Ann. Zool. Fennici 41: 263–270 ISSN 0003-455X
Helsinki 26 February 2004

Growth, annual survival, age and length frequencies for unexploited lake whitefish populations

Kenneth H. Mills[1], Eric C. Gyselman[1], Sandra M. Chalanchuk[1] & Douglas J. Allan[2]

[1)] *Department of Fisheries & Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, Mb., Canada R3T 2N6*
[2)] *Limno Tech Enterprises, 135 Bayridge Ave., Winnipeg, Mb., Canada R3T 5B4*

Received 26 Aug. 2002, revised version received 18 Sep. 2003, accepted 18 Sep. 2003

Mills, K. H., Gyselman, E. C., Chalanchuk, S. M. & Allan, D. J. 2004: Growth, annual survival, age and length frequencies for unexploited lake whitefish populations. — *Ann. Zool. Fennici* 41: 263–270.

We reviewed growth, annual survival, length distributions, and age distributions for unexploited lake whitefish (*Coregonus clupeaformis*) populations. We compared Von Bertalanffy growth curves, catch-curve annual survival, and age distributions based on fin-ray and scale ages for 10 populations and found that growth was slower, annual survival higher, and there were many more age groups in the populations when using fin-ray ages than when using scale ages. The average annual survival of populations based on scale ages was 47% yr^{-1} and 74% yr^{-1} based on fin rays. Independent mark-recapture estimates of annual survival for two populations were almost identical to those based on fin-ray ages. We believe that growth has been overestimated and annual survival underestimated for many unexploited populations when these have been based on scale ages.

Introduction

The lake whitefish (*Coregonus clupeaformis*) is one of the most important freshwater commercial species in Canada. They are widely distributed (Scott & Crossman 1973) and have been the subject of a number of experimental studies to assess their population level responses to exploitation, eutrophication, oligotrophication, or acidification (Healey 1978, 1980, Mills & Chalanchuk 1987, Mills *et al*. 1992, 1995). An essential component of evaluating the responses of lake whitefish populations to these and other stresses is to define the characteristics of unimpacted, natural populations. Healey (1975) reviewed the characteristics of lake whitefish in both exploited and unexploited populations. He reviewed the literature on annual survival, growth, age-at-maturity, and abundance of unexploited populations. He did not find studies where abundance of lake whitefish in unexploited populations was described prior to the time of the review, 1975. He found many studies of annual survival and growth for unexploited populations. He found that estimates of annual survival were derived exclusively from catch-curves based on scale age data. In many cases these same data were used to generate growth curves for the populations. Scales (Van Oosten 1923, 1929) have been the structures normally used to age lake whitefish up to the time of Healey's review.

Power (1978) and Mills and Beamish (1980) questioned the validity of scale aging for unexploited lake whitefish populations. Power believed that scale ages under-aged many individuals in northern populations and that after a period of high mortality during early life stages, lake whitefish mortality was very low for the remainder of a fish's life. He believed this produced northern populations composed of a small proportion of young individuals and a large proportion of older fish from more than 20 age classes. He believed that variance in length of age groups increased as fish became older, and this was the reason that many northern populations had bimodal length-frequency distributions as described by Johnson (1972, 1976). Mills and Beamish (1980) also questioned the validity of scale ages for slow-growing lake whitefish populations. They showed that catch-curve annual survival estimates based on scale ages were much lower than estimates based on fin-ray ages for five unexploited populations. They also showed that growth curves for the five unexploited populations indicated much slower population growth when they were based on fin-ray ages than when they were based on scale ages. The purpose of this study is to review the current knowledge of growth, annual survival, and the length and age distributions of unexploited lake whitefish populations based on fin-ray ages of lake whitefish and compare these with similar scale-based estimates.

