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Age determination and growth of Atlantic redfish (*Sebastes marinus* and *S. mentella*): bias and precision of age readers and otolith preparation methods

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Age determination of Atlantic redfish (*Sebastes* spp.) has proven difficult and has led to inconsistent age and growth estimates in the past. Using otoliths of the two major commercial species, golden redfish (*Sebastes marinus*) and deep-sea redfish (*S. mentella*), a series of exchange schemes was carried out to assess bias and precision of age readings between four readers and between two preparation methods. Considerable bias between readers and moderate precision were observed for the *S. marinus* readings, especially for ages >20 years, with coefficients of variation (CV) of 7.7–12.0% and average percent error (APE) of 5.4–8.5%. Agreement between readers increased from 17–28% to 45–61% when allowing deviations of ±1 year, and to 80–92% with ±3 years tolerance. The age of *S. marinus* determined from broken and burnt otoliths was estimated to be slightly lower than when the age of the same individuals was determined from thin-sectioned otoliths. The bias and precision estimates obtained from the *S. mentella* material were generally poorer than for *S. marinus* (CV 8.2–19.1%, APE 5.8–13.5%), but similar to reported values for other long-lived fish species. Better than 50% agreement was only achieved with ±3 years tolerance. Growth rates differed significantly between species, confirming slower growth for *S. mentella*. For *S. marinus*, only one reader comparison revealed significantly different growth functions, whereas almost all *S. mentella* reader pairs showed significant differences in growth curves. Section and break-and-burn readings of *S. marinus* did not differ significantly. Average ages of around 9–10 years were determined for juvenile *S. mentella* 24–30 cm long, which were likely to have migrated from East Greenland into the Irminger Sea, based on earlier observations. As some of the error in the age determinations presented could be attributed to interpretation differences between readers, further intercalibration of redfish ageing is urgently needed in order to provide consistent input data for stock assessment.

Keywords: age determination, bias, growth, North Atlantic, precision, redfish, *Sebastes marinus*, *Sebastes mentella*.

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Introduction

Age determination provides essential input data for the assessment of marine fish stocks (Hilborn and Walters, 1992). Utilizing the periodicity in the formation of growth increments of calcified hard structures, such as scales, otoliths, fin rays, or vertebrae, the age of fish can usually be estimated by counting annual zones (Campana, 2001). Reliable age estimates, however, are difficult to obtain for species found in tropical regions and therefore lacking seasonality in growth, and for long-lived species, owing to the slow growth and narrow increments in the older growth zones. Redfish of the genus *Sebastes* inhabiting the North Atlantic exhibit longevity of up to 75 years (Campana *et al.*, 1990), leading to problematic age determination (e.g. ICES, 1996). Therefore, most laboratories investigating stock dynamics of redfish have not implemented routine age readings for reasons of concern about the error and poor reliability. In contrast, regular ageing schemes have been established for Pacific *Sebastes* species (MacLellan, 1997; C.A.R.E., 2000), notwithstanding maximum ages of >100 years (Munk, 2001) that were recently confirmed by radiometric ageing (Andrews *et al.*, 2002).

The reliability of hard body structures of fish for ageing has been questioned and addressed several times in the past (e.g. Bortone and Hollingsworth, 1980; Welch *et al.*, 1993; Howland *et al.*, 2004). Various studies (Chilton and Beamish, 1982; Nedreaas, 1990; Saborido-Rey, 1995) and workshops (ICES, 1991, 1996) have shown that otoliths are the most suitable structure for ageing redfish, because scales tend to yield underestimates of older ages and there are serious difficulties in interpreting other structures, such as fin rays or vertebrae. However, otolith-based ageing is also subject to a degree of error, manifested in two major elements: bias and precision. Bias in age readings is caused by a consistent deviation of reading results between readers, and is skewed from the mean to one side or the other, whereas the precision of age readings measures the closeness of repeated independent age estimates (Wilson *et al.*, 1987; ICES, 1996). Precision reflects the degree of agreement among readers, and is not to be confused with accuracy, which relates to agreement with the true age of the fish (Campana, 2001). Although there are routine testing systems and procedures for assessing the bias and the precision of age readings (Kimura and Lyons, 1991; Campana *et al.*, 1995; Hoenig *et al.*, 1995), broad-scale application of these methods in the laboratories carrying out redfish age readings is still missing.

The most recent "Workshop on Age Reading of *Sebastes* spp.", supported by ICES in 1995, revealed considerable bias between readers that improved after discussion of general interpretation of growth structures on the sectioned otoliths (ICES, 1996). Obviously, therefore, there is a need for exchange of material and knowledge on age reading. Before otoliths can be used for age reading, they have to be prepared in a manner that allows clear identification of growth structures. Laboratories in Canada, Iceland, Norway, Spain, and the US mainly use the "break (and burn)" method for ageing *Sebastes* (Chilton and Beamish, 1982; Nedreaas, 1990; MacLellan, 1997; Saborido-Rey *et al.*, 2004), whereas institutes in Germany and the eastern part of the US use thin sections of otoliths (ICES, 1984; Gifford and Crawford, 1988). Only few comparisons have been carried out to assess the variability between both methodologies with regard to Pacific rockfish (Boehlert and Yoklavich, 1984; Stanley, 1987; Andrews *et al.*, 2002), and systematic studies to elucidate advantages or drawbacks of one or the other technique have not been documented.

As part of a multidisciplinary research project on the population structure, reproductive strategy, and demography of redfish in the Irminger Sea and adjacent waters, several otolith exchanges between four redfish age-reading experts of the participating nations (Germany, Iceland, Norway, Spain) were carried out. The first otolith exchange was based on *S. marinus* from the Icelandic shelf. The ages obtained from this exchange were compared between readers and preparation methods with respect to bias and precision. The second set of material exchanged comprised otoliths of pelagic *S. mentella* from the Irminger Sea that were prepared as thin sections to investigate species-specific differences in the level of error. Differences in longevity and growth between *S. marinus* and *S. mentella* were expected (e.g. Nedreaas, 1990; Saborido-Rey *et al.*, 2004), so the age–length relationships and corresponding von Bertalanffy growth parameters were calculated from the data of both exchange programmes. Differences in growth rate between readers, methods, and species were tested for statistical significance, and having estimated ageing errors and growth, the ages of juvenile *S. mentella* involved in migrating from the East Greenland shelf into the Irminger Sea in 1998–1999 (Stransky, 2000) were determined from otoliths of fish of the tracked size groups caught during that period.

Material and methods

The otoliths used for the study were divided into four sets (Table 1), representing the specific tasks of the respective age-reading comparisons. Two methods of otolith preparation (sections and break-and-burn) were used to age *S. marinus*, while the *S. mentella* otoliths were only sectioned. Four age readers from different nations participated in the comparisons.

S. marinus otoliths were collected on board the Icelandic vessel M/V "Brettingur NS" during a groundfish survey carried out in March 1997. The otoliths were taken randomly from five hauls on the Icelandic shelf (ICES Division Va). For age determination, 212 sagittal otolith pairs from fish ranging from 10 to 54 cm total length were selected (Table 1). One otolith from each pair was prepared for age reading using the break-and-burn technique (Christensen, 1964), while the other otolith was thin-sectioned, as described by Bedford (1983). The preparation by break-and-burn was carried out at the Marine Research Institute in Reykjavík, Iceland. Annuli were counted using a range of microscope magnification (up to 100×). A drop of oil was put on the otolith before counting the rings to enhance clarity. Reflected light with an angle of about 30–45° to the otolith surface was used for these readings. The thin sections were produced at the Institute for Sea Fisheries of the Federal Research Centre for Fisheries in Hamburg, Germany. Two diamond-tipped saw blades of 0.3 mm thickness and 100 mm diameter, rotating at

Table 1. Redfish otolith samples exchanged between four age readers.

