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FURTHER STUDIES CONCERNING THE METHODS OF CALCULATING THE GROWTH OF HERRINGS

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SECTION 1.

Introduction.

In a treatise »On the methods used in the Herring Investigations« [6]. I showed, on the basis of measurements of a large number of herrings of all sizes, that the relation between the size of a certain scale and the length of the fish is sufficiently constant to render it possible to calculate, with a considerable degree of accuracy, the length of the fish from the size of the scale. From this I concluded that it must be possible to determine the size attained by the herring in question during the different winters which it had passed, by measuring the size of the scale within each separate winter ring. It should thus be possible to estimate how each individual herring had grown from year to year. The method of procedure in such determinations consisted of measuring, along a line from the centre of the scale to its edge, the distances between the centre and each separate winter ring, as also to the edge. If the growth of the scale corresponded to the growth of the fish, it would then be possible, by means of simple proportion, to calculate how long a herring had been in the previous winters of its life. (Those wishing a detailed description of the practical performance of such growth calculations are referred to HJORT [5]).

During the last few years the individual annual growth of a large number of herrings has been determined by means of such scale measurements. A number of the results obtained have been published by HJORT [5], in the form of tables, including, *inter alia*, for the single herrings of each sample figures showing the length of the fish on formation of the first winter ring (l_1) its length on formation of second winter ring, (l_2) etc.

With the aid of the averages of growth for the different year groups as given in this publication, Miss ROSA M. LEE has, in a treatise entitled »An Investigation into the methods of Growth Determination in Fishes by means of Scales« [9], noted a phenomenon which she calls »the phenomenon of apparent change in growth rate«, and which becomes apparent on comparing the *average growth* of herrings of different age in a sample. Such comparisons can be made from the following table:

Table 1 showing the average calculated lengths of herrings at time of formation of each winter ring. From HJORT [5].

Age group	Number of Fish	Average calculated lengths at time of formation of					Average length of group
		1st winter ring l_1	2d winter ring l_2	3rd winter ring l_3	4th winter ring l_4	5th winter ring l_5	
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

A glance at this table will show that the dimensions l_1, l_2 etc., are greater in the case of the younger fish than in that of the older. It is this continual and almost unexceptional decrease in the calculated lengths, which appears to accompany the increasing age, that Miss LEE calls »the phenomenon of apparent change in growth rate«. One striking consequence of this decrease is the discrepancy between growth curves based upon the calculated values and one based upon the average lengths of each age group. This decrease, which can be traced, practically speaking, in any herring sample in the material collected during the last years for calculation of growth, occurs also in the case of other fish. By comparing the averages in the calculations made by Dr. KNUT DAHL [2] with regard to the trout Miss LEE found similar conditions, and was also able to demonstrate, on the basis of measurements undertaken by herself, the existence of the phenomenon in the case of the haddock. Also in the case of pilchard (*Clupea pilchardus*) the phenomenon can be traced, as shown by FAGE [3] in a treatise recently published.

The first to describe and discuss this phenomenon, which thus appears to be of very common occurrence, is my colleague

Oscar Sund [10], who has, *inter alia*, drawn up and discussed the following table of average growth rate in sprats of different age taken in a seine catch at Langesund, in the south of Norway, on the 10th of June 1908[1].

Table 2.

Year class	Number of individuals	Length after nth growth period						
		1st	2nd	3rd	4th	5th	6th	
1906	45	7.33	12.35	13.31*	—	—	—	—
1905	74	6.59	11.08	13.12	13.64*	—	—	—
1904	59	6.28	10.34	12.69	14.05	14.19*	—	—
1903	28	5.86	10.29	12.79	14.02	14.65	14.98*	—
1902	6	5.41	10.19	12.92	13.89	14.79	15.32	15.58*

* Incompleted increments.

This table shows, as will be seen, an apparent change in growth rate similar to that which has been noted in the case of herring, pilchard, trout and haddock. The sprats to which the measurements above given refer, are sexually mature. Sund [10] has also, with regard to immature sprats, described and discussed the phenomenon, that the younger fish in a sample appear to have grown better than the older specimens in their first year. With regard to this point, he states (pp. 18—19) »The reason of this remarkable disagreement is due to the fact that the groups 1 and 2 in the material employed are not analogous, the last in 1909 consisting of the smaller sizes of the 1907 year class. The larger specimens must have separated themselves from the shoals in the course of the spring and early summer, in order to attach themselves to shoals of spawning fish.«

In her search for an explanation of this phenomenon, which, it is seen, can be observed in the case of various species of fish, Miss Lee has set up a number of hypotheses, the value of which she discusses, without, in my opinion, arriving at any definite conclusion.

I purpose here to deal with the same phenomenon, and shall in the following attempt, firstly, to define, as accurately as possible, the character of the phenomenon, and the conditions which a satisfactory explanation must fulfil; then to discuss more closely

[1] As these sprats were caught in June, they have not completed the whole summers growth; the values marked with an asterisk, represent the average lengths of the sprats actually measured at time of capture and are in consequence not strictly comparable with the other values.

the explanations which Miss LEE considers as possible. Finally I shall describe in detail some points in the biology of the herring leading to the phenomenon here referred to as a consequence. My own determinations of age and measurements of growth having been restricted, in essential, to the herring alone, I shall confine myself to this one species.

Before proceeding further, I will here define some technical expressions which will be employed in the following pages.

The values, arrived at on basis of scale measurements, for the total length of a herring in previous periods of life is called l; thus the calculated total length of a fish at formation of the first winter ring is called l_1; its calculated length at formation of the second winter ring is calted l_2 etc.

The increase in length which a herring has undergone in one year is called t; t_1, which is equal to l_1, is the increase before the formation of the first winter ring, t_2, which is equal to $l_2 - l_1$, is the increase in the time from the formation of the first winter ring to that of the second etc.

The distance between the centre of the scale and the margin along a certain line is called V; the distance from the centre to the first winter ring along the same line is called v_1, the distance between the centre and the second winter ring is called v_2 and so on.

SECTION 2.

Definition of the phenomenon of apparent change in growth rate.

Miss LEE [9] forms her ideas about the change in growth rate of the herring by comparing the different age groups found in a sample. Further, in the case of herrings, she always compares the average calculated lengths (l_1 l_2 l_3 etc.) at time of formation of the different winter rings. This manner of working involves two inconveniences. Firstly irregularities may appear owing to the possibility, that individuals of the different age groups may have grown up under different conditions, and secondly it is impossible to ascertain with any certainty how the change goes on in the different years of growth owing to the fact that all calculated lengths except l_1 are compound quantities consisting of several years' increments.

In order to avoid these inconveniences the material used in this paper is gathered and treated in another way. Instead of comparing different year classes taken simultanously, averages for one and the same year class at different ages are compared, and instead of comparing the compound growth quantities (l_2 l_3 etc.) each single year's increment is kept separate by using the dimensions t_2 t_3 etc.

In this manner we eliminated the possibility of improvement in the growth conditions during a series of years, and on the other hand it can be shown how the single annual increments change, whereby the phenomenon can be much more completely defined.

It is moreover considered desirable to employ as far as possible material gathered from catches made with non-selective implements. Such material has been gathered for the Norwegian herrings during the years 1907—1913; the small meshed seines employed in Norway totally exclude the possibility of artifical selection except among the very youngest fish (0 group and 1-group) and our material of Norwegian herrings must be regarded as the best available for the purpose. Our description of the change in growth rate is deduced mainly from this material which is given in the tables 3—13.

Turning at first to the tables for the immature herrings it will easily be seen, that there is a marked tendency to decrease in all growth values with increasing age; the rule of the decrease holds good here with only few exceptions which are doubtless due to scarcity of material. A closer study of these tables reveals the fact, that the decrease is more marked from the 4th to the 5th year than in other years; thus for the year class 1907 the greatest decrease is found between the years 1910—1911, for the year class 1906 it appears between 1909—1910, for the year class 1905 between 1908—1909, while for the year class 1904 it is found between 1907—1908. From these tables we may therefore deduce the following definition of the phenomenon: 1) Among the immature herrings a continual decrease is observed, but 2) this decrease is more rapid at a certain age of the individuals (4 years). The decrease applies to the growth values t_1 to t_5.

Turning now to the tables for mature fish and looking first at the table for the year class 1904, which is by far the most valuable in the material, we find similar conditions as for the immature fish in the dimensions t_1 and t_2. But for t_3, t_4 and t_5 the decrease is preceded by an increase, while the following dimensions t_6—t_8 seem to remain fairly constant. The values for the year 1910 form an exception in this table being in most cases comparatively low. As this is the case not only for the year class 1904 but for

Tables 3—7 showing average increments of different year classes of Norwegian immature herrings in different years.

Table 3. Year class 1908 among immature herrings.