Methods

We used previously published growth data for 32 unexploited populations of lake whitefish summarized in Healey (1975) and more recent data for 12 unexploited populations. Healey's study is the most comprehensive synopsis of lake whitefish growth that is available. All of the growth curves presented by Healey were based on mean length-at-age data derived from scale ages of lake whitefish. We fit the mean length-at-age data for these unexploited populations to the Von Bertalanffy growth model (Ricker 1975, Haddon 2001) to produce growth curves. It was not clear in Healey's original paper how he fit growth curves to the mean length-at-age-data for each population, but we believe the growth curves were eye-fitted. Using these growth curves, Healey then eye-fitted upper and lower boundaries to describe the range of growth for unexploited lake whitefish populations.

We fit the von Bertalanffy growth model to mean length-at-age data for the 12 unexploited populations that we sampled. We had fin-ray ages for all 12 of our populations and corresponding scale ages for the same individuals for nine populations. Fin-ray and scale ages were read for each population by individuals who had many years aging experience using each method. When we had data for more than one year for a population, we combined these data to calculate single fin-ray and scale growth curves. We used data collected from 1973 to 2001 for lake whitefish from Lakes 226, 258, 259, 302, 305, 310, and 468 located in the Experimental Lakes Area, northwestern Ontario, Canada (Cleugh & Hauser 1971). Experiments occurred in some of these lakes during this time period that either did affect or could have affected lake whitefish growth. Therefore, we excluded data collected during the years that the experiments were conducted as well as six years after the experiments were terminated from our analyses. Although growth had returned to baseline values earlier than six years following the experiments in some populations (Mills & Chalanchuk 1987, Mills *et al*. 1995, 1998, 2002), excluding these years ensured our calculations did not include any residual effects of the experiments. Lake whitefish data were collected using multi-mesh gill nets from Lake Opeongo, eastern Ontario, in 1973, and from Dezadeash Lake, the Yukon Territory, in 1974. Details of sampling are located in Mills and Beamish (1980). Alexie, Baptiste, Chitty, and Drygeese lakes are located in the Yukon Territories (Healey 1975). Lake whitefish in the first three lakes were exploited using gill nets in 1974 and 1975, but the data used in this study were collected using multi-mesh gill nets from 1984 to 1991, nine to 16 years after the exploitation was completed in each lake. Lake whitefish growth had decreased to baseline values in Alexie and Chitty lakes three years after exploitation was terminated

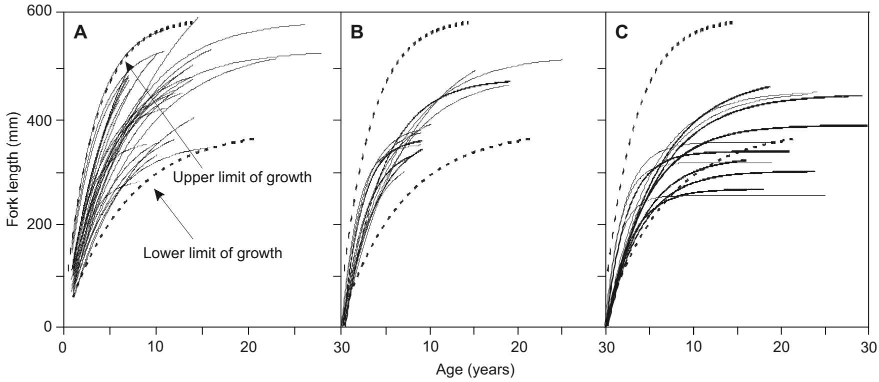

Fig. 1. Growth curves for unexploited lake whitefish populations. — **A**: 32 populations listed in Healey (1975) using scale ages. — **B**: 9 populations in this study based on scale ages. — **C**: 12 populations based on fin-ray ages. The limits of growth (dotted lines) in each figure enclose Healey's (1975) populations in A.

(Healey 1980) and recovery had occurred in Drygeese Lake before our data collection (E. C. Gyselman unpubl. data).

