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ARTICLE

Bomb Radiocarbon Validates Age and Long-Term Growth Declines in American Plaice in the Southern Gulf of St. Lawrence

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Abstract

The growth rate and size composition of American Plaice *Hippoglossoides platessoides* in the southern Gulf of St. Lawrence has changed markedly over the past 40 years. The size at age recorded in commercial fisheries and research survey data has declined, particularly through the mid-1980s. Females of the 1969 cohort grew to an estimated maximum length of 59 cm (males, 42 cm); the 1994 cohort grew to a much smaller maximum of 37 cm (29 cm for males). There is no indication of any reverse trend in growth or size at age in the 2000s, despite reduced harvests and warmer water temperatures. Incorrect aging methods are not the reason for the observed growth trends. Ages were determined by counting the growth increments visible on the surface of whole otoliths, and there is no bias in ages determined by this method (as opposed to those from thin-sectioned otoliths). The accuracy of ages determined by reading whole otoliths was validated to at least 27 years (±2 years) by bomb radiocarbon assays of 39 otoliths collected between 1971 and 1986. While commercial fishing may have contributed to past declines in plaice growth, ongoing natural mortality may be keeping size at age and the growth rate low despite the recent increases expected from low fishing mortality and higher water temperatures.

American Plaice *Hippoglossoides platessoides* is a long-lived, right-eyed flatfish, widely distributed in the Northwest Atlantic Ocean from northern Baffin Island to Rhode Island (Scott and Scott, 1988). American Plaice has been the most abundant groundfish species in trawl surveys of the southern Gulf of St. Lawrence conducted yearly since 1971, the total biomass being second only to Atlantic Cod *Gadus morhua* (Morin et al. 2008). Although still predominant in the demersal fish community, American Plaice have undergone declines in abundance in the southern Gulf of St. Lawrence and throughout Canadian waters over the past 40–50 years. The declining trends in American Plaice abundance have led the Committee on the Status of Endangered Wildlife in Canada to recommend that most Canadian populations be considered as threatened with extinction (COSEWIC, 2009). For some populations, age-based modeling approaches have contributed to understanding their population dynamics.

As a commercially valuable fish species, American Plaice have long been studied for their growth dynamics. Age determination has largely been based on interpretation of the otolith, either through surface reading of the whole otolith (Lux, 1970) or after breaking or sectioning along the transverse axis (Pitt, 1967; Dery, 1988). Age validation was not carried out for any of these methods. Powles (1965, 1966) provided support for the use of otoliths as age indicators of young plaice (<4 years) by showing correspondence with modal lengths from research survey

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catches. Recoveries of tagged plaice were compared with survey estimates of length at age, but were inconclusive. All other published studies have assumed that otolith-based ages were accurate. This assumption has been rejected for many species where surface otolith readings were used (Campana, 2001).

In light of the conservation objectives and economic value of American Plaice, the primary goal of this study was to determine the age and growth characteristics of plaice from the Southern Gulf of St. Lawrence off eastern Canada, and to document the variation in growth over a 40-year time series. In addition to comparing the accuracy of the aging methods for the species, we also report the first application of bomb radiocarbon as an age validation tool for American Plaice otoliths. An additional objective of the study was to test for differences in size at age between sexes, fishing gears, and populations. We conclude by speculating on possible causes for the observed long-term decline in growth rate.

METHODS

Data sources.—American Plaice otoliths for age validation were collected from the southern Gulf of St. Lawrence using both research vessels and commercial fishing vessels. Growth analyses were based on research surveys conducted annually in September since 1971. From 1971 to 1984 the survey gear consisted of a Yankee 36 otter trawl fitted with a 9-mm liner in the cod end; from 1985 on, a Western IIa trawl with a 19-mm liner was used. All otoliths were immersed in a glycerine-thymol clearing agent upon collection.

The stratified mean length at age of plaice was calculated from each survey using standard calculations. For American Plaice, a species with sexually dimorphic growth, this requires length frequencies by sex for each capture location and the sampling of otoliths from all lengths. For large catches a minimum sample of 200 plaice was required, from which length frequencies were made and otoliths for each sex were drawn at a rate of one fish per 1-cm length-group. Exceptions to this were made in four surveys: from 1984 to 1986, when male and female plaice were grouped together in length frequencies, and in 2003 when the survey was not completed due to vessel failure. For growth analyses in this study, length-at-age data were excluded from these four surveys.

Plaice otoliths were also drawn from commercial catches using port and at-sea observer sampling that began in 1976. The fishery is mainly practiced by mobile gear (otter trawls and Danish and Scottish seines) and fixed gear (gill nets and longlines). Mesh size in the mobile gear fishery has increased from about 105 mm before 1976 (Clay et al. 1984) to 155 mm since 1996. Commercial lengths at age are expected to be biased towards larger plaice due to size selection caused by large mesh size and due to at-sea discarding of plaice that was widespread in the southern Gulf of St. Lawrence fishery until the 1990s (Jean, 1963).

Age determination.—All ages were based on counts of presumed annual growth increments (annuli) visible in the sagittal otoliths. Whole otoliths were aged by Department of Fisheries and Oceans (DFO) age readers in the year of collection; the otoliths were immersed in either dilute ethanol or a glycerine–water mixture and examined under a binocular microscope at 96–128 × magnification using reflected light against a black background. About 2,500–5,000 plaice otoliths were aged each year, most of those coming from the annual survey.

The possibility that the long-term (>40-year) growth declines described above were due to differences in age-reading over time was evaluated using calibrations against a reference collection. A single age reader interpreted all plaice otoliths between 1971 and 1982, except 1981. Four age readers were in place between 1983 and 1987, and two readers after 1987. In 1988, an age-determination protocol was established, including an otolith reference collection from which a random selection has been re-aged yearly at periodic intervals to prevent drift in readers' interpretation. The reference collection was established from otoliths drawn from plaice aged prior to 1988 and included age interpretations from the original age reader of 1971–1982. No bias was evident in any of the comparisons, particularly between modern age readers and the age interpretations of the original age reader. A subsequent comparison, made as part of this study, showed no bias between the original and current age interpretations of 59 otoliths collected between 1971 and 1982.

Age validation.—Whole otoliths analyzed in this study represent a subsample of those described previously. Otoliths were immersed in ethanol and viewed and imaged under a binocular microscope at 16–40 × magnification via reflected light. The growth increment sequence was digitally photographed at a resolution of 2,048 × 2,048 and then enhanced for contrast using Adobe Photoshop CS2. Age interpretation was based on the enhanced images. There was no bias between the whole otolith age determinations made as part of this study and those made originally by DFO age readers.

Ages were also determined from transverse sections. Otoliths to be aged were first embedded in a slow-drying hard epoxy (Araldite epoxy GY502 and hardener HY956 in a 5:1 weight ratio). Transverse sections through the core (about 650-μm thickness) were prepared with a single cut using twin blades separated by a spacer on an Isomet low-speed diamond-bladed saw. The sections were subsequently placed on a standard microscope slide under a thin coating of ethanol for imaging using the same protocol as described earlier. Age interpretation was based on the enhanced images. Bias between aging methods and age readers was evaluated with age-bias plots, whereas precision was quantified using the coefficient of variation (Campana 2001).

