Ecology of Freshwater Fish 1998: 7: 25–35
Printed in Denmark · All rights reserved

ECOLOGY OF
FRESHWATER FISH
ISSN 0906-6691

The reliability of whitefish (*Coregonus lavaretus* (L.)) age determination – differences between methods and between readers

Raitaniemi J, Bergstrand E, Flöystad L, Hokki R, Kleiven E, Rask M, Reizenstein M, Saksgård R, Ångström C. The reliability of whitefish (*Coregonus lavaretus* (L.)) age determination – differences between methods and between readers.
Ecology of Freshwater Fish 1998: 7: 25–35. © Munksgaard, 1998

Abstract – Age determinations of whitefish (*Coregonus lavaretus* (L.)) were compared in two different tests. In the first test, the readers determined the age of each individual from one calcified structure (scale, otolith, or opercular bone) at a time. The samples from three populations, 50 specimens in each, were mixed so that the readers did not know which population each calcified structure was from. A sample of known-age whitefish was used in the second age determination test, where information such as time of catch, length, weight, and sex was available to the readers. In each of the 50 envelopes the reader got scale impressions and two otoliths, one of which had been burned and ground. In the first test, the precision of the readers was low both between readers and between different structures. In the samples of slow-growing populations, the determinations made from the otoliths showed older ages than the determinations from the scales. In the second age determination test the results were better; 73–90% (average 82%) of the determinations were correct. The use of two calcified structures and the knowledge of the material were considered to improve the accuracy. Age determination bias may occur that affects the age distribution: even though 80% of the fish were aged correctly, an exceptionally strong or weak year class could remain unidentified. The estimation of growth rate seemed less sensitive to incorrect age determination than age distribution.

J. Raitaniemi[1], E. Bergstrand[2], L. Flöystad[3], R. Hokki[4], E. Kleiven[5], M. Rask[6], M. Reizenstein[2], R. Saksgård[3], C. Ångström[2]
[1]Finnish Game and Fisheries Research Institute, Helsinki, Finland, [2]National Board of Fisheries, Institute of Freshwater Research, Drottningholm, Sweden, [3]Norwegian Institute of Nature Research, Trondheim, Norway, [4]Finnish Game and Fisheries Research Institute, Taivalkoski Game and Fisheries Research, Taivalkoski, Finland, [5]Norwegian Institute of Water Research, Sörlandsavdelningen, Grimstad, Norway, [6]Finnish Game and Fisheries Research Institute, Evo Game and Fisheries Research, Evo, Finland

Key words: whitefish; age determination; reliability

J. Raitaniemi, Finnish Game and Fisheries Research Institute, P.O. Box 6, FIN-00721, Helsinki, Finland

Accepted for publication October 8, 1997

Un resumen en español se incluye detrás del texto principal de este artículo.

Different calcified structures have been shown to give different results in age determination of several fish species, especially in slow growing populations (Jonsson 1976, Harrison & Hadley 1979, Sikström 1983, Mosegaard et al. 1989). Usually age determination from scales underestimates the age of older, slow growing fishes compared with age determination from otoliths or fin rays.

The methods of age determination and the accuracy and precision of the determinations have been dealt with by several authors (LeCren 1947, Beamish & McFarlane 1983, Boehlert & Yoklavich 1984, Mann & Steinmetz 1985, Casselman 1987). Validation has been regarded as important in all studies that involve the extraction of age data from calcified structures of fish (Bagenal & Tesch 1978, Beamish & McFarlane 1983, Casselman 1987). To verify the interpretation, indirect methods have been used more often than direct validation, in which the structures of known-age or partly known-age fish that have grown in natural environment are examined (Casselman 1987).

In this study, the age determinations of whitefish (*Coregonus lavaretus* (L.)) were compared among different calcified structures by different readers from Finland, Norway, and Sweden. Whitefish is a common freshwater species in all three countries and, especially in Finland, it is economically valuable. The validity of age determination of whitefish from scales has been examined earlier by Salojärvi

(1989). The otolith and scale ages of the North-American species *Coregonus clupeaformis* have been compared by Barnes & Power (1984).

The comparability of age determination results between different countries and laboratories is questionable, especially if different methods like age determination from scales or otoliths are used and the age determination conducted in different laboratories have not been compared with each other. Our objective was to test the methods and readers of different laboratories and to find more accurate methods of age determination that could be standardized. We were also interested in the effects of age determination errors on the estimation of age distribution and growth.

In order to compare the accuracy of age determination routines, we conducted two different age determination tests. In the first test, the precision of the readings from calcified structures including scale, otolith (sagitta), and opercular bone, was examined. We compared ages determined from the different structures as well as determinations from each structure by different readers. We tried to use structures that would make it difficult to make presumptions of the fish before examining the age determination structure. To do this, the calcified structures of three whitefish populations were mixed and presented randomly.

In contrast, we conducted another test in which the readers could simultaneously examine the scales and otoliths of individual whitefish. The readers were provided with as much information of the fish as possible, except the actual age, before examining the age determination structure. To know how accurate the determinations are, we used a sample of known-age fish.

Material and methods

The first age determination test of whitefish was done separately with scales, otoliths and opercular bones. A sample of 50 whitefish each were taken from a Finnish, a Norwegian and a Swedish whitefish population. Three readers, one from each Nordic country (A, B, and C), got calcified structures to age, knowing only that the fish had been caught in late summer. The readers got 150 envelopes with scale impressions (five scales per plate), 150 envelopes with otoliths, of which one had been burned and cracked in median cross section through the nucleus, and 100 envelopes with opercular bones. The technique of burning and breaking the otolith was a modification of the method used by Christensen (1964) and more precisely, Power (1977), except that after burning the otolith was dropped hot into water instead of alcohol.