Species	Sampling area (ICES Subarea or Division)	Sampling date or period	Depth range (m)	Length range (cm)	n	Preparation method
S. marinus	Iceland (Va)	March 1997	247–421	10–54	212	Section, break & burn
S. mentella	Irminger Sea (XII)	July 1999	200–350	22–41	213	Section
S. mentella	East Greenland (XIVb)	October 1998	246–389	24–30	60	Section
S. mentella	Irminger Sea (XII)	June/July 1999	200–650	25–30	86	Section

6000 rpm, were used on a geological cutting machine (Conrad, Clausthal-Zellerfeld, Germany) to cut sections about 0.5 mm thick. These thin sections were mounted onto glass plates with translucent polyester resin and read at a magnification of 20–40× using transmitted light. All readers followed the general guidelines from the most recent redfish ageing workshop (ICES, 1996). For the comparison of preparation methods, only the age readings of the Icelandic reader were used.

Pelagic *S. mentella* were sampled from 12 trawls in the Irminger Sea (ICES Subarea XII) within a commercial sampling scheme on board the German F/V "Fornax" in July 1999 (Table 1). From the sampled fish, 213 otolith pairs were selected randomly for thin sectioning and subsequent age determination. *S. mentella* otoliths from fish 24–30 cm long were taken on board the German FRV "Walther Herwig III" off East Greenland (ICES Division XIVb, bottom trawls) in October 1998, and in the Irminger Sea in June/July 1999 (ICES Subarea XII, pelagic trawls).

To compare bias and precision between readers and methods, a suite of statistical tests and graphical methods was applied. Estimates of bias were based on simple linear regression analysis, the parametric paired t-test, and the nonparametric Wilcoxon matched-pairs rank test (Conover, 1998; Hollander and Wolfe, 1999). The slope and the intercept of simple linear regressions were tested for significant differences ($\alpha = 0.05$) from 1.0 and 0, respectively. The parametric paired t-test and the nonparametric Wilcoxon matched-pairs rank test were used to detect significant differences from a paired difference of 0. As error terms, 95% confidence limits were calculated. Age bias plots (Campana *et al.*, 1995) were produced to visualize the deviation of the age readings of two readers or methods from the 1:1 equivalence line. These plots also allowed the detection of non-linear bias, e.g. relative underestimation of age by one reader in one part of the age range and relative overestimation in another part of the age range by the same reader.

Various estimators of precision were suggested to compare age readings. One of the more common indices is percentage agreement, comparing the percentage of age determinations that agree within a specified number of years. This index, however, does not evaluate the degree of precision equally for all species. If, for example, 95% of the age readings agree within a range of ±1 year for cod (*Gadus morhua*), precision would be very poor because there are few year classes in the fishery. For *S. mentella*, 95% agreement within a tolerance range of ±5 years would represent good precision, given the 75-year longevity and 30–40 age groups present in the fishery. Beamish and Fournier (1981) therefore suggested use of an average percent error (APE), which is dependent on the average age of the fish species investigated:

$$\mathrm{APE_j}(\%) = 100 \times \frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij} - X_j|}{X_j}$$

where R is the number of times each fish is aged, X_{ij} the i(th) age determination of the j(th) fish, and X_j is the mean age calculated for the j(th) fish.

Chang (1982) modified this index to a coefficient of variation (CV), substituting the absolute deviation by the standard deviation from the mean age:

$$\mathrm{CV_j}(\%) = 100 \times \frac{\sqrt{\sum_{i=1}^{R}\frac{(X_{ij}-X_j)^2}{R-1}}}{X_j}$$

In addition to these indices, the correlation coefficient r^2 was calculated to evaluate the fraction of variation explained by the linear relationship between readers or otolith preparation methods.

For both *S. marinus* and *S. mentella* age readings, the age–length relationships were plotted and fitted with the von Bertalanffy growth function:

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

where L_t is the fish length (cm) at age t (years), L_{inf} the asymptotic maximum fish length (cm), and t_0 is the theoretical age (years) when the fish was at length zero. L_{inf}, the growth coefficient k, and t_0 were calculated iteratively. To estimate the reader effect on the growth functions, individual sets of growth parameters were calculated for each reader and compared with literature data. The differences in growth curves were tested by a Chow test (Chow, 1960; Saborido-Rey *et al.*, 2004).

Results

S. marinus: comparison of readers

As indicated by the age bias plots for the *S. marinus* readings (Figure 1), all between-reader comparisons exhibit a certain degree of bias, particularly for ages >20 years. In all six cases, the deviation from the 1:1 equivalence line is non-linear, most pronounced in the comparisons between reader 4 and all other readers (Figure 1, right side). Reader 4 generally allocated higher ages in the range 2−12 years and lower ages in the range 13−30 years. However, in the comparisons of readers 1 and 2 and readers 2 and 3, the

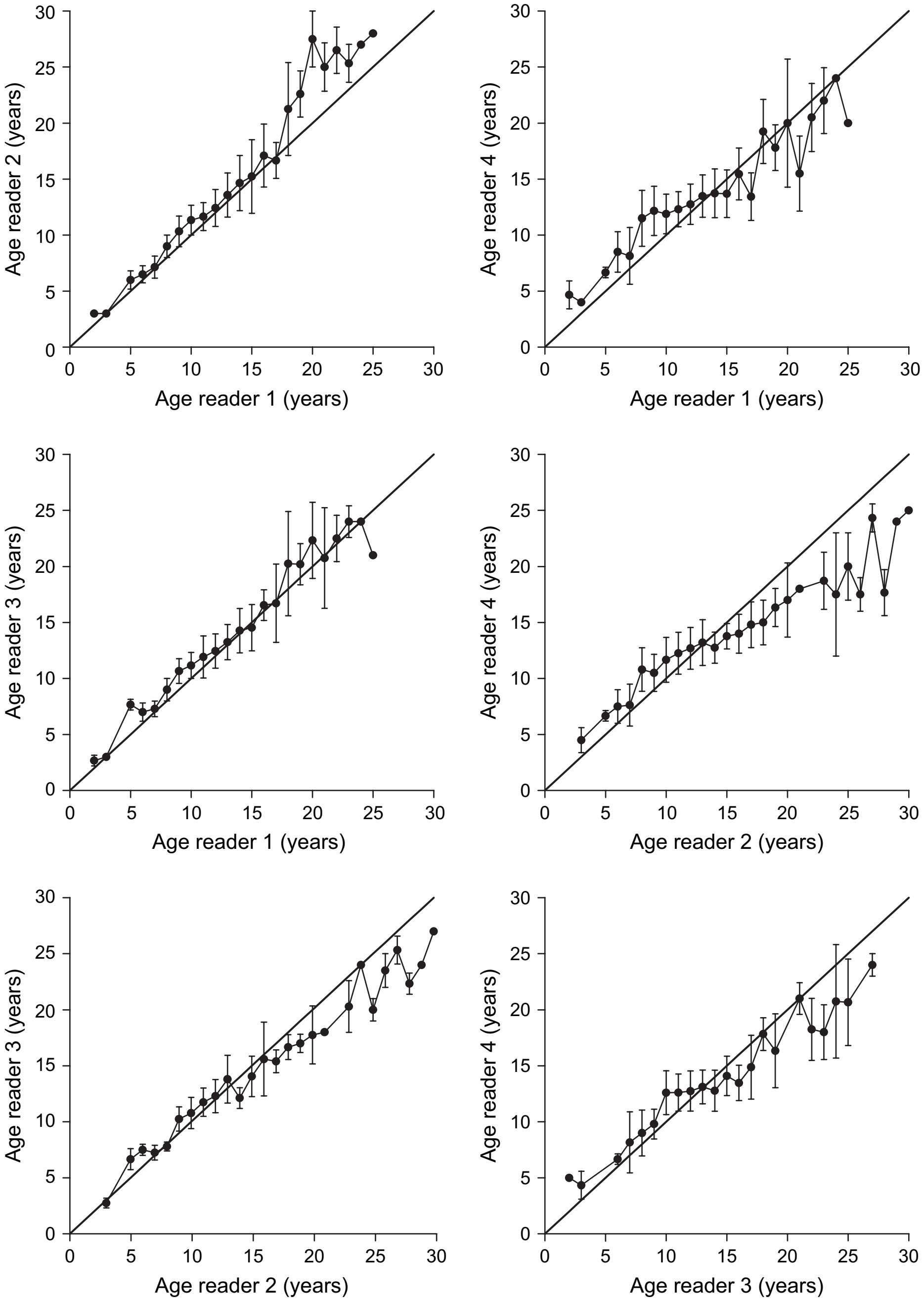

Figure 1. Age bias plots for the reader comparisons based on *S. marinus* otoliths from the Icelandic shelf. Each error bar represents the standard deviation around the mean age assigned by one reader for all fish assigned a given age by the second reader. The 1:1 equivalence (straight line) is also indicated.

