# AN INVESTIGATION INTO THE METHODS OF GROWTH DETERMINATION IN FISHES BY MEANS OF SCALES

BY

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## Introduction.

The Norwegian investigators have for some time been studying in very great detail the methods of age and growth determination from the scales of fishes, their attention being directed mainly at first to the scales of the herring. The great experience to which they have attained, combined with the unique opportunities they have for dealing with a very large mass of collected material, has resulted in the discovery of an extension of the scale method which, if it can be shown to be absolutely reliable, will open up a vast field for investigation and give us most valuable new weapons with which to attack an important question of marine biology, viz., the annual amount of growth of different fishes. Hitherto this problem has only been solved by taking the difference in length between the average sizes of fishes of known age, or by the growth of marked fishes.

However, it will be seen presently that the old method cannot give us *exact* results if this new method is as precise as its exponents believe.

The method consists in determining from the scale not only the age of the individual, but also in demonstrating how the particular individual's growth had occurred during the earlier growth periods.

Mr. Einar Lea, Assistant at Bergen, has arrived at the conclusion that the growth of the scale so closely accords with the growth of the individual, that it is possible with a certain amount of exactitude to describe the growth history by means of measurements of the growth zones of the scale. A full description of these investigations is found in Publications de Circonstance, No. 53, »Report on Herring Investigations until January, 1910«, and the results are continued further in No. 61. »Report on the International Herring Investigations during the year 1910«.

Thus it is that the scale of a fish not only gives data towards determining the size at a given age, but also the size of the fish at each previous year of its existence. Thus one scale gives information for 1, 2, 3, 4, 5 or more years of its existence, and the data become multiplied several fold, and their value is thereby increased enormously. If we suppose it valid, it will be possible to utilise the method to determine growth differences between different years to an extent hitherto unattainable, and to carry back the researches a considerable number of years before the time that the methods were devised, by making use of the scales of very old fish. From these results it should be possible to trace a connection between physical conditions and growth.

## Examination of Norwegian Results.

The results are thus of such far reaching consequences, that it is worth while to try and examine the conclusions, to see to what extent they apply to other fishes, and whether there are any limitations as to their use. For this purpose of examination and analysis of the use of the method. I have taken the *published* results and put certain average values in tabular form and added some slight arithmetical conclusions — so as to show them in a form from which further results may be obtained. In this way some most interesting facts appeared, which I propose setting forth and discussing in the present paper. Besides the published herring results, which were very numerous, there are some for trout investigated in the same manner by the Norwegians, and some for a series of haddock, to which we in England had applied the method; in all these the same law of growth seemed apparent.

The principle of the method employed is to divide the length of each individual fish into parts for each year proportional to the lengths of each yearly ring of the scale, — or more definitely, if $L$ is the length of the fish, and $V$ the length of the scale from the centre to the periphery, $V_1$, $V_2$, $V_3$, etc., the similar lengths to the end of each winter ring, the »calculated« lengths of the fish at the end of the formation of each winter ring in the previous years of its existence are given by

$$l_1 = \frac{V_1}{V} L. \quad l_2 = \frac{V_2}{V} L. \quad l_3 = \frac{V_3}{V} L. \text{ and so on.}$$

The actual increment of growth in each year is given by

$$t_1 = l_1, \; t_2 = l_2 - l_1, \; t_3 = l_3 - l_2, \text{ and so on.}$$

The tables following are made up from values taken directly from the calculated average lengths for each year class — from the various collections, the details of which are given in the papers named above. In all cases in comparing the results of the average calculated lengths as determined from the fish of each single year group, it must be borne in mind that where a group occurs with less than 5 or 6 fish, as is the case in the oldest groups, the resulting average values are unreliable, and we must stop short at such a point where this is the case, for the series and laws that are presently to be deduced generally break down under these circumstances. In the tables a line is drawn to mark these points.

The following facts appear from a study of these figures.

*Collection No. 6. October 1909.* a) The averages under the headings $l_1$, $l_2$, $l_3$, $l_4$ show a regular decrease from the 1st to the 5th year group.

b) Generally speaking, the decrease from one year to the next is greatest between the two first numbers in any series.

c) It can be assumed that, in October, the fish has quite or nearly finished its year's growth, therefore the average size of any age group should equal approximately or be a little less than the length at the end of the following winter which is given by fish of the next year group. But we have 17.5 cm as the average length of the group 1, greater than 14.0 cm the calculated length at the end of the second winter, and 19.9 cm the average length of the group 2, greater than 18.4 cm the calculated length at the end of the third winter, and so throughout the series.

*Collection No. 9.* This consists of 380 fish distributed between age groups 3 to 14. Groups 3, 12, 13 and 14 must be left out of consideration because of their small number of fish.

a) Under $l_1$ we see a decrease from groups 4 to 6 and afterwards an increase. Groups 5 and 6 seem to have had very smal first year lengths, which has consequently affected the results for the succeeding years, and thus to some extent the regularity of the series is marred. In $l_2$ there is a tendency to decrease in the values from the younger to the older age group, — in $l_3$ *an almost steady decrease*, and in the succeeding years, the decrease from the first of each series in the columns is decidedly marked and steady. This group consists of older fish than in Collection 6, and the phenomenon is observed in a greater degree in the calculated values from the 3rd years onwards than in the first two.

**Table 1** showing the calculated lengths of Herrings at the formation of each winter ring.

Herrings from Norwegian waters, from »Herring Investigations until January 1910«, by JOHAN HJORT.

| | Year Class | Number of fish | $l_1$ | $l$ | $l_3$ | $l_4$ | $l_5$ | $l_6$ | $l_7$ | $l_8$ | $l_9$ | $l_{10}$ | $l_{11}$ | $l_{12}$ | $l_{13}$ | $l_{14}$ | Average Length of Group |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Collection 6. 8.10.09. | 1 | 59 | 9.3 | | | | | | | | | | | | | | 17.5 |
| | 2 | 1169 | 7.6 | 14.0 | | | | | | | | | | | | | 19.9 |
| | 3 | 31 | 7.3 | 13.0 | 18.4 | | | | | | | | | | | | 23.2 |
| | 4 | 6 | 7.6 | 12.3 | 16.7 | 20.2 | | | | | | | | | | | 23.2 |
| | 5 | 6 | 6.5 | 11.5 | 15.5 | 19.4 | 22.9 | | | | | | | | | | 26.3 |
| Collection 9. 10.09. | 3 | 1 | 7.9 | 18.0 | 23.6 | | | | | | | | | | | | 27.0 |
| | 4 | 15 | 9.3 | 17.0 | 23.2 | 26.4 | | | | | | | | | | | 28.8 |
| | 5 | 197 | 8.4 | 15.9 | 21.9 | 25.3 | 27.6 | | | | | | | | | | 29.1 |
| | 6 | 38 | 8.3 | 15.5 | 21.3 | 25.2 | 27.4 | 28.8 | | | | | | | | | 29.9 |
| | 7 | 26 | 9.1 | 17.0 | 22.2 | 25.3 | 27.4 | 28.6 | 29.5 | | | | | | | | 30.2 |
| | 8 | 34 | 9.5 | 16.1 | 21.0 | 24.4 | 26.3 | 27.6 | 28.6 | 29.4 | | | | | | | 30.0 |
| | 9 | 22 | 9.3 | 16.0 | 20.7 | 24.0 | 26.2 | 27.5 | 28.5 | 29.3 | 30.0 | | | | | | 30.5 |
| | 10 | 25 | 9.0 | 15.8 | 20.5 | 23.5 | 25.6 | 26.9 | 27.9 | 28.6 | 29.3 | 29.9 | | | | | 30.3 |
| | 11 | 17 | 9.7 | 16.2 | 20.2 | 22.5 | 24.2 | 26.5 | 26.4 | 27.1 | 27.7 | 28.2 | 28.7 | | | | 29.0 |
| | 12 | 3 | 8.1 | 14.2 | 18.4 | 20.5 | 22.8 | 24.4 | 25.7 | 26.6 | 27.1 | 27.6 | 28.1 | 28.6 | | | 29.0 |
| | 13 | 1 | 6.7 | 13.1 | 17.8 | 20.2 | 22.7 | 24.7 | 26.3 | 27.3 | 27.9 | 28.4 | 28.8 | 29.2 | 29.7 | | 30.0 |
| | 14 | 1 | 12.7 | 18.4 | 20.0 | 22.0 | 23.0 | 24.6 | 25.8 | 26.8 | 27.6 | 28.3 | 28.6 | 29.0 | 29.4 | 29.7 | 30.0 |
| | Total | 380 | | | | | | | | | | | | | | | |
| Collection 14. 7.07. | 1 | 153 | 9.5 | | | | | | | | | | | | | | 11.4 |
| | 2 | 37 | 7.8 | 13.3 | | | | | | | | | | | | | 15.2 |
| | 3 | 536 | 6.9 | 12.7 | 17.0 | | | | | | | | | | | | 18.8 |
| | 4 | 22 | 7.0 | 12.2 | 16.8 | 20.4 | | | | | | | | | | | 21.8 |
| | 5 | 6 | 6.3 | 11.7 | 15.4 | 18.1 | 20.2 | | | | | | | | | | 21.5 |
| | Total | 755 | **7.5** | **12.7** | **17.0** | **19.9** | **20.0** | | | | | | | | | | |

