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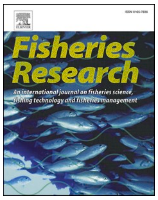

Long-term shifts in otolith age interpretations

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ABSTRACT

Multi-decadal time series using existing age data are increasingly being used to test important issues in ecology. Over the long term however, shifts in age determination protocol are almost unavoidable. This study uses an 86-yr time series of Icelandic cod (*Gadus morhua*) otolith samples (n = 906) to rigorously test the assumption of inter-year comparability of age interpretation across decadal changes in otolith preparation, viewing protocol and age reader. Comparison of the original age estimates with re-ageing of the same otoliths using modern preparation and interpretation protocols and a single age reader revealed a consistent bias, with the original readings over-estimating ages relative to modern. The extent of the bias was minimal at age 8 (0.18 yr), increasing to an average divergence of about 2 yr after age 14. The ageing bias was linked most strongly to the individual ager, whereas the transition from unsectioned (cracked or whole) to sectioned otoliths markedly improved precision. The implications of this study are encouraging, in that they suggest that old data sets incorporating historic age determinations based on specific methods may well be adequate for many purposes.

1. Introduction

Age-structured models form the basis for the assessment for many of the world's most productive fish stocks (Francis, 2015). Large numbers of age determinations are required annually to feed into these stock assessments, most of them based on otoliths. Given that the accuracy of the stock assessment is directly influenced by the quality of the age composition data, considerable attention is now given to ensuring accuracy (lack of bias) and precision (reproducibility or consistency) in age interpretations from year to year (Morison et al., 1998; Spurgeon et al., 2015). Precise age determinations are not necessarily accurate age determinations, and the tests for precision are not necessarily applicable to accuracy (Campana, 2001). In theory, age validation studies to confirm accuracy or test for bias need only be done once to confirm that the ageing method or protocol is providing accurate ages (on average) across all age groups for a given fish stock. In practice, accuracy is often assumed, although the frequency of age validation studies has increased markedly in recent years following cautionary warnings about the implications to fisheries yield resulting from inaccurate ageing methods (Reeves, 2003; Liao et al., 2013). Checks for ageing consistency are far more frequent, and come from quality control programs which may include samples which have been re-aged from the previous year, blind readings of reference collections of known-age material, or exchanges of ageing materials between laboratories (Campana, 2001; Kimura and Anderl, 2005). Programs such as these are useful in ensuring inter-annual replicability, or precision, in the age determinations, at least over short time periods. However, tests for long-term stability in age interpretation are conspicuously rare, despite the fact that long-term drift in interpretation protocol has caused serious breakdowns in the assessment and management of some fisheries (Campana, 1995; Yule et al., 2008; Melvin and Campana, 2010).

Multi-decadal time series of growth and population dynamics using existing age data are increasingly being used to test important issues in ecology (Campana et al., 2023), and all implicitly assume that the ageing protocols were standardized across all years. Over the long term however, shifts in age determination protocol are almost unavoidable, and may potentially introduce bias due to changes in the ageing structure being used (i.e. from scales to otoliths), changes in preparation (i.e. from whole otoliths to otolith sections), changes in interpretation protocol (i.e. from microscope to image analysis system), and changes in age readers (Brouwer and Griffiths, 2004; Duffy et al., 2012). Absolute standardization of the time series would require that a single ageing protocol, and a single age reader, was used for all of the age determinations; such a process would usually require re-ageing of previously collected otoliths, and thus would be both expensive and time-consuming. In practice, the assumption that all sampling years were aged in an identical manner is usually either assumed based on calibration studies reported elsewhere or ignored altogether. But how dangerous is this assumption? Does the use of pre-existing age data necessarily introduce significant error, and if so, how much? Here I take

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advantage of an 86-yr time series of otolith samples used for the stock assessment of Icelandic cod (*Gadus morhua*) to rigorously test the assumption of inter-year comparability of age interpretation across decadal changes in otolith preparation, viewing protocol and age reader. Through comparison of the original age estimates with re-ageing of the same otoliths using modern preparation and interpretation protocols conducted by a single age reader, the sources and magnitude of ageing error can be evaluated over a time scale that has not previously been reported.

