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Comparative study of the age as determined by scales and otoliths of the Lake Trout (Salvelinus namaycush) of Lake Mistassini, Quebec

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COMPARATIVE STUDY OF THE AGE AS DETERMINED BY SCALES AND OTOLITHS OF THE LAKE TROUT (*SALVELINUS NAMAYCUSH*) OF LAKE MISTASSINI, QUEBEC.[1] [2]

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Abstract

Studies made on 603 lake trout (*Salvelinus namaycush*) from Lake Mistassini, Quebec, show that there is a strong discrepancy between ages obtained from the scales and from the otoliths of the same fish. The differences increase with older fish. Growth curves thus obtained (mean individual growth) have different limits and show different patterns of growth. The authors explain this discrepancy by the fact that fish and scale growth may cease or slow down, at sexual maturity, while the otolith continues to register annuli.

Introduction

In the course of an ichthyological inventory undertaken at Lake Mistassini, Quebec, by the Quebec Wildlife Service (LeJeune, 1962, 1964), we realized, during a study of lake trout (*Salvelinus namaycush*) populations, that for this species age determined from scales (scale age) did not agree with age determined from otoliths (otolithic age). Determination of age being an essential technique in the analysis of population structure, we first had to solve this problem.

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[1] Extract from a master's thesis submitted at Laval University (Dubois, 1967).

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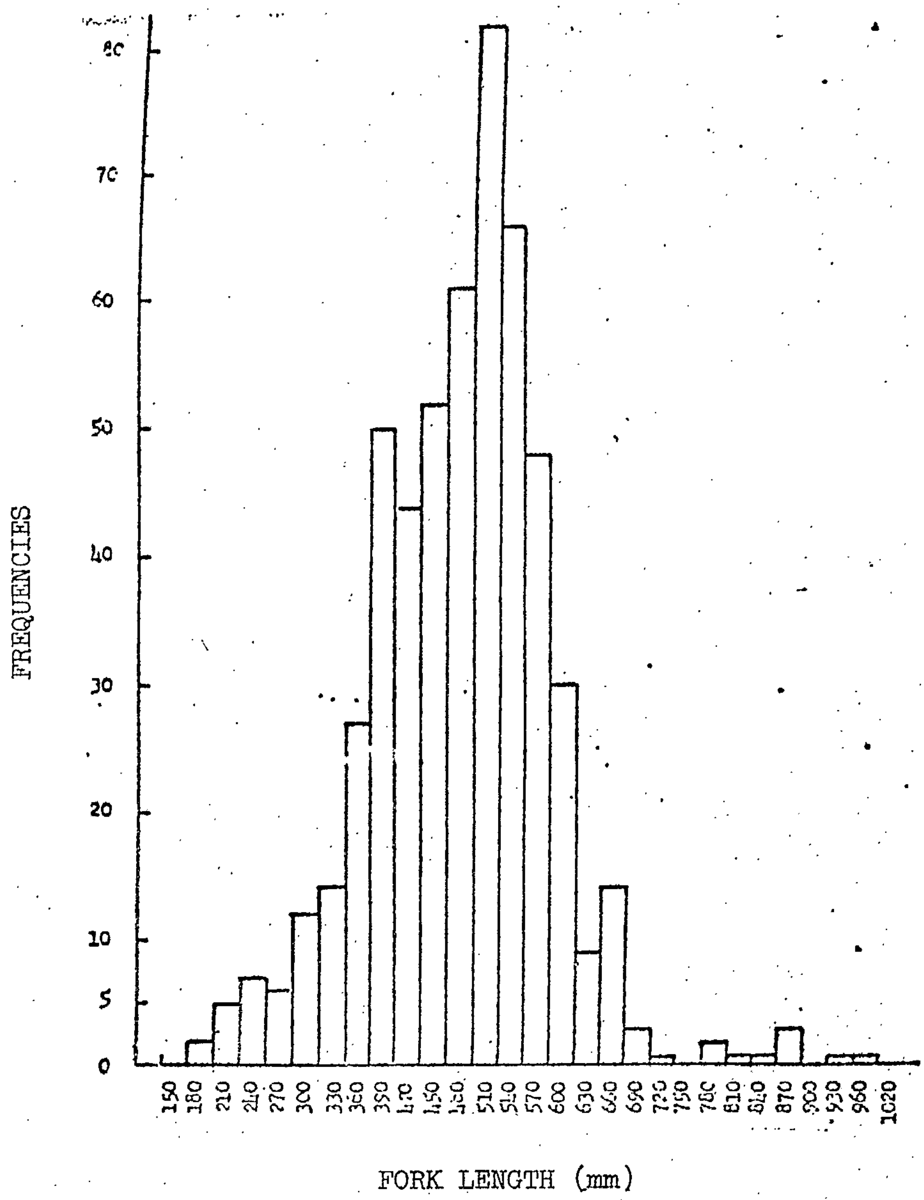

Figure 1. *Salvelinus namaycush*, Lake Mistassini, 1964-66.

Histogram of length frequency (mm F.L.) of material used.