Year of capture	Age	No. of samples	No. of individuals	t_1	t_2	t_3
1909	$1^1/_2$	1	59	[9.3]	—	—
1910	$2^1/_2$	7	815	8.8	7.9	—
1911	$3^1/_2$	2	162	7.9	6.5	5 4

Table 4. Year class 1907 among immature herrings.

Year of capture	Age	No. of samples	No. of individuals	t_1	t_2	t_3	t_4
1909	$2^1/_2$	2	1195	7.6	6.3	—	—
1910	$3^1/_2$	7	681	7.5	6.3	5.8	—
1911	$4^1/_2$	2	63	7.1	5.5	5.3	4.3

Table 5. Year class 1906 among immature herrings.

Year of capture	Age	No. of samples	No. of individuals	t_1	t_2	t_3	t_4	t_5
1907	$1^1/_2$	1	32	[9.8]	—	—	—	—
1908	$2^1/_2$	1	17	9.1	6.9	—	—	—
1909	$3^1/_2$	3	260	8.1	6.3	5.5	—	—
1910	$4^1/_2$	6	13	6.8	5.7	5.3	2.8	—
1911	$5^1/_2$	2	3	[5.0]	[4.7]	[5.2]	[4.8]	[3.6]

Table 6. Year class 1905 among immature herrings.

Year of capture	Age	No. of samples	No. of individuals	t_1	t_2	t_3	t_4	t_5
1907	$2^1/_2$	2	89	9.1	6.5	—	—	—
1908	$3^1/_2$	1	10	8.7	5.5	4.7	—	—
1909	$4^1/_2$	3	97	7.4	5.0	4.5	3.8	—
1910	$5^1/_2$	4	4	[8.3]	[4.6]	[4.9]	[3.7]	[2.6]

Table 7. Year class 1904 among immature herrings.

Year of capture	Age	No. of samples	No. of individuals	t_1	t_2	t_3	t_4	t_5	t_6	t_7
1907	$3^1/_2$	2	69	7.2	5.8	4.8	4.7*	—	—	—
1908	$4^1/_2$	1	58	7.1	5.2	3.7	4.2	3.9*	—	—
1909	$5^1/_2$	3	331	7.1	5.0	3.5	3.9	3.4	3.2*	—
1910	$6^1/_2$	6	78	6.9	5.1	3.5	3.9	2.9	2.8	2.5*

* Incompleted increments.

Tables 8—13 showing average increments of different year classes of mature Norwegian herrings in different years.

Table 8. Year class 1904.

Year of capture	Age	No. of samples	No. of individuals	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9
1907	3	1	4*	11.0	9.5	4.5	—	—	—	—	—	—
1908	4	1	11	9.9	9.8	6.1	3.2	—	—	—	—	—
1909	5	1	33	8.8	7.8	6.7	3.5	2.3	—	—	—	—
1910	6	1	382	*7.7*	*6.6*	*5.3*	*3.9*	2.6	2.2	—	—	—
1911	7	3	1082	8.1	6.8	5.4	4.0	*3.0*	*1.9*	1.3	—	—
1912	8	4	802	7.9	6.5	5.2	4.2	2.9	2.0	1.2	1.0	—
1913	9	2	371	7.8	6.3	5.3	4.0	2.9	1.9	1.2	1.0	0.8

Table 9. Year class 1903.

Year of capture	Age	No. of samples	No. of individuals	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}
1907	4	1	31	10.2	7.8	5.7	3.9	—	—	—	—	—	—
1908	5	1	14	8.7	8.9	6.5	3.7	2.3	—	—	—	—	—
1909	6	1	9	7.7	7.8	6.5	4.5	2.1	1.5	—	—	—	—
1910	7	1	33	*7.2*	*7.1*	*5.8*	*4.4*	*2.5*	1.3	1.2	—	—	—
1911	8	3	76	8.0	7.0	5.6	4.1	2.6	*1.7*	*1.2*	1.0	—	—
1912	9	4	83	7.9	6.8	6.0	4.2	2.5	1.8	1.0	0.8	0.7	—
1913	10	2	32	7.9	6.8	5.9	4.3	2.6	1.3	1.0	0.8	0.7	0.6

Table 10. Year class 1902.

Year of capture	Age	No. of samples	No. of individuals	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}
1907	5	1	26	8.4	8.2	5.8	3.7	2.7	—	—	—	—	—	—
1908	6	1	16	8.7	8.6	6.1	3.8	2.3	1.5	—	—	—	—	—
1909	7	1	2	[9.9]	[6.3]	[5.7]	[4.2]	[2.0]	[1.5]	[0.4]	—	—	—	—
1910	8	1	5	[*7.6*]	[*8.1*]	[*6.0*]	[*3.2*]	[*2.1*]	[*1.3*]	[1.0]	[0.9]	—	—	—
1911	9	3	36	9.1	6.9	5.4	3.9	2.5	1.5	*1.1*	*0.9*	0.9	—	—
1912	10	4	20	8.1	6.8	6.2	4.0	2.9	1.8	0.9	0.7	0.6	0.6	—
1913	11	2	7	8.9	5.4	5.9	4.0	2.9	1.7	1.0	0.8	0.7	0.8	0.6

* In spite of paucity in numbers, these averages must be regarded as fairly representative, since we have found the average length of a large number of fish to be 25.5 cm., while that of these four is 25.0. The dimensions of growth t, t_2 og t_3 are therefore in any case not too high.

Table 11. Year class 1911.

Year of capture	Age	No. of samples	No. of individuals	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}	t_{12}
1907	6	1	15	9.6	6.5	5.1	4.2	2.5	1.9	—	—	—	—	—	—
1908	7	1	16	10.4	6.8	5.7	4.3	2.2	1.4	0.9	—	—	—	—	—
1909	8	1	5	[9.9]	[5.5]	[5.5]	[4.4]	[3.0]	[1.9]	[1.1]	[0.9]	—	—	—	—
1910	9	1	2	[*9.1*]	[*6.9*]	[*5.0*]	[*4.1*]	[*2.5*]	[*1.6*]	[*1.2*]	[1.1]	[1.0]	—	—	—
1911	10	3	29	8.6	5.6	5.0	4.7	2.8	2.2	1.2	*0.9*	*0.8*	0.8	—	—
1912	11	4	15	8.5	5.4	5.6	4.2	3.4	2.1	1.2	0.9	0.6	0.6	0.6	—
1913	12	2	10	8.3	5.1	5.8	4.4	3.3	2.4	1.3	0.9	0.7	0.5	0.6	0.5

Table 12. Year class 1900.

Year of capture	Age	No. of samples	No. of individuals	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}	t_{12}	t_{13}
1907	7	1	12	9.1	6.2	5.5	4.5	2.9	2.0	1.4	—	—	—	—	—	—
1908	8	1	22	8.9	7.5	5.6	3.8	2.5	1.6	1.2	0.7	—	—	—	—	—
1909	9	1	4	[9.2]	[6.5]	[5.2]	[3.8]	[3.2]	[1.7]	[1.1]	[0.8]	[0.8]	—	—	—	—
1910	10	1	7	*7.8*	*4.5*	*6.7*	*4.5*	*3,0*	*2.7*	*1.0*	*0.9*	0.6	0.5	—	—	—
1911	11	3	11	9.1	6.0	5.3	4.3	3.3	1.8	1.3	1.7	*0.8*	*0.6*	0.6	—	—
1912	12	4	16	9.0	4.5	5.4	4.4	3.3	2.3	1.4	1.2	0.8	0.4	0.4	0.4	—
1913	13	2	3	[7.6]	[5.1]	[5.9]	[4.3]	[3.1]	[2.2]	[1.4]	[1.2]	[0.8]	[0.7]	[0.5]	[0.6]	[0.6]

Table 13. Year class 1899.

Year of capture	Age	No. of samples	No. of individuals	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}	t_{12}	t_{13}	t_{14}
1907	8	1	18	9.0	5.4	6.0	4.1	2.9	2.1	1.0	0.9	—	—	—	—	—	—
1908	9	1	15	9.1	6.5	5.7	4.3	2.7	1.8	1.2	0.9	0.6	—	—	—	—	—
1909	10	1	7	*8.8*	*3.9*	*5.4*	*4.2*	*4.0*	*2.3*	*1.5*	*1.0*	0.7	0.6	—	—	—	—
1910	11	1	10	8.7	5.2	5.1	3.9	3.2	1.0	1.4	1.9	*0.7*	*0.6*	0.6	—	—	—
1911	12	3	13	8.6	5.4	5.2	4.1	3.3	2.1	1.4	0.8	0.6	0.7	0.5	0.5	—	—
1912	13	4	20	8.8	4.4	4.9	5.1	3.6	2.4	1.5	1.1	0.7	0.6	0.5	0.4	0.5	—
1913	14	2	2	[8.5]	[8.0]	[5.5]	[3.8]	[3.1]	[1.4]	[1.4]	[0.7]	[0.6]	[0.5]	[0.4]	[0.3]	[0.4]	[0.4]

all year classes, it seems evident that the sample for this year is not quite representative.