2. Methods

The adult Atlantic cod (*Gadus morhua*) sagittal otoliths used in this study represented a subset of the adult otoliths used for a previous study of long-term growth plasticity and synchrony in the northeast Atlantic (Smoliński et al., 2020; Campana et al., 2023). The otoliths ($n = 3278$) from the growth synchrony study were extracted from the archival collection of the Marine and Freshwater Research Institute (MFRI) in Iceland, as representative of longline and bottom trawl catches in the marine areas of southwest Iceland between 1929 and 2015 (see Campana et al., 2023 for a full description of the sampling strategy). Otolith selection within a sampling year was intentionally non-random, and was focused on fish believed to be sexually mature (8 yr of age or older, based on previous age determinations) to meet the objectives of the growth synchrony study. All otoliths had previously been aged, using the methods in practice at the time of sampling. Starting in 1997, all otoliths were embedded in black epoxy and sectioned transversely through the core to a thickness of 1 mm with a Buehler IsoMet 1000 Precision Saw with a diamond blade. Prior to 1997, otoliths were generally cracked through the core, the exposed (transverse) face was coated with water and then aged under a binocular microscope. Some otoliths were microscopically examined whole while immersed in alcohol or water. A total of 6 primary age readers were responsible for cod ageing over the past century, with the ages being used for stock assessment. The sampling years corresponding to each ager are known, but the details of their age interpretation protocol are not.

The objective of the current study was to allow a rigorous comparison of the original ages with those based on modern methods and a single age reader. To meet this objective, a single expert cod otolith age reader re-aged a subsample of the otoliths from the growth synchrony study of Campana et al. (2023), using modern methods and protocols. The otoliths for re-ageing were selected randomly from within each decade of the entire time series, rather than annually, to ensure adequate sample size. The age reader was one of those involved in routine cod ageing by MFRI since 1997. Existing otolith sections were first photographed using a high-resolution digital video camera (Olympus DP74 connected to a Leica S8 APO stereomicroscope) under reflected light. Unsectioned otoliths were embedded, sectioned and photographed as described above. The age reader then re-aged ~28% of the otolith images within each decade of the entire time series ($N = 906$). Re-ageing by a single experienced age reader allowed the detection of possible confounding effects due to changes in ageing method, interpretation protocol or age reader over time.

Matched pair age comparisons between the original and the modern (re-aged) otoliths were made with age bias plots (Campana, 2001); due to the design-based truncation at age 8 in the original sample selection, the original ages were treated as the independent variable in the age bias plot. The mean coefficient of variation (CV) was calculated as the mean of the standard deviation over the mean of each pair of age comparisons, where CV values of less than 5% are generally considered to be precise (Campana, 2001). Symmetry tests (Evans-Hoenig and McNemar tests; Evans and Hoenig, 1998) were implemented in the R package FSA (Ogle, 2018). Differences in the fit between linear models were considered to be significant if AIC deviations exceeded 2.

3. Results

The 906 otoliths analyzed in this study were broadly representative of fully mature cod (total length of 54–136 cm; mean 90 cm) from the southwest of Iceland during the spring spawning season over a period of 86 yr. The median age of both the original and modern ages was 8 yr, with a range of 8–22 yr for the originally-assigned ages and 5–23 yr for the modern ages. Most of the otoliths (82%) were originally aged without sectioning by five of the six age readers, while one of the five readers spent 13 years ageing unsectioned otoliths and a further 7 years ageing sections. All of the age readers spent at least 8 yr ageing cod otoliths, at a rate of > 10,000 otoliths annually, and thus were very experienced.

The age reader who re-aged the otoliths was partially responsible for the original ageing done after 1997, suggesting that there should be no bias between the original (sectioned) and modern ages after 1997. Lack of bias was confirmed with a contingency table (Table 1A), an age bias plot ($n = 162$) and tests of symmetry (Evans-Hoenig, $P = 0.13$; McNemar, $P = 0.11$), with a very precise CV of 3.1%. Thus the re-ageing protocol and interpretation was consistent with that used in the original section-based ageing, with no bias and reasonably good precision.

