Introduction

In the early 1800s Atlantic halibut (*Hippoglossus hippoglossus*, Linnaeus, 1758) were so abundant in the Gulf of Maine (GOM) as to be considered a nuisance to fishermen targeting Atlantic cod (*Gadus morhua*, Linnaeus, 1758) and other groundfish. Halibut were an abundant, low-value species in New England until the mid-nineteenth century when the expansion of railroads, changing social tastes, and declining abundances of other commercial species led to the development of a brief but intense targeted commercial halibut fishery in the GOM. In some areas, fishermen noticed declines in halibut abundances after little more than a decade of targeted commercial fishing. Halibut abundances throughout the GOM collapsed by the turn of the century (Goode & Collins, 1887; Grasso, 2008). The stock remains overfished (Northeast Fisheries Science Center, 2015). The National Marine Fisheries Service considers Atlantic halibut a “species of concern”, a designation for species the agency thinks may warrant listing as endangered or threatened under the Endangered Species Act, but for which insufficient data exist to make such a listing determination.

Both fisheries-independent and fisheries-dependent data on halibut in the GOM are quite limited. Semi-annual fishery-independent bottom trawl surveys that take place in the region catch few halibut each year, in most years catching fewer than ten halibut and in some years catching no halibut (Blaylock & Legault, 2012; Sherman, Stepanek, King, Tetrault, & Eckert, 2012). This is likely the result of low abundances and survey gear selectivity. Fisheries for Atlantic halibut in the GOM are relatively small. Landings throughout the northeast U.S., including state and federal waters,

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averaged 32.5 mt per year from 2007 through 2014 (Northeast Fisheries Science Center, 2015). Maine is the only state which allows a directed fishery in state waters. From 2007 through 2014, the Maine Atlantic halibut commercial fishery averaged 23.00 mt landed per year (DMR, 2016).

The Scotian Shelf and Grand Banks (both in Canadian waters) are generally considered the center of halibut distribution in the Northwestern Atlantic. The GOM is in the southern extent of the species' range (Collette & Klein-MacPhee, 2002, pp. 569–572; Trumble, Neilson, Bowering, & Mccaughran, 1993). Past studies have shown evidence of regional variation in Atlantic halibut growth rates (Armsworthy & Campana, 2010; Haug, 1990; Sigourney, Ross, Brodziak, & Burnett, 2006). A tagging study found extensive movement of Atlantic halibut between the GOM and nearby Canadian waters (Kanwit, 2007). One objective of this study was to compare growth rates of halibut in the GOM to halibut in neighboring Canadian waters to determine if there are differences in growth between these regions.

This study examined halibut growth rates in the GOM using a collection of otoliths obtained from a variety of sources. Most otoliths were obtained from cooperative research efforts carried about by the Maine Department of Marine Resources (DMR) with commercial halibut fishermen and seafood dealers (DeGraaf & Bennett, 2010; Kanwit, 2007). These samples were used to characterize length at age and growth of halibut off the coast of Maine and to evaluate the use of back-calculated size at previous ages based on otolith measurements. Back-calculations based on otolith measurements have proven useful for estimating individual growth for others species, including the closely-related Pacific halibut (*Hippoglossus stenolepis*, Southward, 1962, 1967; Campana, 1990). The authors found no examples of back-calculations of size at previous ages for Atlantic halibut in the peer-reviewed literature.

Back-calculations rely on a number of assumptions, the most important of which is the assumption of a proportional relationship between otolith size and fish size. This assumption is not always met on an individual level and it is often not met when growth rates vary within a population. For example, slow-growing fish can have relatively large otoliths compared to faster growing fish. This can result in underestimation of lengths at previous ages, especially for older fish, and is known as Lea's phenomenon (Campana, 1990; Campana & Jones, 1992). If issues of bias in back-calculated estimates are minimal for Atlantic halibut, this method could provide new information based on existing data. Atlantic halibut are not a research priority in the GOM and are likely to continue to be data-poor, at least for the near future, thus any new information gleaned from existing data may prove useful.

2. Methods

2.1. Origin of otolith samples

A total of 416 left sagittal Atlantic halibut otoliths were examined. Most (i.e. 393) of these otoliths were collected during a cooperative research survey organized by the DMR. Fifteen of the otoliths were collected by the DMR through a sampling program focused on commercial fishermen and fish dealers (Table 1). The DMR collected hundreds of additional otoliths which were not examined because the sex of the halibut from which they were obtained was not known.

All DMR samples (i.e. samples from the cooperative research survey and the commercial fishery) came from halibut caught with circle hooks on demersal longlines (called tub trawls by Maine fishermen). The cooperative survey employed commercial halibut fishermen and their vessels and operated under the same gear, season, and minimum fish size restrictions as the Maine commercial halibut fishery. The survey took place from Penobscot Bay, Maine to the Canadian border, from 3 to about 30 nautical miles from shore (Kanwit, 2007). The Maine commercial halibut fishery is limited to state waters (0–3 miles from shore). All DMR samples were collected during the months of May and June.

Six additional left sagittal otoliths were obtained from halibut caught in Cobscook Bay, Maine as part of a University of Maine bottom trawl survey (Vieser, 2014, p. 133). Two additional left sagittal otoliths were obtained from the GOM Northern Shrimp trawl survey carried out by the Northeast Fisheries Science Center (NEFSC) (Table 1). These eight additional samples from bottom trawl surveys were included in the sample to provide information on small halibut. All samples collected with longline gear were from halibut greater than 86 cm, due to minimum fish size restrictions in the cooperative research survey and the commercial fishery. Longline gear tends to capture larger halibut than bottom trawls gear (Armsworthy & Campana, 2010; Neilson, Waiwood, & Smith, 1989; Scott & Scott, 1988; Sigourney et al., 2006). Additionally, Sigourney et al. (2006) found that longlines capture halibut with larger sizes at age than bottom trawls. The impacts of gear effects on the results of this study are assumed to be minimal because the sample of otoliths from halibut caught with bottom trawls was much smaller than longline sample (Table 1).

One of each pair of otoliths was embedded in resin, cross sectioned, and photographed according to DMR protocols (DeGraaf & Bennett, 2010).

2.2. Growth data for comparison with Canadian waters

The Bedford Institute of Oceanography provided age and length data for 1655 4–15 year old Atlantic halibut caught between 1999 and 2005 in the Canadian commercial halibut fishery on the Scotian Shelf ($n_{\text{female}} = 553$, $n_{\text{male}} = 304$) and southern Grand Banks ($n_{\text{female}} = 497$, $n_{\text{male}} = 301$). These otoliths were from halibut caught with longline gear and circle hooks (Armsworthy & Campana, 2010). These data were only used to compare growth of halibut in the GOM with growth in neighboring regions.