We used Robson and Chapman's (1961) method to calculate catch-curve annual survival rates for our populations using the combined data collected during all years of study, with the same exceptions listed above for growth curves, for the calculations. We calculated separate estimates based on fin-ray and scale ages for each population. We calculated average annual survival from all the scale-based and fin-ray-based estimates weighted by the squared inverse of the standard errors of each individual estimate (Krebs 1999, Sokal & Rohlf 1995).

We compared the catch-curve estimates for lake whitefish from Lakes 226 and 302 with independently derived mark-recapture estimates using the Jolly-Seber full model (Jolly 1965, Seber 1982). We have conducted mark-recapture studies of lake whitefish in each lake using this model for more than 25 years and have calculated average weighted annual survival of each population of lake whitefish using estimates for individual years using the weighting method described above. We excluded mark-recapture annual survival estimates for the same years as described above for growth and catch-curve annual survival for these populations. We had nine annual survival estimates to calculate the average for Lake 226 and 14 for Lake 302.

We constructed age- and length-frequency distributions for our nine unexploited lake whitefish populations based on fin-ray ages and scale ages. When data had been collected for multiple years for a population, we combined them before calculating these distributions. In populations where we had sufficient samples from five or more consecutive years (Lakes 226, 259, 302, 468, Alexie, Baptiste, Chitty, and Drygeese lakes), we constructed age- and length-frequency distributions for each year. We excluded years of data for Lakes 226 and 302 as described above. While there were strong and weak year classes in each population, the general features of the yearly age and length distributions were relatively similar for each lake. We felt that combining data gave a better general overview of the long-term features of each population than examining data for only one year.

Results

When growth curves were based on scale ages, we found that these curves for our 10 populations were in the middle of the range of growth for unexploited populations reported by Healey (1975), based on 32 populations (Fig. 1). In some cases — Opeongo, Alexie, Baptiste, Chitty and Drygeese lakes — we collected data from the same lakes reported earlier by Healey (1975). In these cases, our scale-based growth curves for these lakes were almost identical to those reported by Healey (1975).

The growth curves based on fin-ray ages indicated slower growth than the corresponding curves based on scale ages for all the populations that we sampled (Fig. 1). Growth for many of these populations was slower than the lower growth limit reported by Healey (1975). The differences in the corresponding fin-ray and scale growth curves started at relatively early ages. In some populations, there was a 10–20 mm difference in mean lengths between corresponding growth curves starting at age two (Lakes 259, 302, 305, 310, Dezadeash, and Opeongo) and the differences in mean lengths-at-age became progressively larger with increasing age. For the other populations, this difference first occurred at ages three to five, and differences increased in older age groups.

Catch-curve annual survival of our 12 populations was much higher based on fin-ray ages than scale ages (Table 1). Our calculated annual survival rates, based on scale ages for Alexie, Baptiste, Chitty, and Drygeese lakes (0.52, 0.44, 0.46, and 0.46, respectively) were almost identical to those calculated by Healey (1975) (0.52, 0.44, 0.46 and 0.44) for the same populations using data collected more than ten years prior to our data collections. Similarly, the scale-based annual survival rate we calculated for Lake Opeongo lake whitefish (0.49) was almost identical to the mean of scale age estimates (0.48) for this lake reported by Healey (1975). The average annual survival for all populations using scale ages was 0.47, while the corresponding average annual survival based on fin-ray ages was 0.74. The average mark-recapture annual survival for Lakes 226 and 302 were almost identical to the fin-ray catch-curve rates, while the scale estimates were approximately 50% lower than these estimates.

The length-frequency distributions for each population were usually characterized by two or three modes as described by Johnson (1972, 1976) for many other northern lake whitefish populations. Two examples, one for the southern Lake 226 population and one for the northern Baptiste Lake population are presented in Fig. 2. Lake 226 is much smaller (16 ha) than Baptiste Lake (> 400 ha) and this may be part of the explanation for the smaller modal size (330 mm) of the largest-sized group in this lake when compared with the large-sized group mode in Baptiste lake (430 mm). There were more than 20 age groups in each population and this was typical of all unexploited lakes except Drygeese where there were very few individuals older than 15. There was a general increase in variance of lengths as age became greater in each lake.