The tables for the other year classes (1903—1899) disclose features similar to those described for the year class 1904; tab. 13 especially, for the year class 1899 shows more or less distinctly that t_1 and t_2 decrease a little between the 8th and the 13th year of life, i. e. a long time after all the individuals of the year class had become mature.

Tab. 14 showing differences between average values for t_1, t_2 etc. according to the age at time of capture, a giving the values for fish captured at a relatively young age, b giving values for fish at a more advanced age (compiled by dividing the growth values in tab. 8—13 into two groups, indicated by sloping figures and averaging the values for each group)

Year-class	Minimum age years	t_1			t_2			t_3			t_4			t_5		
		a	b	a — b	a	b	a — b	a	b	a — b	a	b	a — b	a	b	a — b
		Early	Late	Difference	Early	Late	Difference	Early	Late	Difference	Early	Late	Difference	Early	Late	Difference
1904	3	9.4	7.9	1.5	8.4	6.5	1.9	5.6	5.3	0.3	3.5	4.1	—0.6	2.6	2.9	—0.3
1903	4	8.5	7.9	0.6	7.9	6.9	1.0	6.1	5.8	0.3	4.1	4.2	—0.1	2.3	2.6	—0.3
1902	5	8.7	8.7	0.0	7.8	6.4	1.4	5.9	5.8	0.1	3.7	4.0	—0.3	2.3	2.8	—0.5
1901	6	9.8	8.5	1.3	6.4	5.4	1.0	5.3	5.5	—0.2	4.3	4.4	—0.1	2.6	3.2	—0.6
1900	7	8.8	8.6	0.2	6.2	5.2	1.0	5.8	5.5	0.3	4.2	4.3	—0.1	2.9	3.2	—0.3
1899	8	9.0	8.7	0.3	5.3	5.0	0.3	5.7	5.1	0.6	4.2	4.4	—0.2	3.2	3.4	—0.2

Year-class	Minimum age years	t_6			t_7			t_8			t_9			t_{10}		
		a	b	a — b	a	b	a — b	a	b	a — b	a	b	a — b	a	b	a — b
		Early	Late	Difference	Early	Late	Difference	Early	Late	Difference	Early	Late	Difference	Early	Late	Difference
1904	3	2.1	2.0	0.1	—	—	—	—	—	—	—	—	—	—	—	—
1903	4	1.5	1.5	0.0	1.2	1.0	0.2	—	—	—	—	—	—	—	—	—
1902	5	1.4	1.7	—0.3	0.8	1.0	—0.2	0.9	0.8	0.1	—	—	—	—	—	—
1901	6	1.7	2.2	—0.5	1.1	1.2	—0.1	1.0	0.9	0.1	0.9	0.7	0.2	—	—	—
1900	7	2.0	2.1	—0.1	1.2	1.4	—0.2	0.8	1.4	—0.6	0.7	0.8	—0.1	0.6	0.6	0.0
1899	8	2.1	1.8	0.3	1.2	1.4	—0.2	0.9	1.3	—0.4	0.7	0.7	0.0	0.6	0.7	—0.1

A less detailed but more vivid picture of the change in growth rate is obtained when the values under the headings t_1 t_2 etc. are divided into two groups and averaged, one representing the values at a younger stage, the other representing the values when the herrings were older. Thus when the four first values under heading t_1 in tab. 8 are averaged, the figure 9,4 cm. is found to represent the years 1907—1910 while 7,9 cm. corresponds to the same dimension for the years 1911—1913. In such a manner the numbers under headings a and b[1] in tab. 14 are worked out while the figures under heading a—b give the difference between a and b. This table, which gives in condensed form the data of in the tables 8—13 permits us to get a general view of the course of the change in growth rate among mature fish. It will readily be seen that for t_1 t_2 and t_3 all differences except one are positive while all the differences for t_4 t_5 t_6 and t_7 except four are negative. In other words, the three first years' increments decrease with increasing age, while the reverse is the case with the following four increments; as regards the remaining increments t_8—t_{11} the data are too incomplete to ascertain if any change has taken place. It will be seen from the table that in all year classes similar conditions prevail, though the intensity of apparent change varies somewhat.

In order to see if the material used by Rosa M. Lee [9] showed similar features as to the apparent change, I transformed her tables regarding the herring in such a manner as to show the apparent change of each single annual increment. For the three collections (nr. 9, 12, 15) of mature herrings, closely corresponding conditions were observed. Tab. 15 is a transformation of one of the tables used by Rosa M. Lee [9]. In the same manner as employed in the compilation of tab. 14, the averages in a vertical column are divided into two groups one representing younger, the other older fish; the averages of these groups are found in the horisontal columns a and b, and their difference in the column a—b. Here too it will be seen that t_1 t_2 and t_3 *decrease* with age while t_4 t_5 and t_6 *increase.* This peculiar feature, not observed by Rosa M. Lee, will make it a matter of necessity to define the phenomenon of apparent change in growth rate in another manner than she has done. Naturally such a definition will, until more material has been treated, be a provisional one, and it will, obviously, be different for immature and mature herring. For immature herring we may say that all annual increments show

[1] The numbers printed with sloping figures in the tables 8—13 denote the last values referred to category a in tab. 14.

Table 15 showing the average annual increments for different age groups separately and taken together in two groups (younger and sample) in a sample of herrings from South-Iceland, June 1908, Recalculated from Lee (9) p. 7, Collection 15.

Age group	No of individuals	t_1	t_2	t_3	t_4	t_5	t_6	t_7	t_8	t_9	t_{10}	t_{11}	t_{12}	t_{13}	t_{14}
4	49	11.0	8.3	6.1	3.8	—	—	—	—	—	—	—	—	—	—
5	26	10.0	9.4	6.5	3.1	3.2	—	—	—	—	—	—	—	—	—
6	14	9.7	9.3	6.5	3.4	2.3	1.8	–	—	—	—	—	—	—	—
7	19	8.8	7.6	6.4	4.2	2.8	2.2	1.8	–	—	—	—	—	—	—
8	34	9.7	7.9	5.7	4.3	2.7	2.2	1.5	1.0	—	—	—	–	–	—
9	44	9.3	8.1	5.8	4.0	2.7	1.9	1.7	1.2	0.8	—	—	—	—	—
10	47	9.3	7.8	5.9	3.9	2.8	1.8	1.5	1.2	1.0	0.8	—	—	—	—
11	20	8.1	7.5	5.4	4.4	2.9	2.3	1.6	1.3	1.1	1.0	0.6	—	—	—
12	8	8.4	7.5	5.8	4.1	2.3	2.2	1.5	1.2	0.8	0.8	0.7	0.5	–	—
13	8	9.3	7.2	5.1	4.3	2.8	1.8	1.3	1.2	0.9	0.8	0.7	0.7	0.5	—
14	10	8.7	6.4	5.3	4.1	2.8	2.4	1.5	1.1	0.9	0.8	0.8	0.8	0.6	0.5
Early	a	9.8	8.4	6.2	3.8	2.3	2.0	1.6	1.2	1.0	0.9	0.7	—	—	—
Late	b	8.8	7.3	5.5	4.2	2.7	2 2	1.5	1.2	0.9	0.8	0.8	—	—	—
Difference	a — b	1.0	1.1	0.7	—0.4	—0.4	- 0.2	0.1	0.0	0.1	0.1	—0.1	—	—	—

a tendency to decrease with increasing age. For the mature herring we may say:

1) (The first annual increments (t_1—t_3) are on an average larger in the *younger* herrings than in the older (they *decrease* with increasing age). The decrease is greater in the maturing period than before and after.

Table 16 showing average annual increments of different year classes in a sample of sprat from Langesund [10]/6 1908. From Sund (10) p. 30.

Year class	No. of individuals	t_1	t_2	t_3	t_4	t_5	t_6
1906	45	7.3	5.0	—	—	—	—
1905	74	6.6	4.5	2.0	—	—	—
1904	59	6.3	4.1	2.4	1.4	—	—
1303	28	5.9	4.4	2.5	1.2	0.6	—
1902	6	5.4	4.8	2.7	1.0	0.9	0.5

Table 17 showing average annual increments of different age groups in a sample of pilchards from Collioure, April 1912. From Fage (3).

Age group	No. of individuals	t_1	t_2	t_3	t_4	t_5
3	3	8.1	5.1	2.0	—	—
4	12	7.4	4.3	2.4	1.1	—
5	3	7.0	3.4	2.9	1.6	0.7

2) The succeding increments (l_4—l_7) are on an average larger in the *older* herrings than at the younger (they *increase* with increasing age).

3) The last increments (l_8—l_{11}) seem to be constant.