Table 2. Statistical tests for the detection of bias for age readings of *S. marinus* between readers and methods.

	Age reader pair						
Statistic	Reader 1 vs. reader 2 (n = 199)	Reader 1 vs. reader 3 (n = 212)	Reader 2 vs. reader 3 (n = 199)	Reader 1 vs. reader 4 (n = 212)	Reader 2 vs. reader 4 (n = 199)	Reader 3 vs. reader 4 (n = 212)	Sections vs. break & burn (n = 105)
				Regression			
Slope	1.157 ± 0.038	0.950 ± 0.034	0.783 ± 0.024	0.693 ± 0.040	0.588 ± 0.030	0.688 ± 0.035	0.877 ± 0.024
p	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Intercept	−0.993 ± 0.510	1.221 ± 0.460	2.615 ± 0.357	4.345 ± 0.536	5.153 ± 0.435	4.267 ± 0.497	0.987 ± 0.368
p	0.053	0.009	0.000	0.000	0.000	0.000	0.009
				Wilcoxon test			
p	0.000	0.000	0.012	0.006	0.134	0.762	0.000
				Paired t-test			
Mean paired difference	−1.005 ± 0.320	−0.585 ± 0.274	0.372 ± 0.296	−0.406 ± 0.360	0.513 ± 0.401	0.179 ± 0.360	0.771 ± 0.315
p	0.000	0.000	0.014	0.028	0.019	0.327	0.000

mean ages assigned by one reader deviate considerably from the age assignments of the second, particularly in the age range 17–30 years. Table 2 presents the statistical tests applied to the comparison of readers in terms of bias. Regression analysis, the Wilcoxon test, and the paired t-test reveal high levels of significance in most cases, generally indicating bias between readers. The readings of reader pairs 2 vs. 4 and 3 vs. 4, however, did not differ significantly according to the Wilcoxon test, and the comparison between readers 3 and 4 resulted in a non-significant mean paired difference (−0.2 years, $p = 0.327$). The overestimation of ages assigned by reader 2 compared with reader 1 in the older ages (deviation up to 10 years), as shown in Figure 1, results in a slope >1 and a negative intercept of the linear regression. The highest overall bias was between readers 1 and 2, which gave a mean paired difference of about 1 year. Slopes of <1 and positive intercepts are present in all other comparisons. The largest deviation from the 1:1 equivalence line could be detected for reader 2 vs. reader 4, with a slope of <0.6 and an intercept of >5 (Table 2). In all six age bias plots (Figure 1), there is a general trend in increasing standard deviation around the mean with increasing age.

From the precision estimates between readers (Table 3), r^2, the CV, and the APE of the first three comparisons (reader 1 vs. reader 2, reader 1 vs. reader 3, reader 2 vs. reader 3) show relatively good agreement, whereas all comparisons with reader 4 resulted in considerably lower precision. The agreement between readers was 24–28% in the first three cases, but well below 20% in the other cases. If the tolerance level of agreement between readers is raised, as illustrated in Figure 2, a level of around 80% and higher is reached with a tolerance of ±3 years, over the whole age range. For *S. marinus* aged 0–10 years, this tolerance leads to $>95\%$ agreement in the first three reader pairs, and to some 80% for the other readers with reader 4. In the age range 11–20 years, some 90% of the readings agree in all cases, but for older *S. marinus* (21–30 years),

Table 3. Measures of precision for age readings on *S. marinus* between readers and methods.

	Age reader pair						
Statistic or index	Reader 1 vs. reader 2 (n = 199)	Reader 1 vs. reader 3 (n = 212)	Reader 2 vs. reader 3 (n = 199)	Reader 1 vs. reader 4 (n = 212)	Reader 2 vs. reader 4 (n = 199)	Reader 3 vs. reader 4 (n = 212)	Sections vs. break & burn (n = 105)
Correlation coefficient (r^2)	0.824	0.787	0.840	0.590	0.667	0.631	0.930
CV (%)	8.79	8.19	7.66	11.96	11.22	10.61	6.69
APE (%)	6.21	5.79	5.42	8.45	7.93	7.50	2.49
Agreement (%)	24.12	25.00	27.64	16.51	18.59	18.87	28.57

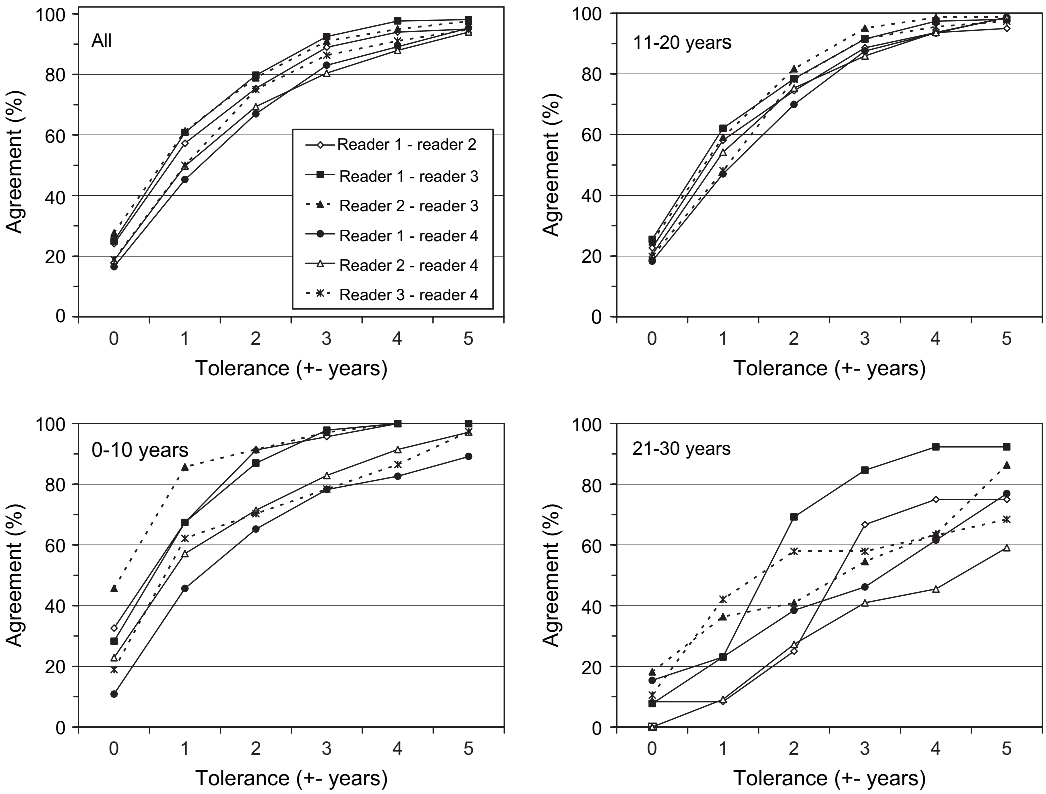

Figure 2. Agreement plots for the reader comparisons based on *S. marinus* otoliths from the Icelandic shelf for a tolerance level (deviation of assigned ages between both readers) of ±0 (total agreement) to ±5 years. These were applied to all age groups and subsets of age ranges assigned by the first reader.

agreement between readers was poor, in the worst case (reader 2 vs. reader 4) <60% even with a tolerance of ±5 years (Figure 2).

S. marinus: comparison of otolith preparation methods

The age bias plot for the comparison of otolith preparation methods (Figure 3a) shows a slight relative underestimation of age from 12 years using the break-and-burn technique. This observation is also indicated by a regression slope of <1 and a positive intercept (Table 2). The mean paired difference between both methods was about 0.8 years. In contrast to the reader comparisons, the variation around the mean of the break-and-burn age readings does not increase steadily with higher age. All precision indices for the comparison between methods were better than between readers (Table 3). The regression explains about 93% of the observed variation, and the CV and APE are relatively low. The agreement between otolith preparation methods is about 29%, a markedly better value than achieved in the reader comparisons. The percentage agreement plot for the comparison of methods (Figure 3b) shows relatively poor agreement in the age range 21–30 years, but considerably better correspondence at younger ages (>90% agreement with ±3 years tolerance).