When we examined age-frequency distributions for each population based on fin-ray and scale ages, we found a much greater proportion of the population in older age groups using the fin-ray ages (two examples are shown in Fig. 3). For Lake 226, more than 20% of the individuals had fin-ray ages greater than 10 while the oldest

Table 1. Catch-curve annual survival estimates and confidence intervals (C.I.) based on scale or fin-ray ages. The average Jolly-Seber mark-recapture annual survival is shown for two populations.

Lake	Scale catch curve			Fin-ray catch curve			Mark-recapture
	Sample size	Annual survival	95% C.I.	Sample size	Annual survival	95% C.I.	Av. annual survival
ELA Lake 226	510	0.59	0.04	2723	0.74	0.01	0.76
ELA Lake 258				220	0.81	0.02	
ELA Lake 259				661	0.78	0.02	
ELA Lake 305				312	0.85	0.02	
ELA Lake 468	145	0.37	0.05	1123	0.77	0.02	
ELA Lake 310	135	0.45	0.03	133	0.78	0.04	
ELA Lake 302	130	0.35	0.11	719	0.76	0.02	0.70
Dezadeash YT	213	0.44	0.08	218	0.79	0.03	
Opeongo Ont	108	0.49	0.07	164	0.75	0.05	
Alexie NWT	320	0.52	0.04	1389	0.73	0.02	
Baptiste NWT	350	0.44	0.03	1630	0.72	0.02	
Chitty NWT	333	0.46	0.03	733	0.76	0.02	
Drygeese NWT	192	0.46	0.05	857	0.71	0.02	

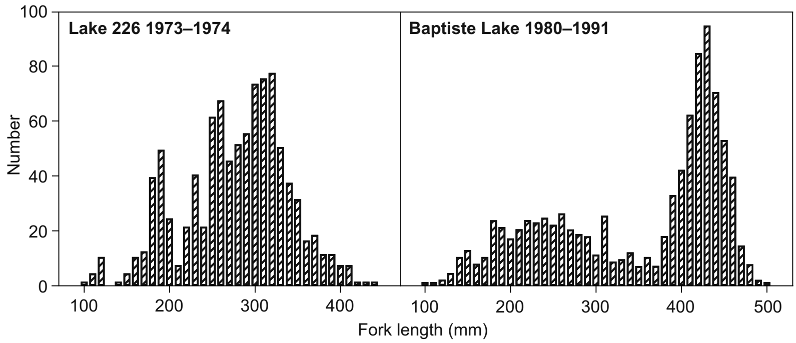

Fig. 2. Length-frequency distributions for lake whitefish in a southern (Lake 226) and a northern (Baptiste Lake) lake whitefish population.