**Table 1.** (Continued).

| | Year Class | Number of fish | $l_1$ | $l_2$ | $l_3$ | $l_4$ | $l_5$ | $l_6$ | $l_7$ | $l_8$ | $l_9$ | $l_{10}$ | $l_{11}$ | $l_{12}$ | $l_{13}$ | $l_{14}$ | Average Length of Group |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Collection 12. 2.08. | 4 | 11 | 9.9 | 19.7 | 25.8 | 29.0 | | | | | | | | | | | 29.0 |
| | 5 | 14 | 8.7 | 17.6 | 24.1 | 27.8 | 30.1 | | | | | | | | | | 30.1 |
| | 6 | 16 | 8.7 | 17.3 | 23.4 | 27.2 | 29.5 | 31.0 | | | | | | | | | 31.1 |
| | 7 | 16 | 10.4 | 17.2 | 22 9 | 27.2 | 29.4 | 30.8 | 31.7 | | | | | | | | 31.7 |
| | 8 | 22 | 8.9 | 16.4 | 22.0 | 25.8 | 28.3 | 29.9 | 31.1 | 31.8 | | | | | | | 31.9 |
| | 9 | 15 | 9.1 | 15.6 | 21.3 | 25.6 | 28.3 | 30.1 | 31.3 | 32.2 | 32.8 | | | | | | 32.9 |
| | 10 | 5 | 10.0 | 16.6 | 21.3 | 25.2 | 28.1 | 29.8 | 30.9 | 31.8 | 32.5 | 33.1 | | | | | 33.2 |
| | 11 | 4 | 9.8 | 17.4 | 22.9 | 26.0 | 28.5 | 29.9 | 31.2 | 32.2 | 33.1 | 34.0 | 34.6 | | | | 34.8 |
| | 12 | 1 | 11.4 | 18.9 | 22.3 | 25.5 | 28.5 | 31.0 | 32.4 | 33.6 | 34.5 | 35.1 | 35.9 | 37.0 | | | 37.0 |
| | 13 | 2 | 10.8 | 17.5 | 22.4 | 26.8 | 30.0 | 31.7 | 32.9 | 33.8 | 34.6 | 35.1 | 35.5 | 36.0 | 36.5 | | 36.5 |
| | 14 | 2 | 8.6 | 15.6 | 21.1 | 24.9 | 27.9 | 29.8 | 30.9 | 31.9 | 32.7 | 33.5 | 34.1 | 34.6 | 35.1 | 35.5 | 35.5 |
| | Total | 108 | **9.3** | **17.1** | **22.9** | **26.8** | **29.0** | **29.0** | **31.3** | **32.1** | **33.0** | **33.8** | **34.8** | **35.6** | **35.8** | **35.5** | |
| Collection 15. 6.08. | 3 | 1 | 8.8 | 16.8 | 24.5 | | | | | | | | | | | | 26.0 |
| | 4 | 49 | 11.0 | 19.3 | 25.4 | 29.2 | | | | | | | | | | | 30.1 |
| | 5 | 26 | 10.0 | 19.4 | 25.9 | 29.0 | 31.2 | | | | | | | | | | 31.8 |
| | 6 | 14 | 9.7 | 19.0 | 25.5 | 28.9 | 31.2 | 33.0 | | | | | | | | | 33.5 |
| | 7 | 19 | 8.8 | 16.4 | 22.8 | 27.0 | 29,8 | 32.0 | 33.8 | | | | | | | | 34.2 |
| | 8 | 34 | 9.7 | 17.6 | 23.3 | 27.6 | 30.3 | 32.5 | 34.0 | 35.0 | | | | | | | 35.3 |
| | 9 | 44 | 9.3 | 17.4 | 23.2 | 27.2 | 29.9 | 31.8 | 33.5 | 34.7 | 35.5 | | | | | | 35.8 |
| | 10 | 47 | 9.3 | 17.1 | 23.0 | 26.9 | 29.7 | 31.5 | 33.0 | 34.2 | 35.2 | 36.0 | | | | | 36.2 |
| | 11 | 20 | 8.1 | 15.6 | 21.0 | 25.4 | 28.3 | 30.6 | 32.2 | 33.5 | 34.6 | 35.6 | 36.2 | | | | 36.5 |
| | 12 | 8 | 8.4 | 15.9 | 21.7 | 25.8 | 28.1 | 30.3 | 31.8 | 33.0 | 33.8 | 34.6 | 35.3 | 35.8 | | | 36.1 |
| | 13 | 8 | 9.3 | 16.5 | 21.6 | 25.9 | 28.7 | 30.5 | 31.8 | 33.0 | 33.9 | 34.7 | 35.4 | 36.1 | 36.7 | | 36.9 |
| | 14 | 10 | 8.7 | 15.1 | 20.4 | 24.5 | 27.3 | 29.7 | 31.2 | 32.3 | 33.2 | 34.0 | 34.8 | 35.6 | 36.2 | 36.7 | 36.9 |
| | Total | 280 | **9.6** | **17.6** | **23.6** | **27.5** | **29.8** | **31.6** | **33.1** | **34.2** | **34.9** | **35.5** | **35.6** | **35.8** | **36.4** | **36.7** | |

b) The phenomenon observed in Collection No. 6 is not so evident in this collection. It is, however, always possible that years of good or bad growth may be a factor in obscuring such a result.

c) The point noticed under c) in Collection 6 is again to be found here. The average of the 4 group in September is greater than the calculated length at the end of the fifth winter, and so on all through the series — the average length of any given group is greater than calculated average lengths at the end of the succeeding winters.

*Collection No. 14.* This includes 755 herring taken in July 1908, and in it age groups from 1 to 5 are found.

The calculated lengths, $l_1$ decrease from 9.5 cm in the first years group to 6.3 cm in the fifth, and $l_2$ from 13.3 cm in the second year to 11.7 cm in the fifth, and similarly in $l_3$ and $l_4$.

b) In this case also the greatest change in any value for any year length between one age group and the next groups older occurs in the age group next to the one which this year length represents.

c) This sample was obtained in July when the fish would not have completed their year's growth. The average values obtained empirically for each group are thus intermediate in value between the calculated value of the last winter ring in that group, and that in the next, and have not yet attained a value which exceeds the winter growth of the next group.

In this series there have also been calculated the average value of $l_1$, $l_2$, $l_3$, etc, for all fish which show the corresponding number of rings on the scales. These figures may be assumed to give the general average for the whole series, of the lengths at the formation of each winter ring. The differences between these give, as the annual growths in the second, third and fourth year respectively, 5.2, 4.3 and 2.9, while on the other hand, the differences in the average lengths of succeeding groups are 3.8, 3.6 and 3.0 cm respectively.

*Collection No. 12.* This collection of 108 fish caught in February 1908, is an important sample, as the scales at this time of the year would show practically no »summer« growth, and the average length for each group coincides fairly nearly with the length at the end of the last winter of that group. The decrease in the values in each column is found from $l_2$ onwards in age groups 4 to 10 with a few minor exceptions. The phenomenon under (b) is not so noticeable in this case.

A comparison of the average length of each group, in this case taken at the end of the year's growth, with, the average calculated values at the end of each corresponding winter based on measurements of scales from all the fish examined, show considerable discrepancies, the empirical values being higher than the calculated from the 4th to the 8th year of age.

e) One other point arises out of these figures. Taking the averages above the horizontal line in the table, it will be seen that in some the lowest values in any column are less than the highest of the preceding column, or that in an older year group the value at the end of a given winter ring is less than the value attained to by the earliest year group for the previous winter ring. Thus $l_5$ in group 9 is 28.3 cm while $l_4$ in group 4 is 29.0 cm. This is not an invariable result, but will be found in an even more marked manner in Collection 9.

*Collection 15.* In this sample practically all the foregoing points are illustrated, viz., the decrease in the calculated lengths for any winter ring with increasing age, the greatest diminuition occurring in the first 2 or 3 years for each column.

## The Phenomenon of Apparent Change in Growth Rate.

Certain very important facts have been derived from a study of these tables.

These facts take the form of a tendency by which with increasing age the groups of fish all show a decreasing rate of growth in the calculated values for *each* year of their lives, that is that as we compare the present with former years the amount of growth at corresponding ages is increasing regularly. For convenience and shortness this tendency will be referred to in this paper as »the phenomenon of apparent change in growth rate«.

This must not be confused with the ordinary law of decrease of growth which is found in so many organisms, viz. that additional length increments decrease with advancing age. In this discussion we an dealing, not with the same organism at different ages, but with different age groups of organisms taken at the same time, and we are comparing, not the growth as the organism gets older, which as a rule naturally decreases, but the growth at *corresponding* periods of life fish born at different times. The *apparent* result from these calculated values is that the growth rate is increasing constantly up to the present time.

It follows from what has been discussed above that some limitations must be observed in employing the method.

*Firstly*, it is obvious that *no single year class* of herrings can by themselves give correct values for the average length at the formation of each winter ring, for no two year classes agree in this point and *all the older fish give lower values in turn than the younger ones.*

A more general result could be expected to be given by employing, not one, but all the year classes, and taking the averages of the ascertained values, as has been done in collections 12, 14 and 15.

To test the validity of this conclusion, it will be necessary to compare these derived values with those obtained empirically from average measures of fish in each age group. A close correspondence between these two series of figures would argue well for the reliability of the method.

Unfortunately, as it has been pointed out above, there is not such close correspondence as would be desired, for not only do the average lengths of an age group exceed the average length of all the fish at the formation of the corresponding winter ring, but also it often exceeds the length at the formation of the next year's winter ring — thus, *calculated and empiric values do not agree.*

*Secondly*, the complications introduced by the presence of these varying growth rates will render more difficult the task of ascribing with any certainty growth differences in several years to variations in physical conditions.