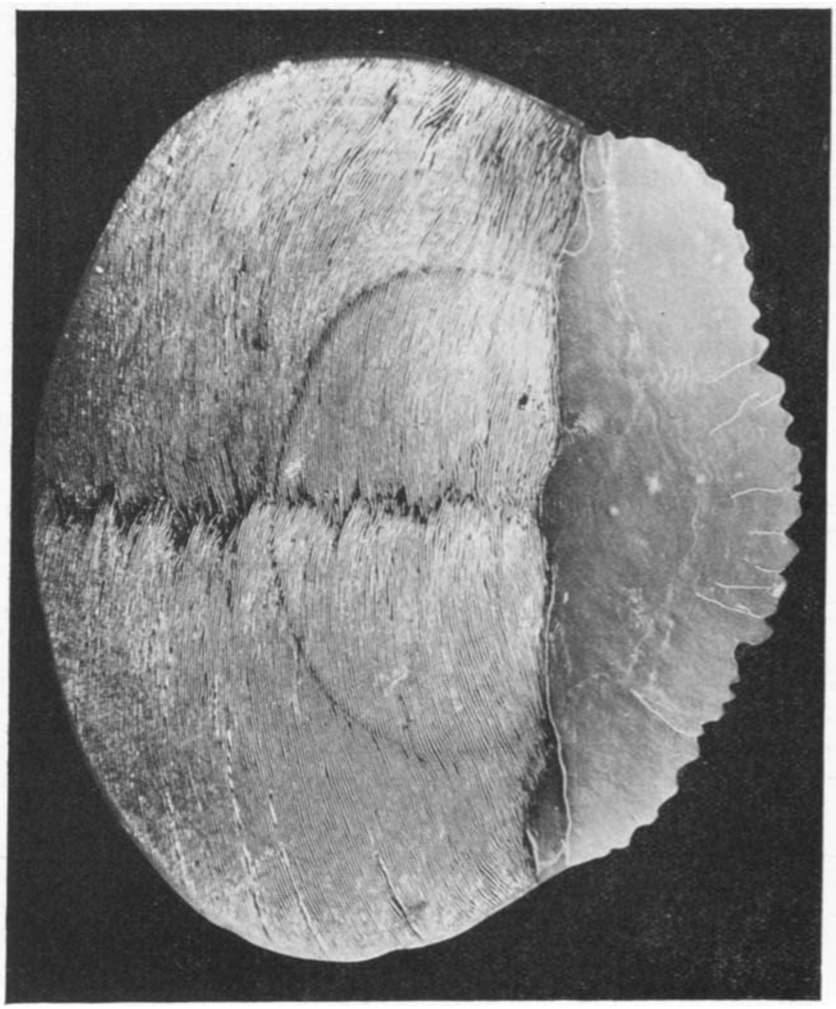

Fig. 1. Scale from a small herring (18 cm) showing one winter ring ($^{22}/_1$).

This definition, which is based on the facts revealed by an examination of the Norwegian herrings, must naturally only be considered valid for this herring group. The table 16 however seems to indicate that analogous conditions prevail for herrings from Iceland and the tables 17 and 18 show that similar conditions are found on examination of sprat and pilchard.

Until more is known it is therefore reasonable to consider the above definition as the most complete, and to reject that given by Miss LEE [9] on p. 9 in her treatise.

From what is now shown regarding the change in growth

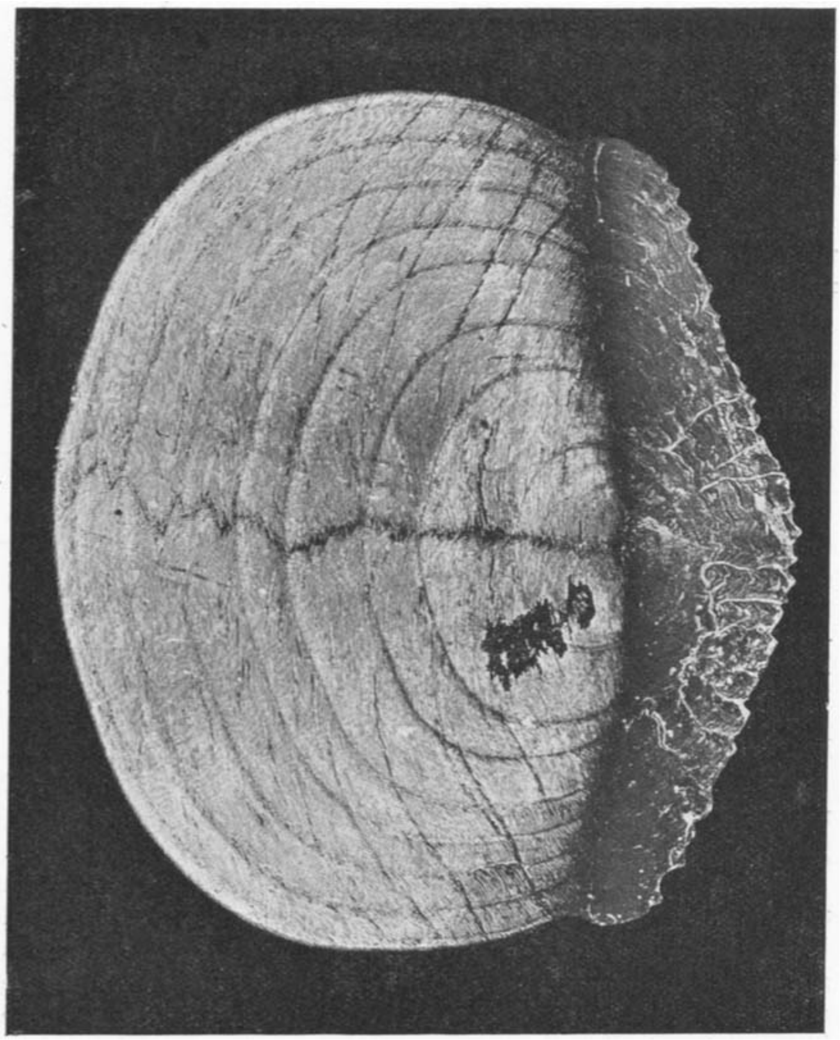

Fig. 2. Scale from a large herring (34 cm.) showing eight winter rings ($^{13}/_{1}$).

rate we can deduce some conditions which must be fulfilled by a satisfactory explanation of the phenomenon. It must be explained:

1) Why the dimensions t_1 t_2 and t_3 decrease while the following increase.

2) Why the decrease is greater at certain ages than before and after. To These may be added the following.

Why is there a discrepancy between the calculated growth curves and that based upon the average length of each age group?

Before proceeding to discuss the various explanations, the appearance and structure of the herring scale may be briefly described.

Fig. 1 is a reproduction from a photograph of a scale from a small herring (18 cm.) while the scale pictured in fig. 2 was taken from a large herring (34 cm.). The scales are from the fore-part of the body, near the lateral line, and have the appearance common to most scales on the body of the herring. As will be seen, the scale is divided into two portions of very different structure. The smaller and posterior portion has a frayed edge and a smooth outer surface, while the larger and anterior portion

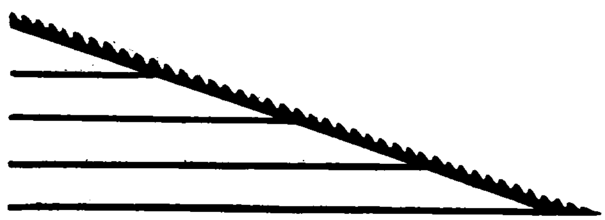

Fig. 3. Arrangement of layers and lamels in the anterior portion of a herring scale.

has an even contour but an outer surface which is transversed by fine parallel ridges giving this portion a striped appearance. The bordering line between the anterior and the posterior portion is as a rule clearly marked, and is by DAHL (1) called the base-line.

The fine ridges on the surface of the anterior portion do not run across the whole scale but cease in the median portion, thus giving rise to an irregular border called by DAHL the median line.

Concentric to the edge of the ridged portion the winter rings are seen as narrow lines darker than the surrounding part. In fig. 1, one winter ring may be seen, while on fig. 2 eight rings are visible inside the edge. They are arranged round the centre of the scale, which is found at the intersection point of the base line and the median line.

If sections are made of a scale, it appears that it is composed of several fibrous lamellae of different extent, those lying near to the inner surface being the most extended. Covering these lamellae a thin homogenous layer of equal thickness extends over the outer surface of the scale. The fine ridges on the surface belong to this thin, homogenous layer and appear in the sections like the teeth of a saw. Fig. 3 is a perfectly schematic drawing intended to illustrate the arrangement of the different layers and lamellae in a section of the ridged portion of the scale perpendicular to the base line. The thickness of the scale is comparatively much more exaggerated than the other extension. Fig. 4

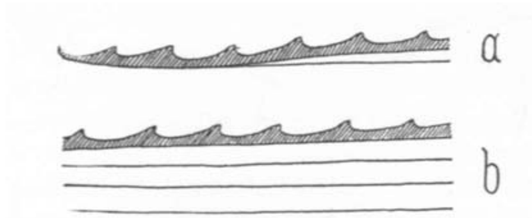

Fig. 4. Parts of a section through a herring scale, perpendicular to the ridges, *a* at the edge, *b* nearer the centre. Schematized but with correct size-proportions ($^{500}/_{1}$).

gives schematized drawings, in whieh, however, the size proportions are correct. They are intended to show the equal thickness of the outer homogenous layer at the edge and nearer to the centre of the scale.