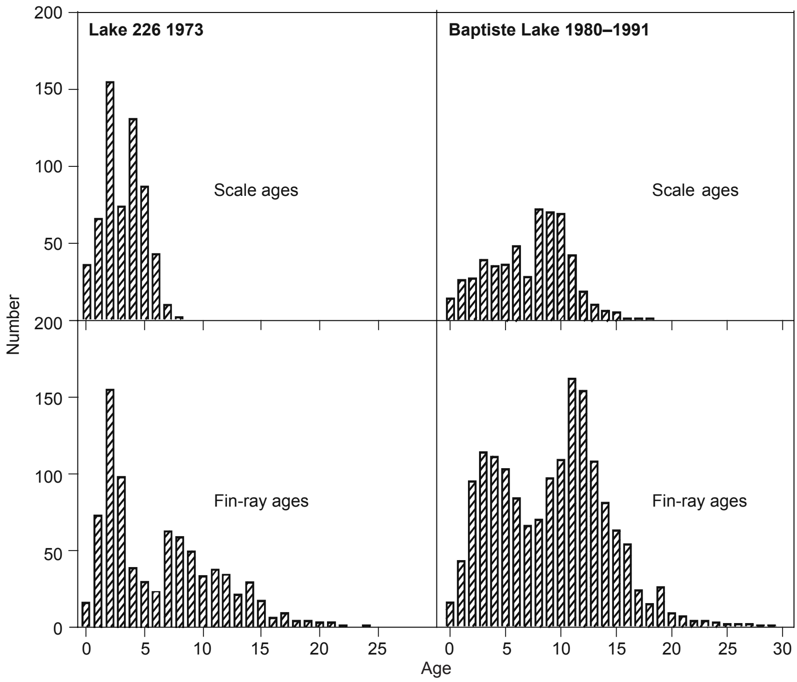

Fig. 3. Age-frequency distributions based on fin-ray and scale ages for a southern population (Lake 226) and a northern population (Baptiste Lake).

fish using scales had an age of eight. For Baptiste Lake, 44% of the individuals had fin-ray ages greater than 10, while only 16% had ages greater than 10 using scales.

Discussion

Characteristics of unexploited populations of lake whitefish

Over the past 30 years, two views of unexploited lake whitefish populations have existed in the lake whitefish literature. The first view, as presented by Johnson (1972, 1976), is that these populations are very stable, varying little through time in age and length structure. Annual recruitment of young individuals into the adult population varies among years. Adults can live more than 20 years and there is low mortality and growth after individuals are recruited from the juvenile population into the adult population. The second view, summarized by Healey (1975), is that some unexploited lake whitefish populations may have slow growth and low natural mortality, but there are also unexploited populations where growth can be rapid and natural mortality high, as high as total mortality in heavily exploited populations.

Contrary to expectations of many researchers and managers, Healey found that unexploited lake whitefish populations in Arctic lakes sometimes grew as quickly as more southerly populations.

Accurate, or nearly accurate, age determinations are essential to describe many characteristics of unexploited lake whitefish populations. Both Johnson (1976) and Healey (1975) realized the potential problems of aging slow-growing individuals, but neither dealt with how systematic, widespread under-aging of individuals could influence their conclusions. Power (1978) suggested that under-aging was responsible for many of the dome-shaped age-frequency distributions described by Johnson. Our results support Power's conclusions (Fig. 3). The lake whitefish populations had very dome-shaped age-frequency distributions based on scale ages, but more complicated structures when based on fin-ray ages. Mills and Beamish (1980) and Mills and Chalanchuk (2004) have validated fin-ray ages using mark-recapture methods for two unexploited lake whitefish populations, giving support for this method for other unexploited populations. Mills and Chalanchuk (2004) also compared pairs of otolith and fin-ray ages for individuals from two unexploited populations and found no significant differences between the corresponding ages, giving support to the conclusions of Power (1978) based on otolith aging. We believe that fin-ray or otolith ages are more likely to be accurate than scale ages for unexploited populations of lake whitefish. Growth of individuals can be very slow, resulting in crowding of annuli on the edges of scales. This makes identifying individual annuli very difficult. Under-aging a few individuals is unlikely to affect growth curves and annual survival estimates, but when this occurs for a large proportion of individuals, which is the case in all the unexploited populations that we examined, there can be significant effects on these parameters. Therefore, we believe that population statistics for unexploited lake whitefish populations, such as growth curves, age-frequency distributions, and catch-curve survival, are more likely to be accurate when using fin-ray or otolith ages than when using scale ages. A similar situation has developed for unexploited or lightly exploited populations of the closely allied European whitefish, *Coregonus lavaretus,* where otolith ages from slow growing populations can be greater than scale ages (Skurdal *et al.* 1985, Raitaniemi & Heikinheimo 1998). Raitaniemi and Heikinheimo (1998) presented a situation where these differences could cause an error in assessing the effects of fishing on a *C. lavaretus* population.