## Conclusions from Phenomenon of Apparent Change and Possible Explanations.

This raises a very serious point which requires a good deal of further investigation. Before accepting the apparent law as a real fact, namely that the growth rate of the herrings at each period of their lives is actually increasing as times goes on, which in itself to very doubtful, it will be necessary to enquire what other possible explanations might be offered to account for the observed phenomenon of changed growth rate in different year groups. Let us examine for the moment the conclusions to which we are forced if we assume that the »calculated values« for the length at the formation of any winter ring are the best to take, on the grounds that they contain all individuals of the samples rather than only the age group which gives the average value for any year. It has been observed that the average lengths of groups tend to be in nearly all cases higher than the »calculated« lengths — (the greatest difference occurring in the first few year groups of the sample). This suggests that these age groups are not really representative, but consist only of the larger individuals of each group, and for this reason they are not adequate to give the average length of the groups, and, in consequence, neither can the amount of growth be determined by taking the difference between the average lengths of succeeding age groups. The fact that these increments are shown to differ considerably from the derived increments $t_1$, $t_2$, $t_3$, etc., throws grave doubt on the method of determining average growths from the differences in the lengths of age groups alone. It is as if, out of the whole sample, the youngest year groups were represented only by their biggest individuals, and as we proceed towards the older groups, more and more of those which *had been* the smaller individuals in their earliest years appear — so that the average sizes of these older groups tend to show a less increment of growth and a levelling up in the values attained. To put this in a more lucid form, I can give a hypothetical example. Of the 1 and 2 group, only the largest individuals appear in the shoal. The three group would consist of those that had been the largest individuals of the 2 group of the year before, together with some of the medium ones of that group; the four group would then consist of the largest individuals of that year's growth, together with some that attained a medium size in their third year, and others that had been small in their second and first year, — and so on, each group adding individuals of the previous year groups which had not attained to a certain size in those years.

Now it is to be understood that this is only a hypothesis. It is yet to be determined whether it is even a working hypothesis or whether we cannot find some other explanations of the phenomenon, which might well occur, and give the same results.

The above is the explanation offered by the Norwegian investigators themselves *), or to quote their own words, there is a rule for herring that »Whenever a year group of herrings makes its entrance into a new phase of life, then the change is generally undertaken earlier by the larger animals in the group than by the smaller, e. g., the larger animals become fully mature before the smaller ones, and they will leave them and congregate with the older spawners, — or at the stage of passing over from the winter's stagnation to the summer's growth, the larger animals begin their summer's growth earlier than the smaller ones. Also in death, the larger ones go first« **).

*) In a private memorandum by Mr. Einar Lea.

**) In order to support this explanation, Lea puts forward some observations for the purpose of showing the selective action of the sexual maturation on a given Year-group of Norwegian herrings. The following Table is qutoed

This explanation may be termed the »Selective effect. of size«, and Lea assumes it to be a *natural* phenomenon. This is probably the case within certain limits, but whether it is so or not, it is at once obvious that if the year classes are only represented in a shoal by certain *selected* individuals, then it is impossible, from these data alone, to arrive at a true estimate of the actual growth rate, and if it can be assumed to be inherent not only in the case of herrings but also of other species as well, it follows that all estimates of the growth rates of certain species of fish which have been already determined by the method of taking the average lengths of distinct year groups must be to some extent accepted with reserve.

There is another factor which might make the selective action on the lengths of herrings an artificial rather than a natural quality. In the case of herring, the selection might arise from the action of the drift nets which cannot catch fish below a certain size, as these would slip through the mesh, or above a certain size as these cannot be caught — the net is arranged to catch a typical size of herrings with a certain deviation on each side of this modal size. The effect is to retain only the larger fish of the youngest age group, the smaller ones escaping through the net, and to exclude the largest fish of the oldest year groups.

Such an artificial selective action of the nets would have the same effect on the size distribution as the natural selection assumed for the herring by EINAR LEA, and may even occur simultaneously. We might consider at this point what other explanations could be offered to account for the phenomena observed.

We have considered selection as a cause and this is one that lies in the nature of the fish themselves. There are others which might be offered, but which, however, have very little to commend them. One is simply that the recorded calculated growths are real, and are actually increasing from year to year, and that for instance all the fish that are now five years old did

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from his memorandum. It demonstrates the great difference in size of the equally old mature and immature Norwegian herrings. All herrings were caught in small-meshed seines which exclude the possibility of artificial selection in this case.

Table showing the average length of year-class 1904 among the Norwegian herrings in different years, in samples of mature herrings (caught in the Spring) and in samples of immature herrings (caught in the Autum).

| Year of Capture | Mature herrings. | Immature herrings. |
|---|---|---|
| 1907 | 25.0 cm | 22.5 cm |
| 1908 | 29.0 - | 24.1 - |
| 1909 | 29.1 - | 26.2 - |
| 1910 | 28.3 - | 27.6 - |

really grow less in their second year than the fish of the third, fourth and second year groups, not because they were selected fish of their own years brood but because the power of growing, or the conditions of growth are improving. But if this were the case we should have to assume unnatural growth conditions, for in nature variatious would occur in a more haphazard fashion than that of increasing each year.

The fact that good and bad years of growth do occur, as has been demonstrated by the Danish and English investigations on the growth of marked fish is, however, a factor which must be definitely reckoned with in accounting for checks or breaks in the regular change demonstrated. Indeed it is such years which the method should be valuable in defining.

Another reason which might help to account for it would be perhaps a varying proportion of male and female fish in the year groups, which have different growth rates. This point has not been investigated in the case of the herring samples already quoted, but will be shown to be insufficient to cause the observed difference in the case of our second sample of haddock, where the sexes are distinguished, and that, in fact, the law is to be observed within a single sex group.

Leaving for a moment the above explanations of the phenomenon which are founded on the growth of the fish, it is evident that the phenomenon could equally well be explanied by peculiarities in the nature of the growth of the scale from which the calculated lengths are derived. It is quite conceivable that the scale adds an increment each year in due proportion to the length of the fish, but that when more additions are made to the scale matter, that which has previously been formed, especially the newest part, may somewhat contract or be pressed inwards by the outside matter. Contraction would tend to make the scale thicker in the centre, and certainly older scales are much thicker than younger ones, but until more is known of the actual growth and texture of the scales, we are not justified in assuming that contraction rather than any other cause, such as the laying of the scale down in plates for each ring, is the source of this thickening.

It is even possible that part of the scale may be absorbed in the maturation of the sexual organs, as is known to occur in Salmon.

The evidence for these hypotheses will be discussed in the following section on haddock scales, where the actual increments of the scale growth in each year have been determined.

The impression has been distinctly felt in working at a very large number of haddock scales that the inner rings in an older scale were appreciably smaller than the corresponding rings in the scale from a younger fish, and at the same time one had the feeling that in the old fish the last, for instance the sixth or seventh ring was even larger and of a looser texture than the one immediately preceding, and it was easy to imagine from this that the previous ring had really been larger in the year preceding, and had somehow shrunk slightly as soon as more scale matter had been added. Direct observation on the scales of fishes kept in tanks over a period of years work go far towards settling this point.

One other possible explanation occurs and this drives at the root of all age determination from scales. It is that the fish may have the power of occasionally putting on more than one ring during the year, so that it would apparently seem older than it really is before it has reached the length proper to fish of its apparent age. Naturally, if such fish are included in an older year group, the average size of that group is lessened, and as such adventitious rings would be more numerous in older fish, the result that in each year the growth rate is rapidly diminished would at once follow.

I know of no evidence that such may happen in herring scales, but in the case of haddock, the most recent information points to the conclusion that in a certain percentage of the fish a secondary ring is very probably formed in the autumn.

## Measurements of Haddock Scales.

We now turn our attention to haddock in order to gain further light on this important question. Two samples of haddock gave scales which were examined in precisely the same way as the herring scales by the method evolved by the Norwegian investigators. They proved all the more valuable in that it was possible to examine the details of the actual measurements of the scales as well as the derived values or calculated lengths on the formation of each winter ring.

The first sample consisted of scales taken from haddock landed at Grimsby on November 14th, 1910, from the Great Fisher Bank, and comprised three boxes of large, medium and small fish respectively, totalling altogether 384 specimens.

The scales were first examined for age, each year group being kept distinct. In this sample 5 scales were selected at random from each fish, and each measured by the image of a micrometer scale which had been previously magnified to the same power as that to which the fish scales were being enlarged. All examinations and measurements were made on Leitz's Projecting apparatus. Measurements were taken from the natural centre along the maximum radius at the broad end of the scale, the whole length being $V$ and those to the periphery of each winter ring being $v_1$, $v_2$ etc. The average of these values for the 5 scales was taken for each fish. The calculated lengths from the formula $l_1 = L\frac{V_1}{V}$ were also determined, and the ratio $\frac{L}{V}$ for each size group. The results were averaged for all fish of the same centimetre size in the same age group and for the whole age group.

Selecting from these results the figures which have most bearing on the matter under discussion, the following table (table 2) of average calculated lengths of haddock at the formation of each winter ring is obtained. After this it will be possible to see the effect of the actual scale measurements on these calculated values.

## Phenomen of Change of Growth Rate prevalent in case of Haddock.

Very striking is the evidence of the presence in this table of haddock of the same kind of phenomena as were shown for herring.

Firstly, the calculated lengths at the end of each winter show a progressive decrease from the second to the fifth age group and the decrease is very considerable.

$l_1$ varies from 18.3 cm in the II group to 15.1 cm in the 5 group, while $l_3$ varies even more, from 40.4 cm in the III group to 30.7 cm in the V group. The average length of $l_4$ in the V group is less than that of $l_3$ in the III group.

As there is not nearly such a large range of years in this case as in the herring (VI and VII should be left out of account) it does not become so evident that the biggest decrease in any particular length is found in the first few year groups where this year length occurs. However, this point becomes much more distinct in the case of the corresponding lengths and increments of the scale.