2.3. Evaluating the relationship between halibut length and otolith length

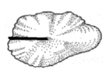
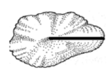
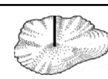
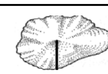
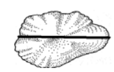
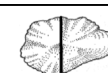
Back-calculations rely on the assumption of a proportional relationship between otolith size and fish size (Campana, 1990). This assumption was tested by performing linear regressions of the length of 100 randomly selected otoliths against the length of the halibut from which they came. These 100 otoliths were selected using stratified random sampling to evenly represent both sexes and the full range of sizes in the DMR sample. The 8 otoliths from halibut caught with bottom trawls were not included in this selection. Linear regressions were calculated using six different ways of measuring the otolith to determine which measurement best predicted halibut length. These six measurements were made using dial-readout calipers and the naked eye and included: the posterior radius, the anterior radius, the dorsal radius, the ventral radius, the dorso-ventral diameter, and the antero-posterior diameter (Table 2).

Measurements of right sagittal otoliths were used for the linear regressions of fish length against otolith length; however, annuli measurements from the left sagittal otoliths were used for back-calculations. The position of the nucleus tends to differ between left and right sagittal otoliths (Forsberg, 2001; Welleman & Storbeck, 1995), thus it would have been preferable to evaluate the relationship between otolith length and halibut length using the same "sided" otolith that was used to measure annuli; however, this was not possible because most left sagittal otoliths in the

Table 1
The source and number of the otoliths samples used in this analysis.

Program	Gear	Size of halibut (total length)	Number of otoliths by year								Total
			2003	2004	2007	2008	2009	2010	2012	2013	
DMR cooperative research survey	Longline	86.4–157.5 cm	329	18	15	31					393
Maine commercial fishery	Longline	96.5–152.4 cm					9	6			15
University of Maine Cobscook Bay trawl survey	Bottom otter trawl	21.0–31.5 cm							4	2	6
NEFSC northern shrimp survey	Bottom otter trawl	35.6 and 37.3 cm							2		2
Total			329	18	15	31	9	6	6	2	416

Table 2
Results of linear regressions between halibut length (cm, total length) and the length of six otolith growth axes (mm).

		 Posterior radius	 Anterior radius	 Dorsal radius	 Ventral radius	 Dorso-ventral diameter	 Antero-posterior diameter
Female ($n = 49$)	Slope	16.67	12.12	23.80	19.85	8.330	14.03
	Intercept	26.09	21.75	19.16	33.76	5.501	0.2756
	Adjusted r^2	0.4151	0.4150	0.4591	0.2145	0.5810	0.4250
Male ($n = 51$)	Slope	5.241	6.331	13.83	11.84	5.341	8.580
	Intercept	80.03	59.48	54.01	61.15	39.62	41.00
	Adjusted r^2	0.07797	0.2807	0.2559	0.3228	0.3336	0.4041
Combined ($n = 100$)	Slope	13.01	10.27	21.67	17.08	7.793	12.15
	Intercept	43.14	33.16	25.98	43.14	10.71	14.79
	Adjusted r^2	0.3208	0.3873	0.4466	0.3003	0.5472	0.4673

sample were embedded in resin and sectioned before this study took place (DeGraaf & Bennett, 2010).

2.4. Estimating age at capture

High-resolution images of thin sections cut through the dorso-ventral diameter of the otolith were used to estimate age at capture (DeGraaf & Bennett, 2010). The primary author was the sole age reader. A validation comparison of her estimates and those of an expert otolith age reader at the NEFSC was performed to ensure that the estimates were not biased (Campana, 1992). The two age readers independently estimated the ages of fifty otoliths selected using stratified random sampling to proportionally represent both sexes and the range of sizes in the overall sample.

2.5. Back-calculating length at previous ages

The diameters of all annuli were measured using ObjectJ, an analysis package designed for use with the open source software ImageJ (Rasband, 2013; Vischer & Nastase, 2013). Sizes at previous ages were back-calculated using these annuli measurements and the coefficients of a linear regression between otolith length and halibut length at capture.

Back-calculations were made using two different equations, one based on a simple linear regression

$$L_t = a + bO_t + \varepsilon_t \tag{1}$$

where L_t is halibut total length at age t, O_t is the length of annuli corresponding to age t, ε_t is an error term, and a and b are the regression coefficients; and the other based on the Fraser-Lee method

$$L_t = a + \frac{L_C - a}{O_C} O_t + \varepsilon_t \tag{2}$$

where L_t is halibut length at age t, O_t is the length of the annuli corresponding to age t, L_C is halibut length at capture, O_C is otolith length at capture, ε_t is an error term, and a is the intercept of the linear regression.

The Fraser-Lee method factors individual variation in the relationship between otolith length and halibut length into the back-calculated estimates. Under-estimation of length at age for older fish is a common problem with unadjusted back-calculations. The Fraser-Lee method usually provides more accurate estimates of length at older ages compared to back-calculations based on simple linear regressions (Campana, 1990).

2.6. Growth rate estimation

Back-calculated lengths were used to estimate von Bertalanffy growth functions (VBGF; Ricker, 1975), described as

$$L_t = L_\infty \left(1 - e^{-K(t - t_0)}\right) \tag{3}$$

where L_t is the mean length at age t (in this case, the back-calculated length), L_∞ is the theoretical maximum length, K is a growth rate parameter, and t_0 is the theoretical age at a length of zero (Ricker, 1975). VBGF parameters were estimated using weighted least squares, with each mean length at age weighted by sample size. VBGFs were estimated using the FSA package (Ogle, 2009) in the statistical analysis program R (version 3.0.2, the R Foundation for Statistical Computing, 2013). VBGF models for the two sexes and for different areas were compared using an analysis of residual sum of squares (Chen, Jackson, & Harvey, 1992), which used an F-statistic (Equation (4)) to determine if VBGFs were significantly different from one another. The F-statistic was calculated as

$$F = \frac{(RSS_P - RSS_S)/(DF_{RSS_P} - DF_{RSS_S})}{RSS_S/DF_{RSS_S}} \tag{4}$$

where RSS_p is the residual sum of squares for VBGFs fitted with combined data (e.g. females and males together), RSS_s is the sum of the residual sum of squares for each VBGF fitted with separate samples (e.g. *RSS* for females and *RSS* for males), DF_{RSSp} is the degrees of freedom for the combined data, and DF_{RSSs} is the sum of the degrees of freedom for the models fitted to separate samples.