Materials and Methods

The materials gathered over a three-year period included a total of 603 lake trout (Figure 1). All were measured (fork length), samples of scales and otoliths were taken, sex was determined and the maturity of gonads assessed.

Scales. All scale samples were taken in the usual manner from the side of the fish in an area located between the dorsal fin and the lateral line. Readings were then taken from impressions on cellulose acetate (Smith's technique, 1954). Each scale was read twice; a third reading was taken when the results of the first two differed. Sixty scales (9.9%) were set aside, and it should be noted that the length of the fish from which these aberrant scales were taken was between 400 and 600 mm (34 fish) and between 600 and 1000 mm (21 fish). It will be seen during a detailed analysis of all the materials that the rejected fish did not represent a particular group, but were spread uniformly throughout the population, and can be eliminated without danger of invalidating the results.

Otoliths. Samples of otoliths were taken by ventral breaking open of the cerebellum using the Lejeune technique (1967); they were kept in a dry place. As for readings, the best results were obtained with the Nordeng technique (1961) in which otoliths are made clearer by a five- to ten-minute bath in 96% alcohol, and then examined in creosote under high intensity lights. Our readings for the years 1964 and 1965 were confirmed by specialists at the Montreal Arctic Biological Station. A total of 109 otoliths out of 603 (18.1%) considered illegible were rejected. For the most part, these otoliths presented a special configuration: shorter anteroposterior axis; less well-defined form; and very numerous, narrower and clearer peripheral growth rings (Table I).

TABLE I

Salvelinus namaycush, Lake Mistassini, 1964, 1965, 1966.

Percentage of otoliths rejected because illegible or doubtful.

Year	Total number	Illegible otoliths	Doubtful otoliths	Total rejected
1964	134	19 (14.1%)	1 (0.7%)	20 (14.8%)
1965	268	27 (10.1%)	18 (6.7%)	45 (16.8%)
1966	201	25 (12.4%)	18 (8.9%)	43 (21.3%)

Results

Determination of Age

Normally one would expect different bone structures in the same fish to register the same age, since theoretically growth of these structures is determined by a common factor - the growth of the fish itself. Bulkley (1960) compared branchiostegal rays of lake trout to their scales and obtained the same results. The comparison between scales and otoliths of haddock by Kohler and Clarke (1958) yielded the same results. Nordeng (1961), however, frequently found a difference, sometimes of several years, between scales and otoliths of the Arctic char, *Salvelinus salvelinus*.

Readings to determine age from scales and otoliths of Lake Mistassini lake trout often gave very different results (Table II). Only 79 readings out of 455 - 17.4% - were identical; the difference between other readings varied from 1 to 18 years, the otoliths always having the greater number of growth zones. A difference of one or two years more or less may be due to a difficulty in interpreting

TABLE II

Salvelinus namaycush, Lake Mistassini, 1964-1966

Difference between the age read from otoliths and the age read from scales of the same fish (455 spp.)

Difference	Number	%	Difference	Number	%
0	79	17.4	10	13	2.9
1	74	16.3	11	9	2.0
2	46	10.1	12	10	2.2
3	50	11.0	13	6	1.3
4	45	9.9	14	10	2.2
5	31	6.8	15	3	0.7
6	20	4.4	16	4	0.9
7	22	4.8	17	2	0.4
8	14	3.1	18	1	0.2
9	16	3.5	-	-	-

growth zones, but when there is a difference as great as 18 years, this explanation is no longer valid. It is obvious that one of the structures is indicating an age that does not correspond to reality.

SCALE GROWTH VERSUS OTOLITH GROWTH

As a result of our readings, for one batch of fish we arrived at two age series - scale age and otolith age - which gave us two completely different pictures of the same population. An initial divergence appeared in the outer limits of extension of distribution by age:

a) The scale age series extends from 3 to 12 years (Table III and Figure 2).

b) The otolith age series extends from 3 to 24 years (Table IV and Figure 2).

TABLE III

Salvelinus namaycush, Lake Mistassini, 1964-1966.
Frequency distribution, growth, standard deviation and standard deviation from the mean according to scale age.

Age	Frequency	Mean fork length (mm)	Standard deviation ($\pm\sigma$)	Standard deviation from the mean ($\pm\sigma_m$)	Outer limits
3	1	205	-	-	-
4	14	233	35.01	9.36	180-315
5	45	342	51.01	7.60	230-450
6	90	401	41.67	4.39	270-500
7	119	468	40.77	3.74	370-550
8	168	523	42.78	3.30	395-650
9	69	560	56.45	6.80	440-790
10	25	623	76.86	15.37	475-830
11	7	719	132.03	49.90	540-950
12	6	795	109.77	44.81	620-920

We also noted a divergence in the lengthwise growth rate:

a) In the scale age series, the growth rate was relatively uniform and high (Table III and Figure 2);

b) in the otolith age series, the growth rate was lower and declined to almost nothing around the age of 12 (Table IV and Figure 2).

TABLE IV

Salvelinus namaycush, Lake Mistassini, 1964-1966.

Frequency distribution, growth, standard deviation, and standard deviation from the mean according to otolith age.