Otolith cores for bomb radiocarbon age validation were isolated from one of three adjacent 1-mm-thick transverse sections through the otolith core made using multiple blades on the Isomet saw. Otolith cores representing the first 3 years of life (5 years in the case of a few samples) were isolated from the central section as a solid piece, which was extracted via a Merchantek computer-controlled micromilling machine using 300-μm-diameter steel cutting bits and burrs. Additional core material from the remaining otolith of the pair was sometimes necessary to maximize the amount of sample material available for assay from each fish (a minimum of 3 mg was usually necessary for radiocarbon assay). The date of sample formation was calculated as the year of fish collection minus the number of growth increments from the edge of the otolith to the midpoint of the range of growth increments present in the extracted core. After sonification in Super Q water and drying, the sample was weighed to the nearest 0.1 mg in preparation for ^{14}C assay via accelerator mass spectrometry (AMS). The assays also provided $\delta^{13}C$ (‰) values, which were used to correct for isotopic fractionation effects and provide information on the source of the carbon. Radiocarbon values were subsequently reported as $\Delta^{14}C$, which is the per mille (‰) deviation of the sample from the radiocarbon concentration of 19th-century wood, corrected for sample decay prior to 1950 (methods outlined by Stuiver and Polach 1977). The mean standard deviation of the individual radiocarbon assays was about 5‰.

The reference $\Delta^{14}C$ carbonate chronology for the Northwest Atlantic (NWA) was derived from 73 otoliths of young known-age fish of various species whose cores were formed between 1949 and 2000 (Campana et al. 2008). Differences in $\Delta^{14}C$ among species are neither expected nor observed if the species inhabit marine waters of similar water mass characteristics. A reference chronology specific to the southern Gulf of St. Lawrence was not available, but would be expected to be very similar to the NWA reference chronology, perhaps beginning by up to 1 year earlier because of freshwater input from the St. Lawrence River.

The feature of a bomb radiocarbon chronology that best serves as a stable, dated reference mark is the year of initial increase above prebomb levels in response to the period of atmospheric testing of nuclear weapons. Comparison of this year of initial increase in the reference chronology with that of the species being tested (in this case plaice) provides a good measure of age-estimation accuracy because consistent overestimation or underestimation of age will shift the calculated year of initial increase in the test chronology to earlier or more recent years (Francis et al. 2010). The year of initial appearance of bomb $\Delta^{14}C$ (YT) was defined as described in Campana et al. (2008).

To detect any subtle differences in age determination accuracy between young and old plaice, a cubic regression was used to describe the relationship between the presumed year of otolith annulus formation (for the period 1952–1977, as indicated by the growth increments in the otolith section) and the corresponding $\Delta^{14}C$ assay values (analogous to Melvin and Campana 2010). The residuals from the modeled fit were then plotted against the otolith section age, with the expectation that a declining trend in the residuals would be suggestive of progressive underaging from increment counts.

Delineation of the otolith core was based on identification of the innermost three growth increments, which were presumed to have formed annually. To confirm the age of the core, the diameter of each of the innermost three growth increments visible in the section was measured and used to estimate corresponding fish length from the regression of otolith width on fish length (Campana 2001). The resulting length-at-age estimates were then compared with length frequency histograms of plaice captured in research vessel surveys of the southern Gulf of St. Lawrence, in which the first few length modes were clearly visible.

Growth analyses.—We modeled the growth of American Plaice from the southern Gulf of St. Lawrence from research survey data on age-2 to age-16 males and age-2 to age-20 females. This range of ages was common to most years and reduced the potential effect of spurious data at older ages, often represented by a single captured fish. For each sex, growth was modeled by survey year (1971–2010, excluding the 1984–1986 and 2003 surveys) and by cohort (1969–1994).

The von Bertalanffy growth function was fitted to the stratified mean length at age, by sex and by survey year and cohort, that is,

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

where L_t is the total length in centimeters of plaice at age t in years, L_∞ is the asymptotic total length, K is a growth coefficient (years^{-1}) and t_0 is the age at zero length. Nonlinear regression was used to estimate the parameters of the model via the NLIN procedure in SAS/STAT software. The models were fitted to the stratified mean lengths at age, weighted by the stratified mean catch at age or by the number of plaice otoliths read at each age. These models assumed normally distributed error terms and made no assumption of age-dependent variance in the observed mean lengths. Either weighting method provided good data fits; however, we found that the number of otolith samples resulted in better fits to the mean lengths at the oldest ages. This was attributed to higher sampling intensity at older ages relative to their abundance in the population. Growth model comparisons were made between cohorts by using the sum of squares reduction test, calculating the F-statistic from a full model that estimates model parameters for each cohort and a reduced model that combines cohorts in a single set of model parameters (Haddon, 2011).

At ages 2 and 3, not all plaice were assigned to sex, thereby introducing potential bias into the sexed length frequencies. We calculated the stratified mean length for all sexes combined for ages 2 and 3 and assigned these values to males and females, assuming no difference in size between sexes. We believe that this assumption is reasonable because both sexes are in early sexual development at these ages. In the nonlinear regressions, the mean lengths of age-2–3 plaice were weighted by half of their combined catch at age or number of samples.

RESULTS

Otolith Growth Patterns in Whole and Sectioned Otoliths

Growth increments, presumed to be formed annually, were visible under reflected light in at least some regions of all of the whole American Plaice otoliths examined (Figure 1). Growth increments were visible in both blind-side (the side of the fish facing the seafloor and having no eyes) and eyed-side otoliths, but they were generally clearer in eyed-side otoliths.

Growth increments were also visible in transverse sections of the otolith (Figure 1). Growth sequences were visible along both the dorsoventral axis and on either side of the sulcal groove, but tended to be most clear (with less splitting) beside the sulcus.

There was no evidence of a systematic difference (bias) between age interpretations of the whole otolith and the sectioned otolith. A scatterplot analogous to an age-bias plot showed minimal deviation from the 1:1 line, indicating that whole and sectioned otoliths showed comparable age readings to at least age 33 (Figure 2). Ageing precision based on replicate age readings of whole otoliths by different readers (historical versus recent) was 5.7%. Ageing precision of a single age reader aging matched pairs of whole and sectioned otoliths was 4.1%. The difference between the two sets of precision values suggests that reader effects were larger than any intrinsic differences between whole and sectioned otoliths.