Regarding the relation between the different layers and lamellae and the winter rings, nothing conclusive can be said for the present, and a discussion of this matter will be postponed to a later publicatiou.

SECTION 3.

Discussion of the various explanations.

When we ask for the cause of the change in growth rate we can now with regard to the material under discussion neglect the possibility of artificial selection caused by the fishing implements as also the hypothesis of improvement in the growth conditions during a series of years. There remain some others, which may be placed in two categories:

A. The apparent change in growth rate is dependent on changes *in the individual growth estimates.*

B. The apparent change in growth rate is not dependent on such changes and can only appear in the averages.

To the first category belong all explanations offered by Miss LEE, while that set forth by myself belongs to the second category.

The following are Miss LEE's explanations:

1) Part of the scale may be absorbed in the maturing of the sexual products.

2) The scale may occasionally put on more than one ring during a year, thus causing a too high age determination.

3) The inner part of the scale may contract or be pressed inwards by the outside matter superimposed upon it during the growth.

I myself have offered an explanation which may be briefly stated as follows:

4) The youngest and oldest individuals in a shoal are selected on account of biological or physiological conditions in such a manner as to give either too high or too low *average* values for the growth of the year class they belong to.

In the following these four hypotheses will be subjected to a closer examination.

EXPLANATION 1.

Absorbtion of matter in the edge of the scale.

On p. 13 of her treatise, Miss LEE puts forward the idea »that part of the scale may be absorbed in the maturation of the sexual organs, as is known to occur in salmon«. This hypothesis, which is not at all supported by any observations is strongly opposed to the facts shown in tab. 3—13 and tab. 14. It is clearly seen from these tables, that the decrease takes place most markedly in the annual increments preceeding sexual maturation (t_1 and t_2) and further that the annual increments fulfilled in the very years of spawning are either *increasing* or constant. Thus the change in growth rate is completely inexplicable by help of this hypothesis.

It is easily demonstrated, that such absorbtion of the scale matter would cause not a decrease but an increase of the dimensions t_1 and t_2. For if the outer scale increments in any way become too small, then the ratio $\frac{v_1}{V}$ (ratio between first years' scale increment and all years' scale increments) becomes larger, and as $l_1 = L \cdot \frac{v_1}{V}$ the calculated length in the first year would increase. As the reverse is the case, we must conclude that such an absorbtion cannot be the cause of the observed change in growth rate.

The structure of the scale would certainly also be affected to a noticeable degree by such an absorbtion. The formation of the spawning mark on the scale of the salmon causes considerable irregularities in the structure, and something similar must be expected in the case of the herring scale, with its fine and delicate ridges. In fact, by examining a large number of scales from a herring it is as a rule possible to find some few, which show traces of being damaged in some way, the result being a disburbance of the continuity of the fine ridges. Fig. 5 is a photograph of part of such a scale. The discontinuity of the ridges is obvious. Fig. 6 is a photograph of part of a scale of which it may safely be said, that it must at a certain time have been dislocated in such a manner as to be turned from its original position in the scale pocket, without however quite falling out. New scale matter has then, in the course of years, formed outside this dislocated part of the scale. The disturbance caused by this dislocation in the continuity of the ridges can easily be seen. Only very few ridges run from the dislocated part to the part outside.

EXPLANATION 2.

Formation of supernumerary rings.

On p. 14 in her treatise Miss LEE says: »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«.

As to this hypothesis the following remarks may be made. In order that the average value for t_1 of a year class should be reduced by inclusion of fish apparently belonging to the same year class by the presence of adventitious rings, the average value t_1, of these last fish must necessarily be less than that of the fish really belonging to the year class. If this lower average t_1 of the fish apparently belonging to the year class should be due to the presence of adventitious rings, *then the adventitious rings must be placed in the first summer belt;* in other words the value of t_1 cannot be lessened by such adventitious rings lying outside the first real one, since the ratio $\frac{v_1}{V}$, which is the element in the equation for growth calculation which can be altered by adventi-

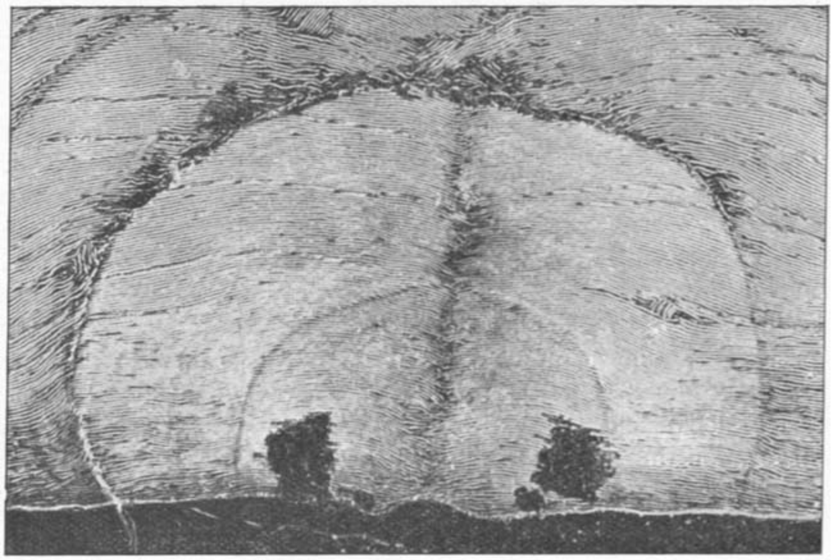

Fig. 5. Part of a herring scale with abnorm structure at the second winter ring ($^{20}/_{1}$).

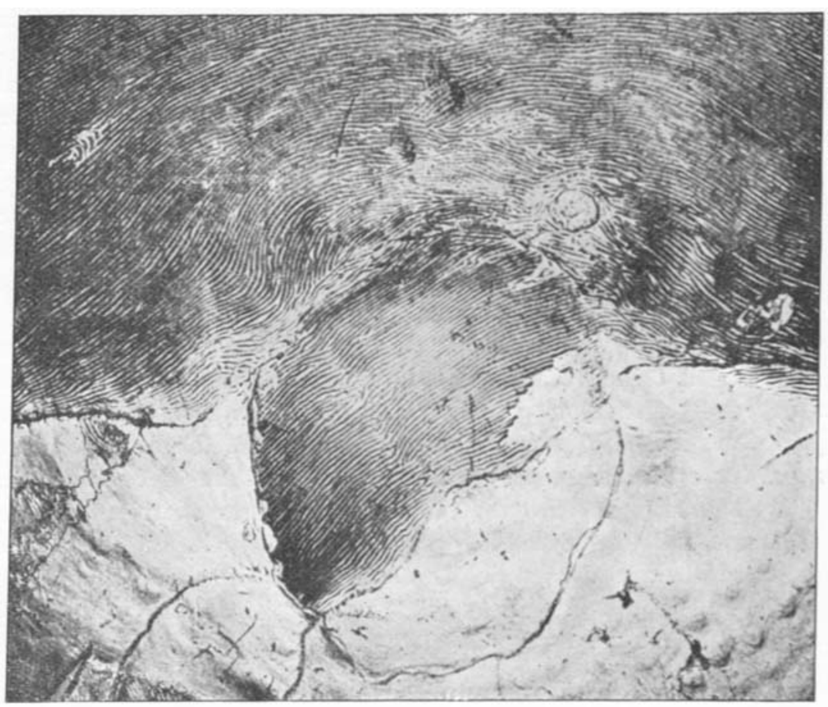

Fig. 6. Part of a herring scale showing a dislocation of the first summer zone ($^{38}/_{1}$).

tious rings, remains completely unaltered by the number of rings lying *outside the real first one*; this becomes evident by drawing a scheme of a scale with its real winter rings and then putting on a »false« ring outside the first real one.

From the above it will be evident, that the decrease in t_1 during several years can only be effected by adventitious rings, when the number of these *inside the first real ring* increases with age. For the growth dimensions t_2 t_3 etc. similar deductions can be made. But it is absurd to suppose that older fish should have a better chance of having adventitious rings *inside* the first real ring than younger fish. We must therefore conclude, that the apparent change in growth rate is not at all explained by the hypothesis of adventitious rings. Such rings will certainly be a source of errors both in age determinations and in growth calculations. But for the growth calculations this source of error is *constant* for each annual increment.