We believe that unexploited lake whitefish populations, whether Arctic or more southerly populations, are characterized by dome-shaped length-frequency distributions (Fig. 2) with one or more modes, and are characterized by slow growth (Fig. 1). This is consistent with the view of Johnson. We have not found any unexploited population with growth as fast as some of the unexploited populations described in Healey (1975) based on scale ages. We believe systematic under-aging could have been responsible for growth appearing rapid in some of the populations summarized by Healey (1975). Although we do not have data from unexploited lake whitefish populations for the northern-most portion of their range, we do have data from the southern Yukon as well as the southern Northwest Territories (Table 1). Growth curves for these populations are similar to those for the more southerly unexploited populations at the Experimental Lakes Area, Ontario. Therefore, the conclusion of Healey (1975), that more northerly populations have growth rates that are similar to those for more southerly populations, is confirmed, but the range of growth among populations is smaller than previously thought.

We believe unexploited populations of lake whitefish are characterized by relatively high annual survival, and that age-frequency distributions reflect this by the presence of more than 20 age groups in the population. This is consistent with the view of Johnson (1972, 1976). Our catch-curve annual survival estimates were very similar to the highest values reported by Healey (1975), but we did not find any estimates for unexploited populations as low as those reported by Healey. Because we validated the fin-ray ages for Lakes 226 and 302 (Mills & Chalanchuk 2004, Mills *et al.* unpubl. data), it is not surprising that the catch-curve rates for Lake 226 and 302 based on the fin-ray ages are almost identical to the average mark-recapture rates (Table 1) for each population, but does add further evidence for the reliability of the fin-ray catch-curve estimates.

Implications for management of lake whitefish fisheries

Unexploited lake whitefish populations are promising targets for new fisheries, or where populations are only lightly exploited, promising targets for increased fisheries. There is a large scope for compensation of populations for this exploitation — increased growth (Healey 1975, Healey 1980, Mills *et al*. 1995), lower age at maturity (Healey 1975, Mills *et al*. 1995), and increased recruitment (Healey 1980, Mills *et al*. 1995). As Mills and Beamish (1980) point out, the greatest danger for assessing the health of new lake whitefish fisheries is when there has been a systematic bias for under-aging individuals, leading to under-estimating annual survival by up to 50% and over-estimating growth. An extensive fishery for lake whitefish can rapidly increase total mortality and cause increased growth, but incorrect aging can lead to estimates of catch-curve survival and growth curves where little or no change is evident because the largest, under-aged older individuals are the first to be removed from the population. A manager might conclude that exploitation can be increased without putting the population at risk of collapse. Increasing exploitation might then cause overfishing to occur very rapidly, with little warning of a fishery collapse based on catch-curve, growth curve, or age-frequency data.

References

Cleugh, T. B. & Hauser, B. W. 1971: Results of the initial survey of the Experimental Lakes Area, northwestern Ontario. — *J. Fish. Res. Bd. Canada* 28: 129–137.

Haddon, M. 2001: *Modelling and quantitative methods in fisheries*. — Chapman and Hall/CRC Press, Boca Raton, Florida.

Healey, M. C. 1975: Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. — *J. Fish. Res. Bd. Canada* 32: 427–448.

Healey, M. C. 1978: Fecundity changes in exploited populations of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*). — *J. Fish. Res. Bd. Canada* 35: 945–950.

Healey, M. C. 1980: Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. — *Can. J. Fish. Aquat. Sci.* 37: 255–267.

Johnson, L. 1972: Keller Lake: characteristics of a culturally unstressed salmonid community. — *J. Fish. Res. Bd. Canada* 29: 731–740.

Johnson, L. 1976: Ecology of Arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic char, *S. alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. — *J. Fish. Res. Bd. Canada* 33: 2459–2488.

Jolly, G. M. 1965: Explicit estimates from capture-recapture data with both death and immigration — stochastic model. — *Biometrika* 52: 225–247.

Krebs, C. J. 1999: *Ecological methodology*, 2nd ed. — Addison Wesley Longman, Inc., Don Mills, Ontario.

