https://doi.org/10.17895/ices.pub.9464

3

A MODIFICATION OF THE FORMULA FOR CALCULATION OF THE GROWTH OF HERRING.

BY

EINAR LEA.

THE growth of an organism is a fundamental part of its life. It is therefore justifiable to assume that, where they are available, descriptions of growth history will be of significance. This does not apply merely to investigations in which growth occupies a prominent place, but also to those in which, although the problem does not directly involve the growth of the organism, the phenomena under consideration are, nevertheless, dependent in one way or another on growth. To mention one or two examples only, it can now be seen that it would have been of material help if growth-data had been at the disposal of Heincke and his successors in the biometric line of work, and that the study of the ramifications of the influence of the sexual functions on the life history of fish, *inter alia*, on their migrations, is rendered more difficult or facilitated all according to whether information on growth is, or is not, available.

From considerations of this nature it must present itself *per se* as a useful and important task to develop methods for individual growth determination in those cases in which this is possible. A possibility of this kind exists in the case of the herring and probably also of those species of fish in which the annual rings on the scales or bones are sufficiently definite to permit of fairly precise measurements being taken.

The conception that the permanent picture of the growth of the herring scales, which is registered by the formation of annual rings, can be employed for calculation of the individual growth of the fish expressed in the conventional measure — the total length — has its origin, to some extent, in a number of more or less precise observations which are brought forcibly to the notice of everyone who performs the basic observational work on actual herring samples and does not start the work from tabulated observations made by others. To some extent the conception arises from more precise observations of the arrangement of the annual rings on the scales.

Irrespective of whether he examines his herring samples biometrically or otherwise an observer cannot avoid noticing such matters as that fish varying greatly in size have, nevertheless, in their broad features approximately the same shape; that the number of scales and their arrangement on the body are, on the whole, the same; that scales which have a definite situation and a characteristic form occur at the same place and with approximately the same form in both small and large fish; and that the size of the fore part of the scales, that which has a fluted surface, corresponds to the width of the muscle segment which the scale overlies and covers.

Observations of this kind naturally give birth to the idea that in its development from a small to a large fish the herring acts approximately as an isomorphous body or, to use Huxley's terminology, the herring has an isogonic growth. In this connexion it is of interest to mention that in his work "Problems of Relative Growth" (1932), which is mainly devoted to organisms and organs with conspicuously heterogonic growth, Huxley cites ichthyometric data as an illustration of isogonic growth.

The simple proportion formula for growth calculation,

$$l = \frac{s}{S} L,$$

is none other than a precise mathematical formulation of this conception of isomorphous growth in so far as concerns the quantities used in the formula, and it is more or less valid in the same measure as the conception corresponds more or less exactly to the actual conditions.

Simultaneously with this conception, certain critical counter ideas also arise from general observations of this nature. To a fairly well-trained observer it is sufficiently obvious merely on inspection and comparison of samples of both small and large herring that the form of the individuals irrespective of size is not exactly the same. There is undoubtedly a small but nevertheless obvious difference in the bodily proportions between the large and the small individuals, and this difference proceeds in a definite direction; for example, the head of the small herring appears comparatively larger than that of the large herring.

The isomorphism (or isogonism) cannot therefore be complete and the proportion formula mentioned above cannot be expected to give an absolutely correct expression of the actual conditions.

The more precise observations, which operate in the same direction to stimulate the idea of exploiting the growth history registered on the scales, concern the arrangement of the annual rings on scales from the same individual. This arrangement, to which numerical expression can easily be given by measuring the distances from the growth-centre of the scale to the winter rings, as well as the scale-edge, and converting all measurements into units or percentages of the last measurement, shows such great similarities when the question is one of measurements from adjacent scales, even if the absolute measurements of the scales happen to be conspicuously dissimilar and such regular changes in the numerical values where entire series of scales are concerned that it is imperatively necessary to seek an explanation. In my opinion, this conformity to rule is incomprehensible unless the facts observed are supplemented by the assumption that the observable growth histories which the scales reveal are very closely allied to the growth of the individual as a whole, and thus also to the increase in the measurement which is conventionally used to indicate the size of the individual — the total length.

Observations of this kind, which can also be extended to several measurement dimensions of the same scale and even to characteristic details of the formation of the winter rings (sharp or diffuse rings, double ring formations and the like), form, in my opinion, the real basis of, and argument for, the conviction that the actually existent and measurable growth history of the herring scales can be converted into expressions which are comparable with the conventional measurements of length ("empirical lengths").