Since this hypothesis has once more appeared in the literature on the subject, the opportunity may be utilized of testing it more thoroughly.

In order to study the seasonal growth of the herring and the time for formation of a new summer belt, 21 collections of young herrings were collected during the time from April 1910 to May 1911. The material thus obtained is published by myself (8) and may easily be used for an examination of the hypothesis of adventitious rings. For if such rings are formed during the summer in a certain percentage of the fish, then the last increment of these fish must be very small, approximate to 0. From the following table 18 it can be seen how large is the average and minimal last increment in each sample, and for purposes of comparison, the last but one increment belonging to the individual having the minimal last increment is also given. This table reveals the facts:

1) That the average and minimal last increments are smaller than 1 cm. only in the spring (April and May).

2) That the minimal last increment increases during summer parallel to the average increment.

3) That the sum of the minimal increment and the last but one is in the summer always very much larger than the average last increment.

We may from these facts conclude:

1) That the new summer's growth begins in the spring.

2) That none of the individuals examined had formed an adventitious ring during the summer.

Table 18 showing for a number of samples the average and minimal last increment and the last increment but one, for the fish having the minimal increment.

Year and date of capture	Number of fish	Last increment		Increment preceeding the minimal last one
		Average	Minimal	
1910, 23/4	13	1.1	0.6	6 8
» 6/5	66	1.0	0.1	9.3
» 11/5	41	1.2	0.6	8.5
» 18/5	38 •	1.9	0.7	8.4
» 25/5	34	2.2	0.7	11.1
» 1/6	39	2.5	1.2	5.1
» 8/6	28	2.9	1.7	7.5
» 15/6	41	3.8	2.3	8.2
» 21/6	37	4.2	1.7	7.7
» 7/7	38	4.8	2.8	8.3
» 27/7	41	5.9	3.0	9.8
» 10/8	31	6.5	4.7	9 5
» 17/8	32	6.9	4.8	8.3
» 29/8	38	6.5	4.1	8 7
» 21/9	35	6.3	3.1	8.0
» 19/10	31	6.9	5.2	7.8
» 14/11	29	7.2	5.4	8.8
1911, 5—7/4	24	0.4	0.0	5.3
» 8/4	26	0.1	0.0	5.3
» 11—12/4	14	0.6	0.0	7.2
» 1/5	27	1.1	0.6	6.0
	703			

There is another manner of investigating the probality of adventitious rings. If a certain year class is very much more numerous than those one year older and younger, then if a certain per cent of the individuals put on more than one ring during a year the result will be that always more and more fish will be reckoned to the oldest year class and the value of the ratio between the number of animals referred to the two year classes $\left(\frac{\text{rich year class}}{\text{poor year class}}\right)$ will in course of time decrease.

As an example, if the relative abundance of three succeeding year classes in a stock be as 10 : 100 : 10 in one year and if in the next year say every ten of all individuals owing to adventitious rings are apparently one year too old then the relative abundance will be 9 : 91 : 19, if the same continue one year more, the relative abundance would be about 8 : 83 : 26 and so on. The different death rate is disregarded as it can be shown to have only an immaterial effect upon the levelling up of the relative abundance of the year classes.

Among the Norwegian spring herrings the year class 1904 has since 1908 been far more numerous than the year class 1905 and 1903 (see HJORT and LEA [6]) and an examination of the ratio between the year classes 1904 and 1903 in different years will be of importance in judging the hypothesis in question. In the following table 19 the ratio between the number of fish referred to year class 1904 and that referred to year class 1903 is found for different years. The table shows the ratio to be constant from 1910

Table 19 showing the ratio between the number of the year class 1904 and 1903 in different years.

Year	1907	1908	1909	1910	1911	1912	1913
Ratio 1904/1903	0.1	2.9	3.7	11.6	14.1	10.7	12.1

on *viz.* from the time when most herrings of the year class 1904 had become mature. The facts shown in this table consequently point to the conclusion that adventitious rings are not formed.

Yet another method can be employed. Among the year class 1904 many individuals can be found which in their third summer have had a very poor increment, about one third of the number having grown better in the fourth year than in the third [$t_3 < t_4$]. (see HJORT and LEA [6]). Among all year classes some few fish are found which show similar growth, but the percentage has never been found so great as in year class 1904 (more than 30 %). Now if a certain percentage of these fish with abnormal growth were referred to an older year class owing to formation of accessory rings, then the percentage will decrease for the year class 1904 and increase for the other year classes. Table 20 shows that this is by no means the case.

Thus the hypothesis of adventitious rings is opposed to the facts as far as regards the Norwegian herrings. Other conditions may however prevail in other herring stocks. Thus HELLEVAARA [4] has found that herrings caught off the coasts of Finland often show faint rings which in his opinion are caused by the rapid development of the sexual products accompanied by fasting, or by lack of nutriment. In spite of this it seems as if those faint rings are easily distinguished from the real winter rings in this case, for the author concludes his interesting treatise in the

Table 20 showing percentage of fish with abnormal growth in third year in different year classes of Norwegian spring herrings in different years.

Year	Percentage of abnormal fish ($t_3 < t_4$)		
	Year class 1905	Year class 1904	Year class 1903
1910	8	32	18
1911	7	30	21
1912	8	34	13
1913	7	35	10

following way: »Determination of the age of the fish by the scales did not present appreciable difficulty after I had practised it somewhat. In such localities where the herring spawn during the whole summer, the scale examination may possibly be more intricate«. [Translated from Swedish]. My own experience includes but few instances, where an age determination by means of scales was a matter of impossibility; as in a sample of small herrings sent by Professor HEINCKE from Helgoland the scales failed in giving certain information of the age, and in some samples from the coasts of Ireland the age determination was difficult owing to the presence of many faint rings in the summer belts.

EXPLANATION 3.

Contraction of the scale.

Regarding this Miss LEE says on p. 13: »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 explained 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«.

Formally this explanation is satisfactory in so far as changes in the relative distances between the winter rings on the scales will imply corresponding changes in the calculated growth dimentions [t_1, t_2 etc.]. But really it is not easily maintained, as it is extremely difficult to conceive, that some parts of the scale contract while other parts must be supposed to expand if the phenomena described as the apparent change in growth rate are to be explained from the hypothesis of a change in the relative distances between the winter rings on the scales. However this may be it has been deemed useful to test this hypothesis according to the following plan. As shown in the foregoing, the dimensions t_1, t_2 and t_3 decrease with increasing age. If this apparent decrease is effected in such a manner, that the scale matter corresponding to these dimensions, contracts or is pressed inwards by the outside matter superimposed upon it, then the average distance between the fine ridges on the scales must be lessened by this contraction. By measurements of the distance between these ridges in young and old scales it is possible to decide whether contraction takes place or not[1]. With this idea in view I collected in April of this year a sample of mature Norwegian herrings consisting of 151 individuals belonging to different age groups:

7	were	born	in	1908,	being	5	years	old
7	»	»	»	1907,	»	6	»	»
8		»	»	1906,	»	7	»	»
9	»	»	»	1905,	»	8	»	»
107	»	»	»	1904,	»	9	»	»
13	»	»	»	1903—1899	»	10—14	»	»

In addition, 26 herrings belonging to the year class 1912 showing two summer belts on the scales, were procured in the first days of September. For each of these 177 fish the average distance between the ridges in the three first summer belts was determined in the following manner. The breadths of the three first summer belts were measured along a line from the centre of the scale perpendicular on the basal line. They are termed b_1, b_2 and b_3 respectively. The number of ridges in each of the three summer belts was counted along a line running from the little bend in the basal line to the side of the centre parallel to the measuring line (see fig. 1 on p. 14). This was done in order to avoid the median line. As the first ridge in the first summer belt was reckoned that lying nearest to the basal line, and as the last one that which crossed the first winter ring at the point, where this is intersected by the median line. The next ridge outside was reckoned as the first ridge in the second summer belt, and

[1] Fage 3) has very recently proposed the very same plan for testing the hypothesis of contraction.

so on. The number of ridges in the summer belts are termed n_1, n_2 and n_3 recpectively. The ratios $\frac{b_1}{n_1}$, $\frac{b_2}{n_2}$ and $\frac{b_3}{n_3}$ express the average distances between the ridges in the three summer belts, and these ratios ought to have lower values in old scales than in young if contraction has taken place.

An analysis of values obtained for each fish showed:

1) That the values varied somewhat from fish to fish from about 0.017 mm to about 0.024 mm in the common manner. This variation is partly due to errors in counting and measuring, and is partly a real individual variation.

2) That there was no correlation between the absolute size of the summer belt and the distance between the ridges, *viz.* that small increments are strictly comparable with large ones. This is proved by the tables 21, 22 and 23 giving the average distance between the ridges for varying sizes of the summer belts in a single year class (1904).