Age	Frequency	Mean fork length (mm)	Standard deviation (±σ)	Standard deviation from the mean ($\pm\sigma_m$)	Outer limits
3	1	205	-	-	-
4	9	231	41.44	13.81	180-315
5	14	315	61.50	16.44	230-400
6	32	362	69.07	12.21	200-515
7	50	412	60.56	8.56	270-550
8	35	428	74.31	12.56	250-575
9	48	483	73.14	10.56	310-640
10	34	491	72.03	12.18	305-615
11	47	511	69.85	10.19	305-670
12	44	542	61.18	9.33	420-710
13	26	528	70.20	13.77	410-690
14	41	528	113.25	17.67	345-840
15	17	528	95.56	23.18	390-815
16	17	543	129.93	31.51	355-825
17	18	521	79.91	18.84	405-645
18	12	568	120.82	34.88	380-775
19	13	576	121.43	33.68	450-920
20	6	520	76.22	31.12	385-615
21	5	599	158.52	70.89	410-850
22	12	588	94.73	27.35	425-790
23	9	618	196.15	65.38	385-1005
24	6	564	150.78	61.56	490-870

In our sampling, only one fish was three years old; its scales and otoliths indicated the same age. At the four- and five-year age level, there was still no significant difference between the mean length of corresponding scale and otolith age groups; this difference appeared only in the age VI group with a "t" of 3.765. There was, however, a rather pronounced variation in the number of specimens for the IV and V age groups; these scale age groups included 14 and 45 specimens respectively,

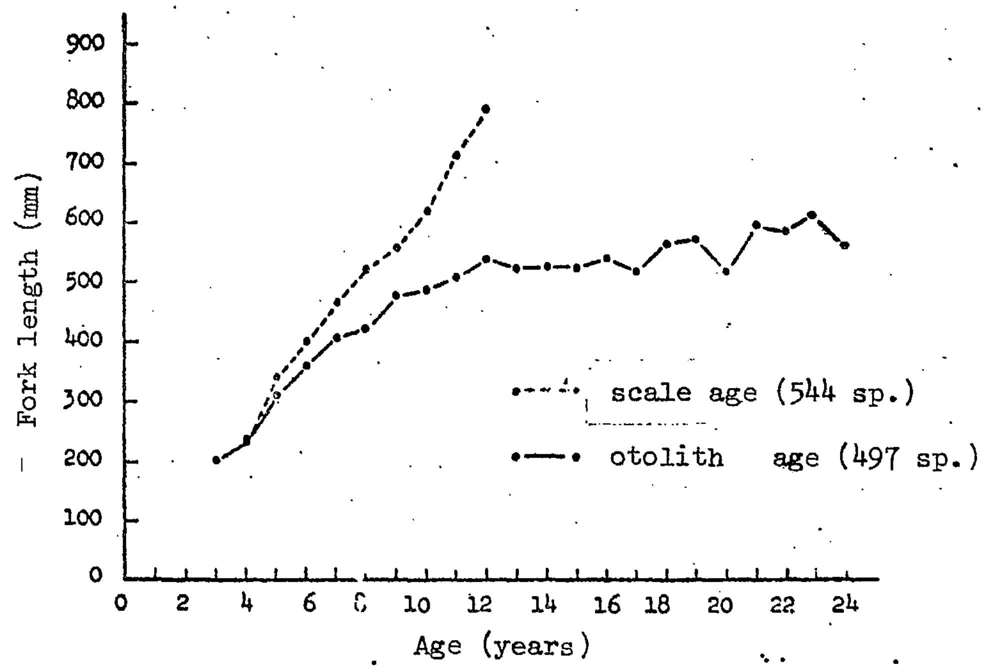

Figure 2. *Salvelinus namaycush*, Lake Mistassini, 1964-66.
Growth curve, or age/length relationship, by scale age and by otolith age.

while the corresponding otolith age groups included 9 and 14 respectively. This is explained by the fact that for most of these lake trout, the otoliths contained a greater number of growth rings than did the scales.

AGE AT FIRST REPRODUCTION

Faced with two age series for one batch of fish, we must take this into account when determining the age at which lake trout first reproduce. Gonads were examined in August of 1965 and 1966. According to Dufour,[4] the lake trout of Lake Mistassini spawn towards the end of September or the beginning of October. One might therefore expect that in August, the gonads of lake trout that are going to spawn in the following month will be sufficiently developed to be easily distinguished.

By scale age - On the basis of these observations (Table V), we see that males begin to mature sexually at the age of 5, and females at the age of 6. At 9, all males are adult and will spawn in the autumn. A male of 10, 690 mm long, and another 965 mm long of uncertain age, had immature gonads;

[4] M. Dufour, biologist with the Quebec Wildlife Service, personal communication, 1966.

it is possible that these fish were sterile or exceptionally slow in their sexual development or were not reproducing that year.

TABLE V

Salvelinus namaycush, Lake Mistassini, August 1965 and 1966. Percentage of lake trout with mature and immature gonads by scale age.