There was a significant bias between the original unsectioned ages and those based on the modern sections, with the means of the original ages exceeding the modern ages at almost every age (Fig. 1). The extent of the bias was minimal at age 8 (0.18 yr), increasing to an average divergence of about 2 yr after age 14. Ages less than 12 yr, which accounted for 85% of the sample size, were biased by less than one year. Both the Evans-Hoenig and the McNemar tests of symmetry were highly significant ($P < 0.001$). The mean CV between the paired age estimates was 6.1%, which is higher than would normally be observed in an ageing study of cod.

A time series of the extent of the ageing bias indicated that the original over-ageing was linked strongly to the individual ager, and not just the transition from unsectioned to sectioned otoliths (Fig. 2). The mean divergence (0.65 yr) between original and modern ages was largest during the period 1929–1967, which spanned 3 age readers. The mean divergence after 1967 was 0.17 yr, which was a period that also spanned 3 age readers, as well as the transition to sectioned otoliths. Notably, the single age reader who spent years ageing unsectioned otoliths before transitioning to sectioned otoliths showed little change before and after the methodological transition, but both periods were significantly biased ($P < 0.05$) relative to modern ages by a mean of 0.26 yr.

A hierarchical sequence of linear models indicated that inclusion of age readers explained most of the variance between the original age and the modern section age (Table 2). Inclusion of ageing method as a factor was not a large improvement over a simple model relating modern and original ages ($\Delta AIC=2$). However, a model where Ager was included as a factor reduced the AIC by 22 (Table 2), a result which was similar to a model which included an Ager x Original Age interaction. The contingency table of Table 1B and the parameter estimates of Table 2 indicate that the largest ager-level divergences were associated with the first two Agers, who collectively worked between 1929 and 1945.

Measures of precision are not particularly useful if there is bias in the age estimates, but a time series of precision estimates can highlight trends. When calculated on a year by year basis, the trend was towards improved precision over the time series, with CV values averaging a relatively imprecise 7.1% before 1946 and a much more precise value of 3.1% after the transition to section-based ageing (Fig. 3). Interestingly, the precision of the single age reader who originally interpreted both unsectioned and sectioned otoliths increased from a CV of 7% with unsectioned otoliths to 2.8% with sectioned otoliths.

4. Discussion

Given the marked improvements in age determination protocols over

Table 1

Contingency tables of modern section ages against: A) Original section ages; B) Original unsectioned ages prior to 1945.

A			Original Section Age (yr)															
Modern Section Age (yr)	5	6	7	8	9	10	11	12	13									
5	0	0	0	0	0	0	0	0	0									
6	0	0	0	0	0	0	0	0	0									
7	0	0	0	27	0	0	0	0	0									
8	0	0	0	99	2	0	0	0	0									
9	0	0	0	20	5	4	0	0	0									
10	0	0	0	1	0	2	0	0	0									
11	0	0	0	0	0	0	0	1	0									
12	0	0	0	0	0	0	0	0	0									
13	0	0	0	0	0	1	0	0	0									
B			Original Unsectioned Age Prior to 1945 (yr)															
Modern Section Age (yr)	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
5	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	30	3	2	0	1	1	1	0	0	0	0	0	0	0	0
8	0	0	0	56	5	2	1	4	1	0	0	0	1	0	0	0	0	0
9	0	0	0	13	8	17	2	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	2	0	10	4	4	0	0	0	0	0	0	0	0	0	0
11	0	0	0	1	2	2	5	7	3	1	1	0	0	0	0	0	0	0
12	0	0	0	0	0	0	3	14	2	3	1	1	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	3	3	0	1	1	0	0	0	0	0
14	0	0	0	0	0	0	0	1	2	1	1	2	0	1	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	1	1	4	1	0	0	1	0
18	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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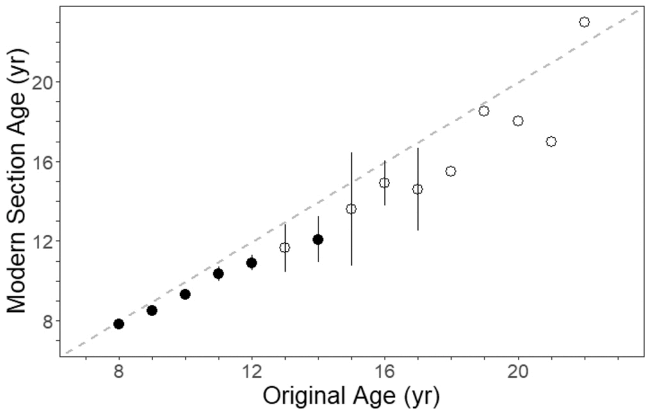