An analysis of covariance was performed to determine if sex had an influence on the slope of the linear regression between halibut length and otolith length (measured along the dorso-ventral diameter).

2.7. Comparing growth through time

Increases in length by calendar year were estimated for every halibut in the sample using back-calculated estimates of length during previous years. Average growth by age class and by sex was plotted across time to look for evidence of changes in growth over time.

3. Results

3.1. The relationship between halibut length and otolith length

All six ways of measuring the otoliths showed moderate linear correlations with halibut length. The dorso-ventral diameter showed the strongest correlation with length for female halibut and for both sexes combined. The antero-posterior diameter showed the strongest correlation with length for male halibut (Table 2).

The influence of sex was not significant when the 8 samples from halibut caught with bottom trawls (all of which were less than 50 cm in length) were included. When the analysis of covariance was performed with only those halibut caught with longlines (all of which were at least 86 cm in length) sex did influence the slope of the regression (Fig. 1, Tables 3 and 4).

3.2. Validation of age estimates

A comparison of the primary author's age estimates with those of an expert otolith age reader showed 62 percent total agreement, 90 percent agreement to within one year, and a CV of 1.35 (Fig. 2). The International Pacific Halibut Commission has estimated the ages of Pacific halibut since the early 1900s and seeks a standard of agreement between age readers based on a maximum CV of 4.0, a

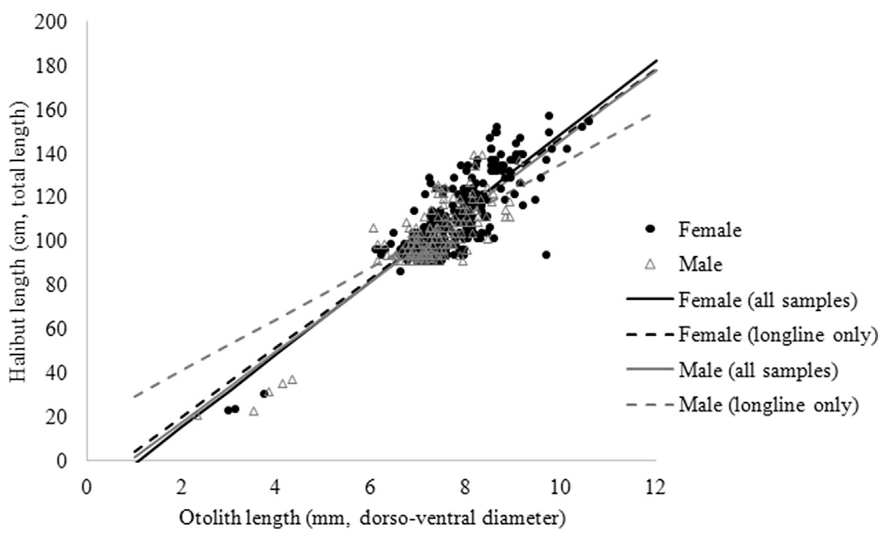


Fig. 1. Otolith length plotted against halibut length, by sex. Solid lines represent linear regressions of halibut length against otolith length including all samples ($n_{female} = 264$, $n_{male} = 152$). Dashed lines represent linear regressions of halibut length against otolith length using only samples from halibut caught with longline gear ($n_{female} = 261$, $n_{male} = 147$). Coefficients of the linear regression are shown in Table 4.

Table 3
Results of an analysis of covariance on a linear regression of halibut length (cm, total length) against otolith length (mm, measured along the dorso-ventral diameter) and sex. The analysis was performed once with all otoliths in the sample (416 otoliths, 264 from female halibut and 152 from male halibut), and once with only those otoliths from halibut caught with longlines (408 otoliths, 261 from female halibut and 147 from male halibut). The halibut caught with longlines were much larger (86.4–157.5 cm) than the halibut caught with bottom trawls (8.5–37.5 cm).

Coefficients	All otoliths ($n = 416$)				Only otoliths from halibut caught with longlines ($n = 408$)			
	Estimate	Std. Error	*T*-value	*P*-value	Estimate	Std. Error	*T*-value	*P*-value
Intercept	−18.26	5.071	−3.601	0.0003560	−11.94	5.797	−2.059	0.04011
Otolith length	16.69	0.6580	25.369	<2 E-16	15.89	0.7487	21.22	<2 E-16
Sex (M)	3.608	8.169	0.4420	0.6589	29.25	0.7487	2.605	0.009540
Oto. length: Sex (M) Interaction	−0.6486	1.0938	−0.5930	0.5535	−4.101	1.496	−2.741	0.006400
Degrees of freedom	412				404			
Adjusted R^2	0.7132				0.5814			

Table 4
Coefficients of linear regressions of halibut length (cm, total length) and otolith length (mm, dorso-ventral diameter). Coefficients are shown for regressions of all samples, by sex ($n_{female} = 264$, $n_{male} = 152$), and for regressions using only the samples caught with longline gear ($n_{female} = 261$, $n_{male} = 147$).

	Female (longline only)	Male (longline only)	Female (all samples)	Male (all samples)
Slope	15.88	11.79	16.69	16.04
Intercept	−11.94	17.32	−18.26	−14.65

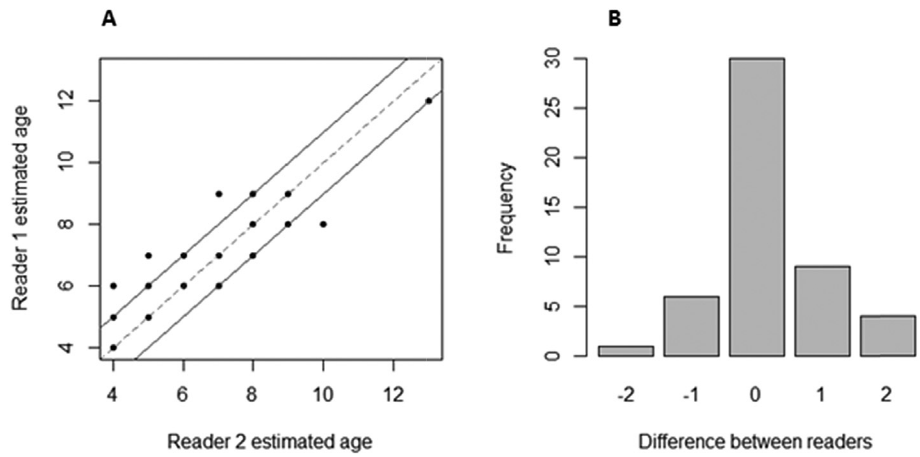


Fig. 2. A) An age bias plot comparing the primary author's age estimates (reader 1) with the estimates of a federal fisheries biologist and experienced otolith reader (reader 2). The dashed line represents total agreement on ages and the solid lines represent agreement to within one year. B) Frequency plot of differences between estimated ages of reader 1 and reader 2.