Mills, K. H. & Beamish, R. J. 1980: Comparison of fin-ray and scale age determinations for lake whitefish (*Coregonus clupeaformis*) and their implications for estimates of growth and annual survival. — *Can. J. Fish. Aquat. Sci*. 37: 534–544.

Mills, K. H. & Chalanchuk, S. M. 1987: Population dynamics of lake whitefish (*Coregonus clupeaformis*) during and after the fertilization of Lake 226, the Experimental Lakes Area. — *Can. J. Fish. Aquat. Sci.* 44 (Suppl. 1): 55–63.

Mills, K. H. & Chalanchuk, S. M. 2004: The fin-ray method of aging lake whitefish. — *Ann. Zool. Fennici* 41: 215–223.

Mills, K. H., Chalanchuk, S. M. & Mohr, L. C. 1992: Effects of acidification on lake whitefish (*Coregonus clupeaformis*). — *Pol. Arch. Hydrobiol*. 39: 423–430.

Mills, K. H., Chalanchuk, S. M., Allan, D. J. & Mohr, L. C. 1995: Responses of lake whitefish (*Coregonus clupeaformis*) to exploitation at the Experimental Lakes Area, northwestern Ontario. — *Arch. Hydrobiol. Spec. Issues Advanc. Limnol*. 46: 361–368.

Mills, K. H., Chalanchuk, S. M., Findlay, D. L., Allan, D. J. & McCulloch, B. R. 2002: Condition, recruitment, and abundance of lake whitefish (*Coregonus clupeaformis*) in a fertilized acid lake. — *Arch. Hydrobiol. Spec. Issues Advanc. Limnol*. 57: 423–433.

Mills, K. H., McCulloch, B. R., Chalanchuk, S. M., Allan, D. J. & Stainton, M. P. 1998: Growth, size structure, and annual survival of lake whitefish (*Coregonus clupeaformis*) during the eutrophication and oligotrophication of Lake 226, the Experimental Lakes Area, Canada. — *Arch. Hydrobiol. Spec. Issues Advanc. Limnol*. 50: 151–160.

Power, G. 1978: Fish population structure in Arctic Lakes. — *J. Fish. Res. Board Can*. 35: 53–59.

Raitaniemi, J. & Heikinheimo, O. 1998: Variability in age estimates of whitefish (*Coregonus lavaretus* (L.)) from two Baltic populations — differences between methods and between readers. — *Nordic J. Freshw. Res*. 74: 101–109.

Ricker, W. E. 1975: Computation and interpretation of biological statistics of fish populations. — *Bull. Fish. Res. Bd. Canada* 191: 1–382.

Robson, D. S. & Chapman, D. G. 1961: Catch curves and mortality rates. — *Trans. Am. Fish. Soc*. 90: 181–189.

Scott, W. B. & Crossman, E. J. 1973: The freshwater fishes of Canada. — *Bull. Fish Res. Bd. Canada* 184: 1–966.

Seber, G. A. F. 1982: *The estimation of animal abundance* *and related parameters*, 2nd ed. — Macmillan Publishing Co. Inc., New York, NY.

Skurdal, J., Vøllestad, L. A. & Qvenild, T. 1985: Comparison of scales and otoliths for age determination of whitefish *Coregonus lavaretus*. — *Fisheries Research* 3: 237–243.

Sokal, R. R. & Rohlf, F. J. 1995: *Biometry*, 3rd ed. — W.H. Freeman & Co., New York.

Van Oosten, J. 1923: The whitefishes (*Coregonus clupeaformis*). A study of the scales of whitefishes of known ages. — *Zoologica (N.Y.)* 2: 381–412.

Van Oosten, J. 1929: Life history of the lake herring (*Leucichthys artedi*) of Lake Huron as revealed by its scales and with a critique of the scale method. — *Bull. U.S. Bur. Fish.* 44: 265–428.