The scales of the Finnish sample had been taken from the area between the tips of the pelvic fins, and the scales of the Norwegian and Swedish samples from the area between the lateral line and the adipose fin. The opercular bones were from the Swedish and Finnish populations, and they were read by only one reader. Scale and otolith envelopes were mixed so that readers could not distinguish the different populations.

Wilcoxon's signed-rank test was used to examine whether differences in age determinations among readers were systematic or random. Similarly, the ages determined from scales, otoliths, and opercular bones were compared. The effects of aging on age distributions were examined. The average lengths of the estimated age groups were also studied to see how much the differences in age determination affected the mean lengths of the estimated age groups.

The whitefish used in the second age determination test had been reared in ponds with a natural food supply and tagged with microtags injected into their snouts (Jefferts et al. 1963) as one-summer-old fingerlings, so their real ages were known. After tagging they had been released into Lake Vuokalanjärvi, Finland. Microtagging of whitefish fingerlings is a common method in Finland, and to our knowledge it does not affect the growth of the tagged individuals.

The sample of 50 specimens consisted of 1- to 6-year-old individuals (calendar age 1–6), and the 6-year-olds were the largest age group. The scales were taken from the area behind the pelvic fins. All eight readers (A, B, C, D, E, F, G and H) were given information about the fish: date of catch, length, weight, and sex. In each of the 50 envelopes the reader got scale impressions and two otoliths, one of which had been prepared for the determination. First, it had been burned as in the first study and then glued to a piece of plastic plate, covering the otolith completely with epoxy two-component glue. After the glue had hardened, the otolith was ground to get a smooth cross section through the nucleus.

There were some differences in the practices of the readers that were revealed in the second age determination test. Readers A, C and F did not age-determine all the 50 individuals, because they were of the opinion that it is better to exclude indistinct individuals than to age them with great uncertainty. There were also unexpected differences in the definition of age. The Finns and Swedes used "+" in marking the marginal growth after the last annulus ("4", "4(+)" [the parenthesis in Sweden if marginal growth was not detected], and "4+" are "4-year-olds" [calendar age from 1 January to 31 December]), and a part of the Norwegians used

Table 1. The number of identical readings made by the readers (A, B and C) from the Norwegian, Swedish and Finnish whitefish samples (50 readings in each). The significance of the difference of the determinations (Wilcoxon's signed-rank test) is shown with a symbol (**P<0.01, *P<0.05, NS: not significant)

Readers Statistical test	Norwegian		Swedish		Finnish	
	scales	otoliths	scales	otoliths	scales	otoliths
A–B	11	7	21	14	28	25
Wilcoxon	**	**	**	**	**	NS
A–C	9	14	9	21	20	8
Wilcoxon	**	**	**	*	**	**
B–C	32	3	32	16	33	6
Wilcoxon	**	**	**	**	**	**

"+" in marking calendar age ("4+" and "5" are "5-year-olds", i.e., the fish have grown 5 summers). One reader did not mark "+" at all. Because of a temporary handicap, one of the eight readers (reader H) aged only 3–5 individuals per day, whereas the others aged the whole material during a shorter continuous period.

The ages determined were compared with the real ages of the fish. Wilcoxon's signed-rank test was used to examine whether the differences were systematic or random. The resulting age distributions were compared with the real age distribution and the mean lengths of the estimated age-groups were compared with the known mean lengths (t-test).

In this article we use the terminology on definition of age presented by Bagenal & Tesch (1978).

Results

Age determination test with mixed samples

The first age determination test showed great variation both between readers (Table 1) and between structures read by the same reader (Table 2).

The differences in the age determination varied between the population samples, and systematic differences between the determinations were common. Of the Norwegian scale sample, the readers B and C got 32 identical readings, but of the otoliths only three. However, according to the otolith ages, a large part of the Norwegian sample consisted of old individuals when compared with scales. On the grounds of the thickness of their otoliths and the structure of the rings (cf. Power 1978) the otolith ages were considered to be closer to the actual age than scale age, which under-estimated the real age (Fig. 1). Discrepancies among Swedish samples were probably also due to inaccurate age determination of scales and opercular bones from older individuals.

The Finnish whitefish sample consisted of 2- to 6-year-old individuals, and systematic differences in the age determination results such as those found in the Norwegian or Swedish material did not appear. However, the age determination of the Finnish fish was not always accurate. Five individuals, all 3 years old, had been microtagged before releasing as fingerlings, and so their real age was known. On the average, two of five were aged correctly, and errors were made with all calcified structures: scale (2–4 correct determinations), otolith (1–2 correct determinations) and opercular bone (2 correct determinations). The errors with scales and opercular bones were mostly over-estimation, the ages from otoliths were both over- and underestimated.

The otolith reading indicated that a large part of the Norwegian sample consisted of older than 9-year-old whitefish, whereas the age determination from the scales revealed no individuals of this age (Fig. 2). A similar phenomenon was found in the Swedish whitefish sample. In addition, reader A determined 2-year-olds to be the youngest age-group in the Swedish sample, while the other readers also found yearlings. In the Finnish sample a systematic difference was found only in the age determination of the reader C who determined the same fish 2 years old from the scales and 3 or 4 years old from the otoliths (Fig. 2).