Fig. 1. Age bias plot between the originally-assigned otolith age and the modern section otolith age. Each error bar represents the 95% confidence interval for the mean modern section age for all fish assigned a given original unsectioned otolith age. Error bars with a solid fill differ significantly from the one to one equivalence line (shown as a dashed line). Error bars for ages 18 + are based on fewer than 10 observations each.

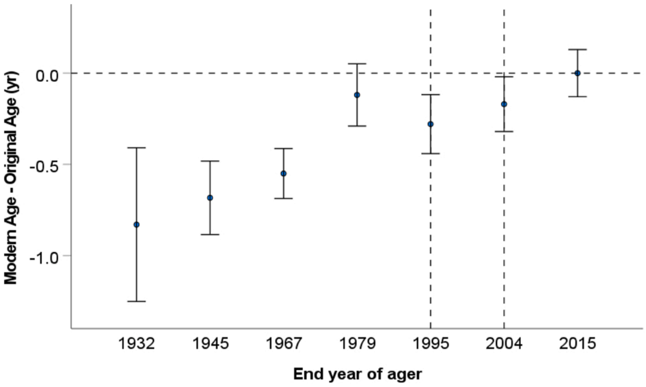

Fig. 2. Divergence (in years) between the modern otolith section age and the originally-assigned age, grouped by ager. The last year of ageing by each ager is shown on the X axis. The dashed horizontal reference line indicates zero net divergence in age estimates. The two vertical dashed reference lines indicate the single ager associated with the transition from unsectioned otoliths to otolith sections, where samples between 1979 and 1995 were unsectioned and those until 2004 were sectioned. Error bars show the 95% confidence interval.

recent years (Campana, 2005), the likelihood of an 86-yr time series of otolith ages showing no bias against modern methods would appear unlikely. Thus the finding that there was significant bias in the original cod ages compared to modern ages is not at all surprising. What is surprising though is that the bias was so small (< 2 yr in fish <14 yr of age), despite spanning changes in otolith preparation, examination, interpretation and age reader. Indeed, it is remarkable that even the earliest decades of otolith ageing (1920–1940 s) were marked by such modest biases. There are few published studies against which such long term comparisons can be evaluated. Morin et al. (2013) sectioned and then re-aged 59 American plaice (*Hippoglossoides platessoides*) otoliths that had originally been aged whole 40 years previous, and found no net difference. In keeping with many flatfish otoliths, these otoliths were dorso-ventrally flattened, and thus showed remarkably clear annual growth increments without sectioning. Zuykova et al. (2009) carried out a similar study on cod, re-ageing otoliths over a 35-yr period, but without any new preparation. Thus the comparison was limited to interpretation, not methodological. In keeping with our results, they reported deviations of less than one year between historical and modern ages before 1960, with historical ages exceeding modern ages. Unlike our results however, the bias was also apparent (and reversed) at ages less than 8 yr. In the absence of revised preparation methods, it is difficult to interpret these results.

The modest over-ageing of the historical cod ages can largely be

Table 2

Output of linear model: Modern Section Age ~ Original Age + Ager, where the parameter estimate for Original Age is a covariate (slope) and the Agers are factors. The model was highly significant ($P < 0.0001$) with an R^2 of 0.73.