Core Age and Identification

Mean diameters of the inner three growth increments along the dorsoventral axis of the 89 American Plaice otolith sections examined were 0.78 mm (age 1), 1.49 mm (age 2), and 2.03 mm

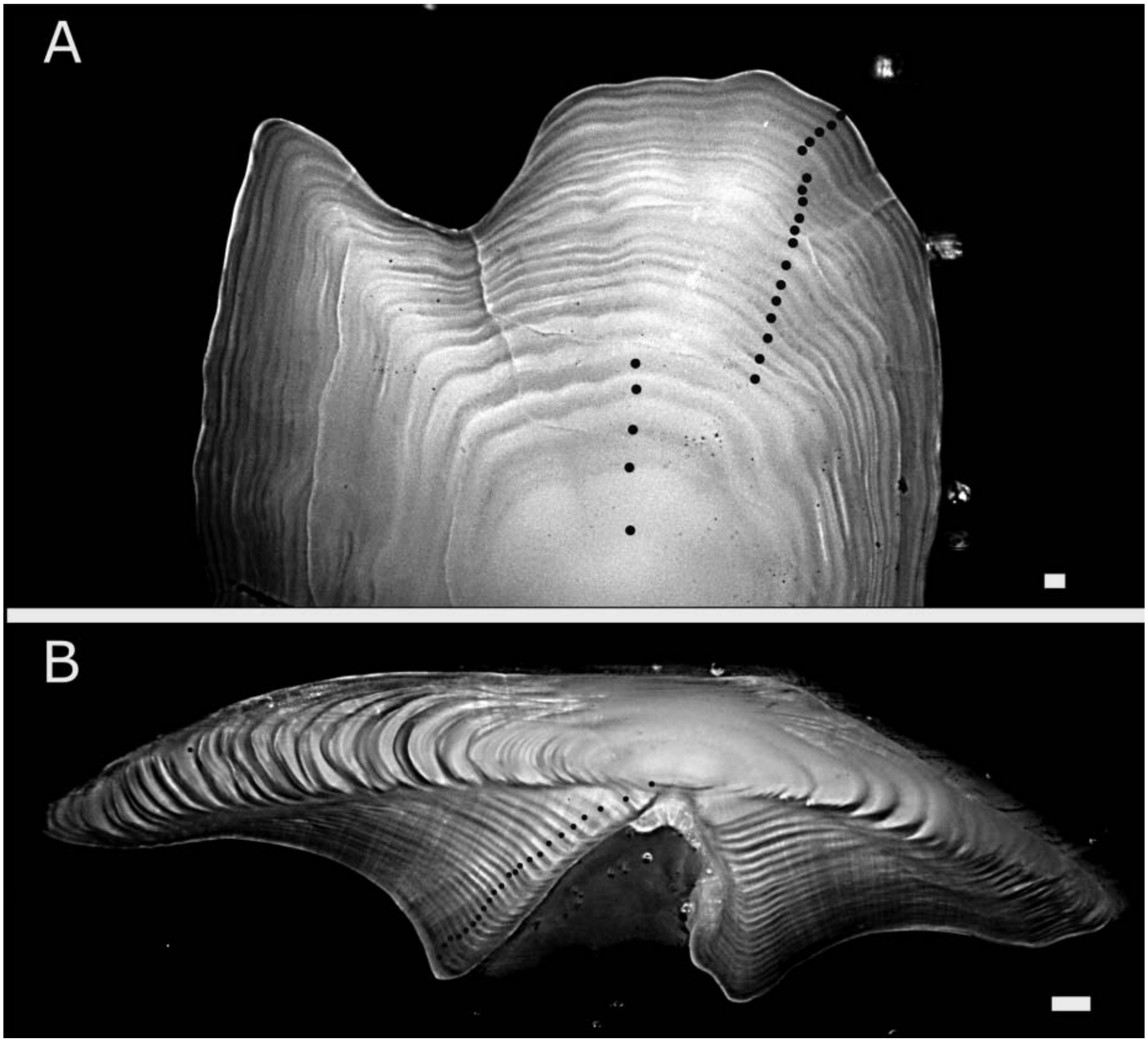

FIGURE 1. Otolith from a 56-cm female American Plaice showing 23 annual growth increments (translucent zones indicated by black circles) in **(A)** the anterior half of the whole otolith and **(B)** a transverse section through the core of the same otolith. Both images have been digitally enhanced for clarity. The scale bar in both images is 0.2 mm.

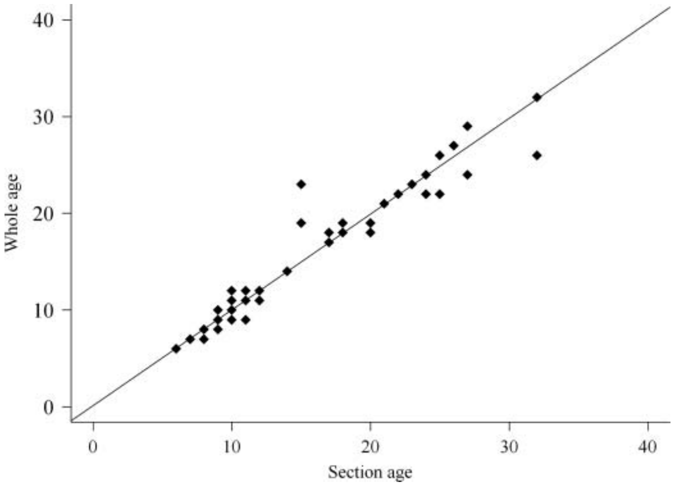

FIGURE 2. Linear regression of American Plaice age determined using whole otoliths on that determined using transverse sections. Since the fitted regression is very similar to a 1:1 line, no bias is evident between the aging methods.

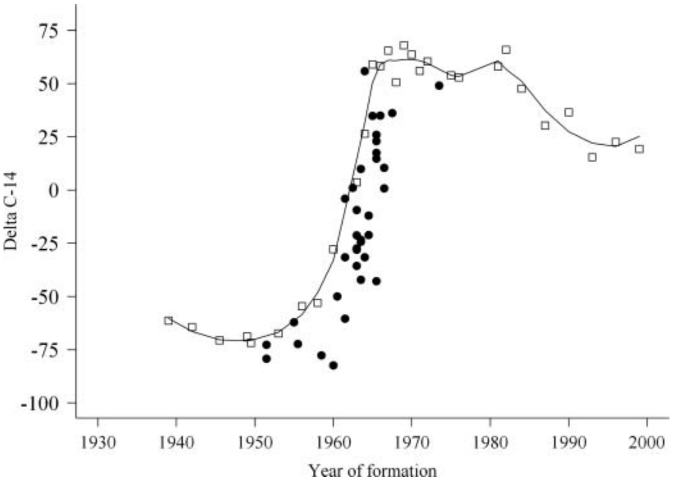

FIGURE 3. Radiocarbon values (reported as $\Delta^{14}C$) in otolith cores (dots) of American Plaice versus year of formation inferred from counts of the growth increments in sectioned otoliths. Also shown is the $\Delta^{14}C$ reference (known-age) chronology for the Northwest Atlantic (squares) with a fitted LOESS smoother. The correspondence between the two radiocarbon chronologies indicates that the ages of the plaice were interpreted relatively accurately based on the growth increment counts.

(age 3). The regression of fish length (dependent) on dorsoventral otolith width (independent) was linear with a slope of 9.22 ± 0.32 and an intercept of -4.43 ± 1.64 (overall regression; $P < 0.001$, $r^2 = 0.84$), yielding predicted fish lengths at age 1 of 2.7 mm, at age 2 of 9.3 mm, and at age 3 of 14.2 cm. Length frequency histograms of survey catches between 1990 and 1994 (corresponding to the years when the otolith measurements were made) showed clear modes at 9–10 and 14–15 cm in each year and a more equivocal mode at 5–7 cm. Small fish observed in the 2006–2010 surveys showed clear length modes at 4, 7 and 12 cm, roughly consistent with the 1990–1994 results. Given the limited recruitment and the ability of the survey gear to capture plaice at lengths <7 cm, the correspondence between the length modes and back-calculated fish lengths suggest that the 9–10-cm fish were age 2 and the 14–15 cm fish were age 3. Doran (1967) observed that American Plaice larvae in southern St. Lawrence Gulf began metamorphosis at approximately 18 mm and that the process was underway or completed by September. The first otolith growth increment typically forms in the winter (Powles 1966), so it would be reasonable to expect that the first growth increment forms at an age of <1 year, implying that the otolith core defined by three growth increments is actually about age 2.5, rather than age 3-year age indicated by the annulus count. Based on weight accretion (which is nonlinear), the median age of the extracted otolith core would be closer to 2 years.