When the average lengths of the estimated age groups were examined in relation to the determined age, the determinations of the Swedish material made from scales or opercular bones showed a faster growth rate than the determinations from otoliths, according to which the population is very

Table 2. The number of identical readings of scales and otoliths, aged by the same reader (for explanation see Table 1)

Reader Statistical test	Norwegian sample	Swedish sample	Finnish sample
A	2	30	24
Wilcoxon	**	*	NS
B	12	26	23
Wilcoxon	**	**	NS
C	4	9	15
Wilcoxon	**	**	**

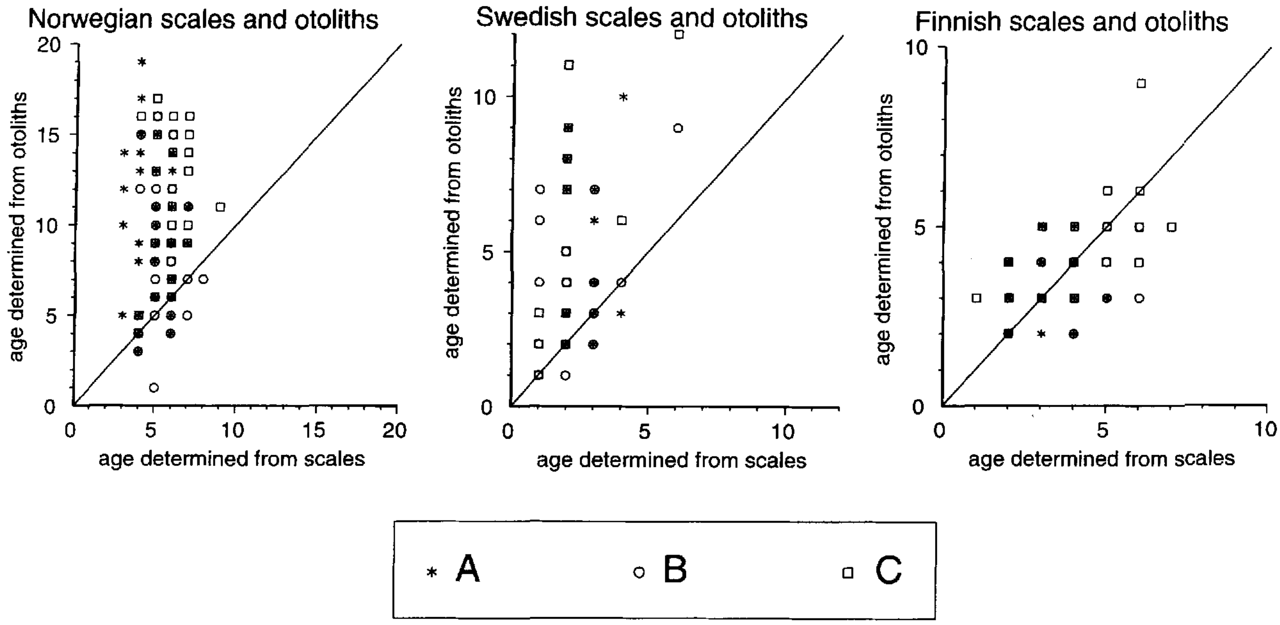

Fig. 1. The relationship of ages determined from otoliths and scales of the Norwegian, Swedish, and Finnish whitefish population samples

slow growing (Fig. 3). The young and old fish in the samples from the Finnish and Norwegian populations were so much of similar size that it could not be examined whether the differences in the determinations would have caused differences in the estimates of growth rates. However, the determinations made from the otoliths of the Norwegian population showed, despite the differences between the age determination, that the whitefish practically ceased from growing when they reached the length of 32–33 cm.

Age determination of known-age whitefish

In the second comparison, the sample consisting of microtagged whitefish with known ages, the results were better than in the first one; 73–90% (average 82%) of the determinations were correct. If the non-aged individuals were included as inaccurate determinations (readers A, C and F did not age the most difficult individuals), 70–90% (average 81%) were correct (Table 3). The determinations of the reader H (46% correct), who aged 3–5 individuals per day, were excluded from these figures. Systematic errors were found towards both younger and older age than in reality (Table 3).

Despite a fairly small number of incorrectly age determined fish per reader, the inaccuracies affected the age distribution of the fish sample. A bias in the determinations tended to make it difficult to distinguish large and small age groups in the sample, even if more than 80% of the determinations were accurate (Fig. 4, Table 3). It was nearly impossible to identify the strength of the age groups 3 and 6 in the age distribution of reader A, although 89% of the age determinations were correct. However, only 82% of the fish in the sample were correctly age determined, since reader A did not determine the age of four individuals in the sample.

The growth of the fish was not as sensitive to inaccuracies as age distribution. All age determinations except the one made by reader H gave a fairly reliable figure of the mean length of each age-group. Only the mean length of the estimated age-group 4 by reader H differed statistically significantly from the real mean length of the 4-year-olds (t-test, $P<0.01$).

The different practices in marking "+" growth did not affect the results, because in this case the number of years was interpreted similarly by all readers.

Discussion

The inaccuracies in the age determination of fish in the first test were probably partly due to the different growth of otoliths and scales, especially among older fish for which growth has slowed. When the growth of the scales had practically ceased, the otoliths still continued to grow. This is because scales reflect somatic growth that slows with age, and otoliths reflect temporal change (cf.