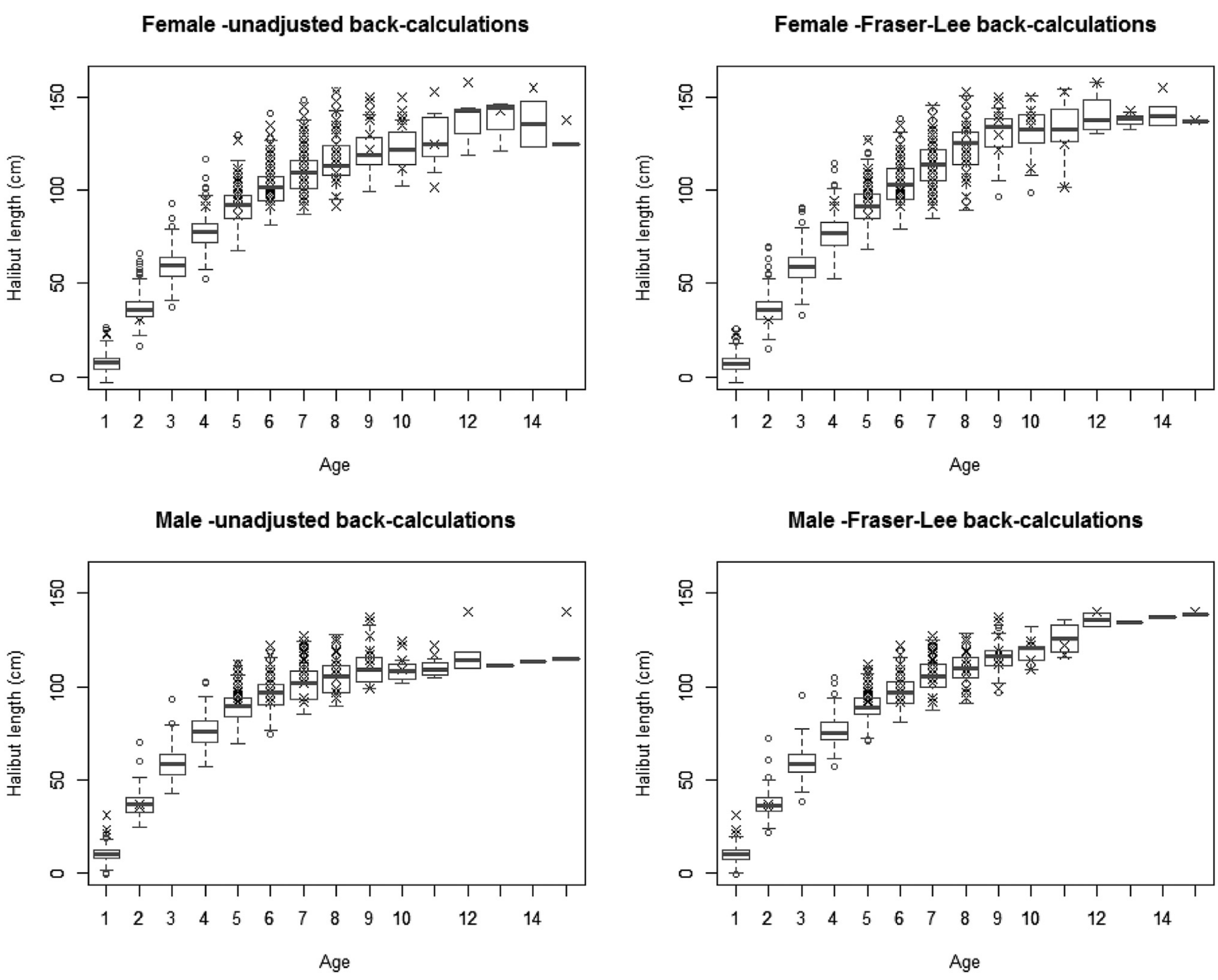


Fig. 3. Observed lengths (cm, total length) at age (symbolized as x's), plotted against back-calculated lengths at age (box plots and circles), by sex, using unadjusted back-calculations and the Fraser-Lee method. Back-calculations shown in this figure were performed using all 416 otoliths, including 408 from halibut caught with longlines (ages 4–15) and 8 from halibut caught with bottom trawls (ages 1–2).

Table 5
Number of samples, mean lengths at age, and standard deviations for both observed lengths at age and back-calculated lengths at age, by sex, using the Fraser-Lee method, including 408 otoliths from halibut caught with longline gear (ages 4–15) and 8 otoliths from halibut caught with bottom trawl gear (ages 1–2). P-values are from Welch's two sample t-tests comparing average observed lengths at age to average back-calculated lengths at age.