## Discrepancies between Empiric and Calculated values.

Another important fact is that the average size of each year group does not correspond very closely with the average calculated length at the formation of the corresponding winter ring based on all the fish examined. They should be expected to correspond very nearly, as in this sample the great number had just completed their last winter ring and some had commenced a little broad growth. It is found that the average length of the second, third and fourth group are 2.1, 3.9 and 4.4 cm, respectively, larger than the corresponding lengths at the end of the winter's growth. Neither do the yearly differences in growth agree too well. We have 10.7, 4.5 and 2.5 cm the increments of the average sizes in the third, fourth and fifth years against 8.9, 4.0 and 2.9 cm in the calculated lengths.

Thus it has been completely demonstrated that the case for haddock is precisely similar to that for herring.

**Table 2** showing the average calculated lengths at the formation of each winter ring, in a sample of haddock taken from the Great Fisher Bank on November 14th, 1910.

| Year Class | Number of fish | $l_1$ | $l_2$ | $l_3$ | $l_4$ | $l_5$ | $l_6$ | $l_7$ | Average length of Group |
|---|---|---|---|---|---|---|---|---|---|
| II | 247 | 18.3 | 29.4 | | | | | | 31.2 |
| III | 87 | 17.6 | 30.4 | 40.4 | | | | | 41.9 |
| IV | 33 | 16.6 | 26.7 | 35.8 | 44.3 | | | | 46.4 |
| V | 13 | 15.1 | 22.9 | 30.7 | 38.1 | 46.1 | | | 48.9 |
| VI | 2 | 15.0 | 21.2 | 27.3 | 32.0 | 36.6 | 41.2 | | 44.5 |
| VII | 2 | 15.9 | 21.9 | 30.5 | 38.6 | 45.0 | 51.6 | 58.0 | 58.0 |
| Average | 384 | **17.9** | **29.1** | **38.0** | **42.0** | **44.9** | **46.4** | **58.0** | |

## Scale lengths and Scale increments.

The following table (3) has been drawn up to show the actual average length in millimetres of the rings on the scale for each age group. At the same time the factor $\frac{L}{V}$ or the average ratio of the length of the fish to the length of the scale is given to show how in each period of life this factor is fairly constant.

From this table one learns that the lengths of the scale occur in a manner strictly analogous to those of the fish in corresponding periods and age groups. Firstly, the scale length (V) increases with each age group, the growth increments showing that the average amount added becomes less in each succeding year with a *very rapid rate of decrease*. Secondly, there is a slight tendency,

**Table 3.** Average Scale lengths in millimetres in each group.

| Year Class | Number of fish | V | $\frac{L}{V}$ | $V_1$ | $V_2$ | $V_3$ | $V_4$ | $V_5$ | Growth |
|---|---|---|---|---|---|---|---|---|---|
| II | 247 | 1.79 | 178 | 1.05 | 1.68 | | | | |
| III | 87 | 2.38 | 180 | 0.99 | 1.72 | 2.28 | | | 0.59 |
| IV | 33 | 2.74 | 171 | 0.98 | 1.58 | 2.11 | 2.62 | | 0.36 |
| V | 13 | 2.88 | 173 | 0.89 | 1.34 | 1.81 | 2.24 | 2.71 | 0.14 |

obscured to some extent by natural irregularities, for the length of the scale to become greater in proportion to the length of the fish $\left(\frac{L}{V}\right)$ in the older groups. This too might be accounted for in several ways. Either the scale does grow more in proportion to the length of the fish, or there may even be a selection or survival of the fish with the larger scales.

Mr. EINAR LEA has gone very thoroughly into this question in the case of herring scales, and has even adopted a correction, which does not, however, very vitally affect either the results or the method. A moment's reflection convinces one that if this small error does introduce an error into the results of the calculated lengths, it will not be of such a nature as to produce the phenomenon we have spoken of as the apparent change of growth in the succeeding years of life*— for if the high ratio is produced because the scale length is relatively small, then the length of the year rings will also be relatively small. On the contrary, it is found that the year rings are relatively larger in these early year groups.

A constant steady decrease in each succeeding age-group is found for the quantities $V_1$, $V_2$, $V_3$, etc. which represent the amount in length of the scale in each year of growth. If we assume that the ratio of the scale length to length of fish is approximately constant, then it is the change in these quantities $V_1$, $V_2$, $V_3$, etc. with the years, which produces the yearly change in the calculated lengths $l_1$, $l_2$, $l_3$, etc., throughout the age groups.

We have thus ascertained the fact that in haddock, the length of the scale to the end of each winter ring decreases regularly from the youngest to the oldest year group sufficiently sampled. It is desirable to see whether the *increment* of growth produced by the scale in each years growth will also show the same phenomenon. The following table shows the average yearly increments in the scale length for each year group.

## Change in older year groups in all corresponding Scale Increments.

This table is of great importance because it shows, with one or two minor exceptions, that not only are the measurements of the corresponding year rings from the centre smaller in the older than in the younger groups, but also that the individual yearly increments of scale length are also less in every case. Therefore, when we compare groups, we find that the IV group has each year ring smaller than those of the II or III group, not only because it contains fish which had been too small to be caught in their first or second year, but also because the amount of growth shown in each individual year is actually less. Consequently the result is that the total length of the scale of the oldest group (V) is only slightly greater (by 0.09 mm) than the IV group, which in its turn is only a little greater, by 0.34 mm, than the III group, and so on. The point at issue is illustrated very clearly by diagram I.

**Table 4.** Average Scale Increments in each Year in millimetres.

| Year Class | Number of fish | 1st | 2nd | 3rd | 4th | 5th | Total | Differences |
|---|---|---|---|---|---|---|---|---|
| II | 147 | 1.05 | 0.63 | | | | 1.68 | 0.60 |
| III | 87 | 0.99 | 0.74 | 0.56 | | | 2.28 | 0.34 |
| IV | 33 | 0.98 | 0.60 | 0.53 | 0.51 | | 2.62 | 0.09 |
| V | 13 | 0.89 | 0.45 | 0.47 | 0.43 | 0.47 | 2.71 | |

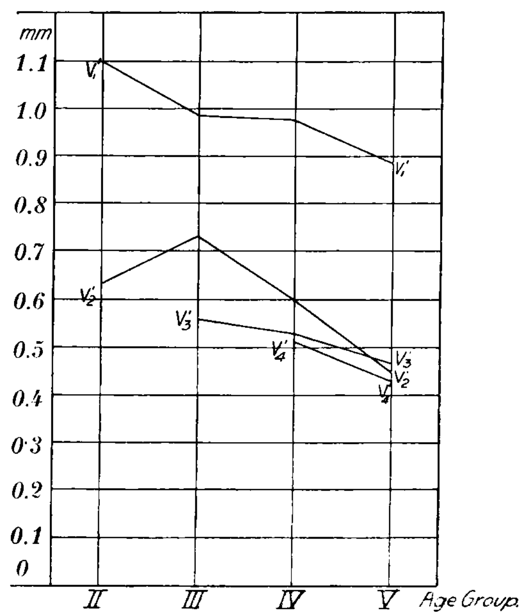


**Fig. 1.** Curves shoving the change with succeding age groups in the annual growth increments ($V'_1$, $V'_2$ etc.) of haddock scales. (Table 2.)

The *important point is that the difference in growth increment* between corresponding ages of successive age groups is not confined to the earliest years of life, but all year groups examined show it up to and for the last year ring. It follows that, if we accept selection as the explanation of the fact, that the change in growth rate is produced by the inclusion of more and more fish in the older groups which have been the smallest of their year group in their youngest ages, these same small fish must be of a slow growth rate all their lives, and have in them an inherent quality of slowness of growth.

This conclusion, which seems to follow from the assumption, is one which I am not prepared to justify. It seems somewhat unlikely, if one regards the amount of growth of a fish in any year mainly as a function of the food and temperature. There seems no reason why, for instance, the fifth and fourth group, which may have lived together for one or two years, should show values of growth in their fourth and third years which differ always in the direction of lesser growth for the older fish.

The scale increments in the last year's growth in each age group are considerable, and as a rule exceed by a significiant quantity the differences in the annual length of the scales.

It is possible to estimate from these figures what the length of the scale would be if neither shrinkage of the scale nor selection of the fish has taken place. In the 2nd year the scale reaches a length of 1.68 mm. In the 3rd year an increment of 0.56 mm, is added: in the fourth an increment of 0.51 mm, and in the fifth year an increment of 0.47 mm, making a total growth of 3,22 mm, which is 19 per cent greater than the value really reached by the fifth group. Now, while the rate of growth does appear to diminish with advancing age, it does not at all seem to be so rapid a diminution as the differences in scale lengths in each age group would seem to indicate. It is impossible to obtain the amount of scale growth in a given year group by simply subtracting the average length of the scale in the previous year group from the length in the given year.

It seems very possible that this effect might be produced by some sort of compression or contraction taking place, and that any yearly ring becomes smaller as soon as the free edge is covered up by succeeding rings superimposed upon it. It appears in some samples where a large number of years are represented, that the effect ceases to be shown in the earliest year rings after a few years have passed since their formation, but the effect is more apparent in the rings nearest the final ring of the scale. Scales are naturally *slightly* elastic, as can be easily tested by measuring them before and after pulling them out of shape, and we may, by virtue of this fact, assume them to be also slightly compressible.

## Investigation for Sex Differences.

A second series of haddock scales was measured, and in this case the sex was generally distinguished. The fish were caught in a haul of one of the Mission Vessels on February 13th, 1911. The results of measurements of the fish and the scales from 178 male, 241 female and 31 whose sex was undistinguished, are given in Table 5. The scales were at the stage of passing over from their winter to the summer growth — some seemed to have quite completed their narrow ring; others to have slight beginnings of the broad ring — all scales with the same number of narrow rings, or so-called winter growth, were classed together.