S. mentella: comparison of readers

An even higher degree in bias was obvious from the comparisons of *S. mentella* age readings (Figure 4). The deviation from the 1:1 equivalence line is non-linear for all reader pairs, and the most pronounced bias was again in all comparisons involving reader 4 (Figure 4, right side). In the age range 15 years and older, reader 4 considerably underestimated most of the ages relative to the other readers, resulting in regression slopes markedly <1 and mean paired differences of up to 5 years (Table 4). Readers 2 and 3 generally assigned higher ages than reader 1 (Figure 4), with mean paired differences of −2.2 and −0.8 years, respectively (Table 4). The nonparametric Wilcoxon test and the parametric paired t-test show high levels of significance in all six comparisons.

A relatively high correlation between *S. mentella* readings (87–95%), but slightly higher CVs and APEs than in the *S. marinus* readings indicated medium precision for most reader pairs, apart from the comparison of readers 2 and 3 with reader 4, which revealed considerably larger

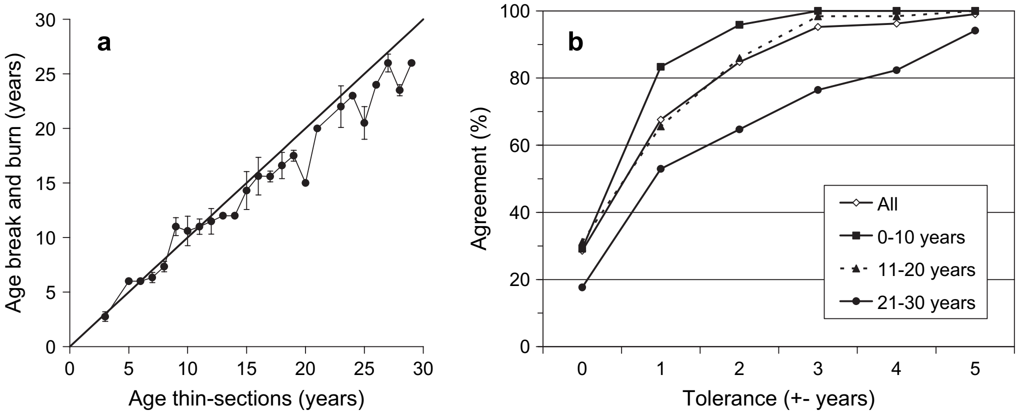

Figure 3. (a) Age bias plot comparing otolith preparation methods based on *S. marinus* from the Icelandic shelf. Each error bar represents the standard deviation around the mean age assigned in the break-and-burn readings for all fish assigned a given age in the thin-section readings. The 1:1 equivalence (straight line) is also indicated. (b) Agreement plot in which tolerance levels (deviation of assigned ages between methods) of ±0 (total agreement) to ±5 years are applied to all age groups and subsets of age ranges assigned in the thin-section readings.

error terms (Table 5). The percentage agreement between *S. mentella* readers was variable (4–19%). If the percentage agreement plots are divided into age ranges of 10 years (Figure 5), the ranges where most of the ageing error occurs become visible. The curves for all reader pairs change from asymptotic to linear with increasing age range, showing that for ages >20 years, tolerance levels of ±1–2 years only lead to moderate improvements in the percentage agreement. The agreement between readers for all age groups increased to 62–87% when ±5 years tolerance was invoked (Figure 5). In the younger age groups (≤20 years), 73–100% agreement was achieved with a tolerance of ±3 years, whereas in the age ranges 31+ years, agreement was mostly less than 50% at this tolerance level. In the age range 21–30 years, clear separation of reader pairs was obvious (Figure 5). The three comparisons with reader 4 revealed agreement of 24–42% applying ±5 years tolerance, while the other reader pairs reached 79–89% on this level.

Age–length relationships and growth parameters

The calculated growth parameters for Icelandic *S. marinus* varied considerably between readers and only slightly between methods (Table 6). The age–length data of reader 2, both from section and break-and-burn readings, led to a relatively low L_{inf} (<48 cm) and relatively high k values (0.12–0.13). Most of the other studies on *S. marinus* reported L_{inf} values of about 50 cm and k values of 0.09–0.12, similar to the parameters obtained from the combination of all readings. The overall growth function derived from the *S. marinus* readings (Figure 6) also shows an asymptotic maximum length of about 50 cm and high variation in age readings, particularly for reader 4.

For *S. mentella* from the Irminger Sea, the asymptotic length was about 40 cm (Figure 7). Markedly slower growth than that of *S. marinus* is also clear, indicated by a lower k value (0.08 for all readers combined, Table 6). In accord with the relative underestimation of age by reader 4, the k value calculated from his results (0.12) well exceeds that obtained for the other readers (0.07). The t_0 values for Irminger Sea redfish also vary between readers and indicate erratic estimates of down to −9.6 years in the worst case (Table 6).

The Chow test results (Table 7) revealed only one significant comparison (reader 1 vs. reader 2) for *S. marinus*, whereas almost all *S. mentella* reader pairs were significantly different. In the latter case, the growth functions of readers 2 and 4 deviated most, while those of readers 1 and 3 did not differ significantly. The growth comparison derived from sectioned and broken and burnt *S. marinus* otoliths was not significant (Table 7). Overall, however, the growth curves differed considerably more between species than between readers or methods (Figure 8). The Chow test confirmed significant differences in growth between species for all readers (Table 7), with reader 4 yielding the lowest F value.

Juvenile *S. mentella*

Comparative readings carried out on *S. mentella* otoliths from fish of a selected size range of 24–30 cm collected off East Greenland and in the Irminger Sea during a period in which migration of fish of that length was very likely, revealed largely differing estimates of age. Most of the readings of readers 1 and 2 were in the range 9–11 years, reader 3 assigned slightly older ages (10–13 years), and reader 4 allocated 8–9 years to the same material (Figure 9). Readers 2 and 3 generally aged pelagic *S. mentella* from the