Age Validation of Plaice

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

The correspondence between the NWA reference chronology and the chronology derived from the plaice otolith cores using section ages was very close (Figure 3). A plaice chronology based on growth increments counted in whole otoliths was very similar to that based on otolith sections. Both the plaice and reference chronologies described a curve that closely resembles that seen elsewhere in the world: a rapid increase between 1959 and the late 1960s followed by a gradual decline through to 1995. The key samples for comparison were the cores formed between 1960 and 1968 (Table 1) because they were formed during the period when environmental ^{14}C levels changed most rapidly. The four cores, formed between 1955 and 1964 (age-22 to age-27 plaice, based on increment counts), were clearly near the onset of the period of bomb radiocarbon increase, as evidenced by their low $\Delta^{14}C$ values; the cores thus must have been within 1–2 years of the ages suggested by increment counts (Table 1).

The feature of a bomb $\Delta^{14}C$ chronology that usually serves as the best dated reference mark is the year of initial increase above prebomb levels (Y_T). The Y_T of the NWA reference chronology was calculated as being 1958 (Campana et al. 2008). Calculation of the plaice Y_T indicated that $\Delta^{14}C$ first increased 1–2 years later (i.e., between 1959 and 1960). This 1–2 year offset is within the 1–3 year range of uncertainty associated with bomb chronologies. Nevertheless, the offset was unexpected and was inconsistent with the close correspondence between the plaice and reference chronologies through the 1960s. Since the Y_T calculation was strongly influenced by the two samples whose cores formed in the late 1950s, it is possible that normal sample

TABLE 1. Summary of δ^{13}C (‰) and Δ^{14}C assay results for otolith cores (3 years of growth) microsampled from American Plaice for age validation. The year of core formation is based on the year of fish collection minus the number of growth increments to the mid-point of growth increments in the extracted core.

Year collected	Fish length (cm)	Whole age (years)	Section age (years)	Core age (years)	Section year of core formation	d^{13}C	Δ^{14}C
1971	30	9	9	3	1963.0	−1.9	−28.1
	26	6	6	3	1966.5	−1.2	10.4
	28	10	10	5	1963.5	−0.9	−24.3
	32	7	7	5	1966.5	−1.5	0.8
	32	7	7	3	1965.5	−1.9	14.7
	27	7	7	3	1965.0	−0.8	34.8
	43	12	12	5	1961.5	−0.9	−60.4
	30	9	9	5	1964.5	−0.9	−12.0
	44	14	14	3	1958.5	−1.4	−77.6
	50	20	20	3	1951.5	−1.5	−72.8
	8	1	1	1	1970.0	−1.5	54.1
	8	1	1	1	1970.0	−1.4	70.2
	18	3	3	3	1969.5	−1.7	72.4
	18	3	3	3	1969.5	−1.6	69.3
	24	6	6	5	1967.5	−1.2	36.1
	63	20	21	3	1951.5	−0.9	−79.2
	38	11	12	3	1960.5	−0.9	−50.0
	34	8	9	5	1965.5	−1.2	17.4
	32	9	11	3	1962.5	−0.9	1.0
1972	34	10	10	3	1963.5	−1.3	−42.1
	43	10	10	3	1963.0	−1.1	−35.6
	42	10	12	3	1961.5	−0.7	−4.1
1973	32	11	11	3	1963.0	−0.7	−9.4
	42	11	11	3	1964.0	−1.2	55.8
	28	11	11	3	1963.0	−1.0	−21.3
1982	51	18	17	3	1966.0	−1.4	34.9
	35	21	10	3	1973.5	−0.6	49.1
	52	18	15	3	1965.5	−0.7	23.0
	58	19	18	3	1964.5	−1.3	−21.2
	49	18	18	3	1965.5	−1.7	25.9
	50	18	15	3	1963.5	−1.0	9.9
	57	19	17	3	1965.5	−0.7	−42.8
	55	20	20	3	1963.5	−1.3	−23.3
1985	66	29	26	3	1960.0	−0.9	−82.4
1986	67	30	33	3	1955.0	−0.7	−62.1
	58	24	27	3	1961.5	−1.1	−31.5
	54	24	25	3	1963.0	−0.9	−27.5
	58	24	23	3	1964.0	−1.1	−31.6
	60	24	22	3	1955.5	−0.9	−72.3

variance associated with these two samples contributed to the apparent offset. An additional (and not mutually exclusive) explanation is that the mean weighted age of the otolith core was actually 2 years, and not the 3 years assumed in the calculation of date of formation (see Methods). Simulated calculations assuming a 2-year core moved the plaice chronology even closer to the NWA reference chronology, although it did not change the calculated value of Y_T.

Small deviations of the early Δ^{14}C history in the southern Gulf of St. Lawrence relative to the NWA reference chronology may also have contributed to the differences in calculated year of bomb radiocarbon onset. Very young plaice otoliths from the 1950s and 1960s were not available to construct a plaice reference chronology specific to the Gulf of St. Lawrence. Therefore the plaice radiocarbon chronology between the years 1952 and 1970 was used as the independent variable in a cubic regression,

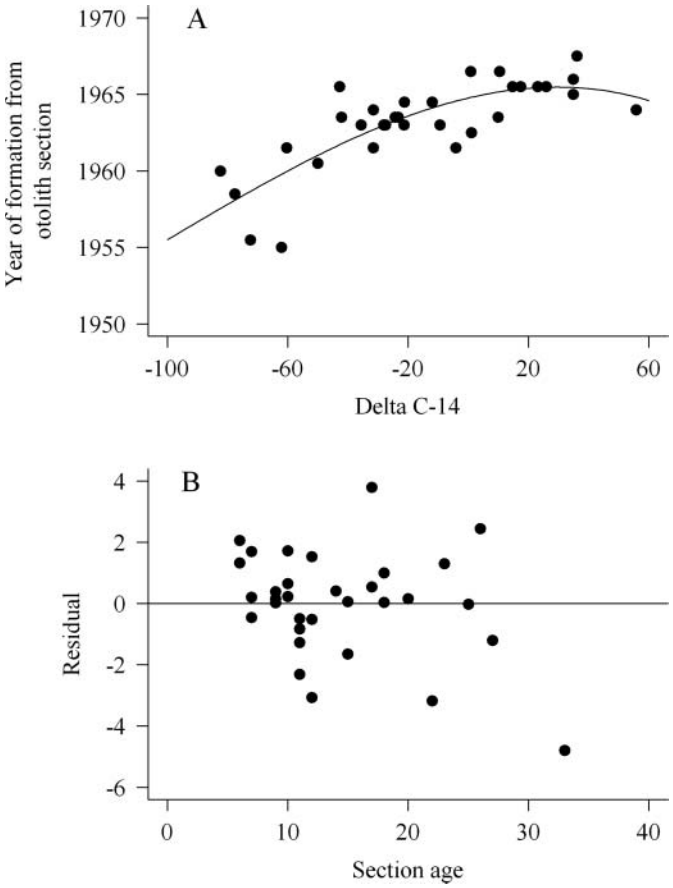

FIGURE 4. **(A)** Cubic regression fit of the presumed year of otolith annulus formation in American Plaice (as indicated by growth increment counts) to Δ^{14}C; **(B)** residuals of the regression fit as a function of the otolith-section age. There was no significant negative trend in the residuals, which would have suggested the underaging of older fish.