3) That the individual variation is too small to cover a difference between the average distance between the ridges of young and old herrings even if it is only a fraction of the difference which must be expected to exist if contraction had caused the change in growth rate (this expected difference can easily be calculated and amounts to at least 0.003 mm while a difference of 0.0015 mm between wo averages can be detected.

Table 21.

Length of b_1 in $\frac{mm}{10}$	No. of observ.	Average distance between ridges in $\frac{mm}{1000}$
9.1 to 10.0	1	23
10.1 » 11.0	0	—
11.1 » 12.0	5	20
12.1 » 13.0	10	21
13.1 » 14.0	19	21
14.1 » 15.0	14	20
15.1 » 16.0	16	21
16.1 » 17.0	12	20
17.1 » 18.0	14	20
18.1 » 19.0	11	21
19.1 » 20.0	3	22
20.1 » 21.0	1	21
21.1 » 22.0	1	22

Table 22.

Length of b_2 in $\frac{mm}{10}$	No. of observ.	Average distance between ridges in $\frac{mm}{1000}$
6.1 to 7.0	4	19
7.1 » 8.0	2	19
8.1 » 9.0	17	20
9.1 » 10.0	17	20
10.1 » 11.0	11	19
11.1 » 12.0	10	20
12.1 » 13.0	14	20
13.1 » 14.0	6	20
14.1 » 15.0	13	20
15.1 » 16.0	5	20
16.1 » 17.0	3	21
17.1 » 18.0	3	19
18.1 » 19.0	2	20

Table 23.

Length of b_3 in $\frac{mm}{10}$	No. of observ.	Average distance between ridges in $\frac{mm}{1000}$
4.1 to 5.0	2	21
5.1 » 6.0	12	20
6.1 » 7.0	12	21
7.1 » 8.0	10	20
8.1 » 9.0	7	19
9.1 » 10.0	18	21
10.1 » 11.0	5	20
11.1 » 12.0	12	21
12.1 » 13.0	13	21
13.1 » 14.0	7	20
14.1 » 15.0	8	20
15.1 » 16.0	1	20

In the following table 24 the average distance between the ridges in the three summer belts is tabulated for each age group together with the variation constant (σ) and the standard error of the averages $\left(\beta = \frac{\sigma}{\sqrt{\text{No. of variates}}}\right)$.

This tables shows in a very convincing manner, that there is no indication of a decrease in the average distance between the ridges.

If we take all possible differences between averages for two years and calculate the standard error of these differences according to the formula standard error $= \sqrt{\beta_1^2 + \beta_2^2}$ and if we demand that a real difference shall be at least three times as large as its error, then we find:

that there is no real difference in 43 cases,

that the older year class has a larger stripe interval in 13 cases

» » younger » » » » » » 1 case.

These facts must be regarded as decisive for the hypothesis of contraction, which appears to be opposed to actual facts, and must consequently be rejected.

Our knowledge of the relation between the growth of the herring and the growth of its scales is enlarged by the above mentioned measurements in a way that makes it possible to consider the method of individual growth calculation as regards the herring as wholly correct within the limitations of exactitude formerly stated [LEA (7)]. For, as it is now prowed that the different zones on a scale really give a *lasting* picture of the growth of the scale, and as the size of the scale grow in proportion to the size of the fish [LEA (7)] then the conclusion must inevitably be drawn that the zones on the scales also give a lasting picture of the growth or the fish.

The conviction of the reliability of the method of individual growth measurements, arrived at by the above mentioned measurements, will facilitate the task of explaining the apparent change in growth rate. For we may now safely neglect the possibility of systematical errors in the numerical data employed and regard the apparent change as an expression of phenomena really occurring in the life of the fish and not as a product of methodical errors.

EXPLANATION 4.

Selection.

Having demonstrated, that no methodical errors can produce the apparent change in growth rate, there remains only one possibility *viz.* that the average do not represent the same things in

Table 24 showing for each age group the average distance between the ridges in the three first summer belts of the scale, with the corresponding indices of variability and the standard errors of the averages.

Year class	Number of variates	Average distance between ridges $^1/_{1000}$ mm			Index of variability $^1/_{1000}$ mm			Standard error of the average $^1/_{1000}$ mm		
		1st summer belt	2nd summer belt	3rd summer belt	1st summer belt	2nd summer belt	3rd summer belt	1st summer belt	2nd summer belt	3rd summer belt
1912	26	19.1	19.6		±0.8	±1.3		±0.2	±0.3	
1908	7	18.8	18.7	20.6	±1.0	±1.5	±1.0	±0.4	±0.6	±0.4
1907	7	18.5	18.0	18.7	±0.5	±1.1	±1.6	±0.2	±0.4	±0.6
1906	8	18.8	18.8	20.5	±1.0	±1.3	±0.8	±0.4	±0.5	±0.3
1905	9	19.9	19.1	20.0	±1.2	±1.2	±1.5	±0.4	±0.4	±0.5
1904	107	20.5	19.7	20.3	±1.3	±1.6	±1.7	±0.1	±0.2	±0.2
1903–1899	13	20.3	20.3	20.5	±1.0	±1.4	±1.2	±0.3	±0.4	±0.3

Table 25 showing relation between growth and development of sexual organs in the year class 1907 in the samples of herrings from the Faroes.

Year and date of capture	Number of individuals	Measured average length	l_1	l_2	Incomplete l_3	State of sexual organs				
						I Immature	II Immature	III Mature	IV Mature	V Mature
1909, 7–8	170	25.4	11.7	8.9	4.8	*120*	18	32	0	0
1909, September	595	26.3	13.8	8.1	4.4	43	27	98	*417*	10

the different years. Upon this idea our own explanation is based. The main assumptions of this explanation are the following:

1) A certain year class of a tribe of herrings is as a rule divided up in components according to the individual state of development.

2) This developmental division is connected with a division according to the growth of the fish, the component of more developed individuals being also the component of the largest ones.

The change in growth rate is effected by segregation from one component and congregation with the other.

In addition the following assumption is made.

3) The annual increment is on an average larger in fish which do not simultanously develope their sexual products than in fish of the same age wich develop their sexual products.

These three assumptions suffice for a complete theoretical explanation of the apparent change in growth rate, and our task will only be to verify the three assumptions. The material at hand is collected for other purposes, but permits us in some cases to demonstrate the selective effect of the development of the sexual organs. The following table 25 is exellently suited for exemplifying our explanation.

It will be seen from this table that the year class 1907 among the herrings caught in the fiords of the Faroes is divided in two kinds of shoals, one comprising mainly immature fish, the other comprising mainly fish in advanced stages of sexual developement (assumption 1). It is further seen, that the average size in the sample of mature fish is larger than that in the sample of immature fish (assumption 2). Moreover it will be seen, that the last increment is larger in the immature fish than in the mature (assumption 3). What will be the result if the immature fish should at some future time mature and, wandering to the spawning places, congregate, with the fish which had matured before? *The t_1 will decrease, while t_2 and t_3 will increase.*

The change has quite the same character as in the case of Norwegian herrings with an increase of some increments and a decrease of others. The difference that only t_1 decreases while t_2 and t_3 increase is immaterial and easily explained by the fact that the first sexual maturation takes place at younger age in Faroese herrings than in Norwegian herrings.

From the tables 26 and 27 it will be seen that analogous conditions prevail among the herrings from Icelandic waters. Individuals of the year classes 1904 and 1903 are found in shoals

Table 26 showing difference in average growth of immature and mature herrings of the year class 1904 from Iceland June and July 1908.

Sexual development	Number of observations	Average length	t_1	t_2	t_3	t_4
Immature	22	21.8	7.0	5.2	4.6	3.6
Mature	55	30.1	10.9	8.5	6.1	3.8

Table 27 showing difference in average growth of immature and mature herrings of the year class 1903 from Iceland June and July 1908.

Sexual development	Number of observations	Average length	t_1	t_2	t_3	t_4	t_5
Immature . .	6	21.5	6.3	5.4	3.7	2.7	2.1
Mature	66	31.8	9.6	9.0	6.5	3.5	2.4

of totally immature fish as well as in shoals of old and mature fish (assumption 1), and the average size of the mature individuals is much larger than the average size of the immature (assumption 2). In these instances all increments up to t_5 will decrease, when the congregation takes place.

The material of Norwegian herrings of the year class 1904 offers exellent material for a study of the developmental division, the correlation between size and state of sexual development, the segregation and congregation, and the effect of sexual development upon the annual growth. And such investigations are greatly facilitated by a peculiar growth-phenomenon causing some individuals to be easily distinguished from others. Fig. 2 on p. 15 is a photograph of a scale belonging to a herring born in 1904. It will be seen, that the third summer belt is not so broad as the fourth, thus indicating that the herring has contrary the general rule, grown better in the fourth year than in the third. Herrings with such an abnormally small growth are very common in the year class 1904 of the Norwegian herrings, and their percentual number in the different localities and at different time varies in so characteristic a manner as to allow of a very close analysis of the above mentioned phenomena.