Several points of interest appear in this sample, and although they have no direct bearing on the question at issue, yet are worth mentioning from the point of view of corroborating or adding to other investigations. In considering the *age distribution*, it is found that the II and III group are the most predominant, and the numbers decrease rapidly in the successive age groups. In the seventh group there is a check in this rapid decline, for there is actually a greater number in the older year group. Now, the fish that were just, or nearly, seven years old would have been born in 1904, and former researches have shown that this was a year of exceptional abundance of newly spawned fish, which was manifested in the enormous quantities of small haddock taken in 1906 and at the end of 1905: that such a predominance of one year group should still be evident after the elapse of so many years is remarkable, and tends to confirm in some degree the hypothesis that the rings are usually annual.

In the distribution of the sexes, the females are the more numerous, especially in groups II, III and IV.

After the fish are four years old, the females show a greater variation in size in each age group than the males. The female fish are very slightly larger than males of corresponding age. The II group is an exception, for in this they are smaller by one centimetre, but in all probability this group is not really representative, as the smaller ones may easily escape capture.

With regard to the growth of the scale, table 5 shows the changes in the calculated lengths to be the same as those already demonstrated for other samples, and this is not only for the whole year class, but also for the males and females separately

**Table 5. Average Measurements of Haddock Scales in millimetres from 7.30 a. m. haul. 13.2.11. Fish of same winter growth combined.**

| No. of fish | Age | Range of size cm | Average size of fish cm | $V_1$ | $V_2$ | $V_3$ | $V_4$ | $V_5$ | $V_6$ | $V_7$ | $V_8$ | $V_1-V_0$ | $V_2-V_1$ | $V_3-V_2$ | $V_4-V_3$ | $V_5-V_4$ | $V_6-V_5$ | $V_7-V_6$ | $V_8-V_7$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Females** | | | | | | | | | | | | | | | | | | | |
| 32 | II | 27—33 | 30.9 | 1.12 | 1.84 | | | | | | | 1.12 | 0.72 | | | | | | |
| 123 | III | 27—45 | 38.2 | 1.07 | 1.75 | 2.33 | | | | | | 1.07 | 0.68 | 0.58 | | | | | |
| 43 | IV | 35—48 | 42.6 | 1.06 | 1.65 | 2.17 | 2.58 | | | | | 1.06 | 0.59 | 0.52 | 0.41 | | | | |
| 14 | V | 37—54 | 45.1 | 0.94 | 1.44 | 1.96 | 2.37 | 2.84 | | | | 0.94 | 0.50 | 0.52 | 0.41 | 0.47 | | | |
| 13 | VI | 39—57 | 48.7 | 0.99 | 1.43 | 1.82 | 2.20 | 2.49 | 2.92 | | | 0.99 | 0.44 | 0.39 | 0.38 | 0.29 | 0.43 | | |
| 16 | VII | 40—66 | 52.1 | 1.01 | 1.44 | 1.88 | 2.28 | 2.58 | 2.93 | 3.30 | | 1.01 | 0.43 | 0.44 | 0.40 | 0.30 | 0.35 | 0.37 | |
| **Males** | | | | | | | | | | | | | | | | | | | |
| 34 | II | 29—36 | 31.9 | 1.09 | 1.86 | | | | | | | 1.09 | 0.77 | | | | | | |
| 73 | III | 29—45 | 37.3 | 1.04 | 1.70 | 2.21 | | | | | | 1.04 | 0.66 | 0.51 | | | | | |
| 28 | IV | 30—49 | 41.1 | 0.89 | 1.53 | 2.05 | 2.50 | | | | | 0.89 | 0.64 | 0.52 | 0.45 | | | | |
| 15 | V | 40 - 51 | 45.5 | 1.04 | 1.51 | 2.00 | 2.46 | 2.82 | | | | 1.04 | 0.47 | 0.49 | 0.46 | 0.36 | | | |
| 11 | VI | 42—50 | 44.4 | 1.04 | 1.50 | 1.88 | 2.10 | 2.56 | 2.88 | | | 1.04 | 0.46 | 0.38 | 0.22 | 0.46 | 0.32 | | |
| 16 | VII | 44—56 | 50.4 | 0.96 | 1.43 | 1.80 | 2.22 | 2.56 | 2.87 | 3.12 | | 0.96 | 0.47 | 0.37 | 0.42 | 0.34 | 0.31 | 0.25 | |
| 1 | VIII | 49 | 49 | 0.70 | 1.00 | 1.40 | 1.88 | 2.20 | 2.60 | 2.80 | 3.30 | 0.70 | 0.30 | 0.40 | 0.48 | 0.32 | 0.40 | 0.20 | 0.50 |
| 178 | | | | | | | | | | | | | | | | | | | |
| **Sex undistinguished** | | | | | | | | | | | | | | | | | | | |
| 18 | II | 25—33 | 30.1 | 1.08 | 1.81 | | | | | | | 1.08 | 0.73 | | | | | | |
| 9 | III | 27—40 | 32.7 | 0.86 | 1.37 | 1.95 | | | | | | 0.96 | 0.51 | 0.58 | | | | | |
| 4 | IV | 29—40 | 32.8 | 0.96 | 1.45 | 1.74 | 1.99 | | | | | 0.96 | 0.49 | 0.29 | 0.25 | | | | |
| **Sexes combined** | | | | | | | | | | | | | | | | | | | |
| 84 | II | 25—36 | 31.1 | 1.10 | 1.84 | | | | | | | 1.10 | 0.74 | | | | | | |
| 205 | III | 27—45 | 37.6 | 1.05 | 1.71 | 2.27 | | | | | | 1.05 | 0.66 | 0.56 | | | | | |
| 75 | IV | 29—49 | 41.5 | 0.99 | 1.59 | 2,10 | 2.52 | | | | | 0.99 | 0.60 | 0.51 | 0.42 | | | | |
| 29 | V | 37- 51 | 45.3 | 0.94 | 1.47 | 1.98 | 2.41 | 2.82 | | | | 0,94 | 0.53 | 0.51 | 0.43 | 0.41 | | | |
| 24 | VI | 39—57 | 46.7 | 1.01 | 1.46 | 1.85 | 2.15 | 2.52 | 2.90 | | | 1,01 | 0.45 | 0,39 | 0.30 | 0.37 | 0.38 | | |
| 32 | VII | 40—66 | 51.3 | 0.99 | 1.44 | 1.84 | 2.25 | 2.57 | 2.90 | 3.21 | | 0,99 | 0.45 | 0.40 | 0.41 | 0.32 | 0.33 | 0.31 | |
| 1 | VIII | 49 | 49.0 | 0.70 | 1.00 | 1.40 | 1.88 | 2.20 | 2.60 | 2.80 | 3.30 | 0.70 | 0.30 | 0.40 | 0.48 | 0.32 | 0.40 | 0.20 | 0.50 |

in each year class. This is demonstrated by Fig. 2 which shows for each annual ring the average amount added in each age group, and how this declines rapidly in the older age groups. We see in each case that the scale increases in length with each succeding age group, but at a rapidly decreasing rate of growth. The total increment in length added in the first year is 1.1 mm, while that in the 7th group is less than 0.1 mm. This rapid decrease is caused, as in other cases, by each age group showing successively a less amount of growth to the end of each winter ring, i. e. the rate of growth is increased in fish born later and the figures under the columns showing the scale increments such as $V_4$—$V_3$ do also become continuously less between the 2nd and the 7th group. Roughly speaking, the biggest decrease in any year's increment occurs during the first three years after its formation. Some exceptions are found to this rule and are probably to be accounted for as the effect of exceptional growth years.

This example may be taken as further evidence of the prevalence of the rule which we have called the Phenomenon of apparent Change of growth rate, but as it stands it offers no support to any theory of the cause of the phenomenon. We do not know whether selective action is sufficient to explain all the observed differences in the growth in the corresponding years of different year groups, or whether it is the result of a shrinking or contraction of the interior portion for the purpose of strengthening and thickening the scale as it becomes larger. It may be conjectured that after a time no further shrinkage can take place, and the inner rings do not show so much decrease, but the new matter superimposed has more effect in causing contraction and thickening in that part of the scale somewhat nearer the edge. Whatever may be the reason, the differences are sufficient to cause the lengths calculated to the end of each winter ring to show serious differences in the various groups.

The actual increments of scale length added in each group as the last year ring are 1.10, 0.74, 0.56, 0.42, 0.41, 0 38 and 0.31 mm, making a total of 3.92 mm at the end of the 7th year — the total length of whose scale is 3.21 mm, the difference amounting to 22 per cent: in the case of the males it is 20 per cent, in that of the females 24 per cent.

It thus appears that the scales of the oldest fish are about one-fifth less in length than they would have been if the had grown at the rate indicated by scales of younger groups.

There are slight sexual differences in the growth of the scale. Corresponding to the higher average size of the female fish in each group, the scales of this sex are also slightly larger.