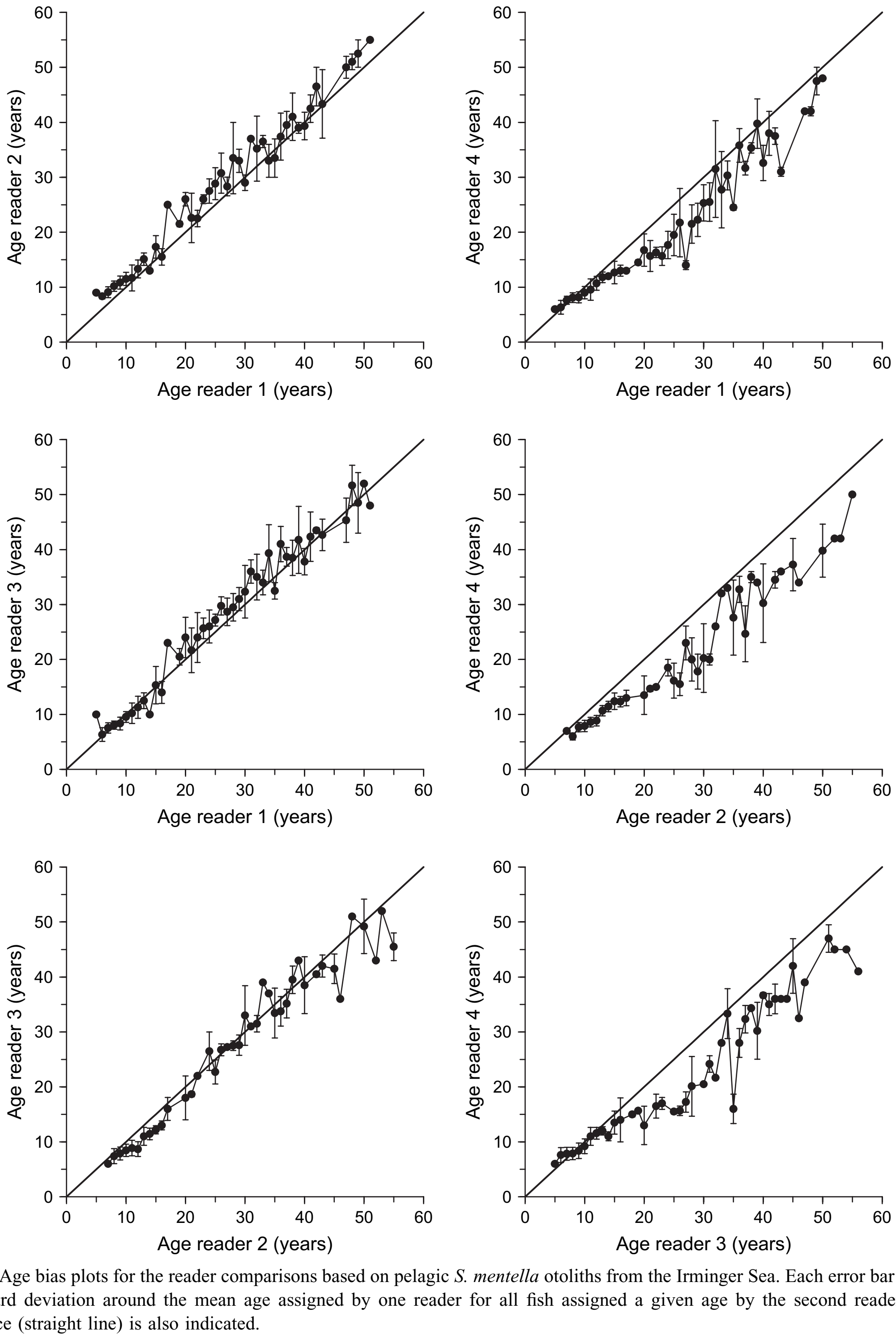

Figure 4. Age bias plots for the reader comparisons based on pelagic *S. mentella* otoliths from the Irminger Sea. Each error bar represents the standard deviation around the mean age assigned by one reader for all fish assigned a given age by the second reader. The 1:1 equivalence (straight line) is also indicated.

Irminger Sea 2–3 years older than *S. mentella* of the same length from the East Greenland shelf, but readers 1 and 4 found only a minor shift in age distribution between areas. Reader 3 contributed the broadest age range (5–20 years), while reader 4 aged the same fish within a narrow range of 5–11 years. From the combination of all readers' results,

Table 4. Statistical tests for the detection of bias for age readings of *S. mentella* between readers.

	Age reader pair					
Statistic	Reader 1 vs. reader 2 (n = 191)	Reader 1 vs. reader 3 (n = 213)	Reader 2 vs. reader 3 (n = 191)	Reader 1 vs. reader 4 (n = 207)	Reader 2 vs. reader 4 (n = 188)	Reader 3 vs. reader 4 (n = 207)
	Regression					
Slope	1.016 ± 0.017	1.055 ± 0.017	1.006 ± 0.017	0.853 ± 0.021	0.787 ± 0.021	0.768 ± 0.021
p	0.000	0.000	0.000	0.000	0.000	0.000
Intercept	1.903 ± 0.396	−0.348 ± 0.408	−1.632 ± 0.448	0.244 ± 0.495	−0.405 ± 0.540	1.310 ± 0.524
p	0.000	0.395	0.000	0.622	0.455	0.013
	Wilcoxon test					
p	0.000	0.001	0.000	0.000	0.000	0.000
	Paired t-test					
Mean paired difference	−2.215 ± 0.412	−0.808 ± 0.431	1.492 ± 0.443	2.729 ± 0.566	5.074 ± 0.660	3.580 ± 0.706
p	0.000	0.000	0.000	0.000	0.000	0.000

the mean age of the East Greenland samples was 9.1 years, and that of the Irminger Sea redfish was 10.6 years.

Discussion

All between-reader comparisons in the *S. marinus* otolith exchange showed considerable bias, caused by relative over- or underestimation of up to 1 year mean paired difference. In the age range >20 years, individual age reading pairs differed by up to 10 years. As maximum ages of >40 years are documented for this species in the Northeast Atlantic (Nedreaas, 1990), the ageing bias for ages >30 years could be even higher. However, when similar ages are produced by different readers on the same fish, similar interpretation of growth structures is not implied. As illustrated in an example overlay of reading marks (Figure 10a), reader 1 had a different perception of the nucleus zone than the other readers, and he used a different reading axis from the eighth reading mark onwards, but came to the same age estimate as reader 4. However, a part of the overestimation of age in the youngest age range by reader 4, relative to the other readers, could be attributed to different interpretation of the first annulus as well as his registration of intermediate zones between the annuli. Differences in the interpretation of marginal zones were more pronounced for fish aged >20 years.

The ranges of the precision estimates calculated for the *S. marinus* reader comparisons (CV 7.7−12.0%, APE 5.4−8.5%), are slightly above the average values in the literature (CV 7.6%, APE 5.5%; Campana, 2001). CVs of 12.9% and 14.8%, however, have been reported for fish species with similar longevity, such as sablefish (*Anoplopoma fimbria*; Kimura and Lyons, 1991), and Atlantic sturgeon (*Acipenser oxyrinchus*; Stevenson and Secor, 1999), respectively. Laidig *et al.* (2003) compared age readings carried out on blue rockfish (*Sebastes mystinus*), and obtained an APE of 5.6% between readers. The agreement of *S. marinus* readings within a tolerance of ±0 years does not exceed 30%, relatively poor compared with age reading results for herring (*Clupea harengus*, 71−90%;

Table 5. Measures of precision for age readings on *S. mentella* between readers.

	Age reader pair					
Statistic or index	Reader 1 vs. reader 2 (n = 191)	Reader 1 vs. reader 3 (n = 213)	Reader 2 vs. reader 3 (n = 191)	Reader 1 vs. reader 4 (n = 213)	Reader 2 vs. reader 4 (n = 191)	Reader 3 vs. reader 4 (n = 213)
Correlation coefficient (r^2)	0.951	0.950	0.947	0.891	0.880	0.869
CV (%)	11.22	8.16	11.06	12.31	19.10	14.22
APE (%)	7.93	5.77	7.82	8.70	13.51	10.06
Agreement (%)	6.81	19.25	11.52	15.46	3.72	16.91