Casselman 1983, Beamish & McFarlane 1995). The results especially from the Norwegian whitefish material show that when using only scales, age can be underestimated more than ten years compared with otoliths. Barnes & Power (1984) found similar differences between the scale and otolith

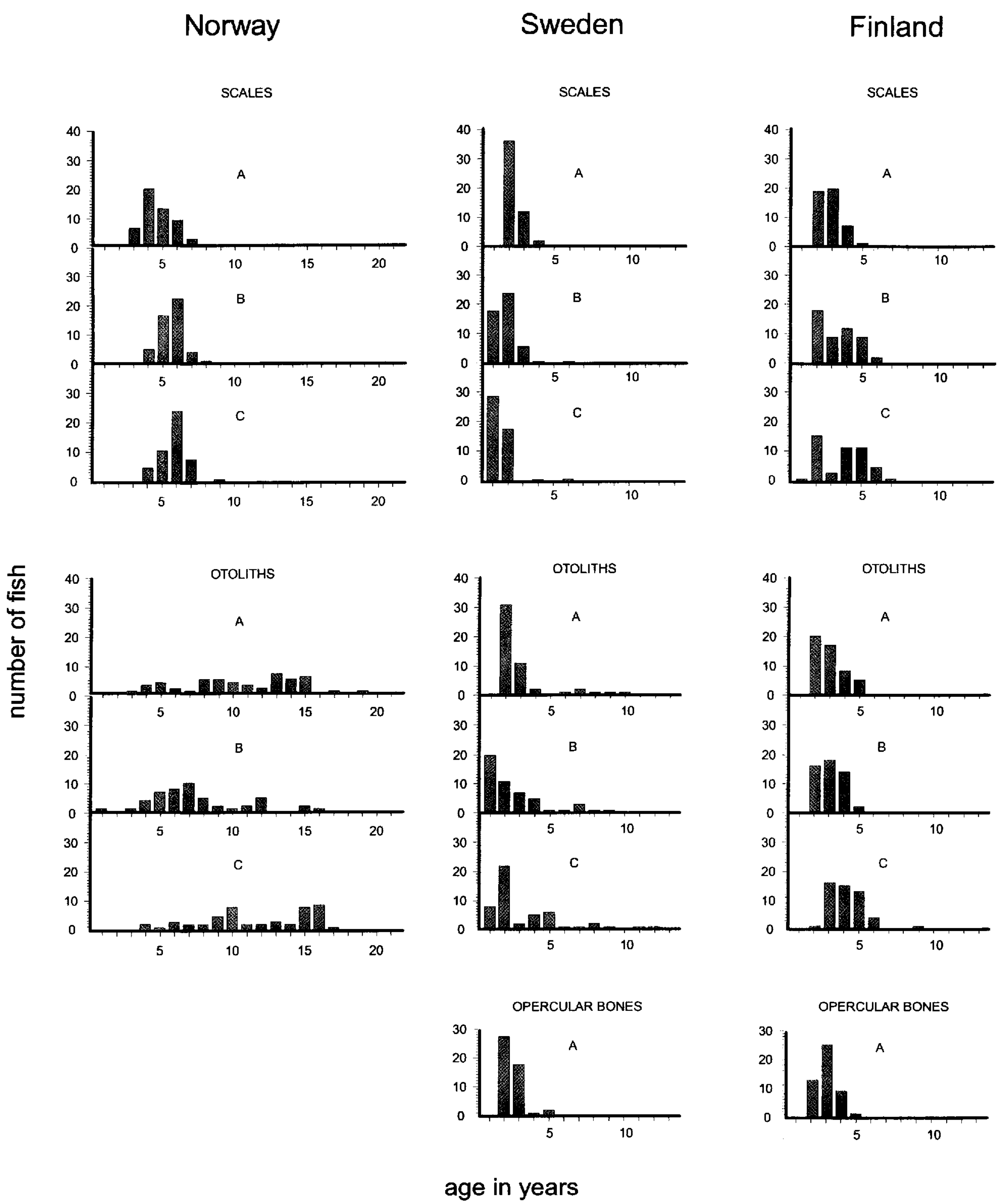

Fig. 2. The age distributions of the Norwegian, Swedish, and Finnish whitefish samples by readers A, B and C. The distributions are based on determinations from otoliths, scales, or opercular bones