The acceptance of this close connexion between that which, for the sake of convenience, we may call the growth in length of the herring and the more special growth histories, which can be observed directly on the bones and scales, is independent of, and thus also compatible with, every conception of how the connexion can best be formulated in a mathematical equation applicable to a definite measurement dimension of a particular scale. It is *per se* possible that the growth in certain definitely localized scales really is sufficiently isomorphous with the growth in length, in which case the already mentioned simple proportion formula is valid for these scales, and it is possible that the connexion for other scales (alternately other scale dimensions) can best be expressed by other mathematical equations. To elucidate this is an important technical or practical task for the development of the growth method, and it can conceivably be done in several ways. But the result of this work cannot be at variance with, nor change anything in, the above-mentioned similarities (or regularities) with regard to the particular growth histories, which are revealed by a consideration of the annual ring system of the scales.

We can even, in principle, renounce, or save ourselves, the work of discovering an equation which connects the growth in length with the growth of a definite scale, namely, by defining the growth history of the individual as that which the scale reveals. We must then, it is true, at the same time abstain from using the length as a conventional expression of the size of the individual, and use instead the size of the scale to express it. Strong objections of a practical nature can be raised to such a change in the conventions, e.g., that a scale is such a small element of the organism, or that it will make it difficult to define the size of individuals which have not yet acquired scales, and so on. But, in principle, as far as I can see, there can be no objection to adopting this line of thought; and, in fact, practical application of this solution has been given effect in a work by E. M. Watkin (1925).

The conviction of the intimate connexion between the thousandfold particular growth pictures, which are registered on the scales of a herring, and the growth of the individual as a whole is thus founded on facts which can be observed in the one individual alone and in repetitions of this class of observations individual by individual. It is not founded on results which are acquired by a collective analysis of samples of herring. It is a different matter that in the course of the work of drawing up calculation formulae it has been found necessary to operate with such collective data. The necessity for this is not a matter of principle but is due to the fact that it has not been technically possible, in any event as far as the herring is concerned, to follow the connexion by means of individual observations. In the case of other species of fish such individual observations may feasibly be carried out in aquarium experiments, as performed by Thompson (1926), and specially arranged marking experiments. Ø. Winge (1915) has succeeded in obtaining a few individual observations of this kind by marking cod.

In the practical-methodical work of developing formulae for the calculation of growth, and in the critical investigations which have been carried out different methods of procedure have been adopted. (As the use of the simple proportion formula has been extended to many species of fish, and as both methodical work as well as valuating views are contained in works on fish other than the herring I refer to some of these in the following remarks).

In one group of investigations represented by K. Dahl's work (1910) on salmon and trout, Rosa M. Lee's (1912) on herring, salmon, trout and haddock, and many others, the statistical tests are intended to decide whether the growth figures which are obtained by the employment of the simple proportion equation are plausible, that is to say, whether they answer to what is considered legitimate expectation. In this class of investigation average values have been chosen for "empirical" length measurements to act as prototypes, and the extent of agreement between these "empirical" average values and the corresponding "calculated" average values has been regarded as expressing the degree of "correctness" of the latter.

A variant of this type of investigation is found in Rosa M. Lee's work (1912) in so far as, in addition to the comparison mentioned, she also uses comparisons between corresponding calculated growth figures for different age-groups. It is by means of this kind of calculation she arrives at what she has termed "the apparent decrease in growth-rate with increasing age", that is to say, the fact that the growth figures for the older animals in a sample generally have, on an average, lower values than the corresponding figures for the younger animals in the samples; and it is mainly on this circumstance that she finds grounds for holding that the growth calculation method cannot yield correct results. C. Segerstråle (1921) has, so to speak, systematized this idea by searching for measurement dimensions on the scales, which, by the use of the simple proportion formula, lead to calculated values with the greatest possible accord with the "empirical" average.

In another form a similar method for testing is taken as a basis in Hodgsons (1929) work. Instead of comparing corresponding average values of calculated lengths for different age-groups (of different year-classes) he compares corresponding length-frequency curves for the same year-class in catches from different years. And as, in his data, these curves have a comparatively characteristic, multimodal form, more and better evidence is provided in the comparison for a critical test than in a comparison of arithmetic means.