which predicted the section-based year of formation quite well (Figure 4a; $P < 0.001$, $r^2 = 0.64$). When plotted against section age, the residuals of the model showed no significant trend, indicating no significant age underestimation with increasing age ($P > 0.1$). Visual assessment of the residuals suggested that most fish were aged within 2 years of their correct age.

As a second test of age underestimation in old fish, a series of age 6–10 plaice were used to prepare a reference Δ^{14}C chronology for that age-group. Comparison of the age-6–10 chronology with age groups corresponding to older plaice (ages 11–19 and age 20 +) showed that each of the chronologies from the older fish were statistically similar to that of the younger (age 6–10) fish (Kolmogorov–Smirnov test, $P > 0.05$), indicating that the growth increments formed after age 10 must have been formed annually; deviations from an annual rate of formation or incorrect interpretation of those increments would have been apparent as a lateral shift in the chronologies of the older fish relative to the younger fish.

These results validate the interpretation of the plaice otolith increments as accurate age indicators (± 2 years) to an age of at least 27 years, and a presumed longevity of at least 33 years.

Variations in Length at Age Based on Gear and Sex

American Plaice in the southern Gulf of St. Lawrence were captured annually from a research vessel trawl survey, as well as by a variety of commercial fishing gears. To determine if calculations of plaice growth rate were sensitive to the fishing gear used, length at age by sex based on whole otoliths was calculated for 1990, a well-sampled year (Figure 5). The length at age of female plaice between ages 6–15 captured with fixed gear (gill nets and longlines) was significantly larger than that captured by seines (Danish and Scottish seines) for all but one age-group (ANOVA, $P < 0.01$). The length at age of females caught with otter trawls tended to lie intermediate between that of fixed gear and seines, many age groups differing significantly among all three gear types (ANOVA, $P < 0.05$). The length at age of plaice caught with research survey gear was significantly smaller than those caught in commercial gear for all but the oldest age groups (ANOVA, $P < 0.05$; Figure 5). A similar pattern was observed with male plaice, whereby the length at age of otter trawl-caught plaice tended to be larger than that of seine-caught plaice, at least until age 13 (Figure 5). Survey-caught males were significantly smaller than commercially caught male fish for most, but not all age-groups (ANOVA, $P < 0.05$). To the extent that these results are representative of other years, plaice length at age appears to vary significantly across gear types.

Growth of Plaice

The mean length at age of plaice declined sharply beginning in the late 1970s, particularly among males and females older than age 5 (Figure 6). This change was observed in both the survey and commercial lengths at age but was more evident at the oldest ages of each sex. In commercial catches, the reduction in mean size at age 10 was less pronounced among females than males but followed the pattern observed in the survey data by age 15.

The von Bertalanffy growth function closely fitted the mean lengths along cohorts, residual sums of squares being <3% of the total sums of squares for females and <4% for males. When fitted to aggregate data from the 1990–1994 cohorts (Figure 7), the resulting asymptotic growth pattern of female and male plaice was typical of all the southern Gulf plaice cohorts that were analyzed in this study. These five cohorts, the most recent in the time series analyzed, represent a period of relative growth stability during which there was no significant difference in the von Bertalanffy growth models between each cohort ($F = 1.71$, $P = 0.17$ for females; $F = 2.48$, $P = 0.09$ for males).

The modeled growth of southern Gulf plaice cohorts indicates a continuous trend of declining growth rate. Parameters of the von Bertalanffy growth model show clear trends, L_∞ declining over time for both sexes (Figure 8A). The first cohort (1969) grew to an estimated L_∞ of 59 cm for females and 42 cm

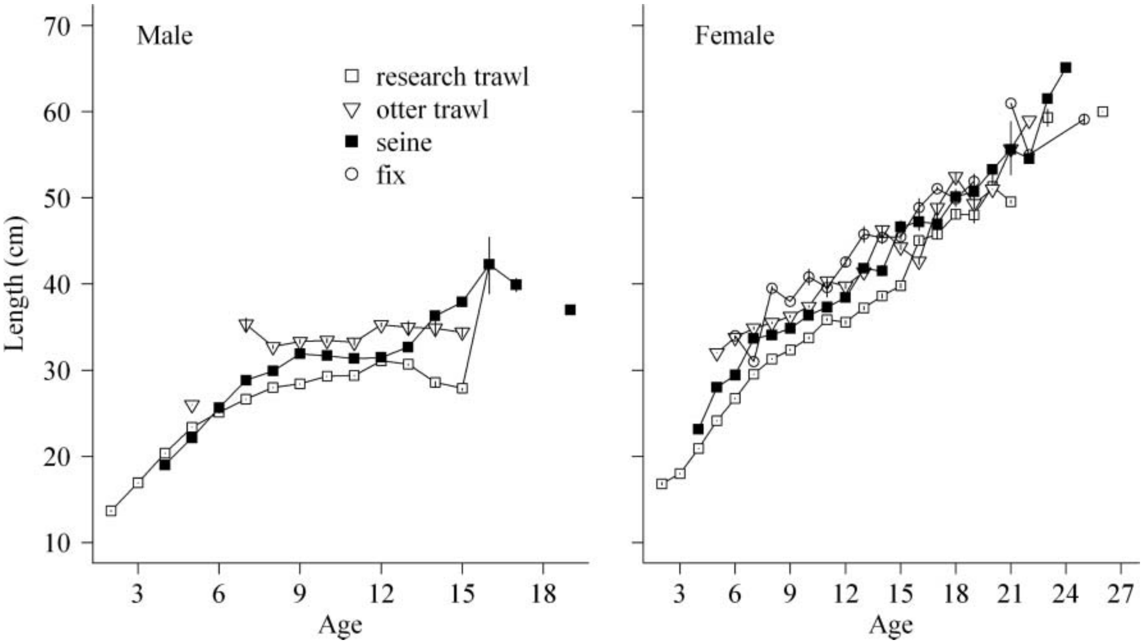

FIGURE 5. Mean lengths at age of male and female American Plaice caught in 1990 by research vessel survey otter trawls and commercial fishing gear (otter trawl, seine, and fixed gear). The error bars denote the 95% confidence intervals. Commercial fishing gear tends to catch larger fish at age than survey gear.

for males; the last modeled cohort (1994) attained corresponding L_∞ values of 37 and 29 cm. Male plaice grow to a smaller size and reach their asymptotic size earlier than females; hence males have consistently higher values of K than females (Figure 8B). For young and old plaice (exemplified by ages 6 and 12 in Figure 8), the estimated size declined sharply from the 1969 to 1974 cohorts, then showed some recovery. Both sexes exhibit a gradual decline in estimated size for cohorts since the mid-1980s (Figure 8C, D).