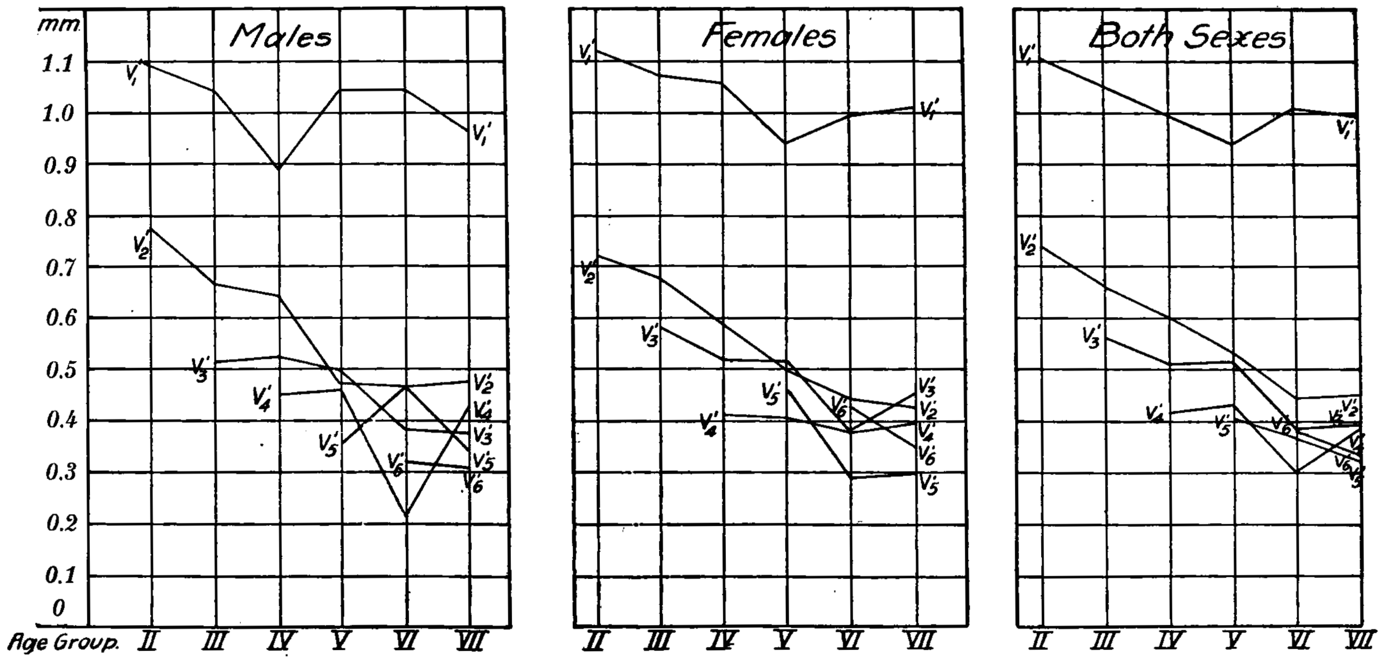


Fig. 2. Curves showing the change in succeding age Groups in the annual growth increments ($V'_1$, $V'_2$ etc.) of haddocks scales (Table 3).

Consider for a moment the sequence of the scale increments from the centre outwards in each age group, as shown by the values in each row of the table. The general rule is for these to decrease with each succeeding increment according to the normal law of decrease of growth rate with age, but towards the end of each line the decrease is not so rapid, and it sometimes happens, as in the case of groups V, VI and VII of the females, and of VIII of the males, that the last increment which is at the free edge is greater than that immediately preceding. This fact gives some support to the idea that when new scale matter is formed on the free edge in the succeeding year, this last ring tends to contract.

## Measurement of Trout Scales.

The next species to be discussed with respect to this feature is trout (*Salmo fario*), and this has its own very peculiar interests and difficulties. Firstly, the trout dealt with have lived only in rivers or lakes under conditions very different and probably far more variable than those which affect the fish of the open sea, such as herring and haddock, and further, they have been caught by very different methods, by nets, by fly and spinner. If it should appear that the same rules of change of growth are to be found under these very different conditions, it will seem to be the effect of something inherent in either the growth of the fish or its scales, rather than altogether the selective action of nets as they fish in the sea. The case is all the more interesting and important for the reason that the Norwegian investigators have further developed the methods they had originated for the herring scales, and have definitely tried to show that the »calculations based on this method of examination will enable them to draw up a growth curve as reliable as one obtained by ordinary methods of analysis of age and size, and that they can accordingly arrive at sound conclusions as to the rapidity of growth by the examination of comparatively few individual specimens«*).

The material discussed here is taken from tables given in a Report on The Age of Growth of Salmon and Trout in Norway, by Knut Dahl, the English translation of which is published by the Salmon and Trout Association. A very large number of calculations of the lengths at the formation of each winter ring are given in tables at the end of the volume, and extracts and deductions from these for the growth of trout in certain waters

*) Dahl. Age and growth of Salmon and Trout in Norway pp. 24 and 29.

appear in Table 6 of this paper. I have included all the material except those which contained so few fish that no definite law could be shown. This is a difficulty throughout several of the samples, viz., that although several years groups are represented in the catch, yet some of the older groups consist of so few fish that the values derived from their scales show irregularities rather than a definite sequence. For this reason they cannot be compared as individual year groups.

Dahl has attempted to show*) a) that there is a close agreement between his calculated values and the empiric curve derived from a classification of age according to size in the case of Trout from the River Chaigijok (Table XXXV b), and b) by dividing his sample into groups of increasing sizes of fish (Table on p. 27) he finds a remarkably close correspondence in these groups for the values to the end of each winter ring. In looking at this table and at that on the next page of his report, there does not appear to be much indication of the apparent change of growth in calculated lengths such as has been found for the species caught in the sea. He, therefore, thinks that he is justified in basing his calculations for a growth curve on a small sample of this material selected at random.

After my experience of the prevalence of the apparent change of growth rate in herring and haddock, this result was somewhat unexpected, but the cause was soon apparent from the fact that his groups of fish are based on size distinctions and not on year of birth. In fact, all of his size groups contain fish of 2, 3 or 4 different years, and this fact alone is sufficient to mask any age differences that may occur.

To show this, I have recast his figures and classified together from his detailed tables all fish of the same year group. The results are given in Table 6.

**Table 6.** Calculated lengths of Trout on the Completion of each Winter Ring, from Table XXII B. Kvern-vand Nærø, July 6, 1909. (Fly).

| No. of fish | Age | Calculated lengths at end of winter band | | | | | Average length of group in July |
|---|---|---|---|---|---|---|---|
| | | 1st | 2nd | 3rd | 4th | 5th | |
| 27 | 2 | 6.0 | 15.6 | | | | 19.1 |
| 46 | 3 | 5.1 | 13.4 | 20.3 | | | 22.5 |
| 19 | 4 | 5.7 | 13.7 | 19.8 | 24.4 | | 25.6 |
| 3 | 5 | 5.7 | 11.3 | 20.2 | 25.1 | 28.9 | 30.3 |

*) See pages 26 and 27, loc. cit.

**Table 6.** (Continued). Calculated Average Lengths from Table XXIII B. (Fly).

| No. of fish | Age | Calculated lengths at formation of winter band | | | | | Average length of group in July |
|---|---|---|---|---|---|---|---|
| | | 1st | 2nd | 3rd | 4th | 5th | |
| 13 | 1 | 7.7 | | | | | 13.6 |
| 39 | 2 | 6.1 | 14.9 | | | | 19.3 |
| 3 | 3 | 6.0 | 13.9 | 19.6 | | | 22.3 |
| 5 | 4 | 6.3 | 15.5 | 20.2 | 23.9 | | 25.8 |
| 2 | 5 | 6.2 | 14.6 | 20.6 | 26.1 | 29.2 | 30.5 |
| 62 | Average | **6.3** | **14.9** | **20.1** | **24.5** | **29.2** | |

Calculated average lengths at formation of winter bands. Table XXXIV B. (Fly, spinner, long line).

| Number of fish | Age | 1st | 2nd | 3rd | 4th | 5th | 6th | 7th | 8th | 9th | 10th | 11th | Average length of group in August |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 7 | 1 | 7.7 | | | | | | | | | | | 13.9 |
| 4 | 2 | 5.8 | 12.1 | | | | | | | | | | 15.5 |
| 8 | 3 | 5.5 | 9.7 | 15.3 | | | | | | | | | 20.6 |
| 23 | 4 | 5.1 | 9.0 | 13.7 | 21.8 | | | | | | | | 24.6 |
| 39 | 5 | 4.3 | 8.8 | 12.5 | 17.3 | 25.3 | | | | | | | 28.4 |
| 22 | 6 | 4.3 | 8.2 | 12.0 | 16.7 | 23.1 | 29.8 | | | | | | 32.2 |
| 5 | 7 | 4.4 | 8.2 | 11.2 | 15.5 | 20.8 | 28.7 | 32.3 | | | | | 34.6 |
| 2 | 8 | 4.1 | 7.7 | 11.5 | 18.4 | 25.4 | 31.3 | 38.6 | 39.4 | | | | 40.5 |
| 3 | 9 | 5.0 | 11 1 | 17.6 | 22.3 | 27.1 | 35.5 | 39.6 | 43.3 | 44.8 | | | 46.0 |
| 1 | 10 | 7.2 | 12.0 | 17.8 | 23.0 | 28.3 | 35.5 | 42.2 | 43.8 | 45.3 | 46.4 | | 47.0 |
| 1 | 11 | 7.2 | 10.6 | 15.6 | 18.7 | 28.3 | 32.5 | 36.9 | 39.8 | 42.1 | 45.5 | 48.2 | 49.0 |
| Average length | | **4.9** | **8.9** | **13 0** | **18.4** | **24.6** | **30.5** | **36.2** | **41.7** | **44.4** | **46.0** | **48.2** | |

Trout from Chaigijok. July 15—25th, 1909. Table XXXV b. (Fly).

| Number of fish | Age | 1st | 2nd | 3rd | 4th | 5th | 6th | 7th | 8th | Average length of group |
|---|---|---|---|---|---|---|---|---|---|---|
| 9 | 2 | 6.3 | 10.9 | | | | | | | 12.8 |
| 6 | 3 | 6.0 | 9.9 | 14.0 | | | | | | 15.5 |
| 34 | 4 | 4.6 | 9.2 | 13.1 | 16.1 | | | | | 17.4 |
| 34 | 5 | 4.7 | 9.3 | 13.2 | 16.5 | 18.7 | | | | 19.7 |
| 18 | 6 | 5.0 | 9.6 | 13.5 | 16.7 | 19.4 | 21.4 | | | 22.3 |
| 6 | 7 | 4.3 | 8.7 | 13.1 | 16.5· | 19.4 | 22.0 | 24.2 | | 25.0 |
| 2 | 8 | 5.3 | 10.4 | 14.0 | 16.1 | 18.4 | 20.5 | 22.6 | 24.2 | 25.0 |
| Average length | | **4.9** | **9.5** | **13.2** | **16.4** | **18.6** | **21.5** | **23.8** | **24.2** | |

## Prevalence of the Phenomenon of Apparent change in Growth Rate in Trout.

The first two of these tables are rather incomplete, but they show a distinct tendency for the apparent rate of growth to be increasing as the years go on i. e. for the lengths under each winter ring to decrease, at any rate between the first and second, and the second and third years of age, — after this the age groups are not adequately represented. In Table XXIII B we see that the average length of each group at the beginning of July tends to be nearer the average value of all fish calculated for the length at the end of the next winter, from which we must conclude that they have nearly completed their year's growth thus early, or that, which is more likely, one year group by itself represents a different rate of growth from that of the whole sample.