Possibly this kind of criterion may be considered as having a certain degree of importance in cases where it is a question of investigating whether the calculated growth figures are fairly correct. But it is clear that great uncertainty attaches to this procedure. It assumes, in effect, a knowledge that the average values of the calculated growth figures must actually agree with the corresponding "empirical" average figures in order to be correct; and in what concrete cases can such an assumption be upheld with certainty? Moreover, the question of what can be regarded as a satisfactory accordance will here, as elsewhere, depend on the requirements of the various problems.

In another group of critical investigations the nature of the calculated growth figures, whether they appear to be plausible or otherwise, has been entirely disregarded, and attempts have been made (a) either to find independent criteria for discussing the legitimacy of the simple proportion formula, or (b) on the basis of such independent criteria to construct other equations for calculating growth. To the first sub-group (a) belongs my work of 1910 and Buchanan-Wollaston's (1934), to mention two extreme points in time. To the other sub-group (b) belong such works as those of Rosa M. Lee (1920), Huntsman (1918), Graham (1929), for cod, and a number of others.

In all investigations within this group use has been made of collective data, but in some cases in very different ways, and in all of them occurs the size S (= a linear dimension as a measure for the total length of the fish). In the majority of the works under sub-group (b) use has also been made of the technique of the correlation theory, either in its more primitive empirical form (e.g., as in Huntsman where S is plotted against L in a co-ordinate system, and a line drawn as nearly as possible to the L—S points), or with the application of the formulae of the theory for the calculation of the correlation co-officiant r and regression lines.

A number of these works (Meek 1916, Rosa M. Lee 1920) also take into account the fact that the scale covering is not formed until the herring are 3—5 cm. long, and it has been asserted that a formula such as the simple proportion equation

$$l = \frac{s}{S} L$$

cannot be valid for this reason, as it of course describes straight lines which all start from the origin.

When we try to decide whether the technical-methodic investigations hitherto carried out have resulted in a clear understanding of the validity of the growth methods, I think that this is not the case. And this applies irrespective of whether we enquire if the simple proportion equation has been more firmly established or whether some other well-founded formula has been advanced which yields results more in accord with reality.

Presumably it is unnecessary here to demonstrate this in detail, particularly in view of the fact that the opinions of the individual workers in regard to methods of growth-study differ so widely, some of them, such as Hodgson, taking the view that the original simple proportion formula is essentially sound whereas others are more reserved and some of them (Molander 1918) to all intents and purposes appear to consider that there is no rational basis for converting the growth history of the scales into terms of the total length.

This does not mean that the work hitherto done in connexion with the methods has been in vain, or that it is of no value. This is not the case since, *inter alia*, the work is of use in drawing up a scheme for new investigations for the establishment of the methods of growth-study.

Nor must the conclusion be drawn from what has been said above, that the great number of biological investigations which are carried out by means of growth calculations are influenced by the consideration. For in the majority of these, regard has been had to the circumstance that the simple proportion formula cannot in general yield numerical results which are entirely faithful to actual conditions. This was expressly emphasized as long ago as in my earliest work (Lea 1910, page 12).

If the foregoing is a fairly correct statement of the state of affairs as they are at present it should, in my opinion, stimulate us to continued efforts to place the growth method on to a more secure basis.

To this motive another must be added, which is of special weight in connexion with investigations relating to herring in Norwegian waters. In regard to this herring the first point to emerge from all previous investigations is that there is a great diversity in the size of the individuals within a single year-class. This is undoubtedly a consequence of the differences in *milieu* over the wide area of distribution of this Norwegian herring. Secondly, great differences are revealed between different year-classes, and this, presumably, is also connected with the difference in the external conditions under which the individuals of the various year-classes have grown up. These diversities, which apply from an early age onward, can be traced without the aid of growth calculations from the scales, merely with the help of data referring to age and size.

As a result of these differences the single individuals of a year-class have, to some extent, a widely varying history, as shown for example by the fact that some of the individuals of a year-class join the spawning shoals when they are not more than 3 or 4 years old, whereas others wait until they are 5 or 6 years, or even 7 or 8 years; or in the proportion in which a number of the individuals of the year-class terminate the coastal period of life as young herring of $1\frac{1}{2}$ or $2\frac{1}{2}$ years and pass into an oceanic stage, while others postpone this until they are $4\frac{1}{2}$ or $5\frac{1}{2}$ years or more. And similarly the result of the differences is that the individuals of the different year-classes act differently in these respects. They are reflected also in the possibilities which present themselves from year to year of catches of young herring, and they also make their influence felt in the fishing for full-grown herring, in as much as, for example, a considerable influx of fish spawning for the first time can cause great changes both in the quality of the catches and in the course of the fishery.