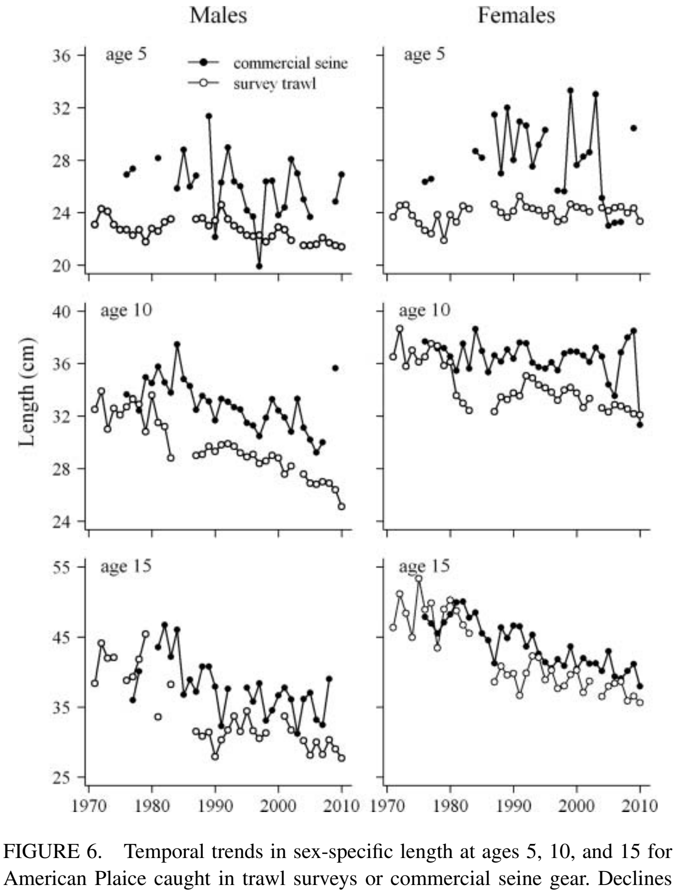

FIGURE 6. Temporal trends in sex-specific length at ages 5, 10, and 15 for American Plaice caught in trawl surveys or commercial seine gear. Declines in length at age are evident in both commercial and survey gear and are most pronounced at older ages.

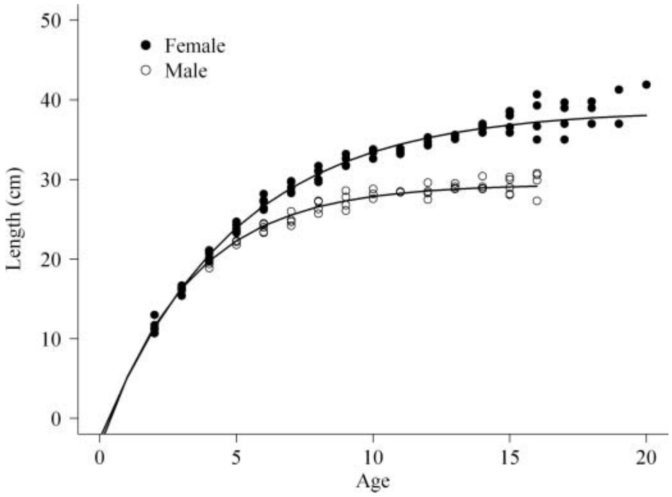

FIGURE 7. American Plaice growth over five cohorts (1990–1994). Shown are the observed mean lengths of females and males from survey data, with fitted von Bertalanffy growth functions.

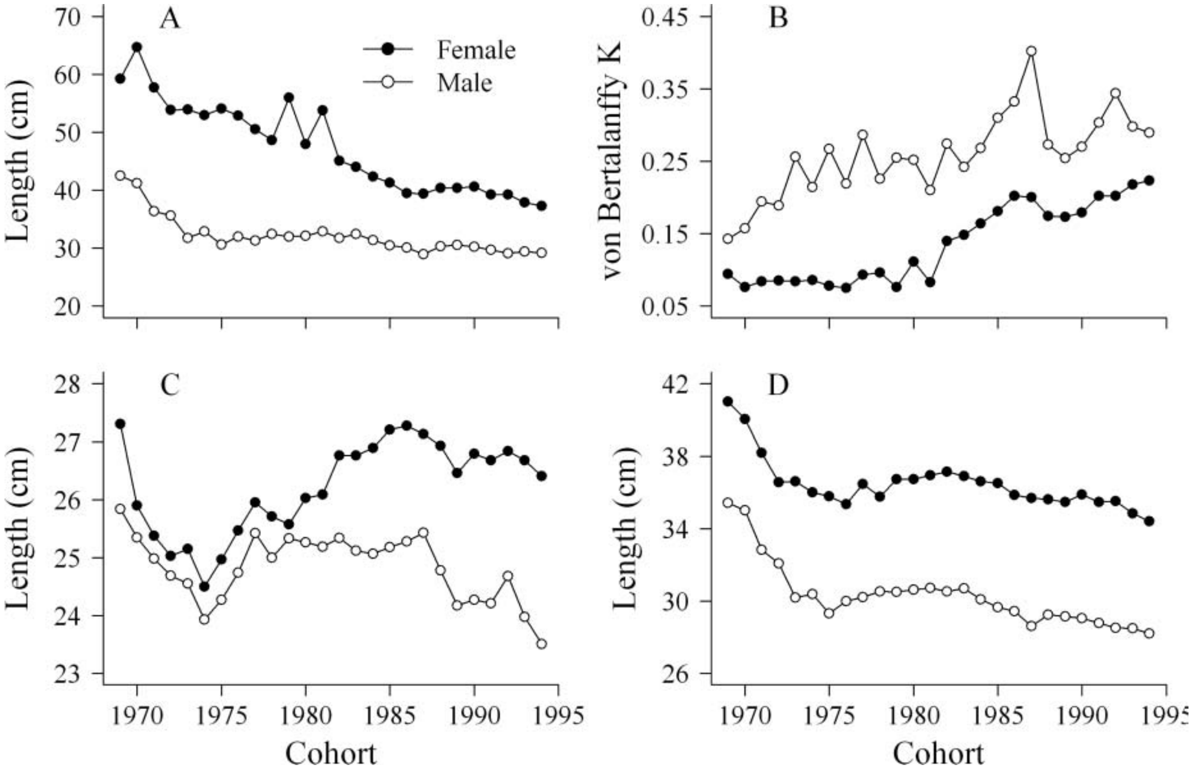

FIGURE 8. Indicators of growth changes in American Plaice in the southern Gulf of St. Lawrence based on the von Bertalanffy growth function fitted to survey data for the 1969–1994 cohorts: asymptotic length, **(B)** the von Bertalanffy growth parameter *K*, **(C)** estimated length at age 6, and **(D)** estimated length at age 12.