Age	Male gonads		Female gonads	
	Immature	Mature	Immature	Mature
3	100.0 (1)	0.0 (0)	-	-
4	100.0 (7)	0.0 (0)	100.0 (7)	0.0 (0)
5	77.3 (17)	22.7 (5)	100.0 (20)	0.0 (0)
6	68.4 (26)	31.6 (12)	85.7 (24)	14.3 (4)
7	28.8 (15)	71.2 (37)	52.6 (20)	47.4 (18)
8	15.9 (10)	84.1 (53)	41.1 (28)	58.8 (40)
9	0.0 (0)	100.0 (15)	26.7 (8)	73.3 (22)
10	16.7 (1)	83.3 (5)	50.0 (4)	50.0 (4)

With the limited observations available, we are unable to determine at what age all females are adult. Even at 9, only 73.3% of the females had mature gonads, and this decreased to 50% at the age of 10. It seems that females do not necessarily reproduce every year. We found eggs from the previous year in the abdominal cavity of 7 females whose gonads were, however, poorly developed. They varied in age from 6 to 8 years, and in length from 420 to 530 millimetres.

One might think that Lake Mistassini lake trout measuring 550 mm or more in length (one could choose 600 mm and the result would be the same) are already adult and would normally spawn in the autumn. However, our sampling included 32 females (37.6%) with undeveloped gonads, and 56 females (62.4%) with developed gonads - a ratio of 1:2. (Taking 600 mm, the ratio 1:2 would be that much closer with respective percentages of 36.1 and 63.9.) The ratio 1:2 leads us to suspect a cycle consisting of two years of reproduction followed by a year of rest. The idea that reproduction of the lake trout might follow a cycle is not a new one: Miller and Kennedy (1948) observed a cycle for Great Bear Lake; and Cuerrier and Schultz (1957) observed one for the Waterton Lakes.

By otolith age - On the basis of otolithic age, males first become adult at the age of 7, and females at the age of 9 (Table VI). We can assume that all males are adult at the age of 15; the few males older than 15 with immature gonads are perhaps sterile or in a period of rest. They account for only 9% of males aged 15 and over; a reproductive cycle is therefore not involved.

For their part, females seem to follow a reproductive cycle. If all females are adult at 17 - and this would not appear to be exaggerated - there were in the group aged 17 and over, 16 females with immature gonads and 17 with mature gonads. Once adult, therefore, females apparently reproduce only every other year.

TABLE VI

Salvelinus namaycush, Lake Mistassini, August 1965 and 1966. Frequencies of lake trout with mature and immature gonads by otolith age (379 spp.).

Age	Male gonads		Female gonads	
	Immature	Mature	Immature	Mature
3	1	-	-	-
4	4	-	5	-
5	7	-	5	-
6	12	-	7	-
7	13	2	11	-
8	6	3	10	-
9	4	14	16	3
10	6	8	6	3
11	6	7	11	10
12	1	12	8	12
13	3	9	2	5
14	9	11	6	9
15	-	8	4	5
16	1	8	3	5

17	–	8	6	3
18	1	6	3	1
19	1	7	1	4
20	–	5	–	1
21	1	1	1	3
22	–	7	3	1
23	–	5	–	3
24	1	2	2	1

Our data is obviously scant and for this reason may not be representative of the population. But our results with the otolithic age series are so different from those obtained with the scale age series that it is important to determine which of these structures - scale or otolith - gives us the real chronological age of the Lake Mistassini lake trout.

Discussion

It is not easy to explain the differences found between the scale age and otolithic age series. With the material we have, the best we can do is suggest a few hypotheses.

HYPOTHESIS: A HALT IN GROWTH

None of the studies made of lake trout (Bulkley, 1960; Cable, 1956; Miller and Kennedy, 1948; Rawson, 1959, 1961, and so on) tackle the problem we are interested in. After showing the validity of scales in determining the age of lake trout, using fish whose age is known, Cable (1956) makes the following remark:

> It should be emphasized that, dependable as lake trout scales may be as indicators of age, they are not read easily. Considerable experience is required before a reader's interpretation of the scale pattern becomes highly reliable. Even the experienced reader can do accurate work only if the scale preparations are clear and they are studied carefully with the aid of the best optical equipment.

We are somewhat surprised that other researchers who have done age studies of lake trout have not tried to draw comparisons between scales and other bony structures. Only Bulkley (1960) has made the attempt, using scales and branchiostegal rays. He noted that it was easy to locate the zones on the rays containing the annuli, but that it was difficult to determine their exact position. As for age, there is agreement between the scales and the branchiostegal rays, but the latter cannot be used for back-calculations.

We are particularly surprised that no one has tried to use otoliths. Nordeng (1961), who worked on Arctic char in northern Norway, provides us with some extremely interesting details which may perhaps shed some light on the problem. An important detail is that this species, the Arctic char, is closely related to the lake trout, also a char. Before Nordeng, scales were commonly used to determine age in Arctic char, as is now the case for lake trout. This author not only questions the value of scales, but proves that age determined by scales is not representative of the population from which samples are taken.

In adult Arctic char, the scale always ends in a zone of varying density (Figure 3) in which it is impossible to distinguish anything, and which corresponds on the otolith to a varying number of zones. These additional annular marks found on the otolith of an adult fish are easily distinguished from the preceding in that they are less opaque and sometimes narrower.