Female								Male							
Age	Observed			Back-Calculated			*P* value	Age	Observed			Back-Calculated			*P* value
	N	Mean estimated fish length (cm)	St. dev.	N	Mean estimated fish length (cm)	St. dev.			N	Mean estimated fish length (cm)	St. dev.	N	Mean estimated fish length (cm)	St. dev.	
1	2	23.50	0.7071	264	7.471	4.443	0.002970	1	3	25.17	5.575	152	10.069	4.123	0.04127
2	1	30.50	NA	262	36.49	7.7129	NA	2	2	36.45	1.202	149	37.36	6.687	0.4627
3	0	NA	NA	261	59.49	8.836	NA	3	0	NA	NA	147	59.18	7.417	NA
4	2	92.71	1.796	261	77.29	9.489	0.02159	4	0	NA	NA	147	76.32	7.718	NA
5	83	98.13	5.947	259	91.57	9.744	3.09E-12	5	52	98.0037	5.560	147	89.42	7.382	1.82E-14
6	69	106.7	10.18	176	102.8	11.28	0.00939	6	40	100.6	7.537	95	97.47	8.410	0.03380
7	53	115.7	12.97	107	112.8	12.66	0.1865	7	19	109.8	10.64	54	105.2	9.247	0.1038
8	29	122.2	15.98	54	121.0	13.61	0.743	8	15	108.4	10.60	35	109.8	9.541	0.6577
9	11	139.2	8.410	25	130.1	11.59	0.01289	9	12	118.1	10.58	21	115.9	9.176	0.5589
10	7	135.7	11.81	14	130.8	14.42	0.4133	10	5	118.9	6.816	9	119.3	7.570	0.9079
11	3	126.2	25.44	7	132.3	17.80	0.7315	11	2	119.4	3.592	4	125.7	8.944	0.2896
12	1	157.5	NA	4	140.5	12.00	NA	12	1	139.7	NA	2	135.9	5.230	NA
13	1	142.2	NA	3	137.5	4.620	NA	13	0	NA	NA	1	134.3	NA	NA
14	1	154.9	NA	2	139.9	7.009	NA	14	0	NA	NA	1	136.9	NA	NA
15	1	137.2	NA	1	136.8	NA	NA	15	1	139.7	NA	1	138.4	NA	NA

Table 6
Number of samples, mean lengths at age, and standard deviations for both observed lengths at age and back-calculated lengths at age, by sex, using the Fraser-Lee method, including only the 408 otoliths from halibut caught with longline gear. P-values are from Welch's two sample t-tests comparing average observed lengths at age to average back-calculated lengths at age.

Female								Male							
Age	Observed			Back-Calculated			*P* value	Age	Observed			Back-calculated			*P* value
	N	Mean estimated fish length (cm)	St. dev.	N	Mean estimated fish length (cm)	St. dev.			N	Mean estimated fish length (cm)	St. dev.	N	Mean estimated fish length (cm)	St. dev.	
1	0	NA	NA	261	12.52	4.312	NA	1	0		NA	152	35.57	3.430	NA
2	0	NA	NA	261	40.14	7.462	NA	2	0		NA	149	55.53	6.0766	NA
3	0	NA	NA	261	61.96	8.624	NA	3	0		NA	147	71.51	8.525	NA
4	2	92.71	1.796	261	78.88	9.323	0.02603	4	0		NA	147	84.00	9.0216	NA
5	83	98.13	5.947	259	92.45	9.673	9.021 E-10	5	52	98.00	5.56	147	93.56	9.344	7.270 E-9
6	69	106.7	10.18	176	103.4	11.29	0.02773	6	40	100.6	7.537	95	98.18	11.15	0.1378
7	53	115.7	12.97	107	113.2	12.69	0.2592	7	19	109.8	10.64	54	103.4	8.935	0.02644
8	29	122.2	15.98	54	121.4	13.64	0.8189	8	15	108.4	10.6	35	105.7	11.090	0.4365
9	11	139.2	8.41	25	130.4	11.54	0.01581	9	12	118.1	10.58	21	108.8	12.94	0.03302
10	7	135.8	11.81	14	131.0	14.40	0.4365	10	5	118.9	6.816	9	107.5	8.0291	0.01932
11	3	126.1	25.44	7	132.5	17.83	0.7216	11	2	119.4	3.592	4	107.2	4.128	0.0485
12	1	157.5	NA	4	140.8	11.85	NA	12	1	139.7	NA	2	122.0	7.220	NA
13	1	142.2	NA	3	137.7	4.752	NA	13	0	NA	NA	1	111.9	NA	NA
14	1	154.9	NA	2	140.1	7.205	NA	14	0	NA	NA	1	121.9	NA	NA
15	1	137.2	NA	1	136.8	NA	NA	15	1	139.7	NA	1	124.7	NA	NA

Table 7
Parameter estimates for von Bertalanffy growth functions (VBGF) for female halibut, for male halibut, and for both sexes combined. Parameters were estimated using Fraser-Lee back-calculated estimates of length at previous ages using 408 samples from halibut caught with longline gear (ages 4–15) and 8 samples from halibut caught with bottom trawl gear (ages 1–2). The residual sum of squares (*RSS*) and degrees of freedom (*DF*) were used to calculate *F*-values to determine if the female and male VBGFs were significantly different from one another. The Critical *F* value represents the threshold *F* value for significance at the level of $P \leq 0.05$.

	Linf	*K*	t_0	*RSS*	*DF*	*F*	Critical *F* ($P < 0.05$)
Female GOM	149.8	0.2242	0.7643	758.1	12	44.04	3.008787
Male GOM	131.494	0.26	0.697	1003	12		
All GOM	142.6117	0.2371	0.7402	11456	24		

minimum total agreement of 55 percent, and a minimum of 80 percent agreement to within one year (Forsberg, 2001). The validation results presented here met these criteria, thus the age estimates can be considered unbiased.

3.3. Observed lengths at age

Estimated ages at capture ranged from 1 to 15 years for both female and male halibut from the GOM. Female observed (as opposed to back-calculated) lengths at age were on average greater than male observed lengths at age after age five (Fig. 3, Table 5).

Fig. 4. Von Bertalanffy Growth Functions (VBGFs) for female and male halibut and for both sexes combined (labeled as "all"). VBGFs were estimated using Fraser-Lee back-calculated estimates of length at previous ages using 408 samples from halibut caught with longline gear (ages 4–15) and 8 samples from halibut caught with bottom trawl gear (ages 1–2). Parameter estimates are listed in Table 7.

This finding corresponds with other studies (Armsworthy & Campana, 2010; Bowering, 1986, p. 32; Haug, 1990; Karlson, Michalsen, & Folkvord, 2013). However, the differences in observed lengths at age between the sexes were only statistically significant for ages 6, 9, and 10.

3.4. Back-calculated lengths at previous ages and back-calculated growth rates

The Fraser-Lee method of back-calculation (Equation (2)) provided estimates that more closely matched observed lengths at age than estimates generated with the simple linear regression equation (Equation (1), Fig. 3). Fraser-Lee back-calculated lengths were more similar to observed lengths at age when all otoliths were used to perform the back-calculations, rather than when only those caught with longline gear were used (Tables 5 and 6). Female and male back-calculated lengths at age were significantly different from one another for ages 5–10.

An analysis of residual sum of squares (Equation (4)) showed that female and male VBGFs based on Fraser-Lee estimates were significantly different from one another (Table 7). The VBGFs predicted similar lengths at age for female and male halibut until age five, after which female lengths at age exceeded male lengths at age (Table 5, Fig. 4).