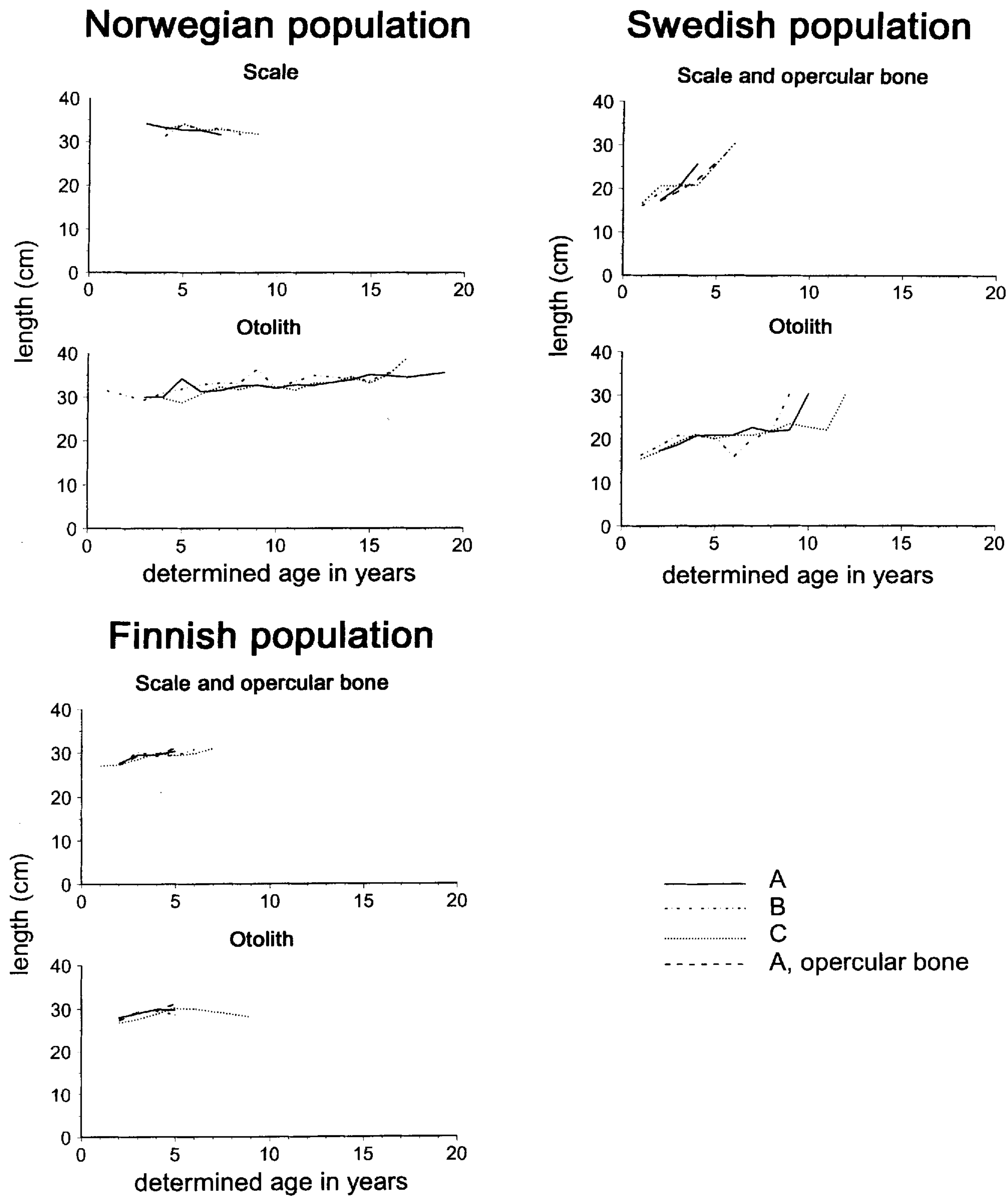

Fig. 3. The mean lengths of the fish of different estimated age groups determined by readers A, B and C in the samples of different countries

ages of the Canadian lake whitefish, *C. clupeaformis*. Although otoliths generally are more reliable than scales, the otoliths of e.g. *C. artedii* (W. MacCallum in Casselman 1983) and *C. lavaretus* (Raitaniemi 1997) can contain multiple zones, due to which the age will be overestimated. In Salojärvi

(1989), the age determination of whitefish from scales gave good results; however, the fish in that study had grown almost as fast as the Finnish whitefish of our first test, and all annuli could be detected in scales.

The discrepancies between the readers in both scale and otolith results indicate a high error rate. An important difference in the first study was the fact that the readers could not use more than one calcified tissue in each determination as in the second study. Using more than one method wherever possible has been recommended by Bagenal &

Table 3. The accuracy of the age determinations of the known-age whitefish sample by readers A–H. The numbers of correct and incorrect determinations are presented in the middle of each table. The percentage shows the proportion of correct and erroneous age determinations from all the 50 fish that each reader got to age-determine. Readers A, C and F aged only 46, 48 and 48 fish respectively of the ones that they read, and the proportions of correct age determinations from the aged fish were 89%, 83%, and 73%, respectively. The significance of the difference of the determined age from the real age (Wilcoxon's signed-rank test) is shown with a symbol (**P<0.01, *P<0.05, NS: not significant)

A

Real age	1	2	3	4	5	6	Sum	%
n	3	8	11	7	6	15	50	
Error (years)							NS	
3								
2								
1	1		1				2	4
0	2	8	9	6	6	10	41	82
−1						3	3	6
−2								
−3								

E

Real age	1	2	3	4	5	6	Sum	%
n	3	8	11	7	6	15	50	
Error (years)								*
3								
2		2					2	4
1	1		4		3	1	9	18
0	2	6	7	5	3	14	37	74
−1				2			2	4
−2								
−3								

B

Real age	1	2	3	4	5	6	Sum	%
n	3	8	11	7	6	15	50	
Error (years)							NS	
3								
2								
1	2	1	2				5	10
0	1	7	9	6	6	12	41	82
−1				1		3	4	8
−2								
−3								

F

Real age	1	2	3	4	5	6	Sum	%
n	3	8	11	7	6	15	50	
Error (years)							NS	
3								
2				1			1	2
1	2	1	1		1	2	7	14
0	1	6	9	4	2	13	35	70
−1			1	2	2		5	10
−2								
−3								

C

Real age	1	2	3	4	5	6	Sum	%
n	3	8	11	7	6	15	50	
Error (years)							*	
3								
2								
1			1				1	2
0	3	8	9	6	5	9	40	80
−1			1	1	1	4	7	14
−2								
−3								

G

Real age	1	2	3	4	5	6	Sum	%
n	3	8	11	7	6	15	50	
Error (years)							NS	
3								
2								
1			3				3	6
0	3	8	7	5	6	14	43	86
−1			1	2		1	4	8
−2								
−3								

D

Real age	1	2	3	4	5	6	Sum	%
n	3	8	11	7	6	15	50	
Error (years)							NS	
3								
2				1			1	2
1			1	1			2	4
0	3	8	9	4	6	15	45	90
−1				2			2	4
−2								
−3								