Table XXIV B is a much more complete sample, and from the first to the seventh year shows all the features that have been shown to occur repeatedly in the case of haddock and herring. The lst. year's growth shows a decrease in size from the lst. to the 5th year, and the 2nd year's growth from the 2nd to the 6th. The later values of lengths to the 3rd, 4th, 5th winter ring are less than the earlier values of the years preceeding. In some groups the average length in August is appreciably greater than the average calculated lengths at the end of the next winter based on all the observations. In this case it is apparent that the empiric and the calculated values for the growth in each year *do not agree.* The examples of fish over seven years old seem to be larger.

Dealing only with the first seven age groups, the following curves, fig. 3, illustrate the difference in the growth curves obtained by different methods.

The thick black line shows the average length of each group and the points are situated a little more than $^2/_3$ the interval between each two succeeding winters (for the reason that these fish were taken in August). The broken line represents the growth curve obtained by averaging up the calculated values to each winter ring of all the individuals measured, and the thin black lines are the same quantities for each year group. This is a most clear illustration of the phenomenon, for all the curves are different and give varying growth rates. The thin black lines for each age group show a distinct sequence of lower average lengths at each year of life, and agree with each other and the thick broken line of average calculated values in being convex to the axis of abscissae.

The thick black line of empiric values is of a different nature, having its ordinates on the whole greater than the corresponding ordinates of the »calculated« curve, and at the same time it is slightly concave to the axis. Most growth curves take a concave form, that is, the older groups add smaller increments in each year. There is something unnatural in the appearance of the »calculated« curves in showing as they do larger and larger growth increments in the later years. Of course, it may be quite possible that the

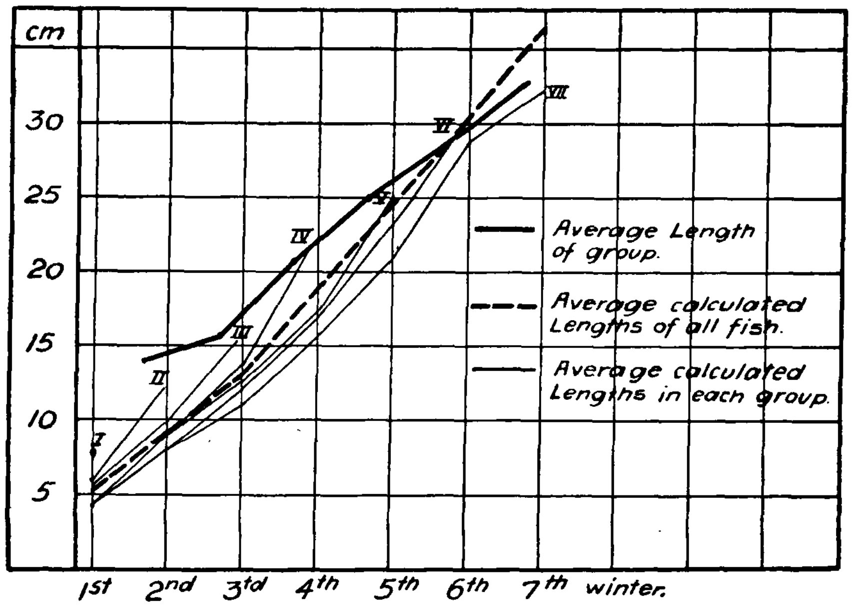


Fig. 3. Growth curves of Trout from Sannavand.
Aug. 1909.

growth increments are really fairly constant within a limited number of years, but in that case declining growth rates as shown by the thick black line and other similar growth curves are unnatural. The question that arises is which of these differing curves will give the best representation of the true growth rate.

Two other cases are left for our consideration. Table XXXV b. shows much the same features as the one fully discussed above, but in this case the decline is not so marked and steady, and in some years there are exceptions. The biggest decrease in any length occurs immediately after the formation of another year's growth. In this case, which is the one illustrated by Dr. Dahl in his text, there is more correspondence between the calculated and empiric values than was observed in the previous example. In both, the yearly increments in length tend to decrease with advancing age, but in the sample from Chaigijok it is shown only up to the first three or four winter rings.

## Prevalence of the Phenomenon in Trout that have Migrated.

Our last example is concerned with trout from Lillehammer (Table XXVII), and is of considerable complexity. All the fish at some period of their life have migrated, and the result has been a great impetus to their growth, which is clearly marked by much larger rings being formed on the scales. The values of length calculated from these show a sudden increase in the size and a rapid rate of growth which is maintained under these favourable conditions.

The calculated lengths to the end of each winter are given for each fish, and from these I have calculated the averages for each group, classifying the fish both according to the number of years before and after migration. The result is set forth in table 7. Although the total number of fish dealt with is 165, very few of the groups obtained in this double classification are really adequately represented, and this may partly explain a result which seems at first sight to contradict the experience of other series. Taking any group such as those that have spent four winters before migration, we find a series of fish of increasing age, not showing very definitely in the winters *after* migration a regular decrease in the lengths to the formation of the winter rings. There is also to be taken into account the fact that the conditions of life in the lake must have been very variable, and unless a large number of fish are present the natural variations are sufficient to mask the general law that may run through these figures. The same thing is seen when we consider the growth in the years before migration, none of the groups of fish which are all of the same age at migration show more than a slight tendency to this change. This may be also explained by the fact that as so many years have been added, the effect of selection or whatever may be the cause of the law it not felt so far back as these youngest year rings, and is has been shown in other samples that the change occurs in its greatest degree in the rings in the first few years after their formation, and when more years have been passed through, the effect is almost inappreciable in the earliest rings.

**Table 7.** Average in each age group of the calculated lengths at the formation of each winter band of Trout from Laagen—Lillehammer. June—September 1909. Table XXVII. c.

| Winters before | Winters after migration | Number of fish | Calculated lengths at formation of Winter band | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1st | 2nd | 3rd | 4th | 5th | 6th | 7th | 8th | 9th | 10th | 11th | 12th | 13th | 14th | 15th |
| 3 | 6 | 1 | 6.0 | 13.0 | 21.0 | 34.0 | 46.5 | 57.5 | 64.0 | 65.5 | 69.5 | | | | | | |
| | 7 | 1 | 6.5 | 14.0 | 18.0 | 28 0 | 38.0 | 50.5 | 62.0 | 71.0 | 72.0 | 75.5 | | | | | |
| | Average | 2 | **6.3** | **13.5** | **19.5** | **31.0** | **42.3** | **54.0** | **63.0** | **68.3** | **70.8** | **75.5** | | | | | |
| 4 | 1 | 1 | 5.0 | 9.0 | 16.5 | 22.0 | 38.0 | | | | | | | | | | |
| | 3 | 22 | 5.9 | 12.3 | 18.8 | 25 0 | 36.8 | 46.9 | 56.9 | | | | | | | | |
| | 4 | 31 | 5.9 | 12.2 | 17.5 | 23.6 | 36.3 | 47.8 | 58.0 | 66.3 | | | | | | | |
| | 5 | 4 | 6.4 | 13.3 | 20.0 | 25.5 | 37.3 | 50.3 | 63.6 | 73.1 | 79.4 | | | | | | |
| | 6 | 3 | 6.2 | 13,3 | 20.8 | 26.2 | 37.0 | 48.3 | 62.2 | 73.2 | 79.7 | 84.7 | | | | | |
| | 8 | 1 | 7.0 | 14.5 | 20.0 | 26.5 | 46.0 | 62.0 | 76.0 | 81.0 | 84.5 | 87.0 | 89.0 | 91.0 | | | |
| | 11 | 1 | 4.5 | 12.5 | 17.5 | 23.5 | 37.5 | 47.5 | 56.0 | 67.5 | 75.5 | 82.5 | 87.0 | 91.0 | 93.9 | 96.0 | 98.0 |
| | Average | 63 | **5.9** | **12.3** | **18.3** | **24.4** | **36.8** | **47.9** | **58.4** | **67.9** | **79.6** | **84.7** | **88.0** | **91.0** | **93.9** | **96.0** | **98.0** |
| 5 | 1 | 2 | 5.5 | 11.5 | 17.0 | 22.5 | 25.8 | 40.0 | | | | | | | | | |
| | 2 | 2 | 5.7 | 10.9 | 17.3 | 23.3 | 28.4 | 39.3 | 50.8 | | | | | | | | |
| | 3 | 24 | 5.2 | 10.9 | 16.2 | 21.5 | 27.3 | 40.1 | 51.3 | 61.1 | | | | | | | |
| | 4 | 26 | 5.9 | 12.0 | 17.6 | 22.8 | 28.5 | 40.6 | 52.9 | 61.9 | 69.8 | | | | | | |
| | 5 | 8 | 5.5 | 11.4 | 17.8 | 23.7 | 28.8 | 41.4 | 53.6 | 64.0 | 71.1 | 76.2 | | | | | |
| | 6 | 7 | 5.8 | 10.9 | 15.8 | 19.9 | 24.9 | 38.1 | 49.2 | 61.5 | 69.6 | 75.1 | 80.1 | | | | |
| | 7 | 1 | 6.0 | 13.0 | 21.0 | 27.0 | 33.0 | 48.5 | 64.0 | 77.5 | 81.5 | 86.0 | 89.5 | 92.0 | | | |
| | 8 | 4 | 5.9 | 13.0 | 18.9 | 24.0 | 30.6 | 45.1 | 56.3 | 67.4 | 77.1 | 83.3 | 87.9 | 91.4 | 93.1 | | |
| | Average | 81 | **5.6** | **11.4** | **17.1** | **22.4** | **27.9** | **40.5** | **52.2** | **62.4** | **70.9** | **77.7** | **83.5** | **91.5** | **93.1** | | |
| 6 | 1 | 3 | 4.8 | 9.0 | 15.3 | 21.7 | 26.5 | 32.8 | 46.0 | | | | | | | | |
| | 2 | 2 | 5.8 | 10.0 | 13.5 | 19.0 | 23.5 | 28.5 | 40.8 | 56.3 | | | | | | | |
| | 3 | 9 | 6.0 | 11.5 | 16.1 | 20.6 | 25.2 | 30.2 | 42.4 | 53.0 | 63.9 | | | | | | |
| | 4 | 3 | 6.3 | 11.8 | 15.5 | 20.2 | 26.2 | 31.8 | 42.3 | 55.0 | 64.8 | 73.7 | | | | | |
| | 5 | 1 | 5.0 | 10.0 | 13.5 | 18.0 | 22.0 | 25.0 | 34.0 | 43.0 | 53.0 | 57.5 | 63.5 | | | | |
| | 7 | 1 | 4.5 | 8.0 | 13.5 | 16.0 | 19.0 | 24.0 | 41.5 | 53.5 | 66.5 | 78.0 | 83.5 | 88.0 | 89.5 | | |
| | Average | 19 | **5.7** | **10.7** | **15.3** | **20.2** | **24 9** | **30.1** | **42.3** | **53.2** | **63.5** | **71.3** | **73.5** | **88.0** | **89.5** | | |