3.5. Temporal variation in growth rates

Temporal trends in growth rates were not evident, based on

Table 8
Growth of year classes through time (average cm per year) based on Fraser-Lee back-calculated estimates of length at previous ages.

Average growth (cm)									
Year	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8
Female									
1988	5.985								
1989	13.868								
1990	9.812								
1991	8.481								
1992	4.679								
1993	9.279								
1994	9.634	32.783							
1995	9.299	28.565	18.889						
1996	7.079	31.182	22.944	16.215					
1997	7.299	27.883	20.963	17.047	15.754				
1998	6.948	30.917	23.460	17.483	17.719	13.133			
1999	8.927	29.119	23.409	17.890	13.991	12.600	10.169		
2000	9.692	28.553	23.590	17.989	14.869	11.970	10.606	7.346	
2001	5.335	23.874	22.347	17.853	13.623	11.488	9.399	8.309	5.379
2002	7.715	26.989	21.440	18.361	13.814	9.396	8.457	6.476	6.416
2003	7.495	25.835	21.228	17.794	16.080	10.609	10.363	3.521	
2004			22.522	17.195	12.909	11.577	11.378	7.124	2.891
2005				18.819	13.449	10.443	8.176	8.021	8.235
2006					16.236	13.267	7.864	7.231	7.455
2007						11.010	10.594	6.764	10.173
2008							9.377	7.364	
Male									
1988	18.363								
1992	12.230								
1993	11.994	23.682							
1994	11.275	27.298	20.549						
1995	11.337	28.192	19.365	16.387					
1996	9.173	27.852	20.529	16.600	14.750				
1997	9.760	26.227	21.076	15.315	14.946	11.576			
1998	9.347	28.475	22.274	19.580	13.213	10.258	7.331		
1999	16.771	25.647	22.369	16.582	11.406	9.705	7.019	4.560	
2000	8.946	27.287	21.251	17.188	12.468	9.436	5.682	5.955	3.740
2001	10.494	28.250	18.948	19.311	13.317	8.909	6.613	3.769	4.090
2002	12.489	25.760	20.915	12.777	14.475	7.998		3.582	
2003	9.792	25.085	20.417	15.735	10.508				3.347
2004			25.849	16.430	12.688	8.103			
2005	8.676			19.820	13.915	9.412	7.525		
2006					15.441	9.921	7.045	5.725	
2007						6.176	6.915	6.347	4.333
2008								6.003	4.509

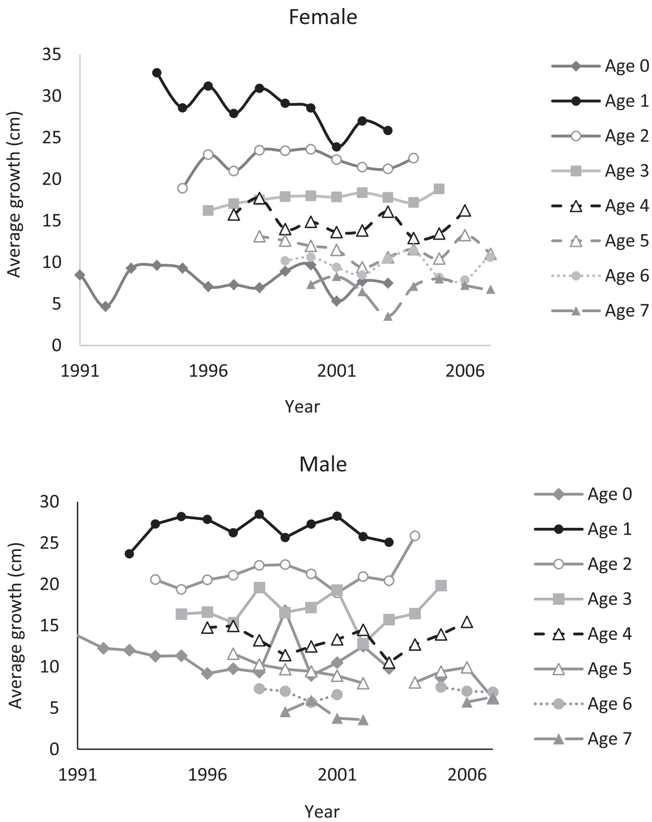


Fig. 5. Average growth (cm) per year, estimated with Fraser-Lee back-calculations, for halibut age 0–7, by age and by sex.

Fraser-Lee estimates of lengths at previous ages (Table 8, Fig. 5). Male halibut showed higher CVs for annual growth (derived from the Fraser-Lee estimates) during 1990–2008, compared to female halibut. When years with three or fewer data points were excluded, no single year between 1990 and 2008 had an average CV for estimated annual growth that fell outside of one standard deviation on either side of the mean for the entire time period, for either sex. Thus, there appears to be no notable trends in growth rates over time in the GOM sample.

3.6. Comparison to growth rates on the Scotian Shelf

VBGFs could not be fit to the age and length data for age 15 and younger halibut caught on the Grand Banks; however, this was possible for halibut caught on the Scotian Shelf. The dataset for halibut caught on the Scotian Shelf did not include female halibut younger than age 5 or male halibut younger than age 4. VBGFs were thus estimated for female halibut caught on the Scotian Shelf using ages 5 through 15 and for male halibut using ages 4 through 15 (to match the maximum age in the GOM sample, though older ages were present in the Scotian Shelf dataset). VBGFs for female and male halibut in the GOM were re-estimated using these same age ranges so direct comparisons between the two regions could be made (Fig. 6). Back-calculated lengths at age were used for the GOM VBGFs. A residual sum of squares analysis (Equation (4)) showed significant differences between growth rates for both sexes between the GOM and the Scotian Shelf (Table 9, Fig. 6); however, the direction of the differences was not consistent between the two sexes. Growth of female halibut in the GOM slowed after about age 9; while growth of female halibut on the Scotian Shelf did not level off between ages 5 and 15. Male halibut showed the opposite trend; growth of male halibut on the Scotian Shelf leveled off at around age 9, while male halibut in the GOM continued to increase between ages 4 and 15. The trend for female halibut in the GOM contradicts previous studies which show that female growth rates continue to increase beyond male growth rates into older ages (Armsworthy & Campana, 2010; Karlson et al., 2013).