It can hardly be contested that the study of these phenomena must form a very important part of the Norwegian herring investigations. Similarly also it cannot be denied that a sound method of calculating growth would be of prime importance in such investigations.

My opinion in this respect has been strengthened by reading Runnstrøm's (1936) paper on the Norwegian herring. In this the author has used growth-data obtained by means of the simple proportion equation from a material divided into groups according to the "character" of the winter rings, a systematization the principles of which I set forth in 1926—1928 (Lea 1929). In conformity with these principles it is possible to divide a sample of Norwegian herring into a large number of categories, (a) according to whether the individual herring has passed the first part of its youth in southern or northern coastal waters, (b) according to whether the coastal life has stretched over 1, 2, — 6 winter seasons, and (c) according to whether the subsequent oceanic young stage, during which sexual maturity is completed, has covered, 1, 2 or 3 winter seasons (more correctly, periods for the formation of winter rings).

The growth-curves which can be drawn up for the various categories have such characteristically different courses (see, for example, Fig. 9, page 77 of Runnstrøm's paper) that, as far as I am concerned, I cannot avoid drawing the conclusion that by combining the two methods of observation (sorting according to the scale character and growth calculation) many fresh possible ways are opened up for investigating several important processes which take place in the Norwegian herring population — the grouping of the young herring on the coast in shoals according to size of fish and the re-grouping among these; the passage from these shoals of the individuals entering the oceanic stage; the accession from this oceanic group to the spawning shoals. All these processes are closely concerned with the growth of the individual and their occurrence can be apprehended by the methods as they now stand. Nevertheless we may hope to describe them more precisely, and perhaps also to calculate them quantitatively, if the methods can be improved.

The disadvantage of using the simple proportion formula

$$l = \frac{s}{S} L$$

as an equation for calculating growth lies in its lack of a term which compensates for heteromorphous growth. In my first work I tried to effect such a compensation in two ways, (1) by setting up a compensation table, valid for the scales immediately behind the gill-cover, and (2) by seeking a part of the body where the scale grew as little as possible heteromorphously with the growth in length. In spite of the fact that the correction table mentioned in (1) still has, in my opinion, a certain value as regards the scales in question, it is readily admitted that it does not fulfil the requirements to-day. And both methods of compensating cannot be said (in any event as far as Norwegian herring are concerned) to be practical. This is because, for determination of age, scales should be taken from the middle region of the 5th—12th muscle segment, and not from immediately behind the gill-cover or from the 25th—28th muscle segment as assumed by alternative (1) or (2). As there is a difference in growth between these three groups of scales, either it will be necessary to collect duplicate sets of scales, one for the age-census and one for the measurement of growth, a cumbersome method, or a new correction table must be drawn up applicable to the scales best suited to age determination. If it is decided to take this course, it must of course be done as efficiently as possible.

The disadvantage arising from the lack of a compensatory term in the calculation formula does not lie in a lower degree of precision in the observations, nor are the advantages of a suitable correction to be found in an increase in the precision, if by precision is understood the chance errors of the observations. The disadvantage arises from the fact that the observations show a systematic error, the numerical value of which is not constant but is dependent, *inter alia,* on the difference in size between the measured total length and the estimated length of the 1st, 2nd, etc., winter ring.

The result of this is a varying degree of comparability in the case of corresponding growth figures (e.g., l_1) from groups of different total lengths. In a carefully made analysis of a material this circumstance involves no small amount of work in ascertaining which observations are really sufficiently comparable for the purpose in question and which of them cannot be regarded as being so. Moreover, the material cannot be so fully utilized, because it is necessary to refrain from drawing comparisons which are desirable in themselves.

In other words, the use of the simple proportion formula is uneconomic, just as it would be uneconomic to use uncorrected thermometers for hydrographic surveys. Furthermore, satisfactory elimination of the systematic error previously mentioned will increase the number of permissible comparisons of growth-data in a given material and make the work easier and more certain. The procedure followed in my work for obtaining a better growth formula is described below.

The Material and Observations.