DISCUSSION

The results of the bomb radiocarbon assays indicate that American Plaice can be aged accurately to an age of at least 27 years using either whole or sectioned otoliths. The close 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 underaging or overaging would have resulted in core $\Delta^{14}C$ values, which were phase-shifted in relation to the reference chronology. Indeed, given the large number of radiocarbon assays that were completed, the growth increment counts must reflect the true age of the fish to within ± 2 years, which is at least as precise as most radiocarbon validation studies (Campana, 2001). Bomb radiocarbon was effective in validating the accuracy of aging methods for other flatfish species, including Pacific Halibut *Hippoglossoides stenolepis* (Piner and Wischniowski, 2004), Yellowtail Flounder *Limanda ferruginea* (Dwyer et al. 2003), Greenland Halibut *Reinhardtius hippoglossoides* (Treble et al. 2008), and Atlantic Halibut *Hippoglossus hippoglossus* (Armsworthy and Campana 2010).

Modern otolith aging methods usually strive to prepare transverse sections for age interpretation, given that surface readings often lead to severe age underestimation in long-lived fish (Beamish and McFarlane, 1983). Therefore, the finding that interpretation of whole plaice otoliths gives age readings that are comparable to those of transverse sections to at least age 33, is somewhat surprising. Whole and sectioned otoliths produced comparable ages in Yellowtail Flounder up to age 7, after which surface readings underestimated the actual age by as much as 50% (Dwyer et al. 2003). Similarly, age underestimation associated with the reading of whole otoliths in old fish has been reported for both Atlantic Halibut (Armsworthy and Campana 2010) and Greenland Halibut (Treble et al. 2008). In general, thin-sectioning and break-and-burn otolith aging techniques would be expected to provide more accurate age estimates for old fish than do surface readings, due to a tendency in old otoliths for growth to occur dorsoventrally (i.e., a thickening of the otolith) rather than peripherally (a widening of the otolith; Chilton and Beamish, 1982; Campana, 2001). However, it appears that the flattened, largely two-dimensional growth pattern of plaice otoliths results in more accurate age readings of whole otoliths in plaice than in many other species. Previous work had reported a correspondence between length modes and the number of otolith annuli in American Plaice in the southern Gulf of St Lawrence, but that work had been restricted to young fish (Powles, 1966). Additional corroboration of annulus formation came from an examination of growth increments in recaptured plaice and long-term persistence of year-classes identified through surface-based age readings (Powles, 1965). However, the current results provide a firm basis for concluding that the age interpretations of southern Gulf plaice based on whole otoliths are accurate across all age groups and no less accurate than those based on transverse sections. In addition to the validation of the aging method, the observed aging precision (CV of 4–6%) indicated that American Plaice otoliths are at least as easy to read as most other species (Campana 2001).

A decline in plaice length at age was evident in both the research survey and commercial data over the past four decades. The decline became most pronounced in the early 1980s, and was most evident among the older age groups (age, >10). Although a change in aging methodology or interpretation would be an obvious possible explanation for the decline, rigorous examination of the data and aging methods revealed no such change. Four pieces of evidence provide a firm basis for this conclusion. Firstly, the radiocarbon assays analyzed otoliths collected between 1971 and 1986 (spanning the period of decline), revealing no change in aging accuracy between the beginning and end of the period. Secondly, the decline in size at age first became evident in the 1970s, a period during which a single age reader using a consistent method aged all otoliths. Thirdly, the development of the otolith reference collection in the 1980s led to numerous age calibrations between age readers spanning the period 1971–2011, preventing drift in age interpretations of otoliths over time. Finally, we compared the historical and modern interpretations of the earliest otolith collections, with no bias observed. Therefore, a change in age interpretation methods cannot explain the observed decline in length at age over the 40-year time series.

Plaice tended to be larger at age in commercial catches than in the research surveys, a result that is consistent with the size selective nature of commercial fisheries. Mobile gear (seines and otter trawls) may remove larger fish at each age than do survey trawls due to their use of large mesh size. Armsworthy and Campana (2010) also found that Atlantic Halibut caught by commercial trawlers were intermediate in size at age between fixed gear (longlines catching the largest halibut) and survey trawls (catching the smallest halibut). The discarding of commercially undersized plaice by mobile gear was widespread in the southern Gulf plaice fishery up to the early 1990s, so the tendency to retain only large plaice (usually >30 cm) also contributed to the larger size at age of plaice reported from mobile gear fisheries.

A 40-year time series of survey size at age enabled us to describe the growth of plaice along cohorts, in contrast to the within-year length-at-age growth curves that are normally fitted. Although some deviation between observed maximum size and the maximum sized predicted from a growth model is common, all of the first 16 surveys (1971–1986) estimated L_∞ as being greater than the observed maximum length, and in 12 cases the difference between $L_{\max}$ and L_∞ was more than one-third of $L_{\max}$ (FishBase criterion for identifying reliable growth models; Froese and Pauly 2012). Thus American Plaice growth models based on annual surveys provided less reliable growth trajectories than those along cohorts, particularly for females. Based both on observed length at age and on the predictions of the along-cohort growth models, southern Gulf cohorts since 1969 have experienced declining growth trends, both sexes attaining smaller maximum size. The decline in asymptotic size was most abrupt for cohorts of the 1970s.

The growth patterns observed for southern Gulf plaice may not be common to other Canadian stocks. On the Grand Bank of Newfoundland, there is no indication of a trend in either the length or weight at age of American Plaice of either sex from 1985 to 2010 (Rideout et al. 2011). Unfortunately, data are limited for other neighbouring populations. Powles (1965) reported comparable growth for American Plaice in the southern Gulf of St. Lawrence and off Labrador, but slower growth than observed for plaice off Cape Cod. Pitt (1967) showed evidence that the growth in the southern Gulf population was intermediate between a low growth rate observed for Labrador plaice and high growth rates observed for Cape Cod, Flemish Cap, and Grand Bank populations. Swain and Morgan (2001) reported smaller size at age for southern Gulf plaice in trawl surveys compared to three Northwest Atlantic populations. Table 2 compares American Plaice growth parameter estimates between southern Gulf of St. Lawrence and other northwest Atlantic stocks in comparable survey years. The southern Gulf stock L_∞ was estimated to be lower than that of the other populations, with two exceptions: the adjacent stock located off the east coast of Cape Breton and one comparison with St. Pierre Bank in 1978.

Perceived differences in growth between populations, based on comparisons between annual surveys, may be due in part to differences in the growth rates of contributing cohorts. It is therefore interesting to compare the growth of plaice, born in the same year, between different populations. González-Troncoso and Paz (2008) reported large differences in growth rates along cohorts among plaice populations of the Northwest Atlantic. When combined with the results from our study, the 1991–1994 cohorts grew to consistently larger L_∞ on the Grand Bank and Flemish Cap than in the southern Gulf (Table 2). Grand Bank plaice tended to grow in a curvilinear fashion, causing the von Bertalanffy function to either fail to converge (male plaice, 1993 cohort; D. González-Troncoso, personal communication) or to converge on extreme values of L_∞ (>90 cm; Table 2). Despite the high values of L_∞ for the Grand Bank population, González-Troncoso and Paz (2008) reported higher growth rates for the Flemish Cap, which they attributed to lower density and better diet than on the Grand Bank.