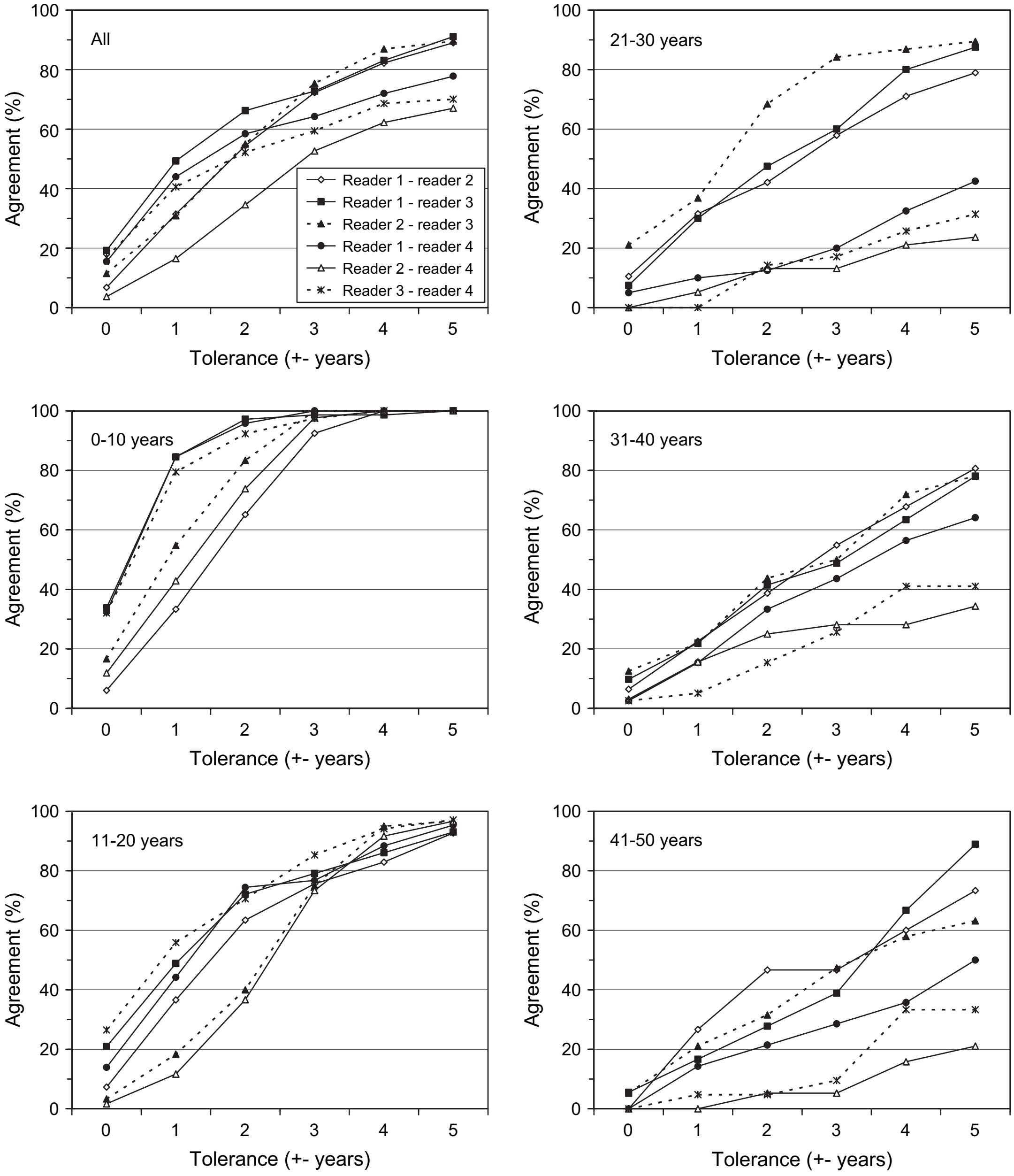

Figure 5. Agreement plots for the reader comparisons based on pelagic *S. mentella* otoliths from the Irminger Sea for a tolerance level (deviation of assigned ages between both readers) of ±0 (total agreement) to ±5 years. These were applied to all age groups and subsets of age ranges assigned by the first reader.

Corten, 1993), mackerel (*Scomber scombrus*, mean 51%; Villamor and Meixide, 1995), or horse mackerel (*Trachurus trachurus*, mean 38%; Eltink, 1997). As the percentage agreement index does not account for the large number of age groups, i.e. the lifespan of the investigated species, comparisons with short-living species can only be approached by applying a higher tolerance of ageing deviations between readers. At a tolerance of ±1 year, more than 60% agreement was reached for the best reader pair, which recently motivated an exploratory analytical assessment of *S. marinus* on the basis of 3-year intervals (Rätz *et al.*, 2004b). The resulting stock projection estimates were similar to those obtained from production models such as BORMICON (Björnsson and Sigurdsson, 2003).

Although the precision of the comparison between otolith preparation methods was generally higher than that for the readers, there was a significant bias between

Table 6. Von Bertalanffy growth parameters derived from this study and other studies (A, unpublished data, T. Sigurdsson, Marine Research Institute, Reykjavík, Iceland; B, Nedreaas, 1990; C, Saborido-Rey *et al.*, 2004; D, unpublished data, K. Nedreaas, Institute of Marine Research, Bergen, Norway).

							von Bertalanffy parameters		
Species	Material	Reference	Reader/laboratory	Method	Length range (cm)	n	L_{inf}	k	t_0
S. marinus	Iceland 1997	This study	1	Section	10–54	212	52.66	0.095	0.470
S. marinus	Iceland 1997	This study	2	Section	10–54	199	46.36	0.131	1.587
S. marinus	Iceland 1997	This study	3	Section	10–54	212	49.55	0.113	1.233
S. marinus	Iceland 1997	This study	4	Section	10–54	212	49.00	0.121	1.427
S. marinus	Iceland 1997	This study	All four	Section	10–54	835	50.50	0.105	0.935
S. marinus	Iceland 1997	This study	2	Break & burn	10–54	108	47.80	0.124	0.913
S. marinus	Iceland 1995–2002	A	2	Break & burn	9–82	12 974	50.33	0.088	−1.427
S. marinus	Norway/ Barents Sea 1985–1988	B	3	Break & burn	8–82	488	50.2	0.11	0.08
S. marinus	Flemish Cap 1990–2000 (males)	C	4	Break & burn	8–51*	3 215	46.40*	0.104	−0.79
S. marinus	Flemish Cap 1990–2000 (females)	C	4	Break & burn	11–57*	2 823	58.15*	0.069	−1.49
S. mentella	Irminger Sea 1999	This study	1	Section	22–41	213	40.08	0.066	−8.531
S. mentella	Irminger Sea 1999	This study	2	Section	22–41	191	39.23	0.073	−6.379
S. mentella	Irminger Sea 1999	This study	3	Section	22–41	213	39.27	0.069	−9.635
S. mentella	Irminger Sea 1999	This study	4	Section	22–41	204	38.82	0.117	−2.293
S. mentella	Irminger Sea 1999	This study	All four	Section	22–41	824	39.31	0.078	−6.797
S. mentella	Irminger Sea 1999	A	2	Break & burn	20–52	920	44.27	0.087	−3.492
S. mentella	Irminger Sea 1999	D	3	Break & burn	21–50	426	43.06	0.107	−0.894
S. mentella	Irminger Sea 2001	D	3	Break & burn	25–49	690	43.69	0.093	−2.463
S. mentella	Irminger Sea 2001	D	3	Section	31–48	115	46.76	0.063	−6.577
S. mentella	Norway/Barents Sea 1985–1988	B	3	Break & burn	8–58	142	49.0	0.06	−2.47
S. mentella	Flemish Cap 1990–2000 (males)	C	4	Break & burn	9–48*	3 588	43.24*	0.107	−1.07
S. mentella	Flemish Cap 1990–2000 (females)	C	4	Break & burn	11–46*	3 454	45.82*	0.096	−1.28

*Fork length.

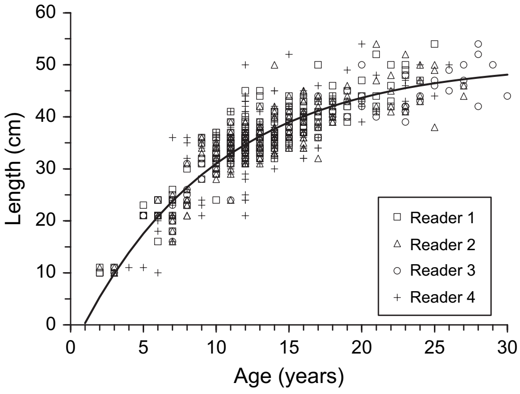

Figure 6. Age–length relationship and fitted von Bertalanffy growth curve of the reading comparison based on *S. marinus* otoliths from the Icelandic shelf. For growth parameters, see Table 6.

methods. Age readings based on broken and burnt otoliths showed a slightly lower estimate of age relative to the results obtained from thin sections. As the primary aim of this study was the comparison between readers by exchange of thin-sectioned otoliths and, in the case of breakage of one of the otoliths of a pair, the other one was kept for sectioning, the number of otoliths available for the break-and-burn preparation was relatively low. One disadvantage of the break-and-burn method is the reading variability introduced by the different angles of light applied to the broken surface. Several laboratories ageing Pacific *Sebastes* species, however, have harmonized their age reading protocols (MacLellan, 1997; C.A.R.E., 2000) in order to reduce reading error caused by systematic differences in interpretation. In an age validation study, Andrews *et al.* (2002) recently compared thin-section and break-and-burn readings on yelloweye rockfish (*Sebastes ruberrimus*), with