The basic observations used are the total length L as an expression of the size of the fish, and a linear dimension S to express the size of the scale, in agreement with previous practice. In my early work (1910), however, I chose a scale which was easy to find but which is not normally used in the ordinary routine collections and investigations, and a dimension for this which, from the point of view of the technique of measurement, was convenient for this particular scale but which is inconvenient when measuring other scales. In the subsequent collection of material I have selected a scale which is situated in the seventh horizontal scale series from the edge of the belly and which is No. 7 from the operculum. This scale was chosen for two reasons, (1) because it is situated in that region of the body of the herring where the age-rings on scales of old animals are easiest to discern, and (2) because there does not appear to be any noticeable difference in average size between this scale and its neighbours. This latter circumstance enables one to substitute one of the adjacent scales for the selected scale if this is missing or must be excluded from the material because it is regenerated or shows signs of mechanical dislocation. In the collection of material two neighbouring scales, Nos. 6 and 8, were included and used in particular cases.

The method of measurement which was used is the same as that employed in the routine work, the distance from the "growth-centre" to the edge of the scale along a line as perpendicular as possible to the somewhat uneven basal line between the fluted and smooth parts of the scale. The growth-centre of the majority of scales used can easily be localized by means of certain peculiarities in the scale surface immediately below the basal line, which has a characteristic bend there.

The material collected consists of samples of Norwegian herring of as many different ages and sizes as possible, from samples of herring of less than a year old to fully grown individuals of more than 15 years. They range over the entire area of growth measurements, from the formation of the first ring to those many years old.

Each sample has been kept separate and divided into sub-groups according to age.

Treatment of the Observations.

The first step in the treatment of the material is dictated by the following considerations:—

If in the case of a sub-sample of old animals, say, 15 years of age, the mean value $\bar{L}$ of the length and the mean value $\bar{S}$ of the size of the scale are taken as co-ordinates in a cartesian co-ordinate system, the point $(\bar{L}, \bar{S})$ will represent the terminus of a line, every point on which represents the mean values of $\bar{L}$ and $\bar{S}$ of the individuals of this group at previous periods in their life, and this applies irrespective of whether the individuals have been in company with each other the whole of the time or separated. The line is called the mean-point line for the group of individuals in question. It is not ascertainable from the observations under consideration. These, however, can supply a mean-point for each sub-group, and as these sub-groups cover widely differing ages and sizes the material provides a collection of different mean-points, each of them valid for its sub-group in the material.

If this collection of mean-points in the co-ordinate system showed no regular order, it would not have been possible to do anything more with it. But it so happens that the points are arranged in such a manner that a representative line can be drawn between them. From this circumstance it can be concluded that these separate mean-points represent something general, which connects the sub-groups investigated, and that the unknown mean-point lines for all sub-groups lie along this representative line.

In this case it is possible to determine all the mean values of L in respect of the earlier periods in the life of a sub-group for which the mean value of S can be established, and this can be done for the times at which the winter rings were formed. We thus have a method for calculating the average size for groups of the above-mentioned kind (age-groups) on the formation of the 1st, 2nd, etc., winter ring. This method is used below as an auxiliary method.

The question of how the series of mean-points can best be represented as a line can be dealt with in several ways. The line can be drawn by eye, a graphic assessment can be made, regard being had to the precision of the individual mean-points, or an arithmetical interpolation or graduation may be performed. In my own material the series of mean-points is grouped with sufficient regularity along a straight line, so that there are no grounds for considering any equation for the representative line other than

$$\overline{L} = a + b\overline{S} \tag{1}$$

By a similar treatment of the observations which are to be found in the papers by Rosa M. Lee (1920) and Molander (1918), and also recasting the observations in my paper of 1910, I can arrive at essentially similar results, in spite of the fact that these three collections are not entirely comparable with my own later observations, since Lee's material cannot be split up into sub-groups according to age, and Molander's collection of scales was not derived from a definite part of the body of the fish.

On the assumption that equation (1) is available for calculating the mean lengths $\overline{L}$ when the mean-values $\overline{S}$ for sub-samples of animals of the same age are known, the further reasoning will be as follows: —

For a sufficiently large material of n older fish of the same age, the mean-point of which for the total length and size of scales ($\overline{L}$, $\overline{S}$) lies on the function line equation (1), measurements are also taken, apart from L and S of the distances between the growth-centre and the 1st winter ring, and are called s. For each individual we have the three observations s, S and L, and to each set of this kind there attaches an unknown l, that is to say, the length which for the individual in question appertains to the s of the individual.