Trends in the abundance of southern Gulf plaice are inconsistent with an expected density-related effect on growth. The survey abundance index was low in 1971 but increased to its maximum level in the late 1970s as abundant cohorts from the 1960s were recruited to the population (Morin and LeBlanc 2012). The abundance declined sharply in the early 1980s, coincident with a drop in mean length at age of older plaice. Southern Gulf plaice abundance continued to decline since the mid-1980s in a more moderate trend, similar to the decline in L_∞ of plaice born in the same period.

TABLE 2. Comparison of von Bertalanffy growth parameters for American Plaice from the southern Gulf of St. Lawrence with those for other populations. The codes for area are as follows: ECB = east of Cape Breton Island, SP = St. Pierre Bank, FC = Flemish Cap, and GB = Grand Bank. For southern Gulf analyses, the standard errors of the growth parameter estimates are in parentheses. Asterisks identify models in which the estimate of L_∞ is extreme relative to the observed $L_{\max}$.

Other population							Southern Gulf of St. Lawrence			
Year(s)	Sex	Area	L_∞	K	t_0[a]	Ref.[b]	Year	L_∞	K	t_0[a]
Parameters obtained from growth models in indicated sample year										
1970, 1971	M	ECB	54.4	0.10	−1.17	1	1971	50.1 (3.34)	0.099 (0.015)	−1.11 (0.359)
	F		78.1	0.06	−1.16			86.2 (4.22)*	0.048 (0.004)	−1.48 (0.172)
1971	M	SP	65.6	0.08	−1.21	1				
	F		80.7	0.06	−1.45					
1974	M	SP	73.5	0.093	0.75	2	1974	42.6 (2.811)	0.149 (0.025)	−0.13 (0.345)
	F		96.5	0.071	1.45			69.4 (5.66)	0.073 (0.011)	−0.58 (0.321)
1978	M	SP	68.4	0.078	−0.17	3	1978	61.8 (10.94)	0.065 (0.021)	−1.96 (0.726)
	F		87.2	0.058	−0.28			86.0 (12.92)	0.051 (0.013)	−1.10 (0.594)
1978, 1985	M	FC	53.7	0.21	1.49	4	1982	43.6 (8.407)	0.105 (0.045)	−1.69 (0.963)
	F		60.0	0.20	2.18			327.1 (518.2)*	0.008 (0.014)	−3.71 (1.114)
1990	M	SP	66.3	0.098	1.01	5	1990	31.6 (0.77)	0.273 (0.028)	0.22 (0.219)
	F		90.4	0.063	0.58			49.9 (3.10)	0.111 (0.017)	−0.79 (0.420)
Parameters obtained from growth models by cohort year										
1991	M	FC	40.3	0.371	−0.27	6	1991	29.7 (0.70)	0.303 (0.027)	0.42 (0.163)
	F		58.4	0.151	−1.52			39.2 (0.83)	0.202 (0.013)	0.35 (0.130)
1992	M	FC	40.3	0.453	0.59	6	1992	29.1 (0.54)	0.344 (0.033)	0.52 (0.208)
	F		58.4	0.163	−0.52			39.2 (0.78)	0.202 (0.014)	0.28 (0.158)
	F	GB	96.1	0.06	−0.10					
1993	M	FC	42.5	0.264	−0.73	6	1993	29.4 (0.47)	0.298 (0.021)	0.32 (0.136)
	F		54.9	0.215	0.04			37.9 (0.99)	0.218 (0.019)	0.40 (0.164)
	F	GB	71.4	0.100	0.11					
1994	M	FC	44.2	0.250	0.05	6	1994	29.2 (0.48)	0.289 (0.021)	0.35 (0.133)
	F		55.4	0.199	−0.12			37.3 (0.77)	0.223 (0.016)	0.46 (0.134)
	M	GB	114.8	0.034	−2.89					
	F		73.7	0.088	−0.70					

[a] Provided by D. González-Troncoso (personal communication).

[b] References (Ref.) are as follows: 1 = Minet (1994), 2 = Pitt (1975), 3 = unpublished, cited in Mahé and Moguedet (1991), 4 = Bowering and Brodie (1994) , 5 = Mahé and Moguedet (1991), and 6 = González-Troncoso and Paz (2008) for parameters L_∞ and K.

Ambient bottom water temperature may influence both growth rates and the local distribution of fish. Pitt (1967) showed that the mean size of American Plaice at ages 5 and 15 across numerous stocks was positively correlated with average bottom temperatures. However, they occupy temperatures that may not necessarily optimize growth. Swain (1997) showed that American Plaice in the southern Gulf of St. Lawrence occupied mean temperatures during the annual surveys that were below the mean ambient bottom temperatures. Females tended to occupy larger areas and significantly warmer water temperatures than males. The tendency for American Plaice to occupy colder temperatures than those available in their environment has also been observed for three populations off Newfoundland and in the southern Gulf (Swain and Morgan, 2001). Water temperature in the southern Gulf from the mid-1980s to the end of the 1990s were below average, with a maximum extent of cold water ($<0^\circ$C) at bottom (DFO 2009). The onset of the cold-water period corresponded with the drop in the mean size of some ages; however, warmer bottom temperatures in the 2000s have not resulted in an increase in size at age.

The past and ongoing influence of human exploitation is another potential explanation of the long-term decline in American Plaice growth rate. From 1965 to the 1980s, reported landings from the southern Gulf stock ranged from 6,000 to 12,000 metric tons (Morin and LeBlanc 2012). Commercial fishing declined sharply in the early 1990s and recent annual harvests have been less than 500 metric tons. Size-selective mortality caused by fishing gear is believed capable of biasing the estimation of fish growth (Ricker, 1969). Size-selective mortality was documented in Atlantic Cod in the southern Gulf of St. Lawrence by reconstructing the growth histories of individual fish via back-calculations on otoliths (Sinclair et al. 2002). Since southern

Gulf stocks of Atlantic Cod and American Plaice were historically exploited by a common fleet with landings related through bycatch, it seems reasonable that the fishery exerted a similar growth influence on the two stocks. Therefore, size-selective fishing mortality of southern Gulf plaice seems a plausible explanation of at least some of the observed decline in plaice length at age.

In summary, the evidence provided in this paper of declining length at age of American Plaice in the southern Gulf of St. Lawrence cannot be attributed to inaccuracies or bias in age determination methods. However, theoretical and empirical studies suggest that the positive trend in the growth parameter K may be related to increases in natural mortality (see Gislason et al. 2010). Natural mortality is thought to increasingly affect the dynamics of southern Gulf groundfish stocks over recent decades (Benoît and Swain 2008) and may have contributed to the observed growth declines of plaice. Recent assessments of southern Gulf plaice (Morin et al. 2008, Morin & LeBlanc 2012) point to high natural mortality as the key factor restricting stock recovery. Predation by grey seals *Halichoerus grypus* is considered to be an important component of mortality on adult plaice in the southern Gulf (Savenkoff et al. 2007).While commercial fishing may have contributed to past declines in plaice growth, ongoing natural mortality may be keeping size at age and growth rate low despite the recent increases expected of low fishing mortality and higher water temperatures.

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