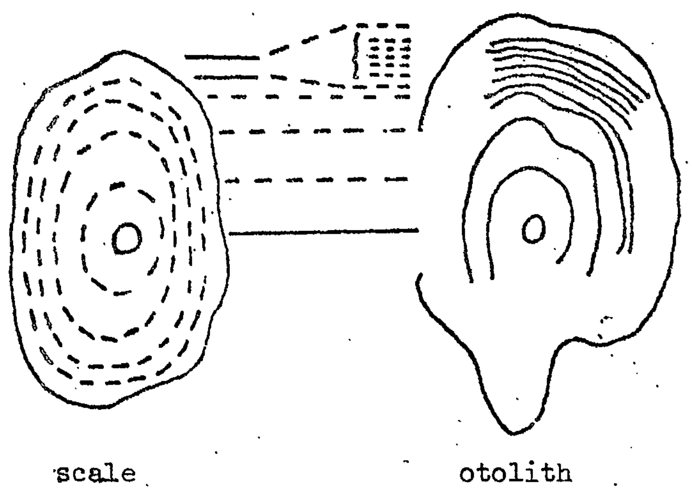

FIGURE 3. *Salmo alpinus*, 24 cm (adapted from Nordeng, 1961). Scale and otolith from the same fish; the annular marks on both structures correspond until sexual maturity, after which the otolith shows six years which appear as a single, concentrated zone on the scale.

By means of marked fish recaptured some years later, Nordeng was also able to verify the fact that zones are really annual on the otolith and that the additional marks, less opaque, correspond to years of reproduction. Finally, and not the least important, these same marked fish have made it possible to show that once sexual maturity is reached - that is, once the Arctic char has begun to reproduce - growth of the body and of the scales becomes very slow, or practically ceases, while the otolith continues its annual growth. Here then is a good explanation of the age difference between scales and otoliths. Briefly, the scales register only the years preceding the first reproduction, while otoliths continue to register years even after that time, and accordingly are the only valid structures for determining the age of an adult fish.

There is reason to think that this phenomenon of a halt in growth occurs in the Lake Mistassini lake trout. We very often found a difference between scale and otolithic age in this species which, as we have shown earlier, can be as large as 18 years. And when this difference exists, the otoliths always have the greater number of annual marks. In lake trout, there are also the additional zones described by Nordeng; these are clearer than the preceding and often narrower. This suggests that if there is a halt in growth, it occurs at the time of the first reproduction. But for the time being, we will try to determine whether or not the hypothesis of a halt in growth can be used to explain the difference between the two growth curves (Figure 2).

TABLE VII

Salvelinus namaycush, Lake Mistassini, 1965-66. Scale age frequencies by otolith age group.

Otolithic age	Scale age									
	3	4	5	6	7	8	9	10	11	12
3	1	-	-	-	-	-	-	-	-	-
4	-	9	-	-	-	-	-	-	-	-
5	-	4	10	-	-	-	-	-	-	-
6	-	1	11	19	-	-	-	-	-	-
7	-	-	8	23	18	-	-	-	-	-
8	-	-	5	5	14	11	-	-	-	-
9	-	-	3	9	14	13	6	-	-	-
10	-	-	5	3	6	9	7	3	-	-
11	-	-	-	6	9	20	6	1	2	-
12	-	-	-	1	4	21	7	3	1	-

13	-	-	-	2	4	11	6	2	-	-
14	-	-	1	7	5	13	5	3	-	-
15	-	-	-	2	2	10	1	-	-	1
16	-	-	1	2	4	4	2	1	-	-
17	-	-	-	-	7	7	-	1	-	-
18	-	-	-	2	2	2	-	1	1	-
19	-	-	-	1	2	4	2	2	-	1
20	-	-	-	1	-	3	1	-	-	-
21	-	-	-	-	1	2	1	-	-	-
22	-	-	-	-	2	4	3	1	-	-
23	-	-	-	1	1	1	4	-	-	1
24	-	-	-	1	1	3	-	-	-	1

Growth on the basis of the otolith age series - The shape of the otolithic age/length curve (Figure 2) seems to imply a halt in growth around the age of 11 or 12, while its slope approaches an asymptote and practically ceases. One may, however, question this. The levelling out that begins around the age of 11 or 12 actually indicates a balance between large fishes and other smaller ones that stopped growing at an earlier age. For example, from the scales and otoliths of a lake trout of 490 mm, we read 6 and 24 years respectively. In the case of another lake trout of 870 mm, we read 12 years from the scales and 24 from the otoliths. If we agree that when there is a difference between the scales and otoliths of the same fish, there was a halt in growth at the age indicated by the scales, we note that this could have taken place any time between the ages of 5 and 12 (Table VII). Furthermore, between 4 and 12 years, there are fewer and fewer scales indicating the same age as the corresponding otoliths (Table VII), but more and more at a lower age. At the same time, it can be seen that the slope of the curve is decreasing steadily. On the other hand, more than 80% of the lake trout in our sampling showed a scale age of 8 or less, and almost all of them were less than 600 mm long. Since these fish are found at all otolith ages, we can see that they eventually maintain a zero slope.