H

Real age	1	2	3	4	5	6	Sum	%
n	3	8	11	7	6	15	50	
Error (years)							**	
3								
2								
1								
0	3	8	8		3	1	23	46
−1			3	7	3	10	23	46
−2						2	2	4
−3						2	2	4

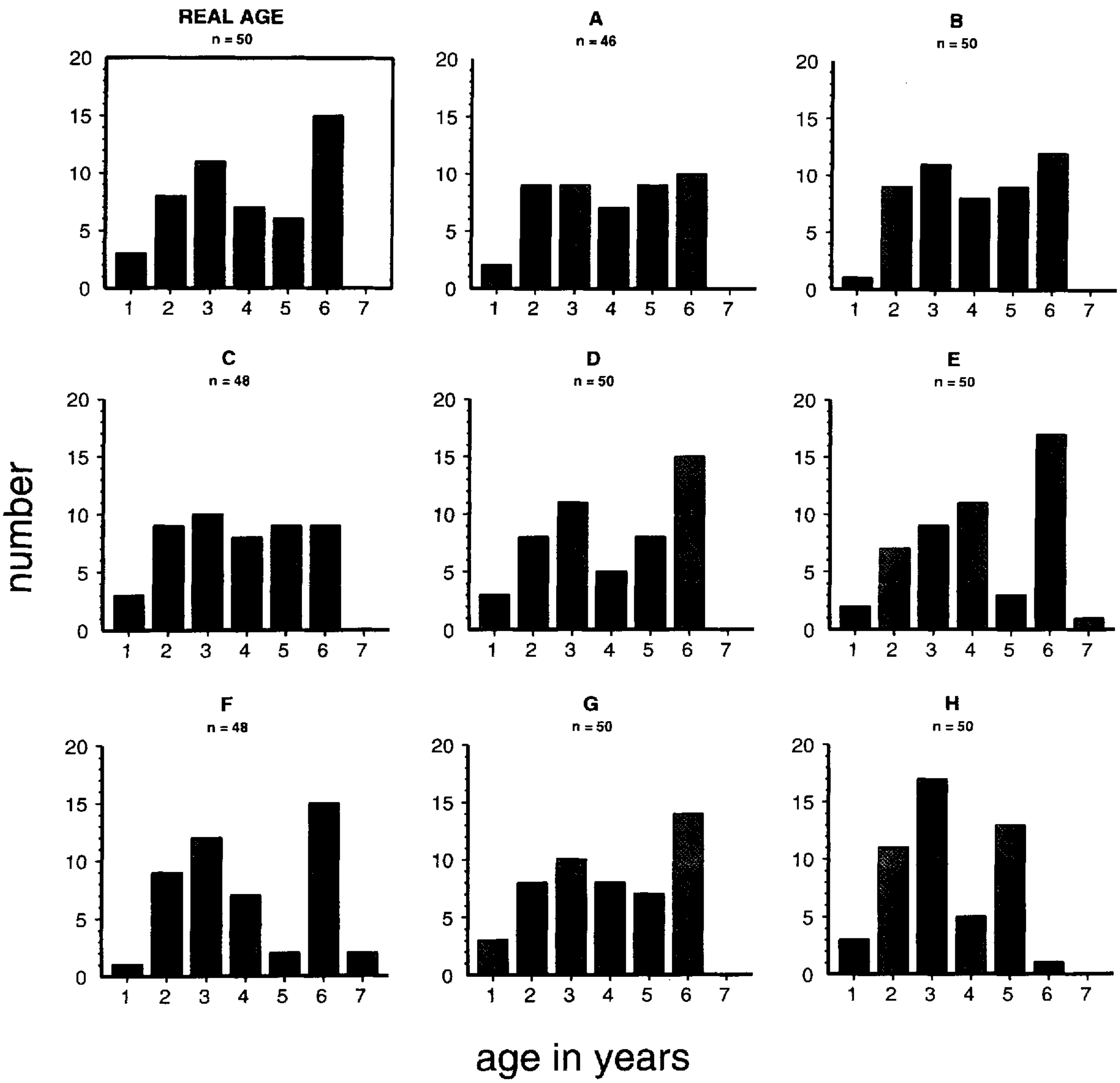

Fig. 4. The real age distribution of the known-age whitefish sample and the age distributions based on the determinations of readers A–H

Tesch (1978) as one way to improve the reliability of age determination.

Because of the mixing of the population samples the readers could not calibrate their determinations with any checks like growth changes from exceptionally good or bad years or regularly occurring false annuli. This may also have been true with reader H in the second study, being able to read the calcified structures of only a few fish per day. Although the mixing of population samples may have prevented the readers from getting presumptions of the age and growth of the fish, it did not improve accuracy, but rather caused confusion in the readers.

The method of preparing the otoliths for the readers in the first age determination test probably caused difficulties in the interpretations. Burning and breaking may give a satisfying cross section with some populations. This study showed, however, that whitefish otoliths may be difficult to read if the otolith is just burned and broken. This is because the cross section will easily have a rough surface. Furthermore, the otoliths of especially fast growing whitefish are often so fragile that they break not only laterally but also longitudinally. It is more favorable to stiffen the otolith with wax or glue or corresponding substance and then grind it to get a readable cross section through the nucleus. This is especially important in comparisons where several persons handle the otoliths.