NB. The age at migration and accelerated growth is marked by a double line.

To enter into this question more thoroughly, it will be necessary to compare the years before and after migration separately. The average of all fish that had spent three, four, five or six winters previous to migration are given, irrespective of the years that come afterwards, and these figures up to the year of migration, based on substantial numbers, show precisely the same kind of regular decrease in all rings formed prior to migration. Thus the 3rd year's growth decreases from 19.5 cm in those fish that have spent 3 years in the river to 15.3 cm in those that have spent six. In this case there is no break in the law. One obvious explanation of the phenomenon in this instance is the hypothesis that the time of a trout's migration depends on length rather than age, and it is those fish which have attained to a good size early in life which will migrate at an early age.

**Table 8.** Showing the average amount of growth in centimetres of Trout after Migration, classified according to the number of years before migration. (Table XXVII. c.)

| Winters before Migration | Number of fish | Winters after migration | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1st | 2nd | 3rd | 4th | 5th | 6th | 7th | 8th | 9th | 10th | 11th |
| 3 | 2 | (11.5) | (22.8) | (34.5) | (43.5) | (48.8) | (51.3) | (56.0) | | | | |
| 4 | 63 | 12.4 | 23.5 | 34.0 | 43.5 | 55.2 | 60.3 | (63.6) | (66.6) | (69.5) | (71.6) | (73.6) |
| 5 | 81 | 12.6 | 24.3 | 34.5 | 43.0 | 49.8 | 55.6 | (63.6) | (65.2) | | | |
| 6 | 19 | 12.2 | 23.1 | 33.4 | 41.2 | 43.4 | (57.9) | (59.4) | | | | |

NB. The averages in brackets are unreliable, being based on a very small number of fish.

The same table gives the amount of growth in the years after the migration age, which is put in a form more strictly comparable by subtracting the amount of growth prior to migration — and given in table 8. Certain of these values are put in brackets as based on very few individuals. The same rule is apparent here. Thus, when the fish are classified according to the winters before migration, the growth of the winters after migration also has a distinct tendency to decrease in the age groups of the older fish at migration.

These facts seem to lead us to a somewhat different conclusion from that reached by Dahl. He states that the younger the trout are on migration, the less do they grow after migration, and that (quoting his own words), »there must be some cause at work which provides the older and slightly larger migrant with a capacity for growth and for utilising its surroundings, surpassing the capacity possessed by the younger and smaller migrant, for the former not only maintains its slight start, but increases it very considerably«. He suggests that in transplantation of trout it would pay to turn out the oldest fish, for the reason that they grew far better than those which commenced their vigorous growth at an early age.

It follows that either these contrary views must be reconciled, or that one must be abandoned.

In explanation, I may say that DAHL obtains his results from the comparison of the *weights* of the fish, whereas in my comparison I have only drawn on the lengths, and the growth rates of the lengths and weight are very different. If we compare the *lengths* in the corresponding winters after migration, we find that they also increase from those that have spent 3 winters prior to migration, to those that have spent 6, but it must not be forgotten that these fish have had one, two or three years longer to grow during their prolonged stay in the river, and such a result is only what would be expected. Where we differ from DAHL is in the fact that the initial difference in size in the groups at migration *does* more than compensate for the difference in growth after migration, as was shown in table 8. So it would appear, that although the rule of decrease of growth in length of trout is really in operation, and that those fish which had a slow growth before migration, continue to have a slower growth rate afterwards, yet the effect of migration to surroundings conducive to more vigourous growth, is to produce such a great and rapid increase in *weight* as to more than compensate for the slight difference in weight at the time of migration. As he suggests it might even be advantageous to transplant the oldest fish. One objection to this seems to me to be in the fact that they will not be so numerous.

## Conclusion.

The important methods originated by the Norwegians for the study of fish scales have thus brought to light some interesting facts with regard to the growth of fish. We have determined the prevalence of an apparent change in the growth rate from the calculated values of lengths of fish of different age at corresponding years of their existence, by which it appears that in older and older fish less growth is attained in each year of their existence. And this phenomenon is seen to be operating in fish of such different kinds, such as herring caught in drift nets in the open sea, such as haddock caught by the trawl net at the bottom of the sea, and as trout which live under the totally different conditions of a river and are caught by such varying means as rods, spinner, long lines and nets. It would thus seem that the phenomenon is, in part at any rate, independent of the means of capture and that the explanation must be sought in some natural feature of the growth of the fish or in that of the scales from which the calculations are made.

Certain facts with regard to herring seem to indicate that there is in some age groups a segregation of fish, according to size, such as might occur at the onset of maturity, but it is not quite evident how such a fact would explain all the phenomena observed. The older fish might have shorter lengths in the years succeeding maturity, owing to the inclusion of the smaller fish that had matured a year later, but there seems no obvious reason why the successive *increments* after maturity should be smaller as well and this seems to be the case.

Unfortunately, the scarcity of numbers in the very oldest age groups from about 9 to 14, makes it impossible to establish the phenomenen with certainty amongst these.

To investigate this possibility more thoroughly, it will be necessary to know more about the time and range of years in which maturity first occurs in these three species, and to estimate the difference in size between immature and mature specimens of the same age.

It has been shown how the phenomenon cannot be explained away as the result of sex differences in growth and distribution, for in each sex the law is apparent, nor is it likely to be the result of external growth conditions which could hardly be expected to act in one direction always, — that of continually increasing the growth rate in each year of life of the younger fish. The remains then the explanation due to the growth of a scale in which hypothesis the rings are supposed to contract slightly as soon as new matter is superimposed upon them and thus the ratio which gives the calculated lengths becomes incorrect. The reasons for this supposition have been set forward above.

It is very possible that not only one but several of these causes may have some power in bringing about the phenomenon that has been described, and the problem is to disentangle the various effects on the growth curve. If the last cause mentioned, alone operated, which is unlikely, the average size for each group might be taken as representative, and the real amount of annual growth obtained by subtracting the successive average lengths from one another, but in this case the calculated lengths would be of no value. If, on the other hand, it is found that selection, either natural or artifical, is the real cause of the phenomenon, one or two results of importance follow out of this.

In the first place, the calculated lengths are assumed correct, and as these generally differ from the empirical values, these latter must be incorrect in so far as they are concerned in giving us a value for annual amount of growth. These would be better determined by the last increments in length in each group, such as the values 9.3, 6.4, 5.4, 3.5, 3.5, obtained by subtraction of the last value but one from the last in each row of collection 6, Table I, page 6. It will be readily seen why growth curves generally take such a concave form showing a rapid falling off with age in the rate of growth, as the individuals constituting these older groups seem to have had a very slow growth rate throughout their lives. In the second place, it will be necessary to be very careful in using these calculated values to compare growths in different years in time to discover effects of various physical conditions. For it is evident that no single differing age groups can give comparable values for the growth in any particular year, for each group consists of selected individuals with different growth rates. The only way in which strict comparisons can be made is to confine them to the same year group from different localities or from the same locality at different times.

With the adoption of these new methods the whole problem of growth seems to have become more intricate and complex, but there seems no reason why these questions should not be solved by further investigations. Experimental work on fish kept under observation would go far to clearing up doubtful points.