TABLE VIII

Salvelinus namaycush, Lake Mistassini, 1964-66.

Percentage of scale age readings identical to otolith age readings.

Otolithic age	4	5	6	7	8	9	10	11	12
Percentage	100	71.4	61.3	36.7	31.4	13.3	9.1	4.5	0.0

Growth on the basis of the scale age series - The growth rate as shown by the scales (Figure 3) is relatively uniform. The scale registers the growth of the fish; it grows and records years as long as the fish grows. As soon as growth stops, the scale no longer records years, even if the fish grows older. Even if growth ceases at the age of 9, 5 years later the scales will still show the same 9 years' growth. Thus it will always be necessary to examine the scales to determine the growth of the fish, whether or not these structures are valid in determining its exact age.

On the whole, the scale curve shows us the average growth of lake trout, without taking into account any halts that may have taken place. The otolith age/length curve, however, shows the true mean growth of the population, since it takes into account any halt in growth.

TABLE IX

Salvelinus namaycush, Lake Mistassini, 1964-66

Scale age frequencies and means by otolith age group.

Otolithic age	Frequency	Mean scale age	Standard deviation ($\pm\sigma$)	Standard deviation from the mean ($\pm\sigma_m$)	Extreme values
3	1	3.0	-	-	-
4	9	4.0	-	-	-
5	14	4.7	0.469	0.125	4-5
6	31	5.6	0.555	0.100	4-6
7	49	6.2	0.699	0.100	5-7
8	35	6.9	1.008	0.170	5-8

9	45	7.2	1.113	0.166	5-9
10	33	7.6	1.518	0.264	5-10
11	44	7.8	1.167	0.176	6-11
12	37	8.3	0.935	0.154	6-11
13	25	8.1	1.038	0.208	6-10
14	34	7.7	1.277	0.219	5-10
15	16	8.1	1.340	0.335	6-12
16	14	7.5	1.344	0.359	5-10
17	15	7.6	0.816	0.211	7-10
18	8	7.9	1.808	0.639	6-11
19	12	8.5	1.624	0.469	6-12
20	5	7.8	1.095	0.490	6-9
21	4	8.0	0.816	0.408	7-9
22	10	8.3	0.949	0.300	7-10
23	8	8.6	1.768	0.625	6-12
24	6	8.2	2.037	0.832	6-12

Comparison of the otolith age/length and otolith age/scale age curves - There is therefore a strong correlation between scale age and the length of lake trout; that is, scale age is an indicator of length. As for otolith age, it is a good indicator of real age, but seems to be independent of length. Figure 4 illustrates what we have just said. Keeping the otolith age as the abscissa, the length (Table IV) or the scale age (Table IX) can be plotted as an ordinate. The resulting curves, otolith age/length and otolith age/scale age, are similar and superposable. Their simple, curvilinear correlation rates are 0.665 and 0.683 respectively, with a "t" of 0.515. In other words, length could be replaced by scale age and the two would give the same result, evidence of a connection between scale age and length.

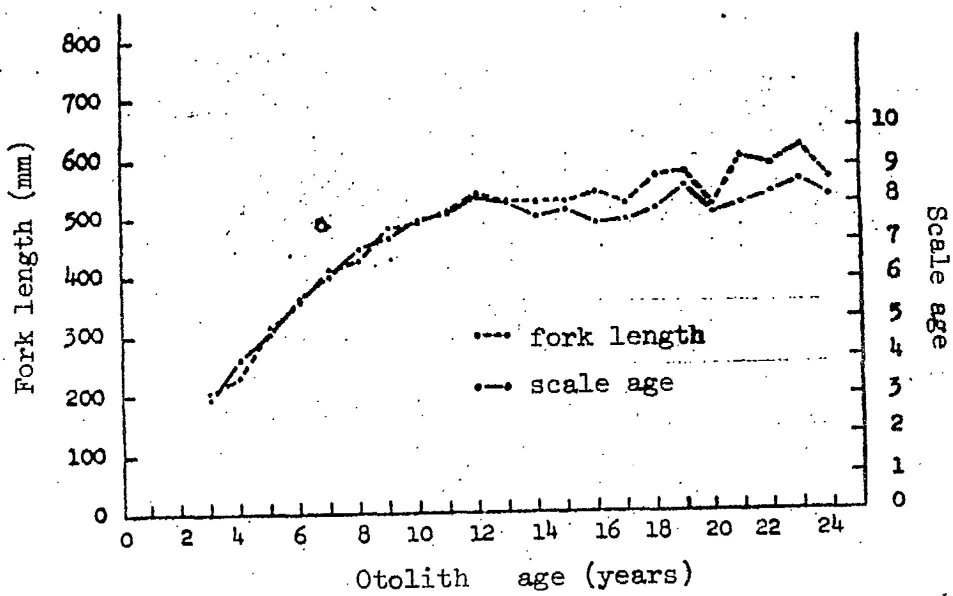

FIGURE 4. *Salvelinus namaycush*, Lake Mistassini, 1964-66. Comparison between the otolith age/length (mm F.L.) curve, 495 spp., and the otolith age/scale age, 454 spp., curve. Note that it is possible to replace the length by scale age for the ordinate.