Only one reader in the first study had experience of whitefish opercular bones and determined ages from them. The annuli of the slow growing Swedish whitefish were hardly distinguishable. In both of the aged samples, there were difficulties in distinguishing the first annulus, typical for the opercular bone. Furthermore, the results showed that, as in age determination from scales, years of slow growth can be missed. On the other hand, the regular form of the opercular bone is an advantage in back-calculation compared with scales.

During age determination, a reader inevitably forms an opinion of typical types of annuli for the population and about where to find the annuli most expectedly in the calcified tissue. According to Bagenal & Tesch (1978), it is important not to know the length of the fish before examining the aging structure, because when knowing the length one is unconsciously tempted to make the visible ring structure fit the age that would be likely for the fish of that length. However, examining the calcified structures alone is enough for presumptions to be formed, and to an experienced reader the size of the calcified structure of a familiar fish species gives a fairly accurate representation of the fish length. In routine age determination it may be impossible to avoid paying attention to the fish length, consciously or unconsciously.

An example of the effects of assumptions on age determination was presented by Beamish & McFarlane (1995). In a time series for Pacific hake ages, all but a few age-groups with above average abundance were equally represented and moderately abundant in the yearly samples, until it became clear that the fish population consisted of a few strong year-classes, occurring every 3rd or 4th year. After getting this knowledge the age distributions differed from the earlier ones, and were either accurate or they reflected a bias toward assigning fish to the known strong year-classes. A similar type of bias seemed to appear in the determinations of the readers A, B and C in the second study (Fig. 4).

Our results from the age determination tests suggest that when the reader has more information about the fish, presumptions of growth, and number of annuli, age determinations are more likely to be accurate. Nevertheless, it is important for the reader to be conscious that growth patterns can be unexpected or that there can always be individuals in the sample that have grown in an exceptional way.

Practicing and testing age determination methods with known-age fish raised under natural conditions is recommended. We used naturally raised fish of known ages in our second study. In the study of Salojärvi (1989), only 4.6% of 680 whitefish were aged incorrectly from scales. The whitefish of Salojärvi's study had grown faster than the individuals in our second study, so they were possibly easier to age. The large sample size allowed readers to become more familiar with the material than in our studies. Known-age fish have been used before in the validation of age determination with several fish species, like roach (*Rutilus rutilus)* and dace (*Leuciscus leuciscus*, Hofstede 1974), or bream (*Abramis brama*) and rudd (*Scardinius erythrophthalmus*, Steinmetz 1974), and they have been recommended by Casselman (1987).

The second age determination study showed that even if 80% of the individuals are aged accurately, an exceptionally strong or weak year-class may remain unidentified due to a bias in the determination. This may cause problems with the reliability of methods in which age distribution is needed for the calculations, e.g. virtual population analysis, calculation of instantaneous mortality, and calculations of yield per recruit.

If individuals that are difficult to determine are excluded from the age determination and thereby from age distribution as well, the error will be smaller than when they are aged incorrectly. However, if their proportion in the sample is large, they may cause a bias in the age distribution despite a high percentage of correctly aged fish.

The calculation of growth rate seems to be less sensitive to incorrect age determination than age distribution, and it can be regarded as more reliable when making conclusions of a small fish population sample. This is also because even a correctly determined age distribution in a fish sample may essentially differ from the age distribution in the population due to sampling error.

Bagenal & Tesch (1978) and Casselman (1987) agree that "+" is a symbolic notation signifying growth distal to the last annulus. If this new growth is not detected, "+" should not be used. Because of the different practices in marking "+" growth due to different definition of age, in some cases it is possible that the age marked by a reader is misinterpreted by a person from another laboratory. This example showed how important it is in cooperative studies to agree on the practices that are used. In future comparisons we agreed to use "+" in brackets "(+)", when the growth of the calendar year (of catch) is not yet discernible in the structures.

Conclusions

The age of slow-growing whitefish should be determined from the cross section of otolith, because years of very slow growth cannot be detected from scales. The chance of correct determination is highest when the reader uses more than one calcified structure as well as biological information of the fish and the population. The validation of age determination with known-age fish is recommended. Less than 20% of incorrect age determination in a sample may cause problems with the reliability of methods in which age distribution is needed for calculations. The calculation of growth rate, at least when using the mean lengths of age groups, seemed less sensitive to incorrect age determination than age distribution.

Resumen

1. Empleando dos análisis diferentes, comparamos determinaciones de edad de *Coregonus lavaretus* (L.). En el primer análisis, varios lectores determinaron la edad de cada individuo sobre una estructura calcificada, escama, otolito o hueso opercular. Mezclamos las muestras de tres poblaciones, con 50 individuos cada una, de manera que los lectores desconocían la población a la que pertenecía cada una de las estructuras calcificadas. En el segundo análisis utilizamos una muestra de *C. lavaretus* de edad conocida y además, facilitamos a los lectores la fecha de captura, la longitud, el peso y el sexo de cada uno de los individuos. En cada una de las 50 muestras, incluimos escamas y dos otolitos, uno de los cuales fué quemado y cortado.

2. En el primer análisis, la precisión de las lecturas fué baja, tanto entre los lectores como entre las diferentes estructuras analizadas. En las muestras de poblaciones de crecimiento lento, las determinaciones de edad realizadas sobre otolitos resultaron en edades mayores de las obtenidas sobre escamas. En el segundo análisis, los resultados fueron mejores, en un 73–90% (media=82%) de los casos las determinaciones de edad fueron correctas.

3. Creemos que el uso de dos estructuras calcificadas más una cierta información sobre los individuos mejora la precisión en la determinación de las respectivas edades. Nuestros resultados no apoyan la idea de que el conocimiento de la longitud u otra información sobre el pez en cuestión dificulta la interpretación correcta de la edad. Muy por el contrario, un cierto conocimiento sobre el pez, dá al lector mayor posibilidad de realizar una correcta determinación de su edad.