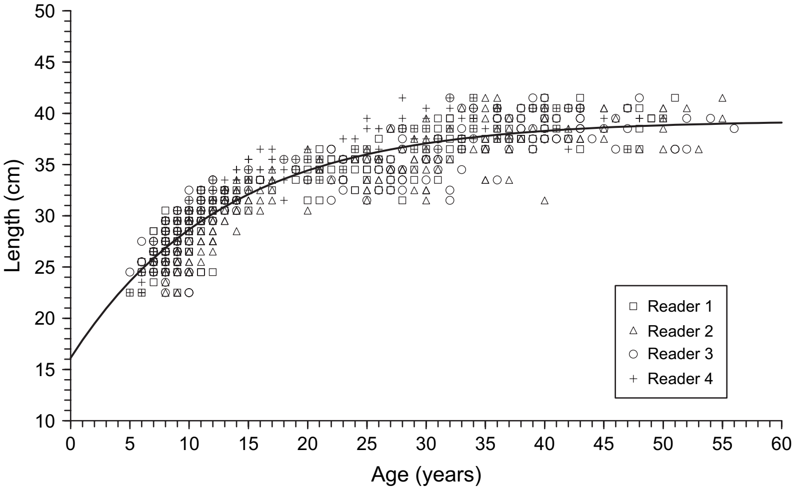

Figure 7. Age−length relationship and fitted von Bertalanffy growth curve of the reading comparison based on *S. mentella* otoliths from the Irminger Sea. For growth parameters, see Table 6.

ages of 15−117 years, and noted slightly higher correspondence between methods ($r^2 = 0.971$) than in our study ($r^2 = 0.931$). In contrast to our results, they found slight overestimation of age using the break-and-burn technique.

The bias of the *S. mentella* readings was particularly apparent in the comparisons of reader 4 with the other readers, resulting in up to 5 years mean paired difference, with individual deviations reaching 20 years. These inconsistencies between readers can be attributed partly to different interpretation of the nucleus zone (Figure 10b). Considering the expected longevity of *S. mentella* of 75 years (Campana *et al.*, 1990), elevated reading bias in data obtained for older individuals of this species is common and often caused by the difficult differentiation of marginal increments. These interpretational differences also affect the precision of readings to a large extent, which was markedly poorer in the *S. mentella* reader comparisons than in the *S. marinus* readings. Regular otolith exchange schemes between Canadian and US ageing laboratories for Pacific *Sebastes* species (C.A.R.E., 2000) of similar longevity as *S. mentella* have revealed only slightly better CVs of 8.2−12.2% and APEs of 5.7−9.1% (C.A.R.E., 2002). Andrews *et al.* (2002), however, noted a CV of 4.5% and an APE of 2.6% for section readings of *S. ruberrimus*. Among reader intercalibration studies for other long-lived species,

Table 7. Results of the Chow test comparing von Bertalanffy growth functions for different readers and methods.

Comparison		F*	d.f.†
S. marinus	Reader 1 vs. reader 2	6.3	405
	Reader 1 vs. reader 3	2.3	418
	Reader 2 vs. reader 3	0.7	405
	Reader 1 vs. reader 4	2.8	418
	Reader 2 vs. reader 4	0.4	405
	Reader 3 vs. reader 4	0.8	418
	Section vs. break and burn	3.2	301
S. mentella	Reader 1 vs. reader 2	12.0	398
	Reader 1 vs. reader 3	1.3	420
	Reader 2 vs. reader 3	11.6	398
	Reader 1 vs. reader 4	25.2	414
	Reader 2 vs. reader 4	62.4	392
	Reader 3 vs. reader 4	20.6	414
Reader 1	*S. marinus* vs. *S. mentella*	183.0	419
Reader 2	*S. marinus* vs. *S. mentella*	249.9	384
Reader 3	*S. marinus* vs. *S. mentella*	122.5	419
Reader 4	*S. marinus* vs. *S. mentella*	40.2	413

*Critical F = 5.42 (α = 0.001) for all tests.
†Denominator d.f. (numerator d.f. = 3 for all comparisons).

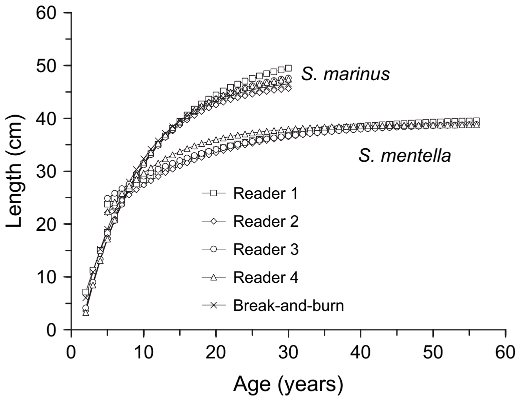

Figure 8. Fitted von Bertalanffy growth curves for all comparisons between readers, methods, and species.

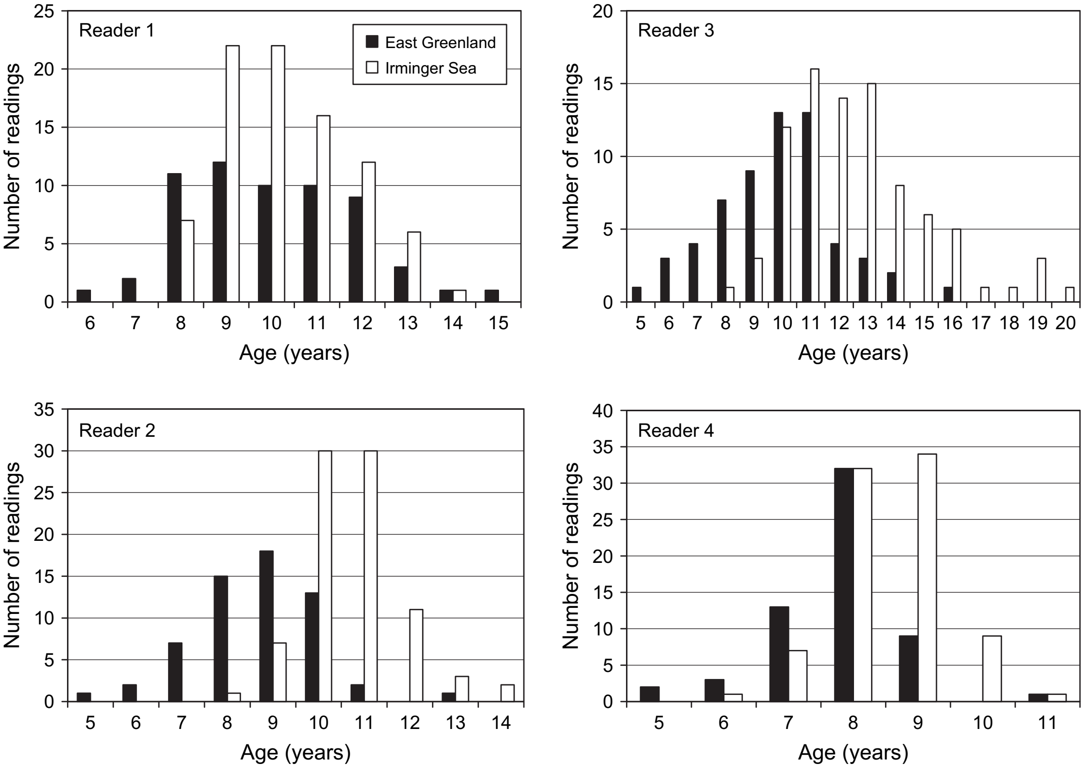

Figure 9. Age distribution of demersal *S. mentella* from the East Greenland shelf (24—30 cm total length) and pelagic *S. mentella* from the Irminger Sea (25—30 cm total length).

APEs of 4.3—10.6% have been reported for Patagonian toothfish (*Dissostichus eleginoides*) with ages of 2—53 years (Horn, 2002). Bergstad *et al.* (1998) showed a significant improvement in the CVs for tusk (*Brosme brosme*) age readings after consensus on a common interpretation principle, decreasing from 11.6% to 7.6% and resulting in non-significant differences between three readers in the final exchange. Keeping the commercial importance of pelagic *S. mentella* in the Irminger Sea in mind, a comprehensive reader intercalibration and standardized ageing protocols (e.g. Beanlands, 1997; Walsh and Burnett, 2002) are urgently needed.