We know that the lake trout is a slow-growing fish usually reaching sexual maturity between the ages of 6 and 8 or 9 (Martin, 1951 and 1957; Rawson, 1961; Royce, 1951). It might therefore be expected to have a long life span, and consequently a low mortality rate. Histograms of frequencies by age group (Figure 5, A and B) should show this. The first (A) is constructed on the basis of the scale age series, the second (B) on the basis of the otolithic age series. The fact that there are fewer specimens 3, 4 and 5 years old, for example, is undoubtedly due to the limits imposed by the sampling method; almost all these fish were captured using nets with a 4-inch mesh. In the first histogram (A), most specimens are found at 8 years, but at 9 years there is an immediate drop of over 50%; the same thing happens at 10 years. This would imply a very high mortality rate and a very rapid disappearance of the adult population, thus endangering the existence of the whole population, which seems inconsistent with the actual situation, since the population is being maintained.

According to the second histogram (B), in which we have used the otolith age series, the mortality rate is not as high and is much more normal. This histogram certainly provides us with the picture closest to what we expected to find.

Having compared our data with this hypothesis, according to which there is a halt in growth in the Lake Mistassini lake trout, we feel it should be retained, even if it is impossible to prove for the time being. It offers a simple and logical explanation of the differences found between scale and otolithic ages, and also explains the differences encountered between the two growth curves. Finally, it becomes more valid following an examination of the two histograms plotted using both age series - scale age and otolithic age.

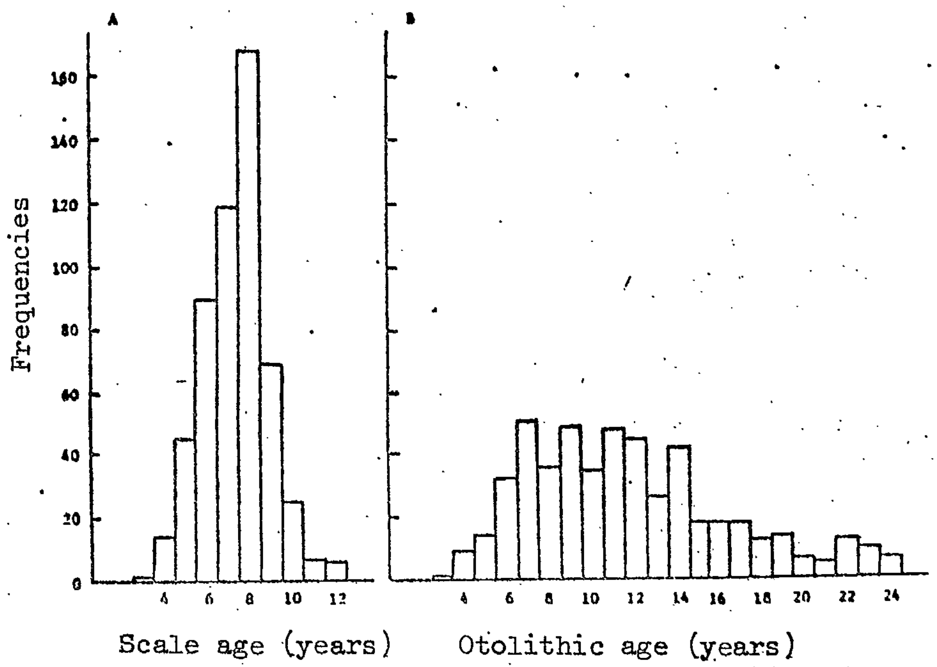

FIGURE 5. *Salvelinus namaycush*, Lake Mistassini 1964-66.

A: Scale age frequencies (544 spp.)

B: Otolith age frequencies (497 spp.)

Halt in growth and sexual maturity - Nordeng (1961) noted very little or practically no growth in the Arctic char of northern Norway after sexual maturity. It is acknowledged that sexual maturity generally requires extreme physiological effort on the part of Salmonidae. Miller and Kennedy (1948) also attributed to sexual maturity a halt in growth of lake trout in Great Bear Lake between 11 and 13 years.

For Lake Mistassini we have suggested, as an interpretation of the difference between the age read from the scales and that read from the otoliths, that there is a halt in growth of the scale and of the fish. If, in addition, we assume that this halt in growth takes place at the time of sexual maturity, we should see that the three following points are verified:

1) As soon as there is a difference between the age read from the scales and that read from the otoliths, the fish is adult.

2) The age read from the scales of an adult lake trout corresponds to the age at which it reached sexual maturity.

3) The divergence between scales and otoliths must begin at about 5 years of scale age, just as sexual maturity does, and this divergence must also become more pronounced with the gradual increase in the number of adult fish to finally reach a maximum around 9 years of scale age, when all fish have reached the adult stage (Table V).

At 4 years, this divergence is already present between the age read from the scales and that read from the otoliths of 5 specimens. But we strongly doubt that these fish are already adult for two reasons; first of all, because we did not find any lake trout of this age in the 14 captured with mature gonads, and also because of the small size of these fish.