Table 28 shows for several years what percentage the fish of the year class 1904 constituted of the total number among spawning and immature fish. It is seen that the year class is divided up into (at least) two components during 4 years (assumption 1).

Table 28 showing for different years the percentage of fish belonging to year class 1904 in total number, and the percentage of abnormally grown fish in the year class 1904. The spawning fish caught in spring off the west coast of Norway The immature fish caught in autumn in the northern Norwegian waters.

Year of capture	Spawning fish		Immature fish	
	% of year class 1904	% of abnormal	% of year class 1904	% of abnormal
1907	1.6	—	51.3	52*)
1908	34.8	—	37.8	65
1909	43.7	—	16.9	67
1910	77.3	32	4.8	69
1911	70.0	30	—	—
1912	65.6	34	—	—
1913	63.1	35	—	—

*) This figure is too low owing to the fact that t_4 was incomplete at the time of capture.

The percentage of abnormally grown fish will serve to prove, that the year class 1904 has been divided into at least three components. For it is seen, that no abnormal fish appeared among the spawning herrings until 1910 and on the other hand there has evidently before that time taken place an intensive immigration into the shoals of spawning herrings, raising the percentual number from 1.6 in 1907 to 43.7 in 1909. As none of the herrings immigrating before 1910 had grown abnormally we may infer that the northern Norwegien stock had not at that time contributed to the increase of the year class 1904 among the mature herrings. Consequently we find for 1907 one component consisting of mature fish, another component consisting of immature fish increasing during 1908 and 1909 the relative abundance of the year class 1904 among the spawning herrings, and lastly a third component of immature herrings appearing for the first time among the spawning herrings in 1910 (Assumption 1).

The immigration into the shoals of spawning fish of individuals belonging to the second component can be followed in our samples of spawning herrings.

In February 1908 relatively few individuals belonging to the year class 1904 were present among the spawning fish, but in April of the same year the relative abundance had increased considerably, as is shown by table 29.

The difference in size is also obvious (assumption 2).

Table 29 showing the increase in relative abundance of the year class 1904 among spawning herrings and the difference in size between those present in February and those, which immigrated later on.

Locality and date	Number of individuals of the year class 1904	Percentage of the year class 1904 in the total sample	Average length cm
Føina, February, 1908. . . .	140	15.9	28.6
Bakkesund, April 4, 1908. .	358	65.2	27.6

None of these herrings immigrating in 1908 had grown abnormally in the third year, thus evidencing, that they do not belong to the component from the northern part of Norway. The immigration of fish of this third component took place for the first time in 1910, as is seen from table 28, but as some individuals of this component were still present in the northern Norwegian stock in 1910 we are justified in inferring that the immigration of the component was not completed before 1911. Table 30 shows the difference in average length between the individuals which in certain years had become mature and those still remaining immature in the northern part of Norway.

Table 30 showing for four years the average length of the herrings belonging to the year class 1904 among mature and immature fish, the last having had nearly a whole summer's more growth.

Year of capture	Mature fish spring		Immature fish autumn	
	No. af fish measured	Average length	No. of fish measured	Average length
1907	15	25.5	1175	22.0
1908	498	27.8	804	24.2
1909	248	29.1	331	26.2
1910	382	28.3	78	27.4

That the immigration of the immature herrings from the northern Norwegian stock will cause a change in the growth dimensions is evident. The character of this change will be seen by comparing the single growth dimensions in the mature and immature fish. From tables 7 and 8 the following table 31 is compiled.

It will be seen that t_1 t_2 and t_3 will decrease, and that t_4 and t_5 wil increase if the immature fish of the northern compnonent

Table 31 from which it can be deduced that t_1 t_2 t_3 must decrease, while t_4 and t_5 must increase if an immigration takes place into the shoals of spawning herrings of hithertho immature fish of the component from the northern Norwegian waters.

Kind of herring, year of capture	t_1	t_2	t_3	t_4	t_5
Spawning fish in spring 1909	8.8	7.8	6.7	3.5	2.3
Immature fish in autumn 1909 . . .	7.1	5.0	3.5	3.9	3.4
Spawning fish in spring 1910—1913	7.9	6.6	5.3	4.0	2.9

immigrate into the shoals of mature fish. It will further be seen that this is exactly what has taken place, and that the change caused by the immigration corresponds in detail with the change really observed.

No better agreement can be expected than that found between our explanation of the apparent change in growth rate and the facts observed.

The phenomena actually taking place are:

1) When a certain year class is approaching the period of sexual maturation, the larger individuals will develop their sexual products earlier than the smaller.

2) Those individuals which have reached maturity will congregate with the older spawning herrings.

3) Among the herrings remaining in an immature state some, and also in this case the larger ones, will be ready for spawning the next year and then congregate with the spawning herrings, and so on until all herrings of the year class have become mature.

4) The development of the sexual products has the effect of depressing the length increment simultanously taking place.

Besides the proofs set forth above of the correctness of our assumptions the following may be given. Table 32 supports assumption 3, showing for the individuals of a year class in a single sample, that those fish which have developed their sexual products have simultanously had a lesser increment than those remaining undeveloped.

Table 33 furnishes evidence of the correlation between sexual developement and average length for a whole number of samples and for very different stages of sexual developement.

The evidences set forth will, it is to be hoped, suffice for an analytical proof of the correctness of our explanation of the

Table 32 showing the last increment (t_6) as a function of the sexual development simultaneously taking place. (Year class 1904, Collection 5, Publ. de Circonst. No. 53, 1910.)

Sex	Stages of sexual development					
	I	Number	II	Number	III—IV	Number
Males	3.4	70	3.3	34	2.6	20
Females	3.3	73	3.2	78	1.9	7

Table 33 showing difference in length between sexually less developed and sexually more developed herrings of the same age in the same sample.

Collection nr, Date, Locality	Condition	Year class	Stages	♂ Average length	♂ No. of observ.	♀ Average length	♀ No. of observ.
Coll. 5 (1909) Aug., Northern Norway	Immature	1904	I II—IV	25.5 26.7	70 54	25.2 26.4	73 85
Coll. 10 (1910), Nov., Western Norway	Large, not fully mature	1904	I—III IV—V	29.6 30.5	72 73	30.1 31.2	167 31
1911, Jan., Western Norway	Nearly mature	1904	I—III IV—VI	29.8 30.8	94 187	30.0 30.7	83 189
1911, ult. Feb., Western Norway	Fully mature	1904	III—IV V—VII	31.1 31.4	50 68	30.9 31.8	41 89
1911, April, Western Norway	Fully ripe, partly spent	1904	II—IV V—VII	29.5 29.8	50 114	29.6 29.8	7 86
Coll. 10, 1909, Sept. North, eastern North-Sea	Recovering	1904	II III—IV	28.8 29.0	71 69	29.1 29.2	84 22
Coll. 19, 1909, Aug., Faroes	Immature	1907	I II—III	24.8 26.0	65 33	25.1 26.8	67 17
Coll. 21, 1909, Sept. Faroes	Nearly mature	1907	I—III IV—V	26.0 26.3	84 414	26.5 26.4	85 18

apparent change in growth rate going on during the time, when the individuals of the year class become sexually mature. But as the apparent change is possibly going on after all the individuals of a year class have congregated with the spawning herrings, the assumption must be made that similar selective processes take place at a later stage in the life of the fish. If the death rate is correlative to the number of spawnings effected in such a manner that a herring with say 6 spawning periods behind it has a greater life probability than a herring of the same age with 10, then the herrings which attain the highest age will be those which have reached maturity relatively late in life viz. the herrings with low growth rate. SUND (10) has, with regard to the sprat, expressed this idea in the following words: »The originally small individuals will generally attain a higher age than those who grow fast in early life«. It results from the nature of the case that a verification of this assumption by more direct observation is extremely difficult, and the material at present available gives only a very faint hint. Looking at the table 20 or 28 it will be seen that the percentage of abnormally grown fish has increased slightly from 1911 to 1913 (after all fish of the year class had reached maturity). Recognizing of the fact that these abnormal fish attained maturity at a higher age than other fish of the year class, and consequently have not spawned so many times as others, this increase is not without importance. If it is shown by future investigations that the percentual number of abnormal fish increases as time goes on, a convincing explanation will be at hand of the apparent change in growth rate during the later years of the life of the herring.

Conclusions.

1. The phenomenon of apparent change in growth rate, as it appears in the numerical data, is observed as a difference in the average values of corresponding growth dimensions of younger and older fish. Some growth dimensions have a tendency of being greater in the younger fish than in the older, while the reverse is the case with other growth dimensions.
2. These differences are not due to methodical errors occurring in the material used.
3. On the contrary they represent important features in the biology of the fish, *viz.* sexual development correlated to the growth, separation of the individuals of a year group in components of different sexual development and intermingling of these components in the course of time.

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