4. Discussion

Moderately accurate lengths at previous ages were estimated using Fraser-Lee back-calculations based on measurements of Atlantic halibut annuli. To the best knowledge of the authors, this study is the first to do so for Atlantic halibut, though back-calculations have been used for other species, including the closely related Pacific halibut (Campana, 1990; Southward, 1962, 1967). Back-calculations are especially useful in the GOM where data on halibut in general, and small halibut in particular, are limited. Back-calculations of size at previous ages allow reasonable estimates to fill data gaps on small halibut.

The inclusion of 8 samples from small halibut caught with bottom trawl gear, alongside 408 samples from much larger halibut caught with longline gear, may have introduced some minor confounding effects into the analysis; however, it also improved the accuracy of the estimates. Campana and Jones (1992) showed that biologically-based regression intercepts, such as intercepts defined based on fish and otolith measurements from laboratory-reared larvae, can improve back-calculated estimates of length at previous ages. The inclusion of 8 otoliths from small halibut likely allowed for more biologically-accurate estimates of the intercept for the GOM back-calculation regression.

Both the observed lengths at age and the VBGFs showed similar

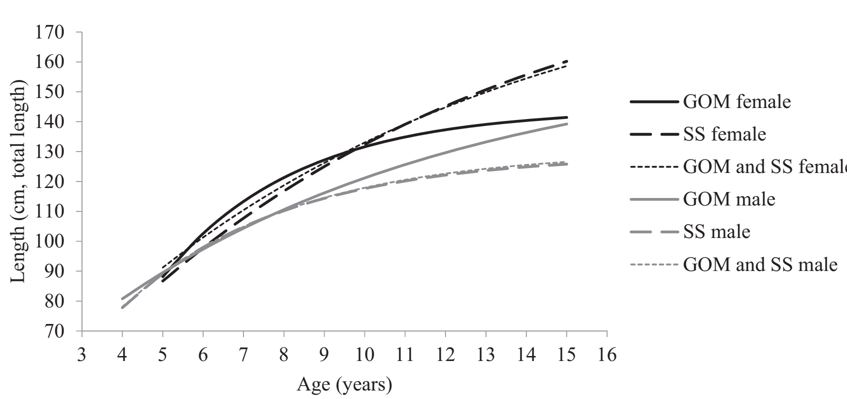


Fig. 6. Von Bertalanffy Growth Functions (VBGFs) by sex for halibut caught in the Gulf of Maine (GOM) and on the Scotian Shelf (SS). GOM VBGFs were estimated using Fraser-Lee back-calculated estimates of length at previous ages. SS VBGFs were estimated using observed lengths at age. Parameter estimates are listed in Table 9.

Table 9
Parameter estimates for von Bertalanffy growth functions (VBGF) for female and male halibut caught in the Gulf of Maine (GOM) and on the Scotian Shelf (SS). Parameters of the GOM VBGFs were estimated using Fraser-Lee back-calculated estimates of length at previous ages. Parameter estimates for the SS VBGFs were estimated using observed lengths at age. Both the GOM and the SS data used to estimate VBGFs were restricted to ages 5–15 for female halibut and 4–15 for male halibut. The residual sum of squares (*RSS*) and degrees of freedom (*DF*) were used to calculate *F*-values to determine if GOM and SS VBGFs were significantly different from one another. The Critical *F* value represents the threshold *F* value for significance at the level of $P \leq 0.05$.

	Ages	*Linf*	*K*	t_0	*RSS*	*DF*	*F*	Critical *F*
Female GOM	5–15	144.3	0.2976	1.827	369.2	390	632.0	2.614
Female SS	5–15	203.2	0.09960	−0.5853	2192	550		
Female GOM and SS	5–15	199.1	0.098040	−1.251	7727	943		
Male GOM	4–15	163.1	0.1125	−2.0763	173.9	367	72.42	2.618
Male SS	4–15	129.1	0.2495	0.3009	2320	301		
Male GOM and SS	4–15	130.3	0.2398	0.1856	3305	671		

lengths at age for female and male halibut until age 5, after which female halibut reached greater lengths at age than male halibut. Sigourney et al. (2006) and Armsworthy and Campana (2010) found similar patterns for halibut in the GOM, and on the Scotian Shelf and Grand Banks, respectively. Sigourney et al. (2006) analyzed some of the DMR samples used in this study. The Scotian Shelf and Grand Banks samples examined in this study were also used by Armsworthy and Campana (2010). Similar patterns in female and male halibut growth rates have been found in other areas, including Norway (Karlson et al., 2013) and Newfoundland and Labrador (Bowering, 1986, p. 32).

To compare VBGFs that were estimated with comparable age ranges, only growth rates between the GOM and the Scotian Shelf were compared with an F-statistic (Equation (4)). The GOM sample included halibut 15 years old and younger, which is characteristic of catches in surveys and fisheries in the GOM, but much younger than the age ranges used to estimate VBGFs in other published studies. For example, Armsworthy and Campana (2010) included otoliths from a 50-year-old halibut in their analysis. For this reason, the GOM VBGF estimates were not compared to other published studies. It was possible to compare GOM and Scotian Shelf VBGFs because scientists at the Bedford Institute of Oceanography shared data which allowed estimation of VBGFs for age 15 and younger halibut. Given that the species can live to at least 50 years of age, it cannot be assumed that the GOM VBGFs are representative of the entire life cycle of Atlantic halibut.

Differences in growth rates were found between the GOM and the nearby Scotian Shelf; however, the direction of the differences was not consistent between the two sexes. Previous studies have found regional differences in halibut growth (Bowering, 1986, p. 32; Haug, 1990; Armsworthy & Campana, 2010; Karlson et al., 2013); however, due to the inconsistent pattern between the sexes, the authors of this study are hesitant to draw strong conclusions about differences between the GOM and neighboring Scotian Shelf.

There was no clear evidence of temporal trends in growth rates in the GOM based on the back-calculations. Growth at age over a relatively short year time period (about 15 years) was examined. Tagging studies in the GOM show that halibut move extensively between the GOM and nearby Canadian waters (Kanwit, 2007). This mobility may allow them to avoid extreme environmental conditions that would impact growth rates.

In conclusion, this study suggests that back-calculations can provide reasonably accurate back-calculated lengths of Atlantic halibut at previous ages and that these estimates can be used to examine patterns in growth rates. Back-calculations increase the amount of information that can be obtained from otoliths, which is beneficial for data-poor species such as Atlantic halibut.

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References

Armsworthy, S., & Campana, S. E. (2010). Age determination, bomb-radiocarbon validation and growth of Atlantic halibut (*Hippoglossus hippoglossus*) from the Northwest Atlantic. *Environmental Biology of Fishes, 89*, 279–295. http://dx.doi.org/10.1007/s10641-010-9696-8.