Parameter	Estimate	Std Error	P
Intercept	2.03	0.20	< 0.01
Original age	0.75	0.02	< 0.01
Ager 1 whole	-0.35	0.13	< 0.01
Ager 2 whole	0.69	0.22	< 0.01
Ager 3 whole	-0.21	0.13	0.09
Ager 4 whole	-0.11	0.15	0.47
Ager 5 whole	-0.23	0.12	0.06
Ager 5 section	-0.16	0.17	0.35
Ager 6 section	-	-	-
Model $R^2 = 0.73$			

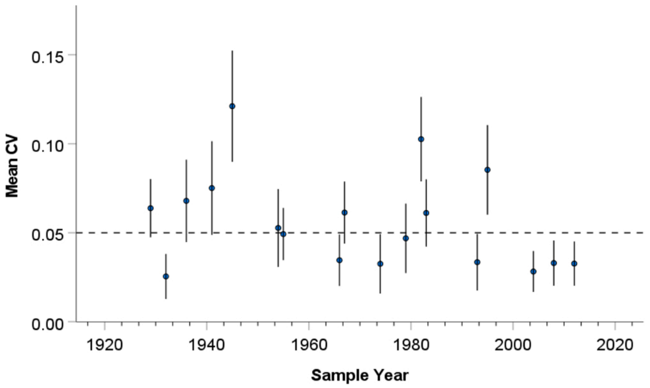

Fig. 3. Ageing precision (Coefficient of variation, CV) between the modern otolith section age and the originally-assigned age, grouped by year of sample collection. The dashed horizontal reference line indicates a CV of 5%, typically associated with acceptable ageing precision. Samples collected after 1997 were all aged with sections. Error bars show the 95% confidence interval.

attributed to the structures and methods that were originally used. Scales and vertebrae are well known for under-ageing longer-lived fish (Gunn et al., 2008), yet those structures were not used for Icelandic cod, at least after 1929. Whole otoliths are suitable for ageing many fish species of moderate longevity, but tend to underestimate age in long-lived fish (Dwyer et al., 2003; Gunn et al., 2008). For this reason, otolith sections have become the preferred approach for ageing all but short-lived species. It is fair to ask then, why the historical ages in this study tended to be older, not younger, than those based on sections. Consistency between the original ages and the modern section ages can be explained by the fact that the original cod agers usually cracked the otoliths of the larger fish in half, so as to reveal the growth pattern along the dorso-ventral (thickened) axis. In principle, an otolith cracked through the core reveals the same growth bands that would be visible in a section, albeit over a rugged surface. Age comparisons between cracked and sectioned otoliths have seldom been reported, but a study of Atlantic redfish (*Sebastes* spp) otoliths revealed that cutting an otolith in half (which exposes the same surface as a section) provided accurate ages to at least 70 yr of age, whether burned or unburnt (Campana et al., 2016). The absence of a change in bias associated with the transition from cracked to sectioned Icelandic cod otoliths is consistent with this hypothesis. It is also consistent with the improved precision evident in the transition to sections, due to the relative ease of ageing flat sections compared to a three-dimensional cracked surface. However, it does not explain why the historic (cracked) ages might be older. Presumably, some aspect of growth band interpretation was involved here, perhaps associated with the otolith margin, for which specific protocols have only been developed in recent decades.

The single largest contributor to age deviations in this study was associated with the individual age reader. Systematic age differences due to individuals are common, and can account for consistent differences among agers of up to a year, even across abundant age classes (Power et al., 2006; Hanselman et al., 2012; Hüssy et al., 2016). In this study, individual differences were due not only to interpretation, but to protocols associated with preparation and examination as well. Perhaps not surprisingly, the largest individual biases, and the poorest precision levels, were associated with the earliest age readers. The fact that they aged as well as they did, in the absence of any modern protocols, is remarkable.

The implications of this study are encouraging, in that they suggest that old data sets incorporating historic age determinations may well be adequate for many purposes in species where the growth increments do not become inordinately narrow with age (as they do in many *Sebastes* species). A gradual increase in bias with fish age is commonly observed (Dwyer et al., 2003; Gunn et al., 2008), but if limited to ages beyond those of major interest (as it was in this study), may remain largely irrelevant. Conservation studies requiring longevity estimates would suffer; stock assessment time series using a plus group in the catch at age matrix would not. However, our conclusions would have been very different if other structures had been used in the original ageing. Scales, vertebrae and whole otoliths can result in a compressed and truncated age composition, implying that a simple transformation cannot be used to reconstruct the correct age composition, as could be done here.

CRediT authorship contribution statement

Steven Campana was sole author of this manuscript, and is fully responsible for all aspects of its preparation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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