4. Es recomendable validar las determinaciones de edad con individuos de edad previamente conocida. Menos de un 20% de las dataciones incorrectas o de los individuos no datados puede causar problemas de fiabilidad en los métodos en los que las distribuciones de edades son necesarias. Calcular la tasa de crecimiento parece menos sensible a dataciones incorrectas que a las distribuciones de edad.

Acknowledgements

A working group of fish researchers from three Nordic countries, Finland, Norway and Sweden, has been dealing since 1991 with the questions of the methods used in acidification studies. In order to increase the comparability of the results, the group has considered it important to calibrate the methods used in each country. Age determination has been one of the important topics examined in the group that we call the Nordic Freshwater Fish Group (NOFF). One goal has been to test the accuracy of age determination of different fish species that live in the fresh waters of the Nordic countries and the precision between different readers from different laboratories and countries. The authors got very valuable comments for this text from Magnus Appelberg, Trygve Hesthagen, Mika Kurkilahti, Kari Nyberg, and the referees. Kari Nyberg also treated the otoliths and scales of the second study for determination. Helena Halme edited the text.

References

Bagenal, T.B. & Tesch, F.W. 1978. Age and growth. In: Bagenal, T., ed. Methods for assessment of fish production in fresh waters. Oxford: Blackwell, pp. 101–136.

Barnes, M.A. & Power, G. 1984. A comparison of otolith and scale ages for western Labrador lake whitefish, *Coregonus clupeaformis*. Environmental Biology of Fishes 10: 297–299.

Beamish, R.J. & McFarlane, G.A. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Society 112: 735–743.

Beamish, R.J. & McFarlane, G.A. 1995. A discussion of the importance of aging errors, and an application to walleye pollock: the world's largest fishery. In: Secor, D.H., Dean, J.M. & Campana S.E., ed. Recent developments in fish otolith research. The Belle W. Baruch Library in Marine Science Number 19. Charleston: University of South Carolina Press, pp. 545–565.

Boehlert G.W. & Yoklavich M.M. 1984. Variability in age estimates in *Sebastes* as a function of methodology, different readers, and different laboratories. Californian Fish and Game 70: 210–224.

Casselman, J.M. 1983. Age and growth assessment of fish from their calcified structures – techniques and tools. In: Prince, E.D. & Pulos, L.M., ed. Proceedings of the international workshop on age determination of oceanic pelagic fishes: Tunas, billfishes, and sharks. NOAA Technical Report NMFS 8: 1–17.

Casselman, J.M. 1987. Determination of age and growth. In: Weatherley, A.H. & Gill, H.S., ed. The biology of fish growth. London: Academic Press, pp. 209–242.

Christensen, J.M. 1964. Burning of otoliths, a technique for age determination of soles and other fish. Journal du Conseil 29: 73–81.

Harrison, E.J. & Hadley, W.F. 1979. A comparison of the use of cleithra to the use of scales for age and growth studies. Transactions of the American Fisheries Society 108: 452–456.

Hofstede, A.E. 1974. Studies on growth, aging and back-calculation of roach *Rutilus rutilus* (L.), and dace *Leuciscus leuciscus* (L.). In: Bagenal, T.B., ed. Ageing of fish. Proceedings of an International Symposium. Surrey: The Gresham Press, pp. 137–147.

Jefferts, K., Bergman, P. & Fiscus, H. 1963. A coded wire tagging system for macro-organisms. Nature 198: 460–462.

Jonsson, B. 1976. Comparison of scales and otoliths for age determination in brown trout, *Salmo trutta* L.. Norwegian Journal of Zoology 24: 295–301.

Le Cren, E.D. 1947. The determination of age and growth of the perch (*Perca fluviatilis*) from the opercular bone. Journal of Animal Ecology 16: 188–204.

Mann, R.H.K. & Steinmetz, B. 1985. On the accuracy of age-determination using scales from rudd, *Scardinius erythrophthalmus* (L.), of known age. Journal of Fish Biology 26: 621–628.

Mosegaard, H., Appelberg, M. & Ångström-Klevbom C. 1989. Skillnader i åldersbestämning från fjäll och otoliter hos mört (English summary: Differences in age determination of roach using scales and otoliths). Information från Sötvattenslaboratoriet, Drottningholm 3: 19–27.

Power, G. 1978. Fish population structure in Arctic lakes. Journal of Fisheries Research Board Canada 35: 53–59.

Raitaniemi, J. 1997. Rannikon siikojen iänmäärityksen luotettavuus (In Finnish with an English abstract: the reliability of the ageing of whitefish (*Coregonus lavaretus* (L.)) on the Finnish Baltic coast). Kalatutkimuksia – Fiskundersökningar 121. 23 pp.

Salojärvi, K. 1989. Validity of scale ages determined for whitefish (*Coregonus lavaretus* L. s.l.) checked by microtagging in lake Oulujärvi, northern Finland. Aqua Fennica 19: 119–122.

Sikström, C.B. 1983. Otolith, pectoral fin ray, and scale age determinations for Arctic grayling. Progressive Fisheries-Culture 45: 220–223.

Steinmetz, B. 1974. Scale reading and back-calculation of bream *Abramis brama* (L.) and rudd *Scardinius erythrophthalmus* (L.). In: Bagenal, T.B., ed. Ageing of fish. Proceedings of an International Symposium. Surrey: The Gresham Press, pp. 148–157.