Blaylock, J., & Legault, C. M. (2012). Section M: Atlantic halibut. In *Northeast Fisheries science center reference document 12-06. Assessment or data updates of 13 northeast groundfish stocks through 2010* (p. 37). Woods Hole: Massachusetts.

Bowering, W. R. (1986). *The distribution, age and growth and sexual maturity of Atlantic halibut (Hippoglossus hippoglossus) in the Newfoundland and Labrador area of the Northwest Atlantic*. Canadian technical report of fisheries and aquatic sciences 1432. St. John's, Newfoundland: Department of Fisheries and Oceans, Fisheries Research Branch.

Campana, S. E. (1990). How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Sciences, 47*(11), 2219–2227.

Campana, S. E. (1992). Measurement and interpretation of the microstructure of fish otoliths. In D. K. Stevenson, & S. E. Campana (Eds.), *Analysis of otolith microstructure data* (pp. 59–71). Ottowa, Canada: Department of Fisheries and Oceans.

Campana, S. E., & Jones, C. M. (1992). Analysis of otolith microstructure data. In D. K. Stevenson, & S. E. Campana (Eds.), *Analysis of otolith microstructure data* (pp. 73–100). Ottowa, Canada: Department of Fisheries and Oceans.

Chen, Y., Jackson, D. A., & Harvey, H. H. (1992). A comparison of von Bertalanffy and polynomial functions in modeling fish growth data. *Canadian Journal of Fisheries and Aquatic Sciences, 49*, 1228–1235.

Collette, B. B., & Klein-MacPhee, G. (2002). *Bigelow and Schroeder's fishes of the Gulf of Maine* (3rd ed.). Washington, D.C.: Smithsonian Institution Press.

DeGraaf, T. C., & Bennett, T. D. (2010). *Aging manual for atlantic halibut: Procedures and methods used at the Maine*. West Boothbay Harbor, Maine: Department of Marine Resources.

DMR (Maine Department of Marine Resources). (2016). *Historical Maine fisheries landings data, Atlantic halibut, 1950-2015*. Hallowell, Maine.

Forsberg, J. E. (2001). *Aging manual for pacific halibut: Procedures and methods used at the international pacific halibut commission (IPHC)*. International Pacific Halibut Commission Technical Report No. 46. Seattle, Washington.

Goode, G. B., & Collins, J. W. (1887). The halibut fisheries. In G. B. Goode (Ed.), *Section V: The History and Methods of the Fisheries: vol. 1. The fisheries and fishery industries of the United States*. Washington, DC: Government Printing Office.

Grasso, G. M. (2008). What appeared limitless plenty: The rise and fall of the nineteenth-century atlantic halibut fishery. *Environmental History, 13*(1), 66–91.

Haug, T. (1990). Biology of the atlantic halibut, *Hippoglossus hippoglossus* (L., 1758). *Advances in Marine Biology, 26*, 1–70.

Kanwit, J. K. (2007). Tagging results from the 2000-2004 federal experimental fishery for Atlantic halibut (*Hippoglossus hippoglossus*) in the eastern Gulf of Maine. *Journal of Northwest Atlantic Fishery Science, 38*, 37–42. http://dx.doi.org/10.2960/J.v38m594.

Karlson, S., Michalsen, K., & Folkvord, A. (2013). Age determination of atlantic halibut (*Hippoglossus hippoglossus* L.) along the coast of Norway: Status and improvements. *ICES Journal of Marine Science, 70*(1), 50–55.

Neilson, J. D., Waiwood, K. G., & Smith, S. J. (1989). Survival of Atlantic halibut

(*Hippoglossus hippoglossus*) caught by longline and otter trawl gear. *Canadian Journal of Fisheries and Aquatic Sciences, 46*, 887–897.
Northeast Fisheries Science Center. (2015). *Operational assessment of 20 northeast groundfish stocks, updated through 2014*. U.S. Department of Commerce Northeast Fisheries Science Center. Reference Document 15–24.
Ogle, D. H. (2009). *FSA: Fisheries stock analysis*. R package version 0.4.2.
Rasband, W. (2013). *ImageJ 1.47v*. USA: National Institutes of Health.
Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada, 191*, 382.
Scott, W. B., & Scott, M. G. (1988). Atlantic fishes of Canada. *Canadian Journal of Fisheries and Aquatic Sciences, 210*, 730.
Sherman, S. A., Stepanek, K. L., King, C. A., Tetrault, R., & Eckert, R. (2012). *Annual report on the Maine-New Hampshire inshore trawl survey*. January 1, 2011 – December 31, 2011. Hallowell, Maine: Maine Department of Marine Resources.
Sigourney, D. B., Ross, M. R., Brodziak, J., & Burnett, J. (2006). Length at age, sexual maturity and distribution of Atlantic halibut, *Hippoglossus hippoglossus* L., off the northeast USA. *Journal of Northwest Atlantic Fishery Science, 36*, 81–90. http://dx.doi.org/10.2960/J.v36.m574.
Southward, G. M. (1962). A method of calculating body lengths from otolith measurements for Pacific halibut and its application to Portlock-Albatross grounds data between 1935 and 1957. *Journal of the Fisheries Research Board of Canada, 19*(2), 339–362.
Southward, G. M. (1967). *Growth of pacific halibut*. Seattle, WA: International Pacific Halibut Commission. Scientific Report No. 43.
Trumble, R. J., Neilson, J. D., Bowering, W. R., & Mccaughran, D. A. (1993). Atlantic halibut (*Hippoglossus hippoglossus*) and Pacific halibut (*Hippoglossus stenolepis*) and their North American fisheries. *Canadian Journal of Fisheries and Aquatic Sciences, 227*, 84.
Vieser, J. D. (2014). *Collaborative research on finfish, their distribution, and diversity in Cobscook Bay, Maine*. Masters Thesis. Orono, ME: University of Maine.
Vischer, N., & Nastase, S. (2013). *ObjectJ v.103.d. Non-destructive marking and linked results plugin for ImageJ*. University of Amsterdam.
Welleman, H. C., & Storbeck, F. (1995). Automatic aging of plaice (*Pleuronectes platessa* L.) otoliths by means of image analysis. In D. H. Secor, J. M. Dean, & S. E. Campana (Eds.), *Recent developments in fish otolith research*. Columbia, SC: University of South Carolina Press.