At 5 years of scale age, we encounter this divergence between scales and otoliths in 34 out of 44 lake trout - slightly over 75%. If at this age 3/4 of Lake Mistassini lake trout were already adult, we would have to find more than 5 specimens with mature gonads out of 42. Since the same phenomenon recurs at later ages, it becomes impossible to attribute as large a role to chance in the distribution of specimens. It is certain that all females do not necessarily reproduce every year. It is also possible that these results are due in part to incorrect readings, from scales in particular, but we do not think that this accounts for the divergencies encountered.

If the halt in growth of the lake trout takes place independently of sexual maturity, then of the results we presented on reproduction in the lake trout, we must retain only those based on otolithic age. In other words, the lake trout becomes adult between 7 and 9 years of age, sexual maturity takes place over a large number of years, and once adult, females probably reproduce only every other year.

This is still somewhat surprising. Until now, everything was consistent with Nordeng's observations on the Arctic char, including reproduction marks on the otolith as described by the same author. Perhaps the number of small lake trout in our sampling is not large enough to give us an accurate picture of the situation. Perhaps we must examine the life of the Lake Mistassini lake trout for another event capable of producing this halt in growth, and independent of the age or size of the fish. Or perhaps we must quite simply reject the hypothesis of a halt in growth.

HYPOTHESIS: OTOLITHS REGISTER MORE THAN ONE GROWTH ZONE A YEAR.

If we reject the hypothesis of a halt in growth, the only other possibility is that the scales of Lake Mistassini lake trout indicate the true age, and that otoliths register more than one growth zone a year. It is possible that otoliths are more sensitive than scales when it comes to registering cyclic midseasonal growth variations due to a more or less rigorous climate and a greater or lesser supply of food, with the result that they would often register more than one growth mark a year. Any cyclic or acyclic factor in one way or another affecting the growth of a fish has its repercussion on the development of bony structures.

However, we see a few objections to this hypothesis. Assuming that the age indicated by the scales is correct, we are faced immediately after sexual maturity with a mortality rate that seems too high (Figure 5A). If scales lead us to equally doubtful results, it would seem that their validity must also be questioned.

On the other hand, if Lake Mistassini lake trout register more than one growth mark a year, should there not be almost the same number of additional marks on the otoliths of fish of the same scale age class? All were subject to the same factors capable of affecting their growth. Yet otoliths of fish whose scales contained 6 annuli, for example, registered from 6 to 24 growth marks (Table VII). In order to accept this hypothesis, one would have to conclude that growth zones are registered somewhat incoherently on otoliths; or better, that each fish responds in its own way to factors in the environment which may affect its growth, and that otoliths reflect the after-effects in their own particular way also.

This is inadmissible. Where scales are concerned, all the fish of one population usually carry the same false annulus; for this reason, one would also expect to find them on otoliths of all fish that have lived in similar conditions.

Still another objection arises. If we agree that scales register the age of lake trout accurately, and that females rest for a year after two years of reproduction, as we saw earlier, we would then have to conclude that female lake trout can be adult at 5 and even 4 years. We were saying earlier that we had found ripe eggs in lake trout of 6 to 8 years with undeveloped gonads. This would mean that these females had become adult between 4 and 6 years, had spawned for two consecutive years and had been captured during their year of rest. But it seems rather unlikely, with the data we have, that females are already adult at 4 and even 5 years. It is also worth noting that all otoliths from these few lake trout, except in one case where they indicated 17 years, are illegible because of an excessive number of growth marks: these lake trout may therefore be much older than their scales indicate.

Conclusions

Neither of these hypotheses can be verified with the data we have. Furthermore, it is not impossible that both are partly correct; that is, that there is a halt in the growth of the fish and of the scale, and that otoliths frequently register more than one annual growth mark.

The most effective means of verification would consist of intensive marking of lake trout, and recapturing over a period of a few years. Comparison of scales taken during tagging and at the time of recapture would enable us to see whether or not they had registered exactly the number of years that had passed between these two events. Setting up such a tagging operation is unfortunately outside the scope of this study. As for otoliths, we will be able to see whether or not their growth marks are annual only through marking and recapturing lake trout of known age, or through a method of marking the edge of the otolith at the time of initial capture. Such methods now exist for marking the edge of scales (Fry, Cucin and Kennedy, 1960; Hijama and Ichikawa, 1952; Van Coillie, 1967), and there is no reason why such a technique could not be applied to other bony structures such as otoliths (Jensen and Cumming, 1967).

In the case of the Lake Mistassini lake trout we have thus noted that there is a marked difference between scale age and otolith age for the same fish, and between the growth curves derived from these two techniques. Our explanations are still only hypotheses, but one important fact remains: the gap between the results obtained using two techniques recognized as classic. We are puzzled by the fact that in the numerous studies made of lake trout, especially in the Great Lakes, only scales were used to determine age. Only Bulkley (1960) draws a parallel between scales and branchiostegal rays, and to our knowledge, nowhere are otoliths mentioned.

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