Although relatively high bias was observed between *S. marinus* readers, the age—length relationships and growth parameters only varied modestly. Notably, the von Bertalanffy parameters derived for reader 1 came closest to those from the largest data set available (almost 13 000 readings of *S. marinus* around Iceland). An asymptotic maximum length of >50 cm and a growth coefficient k of <0.1 were calculated for both data sets, whereas the relative underestimation of ages by reader 4 did not lead to an extraordinarily high k. The break-and-burn results of reader 2, however, indicated faster growth ($k = 0.12$) than suggested by all thin-section readings combined ($k = 0.11$), but slower growth than derived from the section readings of reader 2 only ($k = 0.13$). Only the results of readers 1 and 2, however, differed significantly, with a slightly higher F than the critical value.

A more pronounced difference in k was observed in the *S. mentella* readings, with the relative underestimation in the age readings of reader 4 leading to a k of 0.12, in contrast to the 0.07 inferred from the data of the other readers. Most other studies have suggested k values below 0.10, but the narrow length range of the *S. mentella* investigated in this study (22—41 cm) makes comparison with other studies based on material from an extended length range problematic. As the smaller juveniles <20 cm long inhabit demersal nursery areas on the shelf (Magnússon *et al.*, 1988), the lack of younger age groups in the Irminger Sea (Magnússon and Magnússon, 1995) contributes largely to the remarkably low t_0 values found for Irminger Sea redfish. The *S. mentella* aged in this study were caught in comparatively shallow water, where larger fish are underrepresented, probably causing the relatively low L_{inf} of 39 cm. Pelagic redfish in the Irminger Sea are found down to 1000 m, with maximum lengths of >50 cm (Sigurdsson *et al.*, 1999), suggesting higher L_{inf} values when including fish from deeper layers, where the larger specimens usually occur. Apart from the comparison of readers 1 and 3, all *S. mentella* reader pairs showed significant differences in growth curves. The reader pair 2 vs. 4, which exhibited the lowest precision and highest

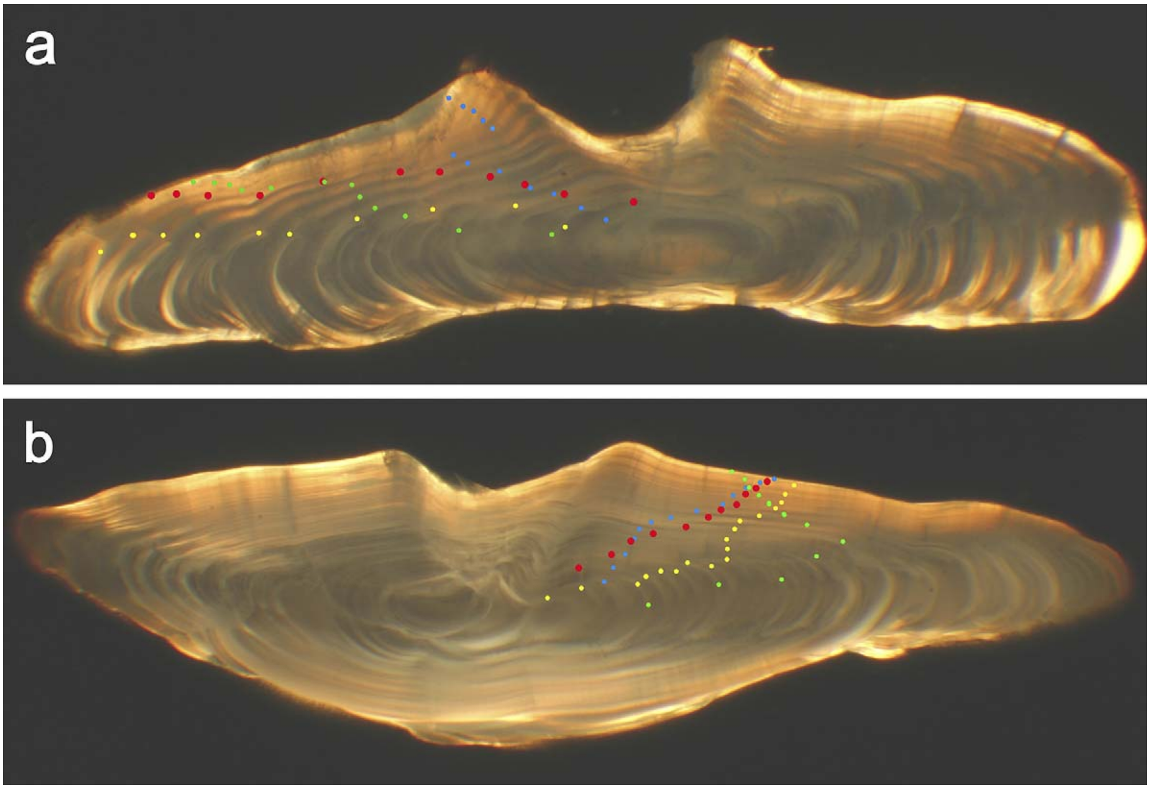

Figure 10. Examples of (a) *S. marinus* and (b) *S. mentella* otolith thin sections, including age reading marks of readers 1 (blue), 2 (red), 3 (yellow), and 4 (green). The reading results are (a) 12, 11, 10, 12 years, and (b) 13, 11, 18, 12 years, respectively.

overall bias, also revealed the highest differences in growth curves, illustrating the effect of deviation in readings on growth estimations.

An additional error might be introduced by the presence of relatively large fast-growing juveniles that have been recruited from the highly productive shelf areas off East Greenland and Iceland. According to our results, a 25 cm pelagic *S. mentella* would be around 6 years old, while in shelf areas of the Flemish Cap (NAFO Division 3M), in the Northeast Arctic (ICES Subareas I and II), and off East Greenland (ICES Division XIVb), demersal *S. mentella* of the same size would be 7, 8 and 8.5 years old, respectively (Nedreaas, 1990; Kosswig and Rätz, 1995; Saborido-Rey *et al.*, 2004). As the L_{inf} and k values were reported to be higher for the shelf areas, faster growth of demersal *S. mentella* compared with pelagic *S. mentella* was observed for ages >10 years. By tracking strong cohorts in the length frequency distributions derived from regular monitoring programmes, a corroboration of age-reading results is possible (e.g. Mayo *et al.*, 1981; Beamish and McFarlane, 1983; Nedreaas, 1990). The investigated *S. marinus* material includes two strong year classes, most probably 1985 and 1990, dominating the length distributions in regular surveys and commercial sampling (ICES, 2003). After 10 years, the length peaks had reached 28–29 cm, which corresponds with the age–length relationship inferred from the data presented here and recently undertaken through radiometric ageing (Stransky *et al.*, unpublished data).

Differences between readers were also considerable for *S. mentella* of length range 24–30 cm, selected with regard to evidence of migration found for the same length groups from East Greenland into the Irminger Sea during 1998 and 1999 (Stransky, 2000). The extraordinarily strong cohort that could be tracked in the length distributions of *S. mentella* <20 cm long off East Greenland (Rätz *et al.*, 2004a), however, most likely contains fish from the 1991 year class, so the ageing results of reader 4 are closest to this estimate (age 7 in 1998, age 8 in 1999). In contrast, 0-group indices from the Icelandic surveys (Magnússon and Jóhannesson, 1997) did not match the observed strong cohorts.

Based on the observations made in this study, expansion of the general redfish otolith reading guidelines of the most recent ageing workshop (ICES, 1996) is clearly necessary. As the size and the importance of the pelagic *S. mentella* stock in the Irminger Sea were explored only recently, the special ageing problems related to that stock should be addressed in future age-reading workshops. In this respect, the latest age validation results (Stransky *et al.*, unpublished data) should be taken into consideration. Further otolith exchange programmes with a focus on pelagic *S. mentella* are encouraged, making use of digital imaging techniques to illustrate interpretational differences between readers. Although the differences between readings of sectioned and broken and burnt otoliths were minor, readability of redfish otoliths was improved by the thin-sectioning method, and this method should therefore be implemented as the standard means of preparation.

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