For the total of n individuals we have

$$\frac{\Sigma l}{n} = a + b\frac{\Sigma s}{n},$$

this equation being merely a transcription of equation (1).

For each single individual in the material we can state a strictly valid equation of the form

$$\frac{L - \alpha}{l - \alpha} = \frac{S}{s} \tag{2}$$

This equation expresses nothing more than that a straight line can always be drawn between two points (L, S) and (l, s). As l is unknown in each individual case α cannot be assumed to be common to all individuals and must be furnished with an index in common with the unknown l and the known magnitudes s, S and L. Solving equation (2) for l we obtain

$$l = \frac{s}{S}L + \alpha\left(1 - \frac{s}{S}\right) \tag{3}$$

In this equation, as will be seen, the first term to the right is identical with the calculated lengths obtained by the use of the simple proportion equation and this value is called below l'.

The second term is a correction on l', the magnitude of the correction depending on the unknown α and the known expression $1 - \frac{s}{S}$, the numerical value of which is equal to $1 - \frac{l'}{L}$ and is always a proper fraction.

For the complete sample the following equations can be stated:—

$$\begin{aligned} l_1 &= l'_1 + \alpha_1\left(1 - \frac{l'_1}{L_1}\right) \\ l_2 &= l'_2 + \alpha_2\left(1 - \frac{l'_2}{L_2}\right) \\ l_n &= l'_n + \alpha_n\left(1 - \frac{l'_n}{L_n}\right) \end{aligned} \tag{4}$$

which on adding yields

$$\Sigma l = \Sigma l' + \Sigma\alpha\left(1 - \frac{l'}{L}\right). \tag{5a}$$

Divided by n (the number of individuals) this produces

$$\overline{l} = \overline{l'} + \frac{1}{n}\Sigma\alpha\left(1 - \frac{l'}{L}\right) \tag{5b}$$

If now, in the equations (4) instead of the individual quantity α we introduce a quantity A common to all individuals we obtain

$$
\begin{aligned}
l_1 &= l'_1 + \mathrm{A}\left(1 - \frac{l'_1}{\mathrm{L}_1}\right) \\
l_2 &= l'_2 + \mathrm{A}\left(1 - \frac{l'_2}{\mathrm{L}_2}\right) \qquad (6) \\
l_n &= l'_n + \mathrm{A}\left(1 - \frac{l'_n}{\mathrm{L}_n}\right)
\end{aligned}
$$

which on totalling gives

$$\Sigma l = \Sigma l' + \mathrm{A}\Sigma\left(1 - \frac{l'}{\mathrm{L}}\right). \qquad (7\mathrm{a})$$

this on division by n yields

$$\overline{l} = \overline{l'} + \mathrm{A}\frac{\Sigma\left(1 - \frac{l'}{\mathrm{L}}\right)}{n} \qquad (7\mathrm{b})$$

Comparing (5 b) and (7 b) it will be seen that the latter equation gives the same result as the first if

$$\frac{1}{n}\Sigma\alpha\left(1 - \frac{l'}{\mathrm{L}}\right) = \frac{1}{n}\mathrm{A}\Sigma\left(1 - \frac{l'}{\mathrm{L}}\right) \qquad (8)$$

and as in (7 b) all quantities except A are known this equation serves to determine A.

It is thus possible to work out an equation of type (6) for individual calculation of the growth, which is of such a nature that it causes the mean values of the calculated growth figure to be equal to the mean values which are obtained by calculation according to equation (1). In this way, presumably, the systematic error in the simple proportion equation should be eliminated to an extent which depends only on the accuracy with which equation (1) can be established once and for all. This, in the main, is a question of the number of observations made with a given degree of accuracy.

The numerical value of A lies, according to the calculations so far made, between 8 and 12 mm., varying according to the assumptions upon which the quantity a in equation (1) is computed. On this point my work on the material is not complete and I therefore state the value of A as 10 mm. provisionally only, though I believe it to lie close to the true figure.

In the construction of this new growth equation the quantity A is not invested with any biological or morphogenetic significance and must by no means be connected with the apparently similar constant a which occurs, for example, in Lee's (1920) proposed growth formula. This quantity a, the numerical value of which is put at 30—40 mm., by Molander at 50 mm., represents the length of the herring immediately before the scales begin to grow out on the herring, and it is placed directly in the equation without any attempt being made to demonstrate that the

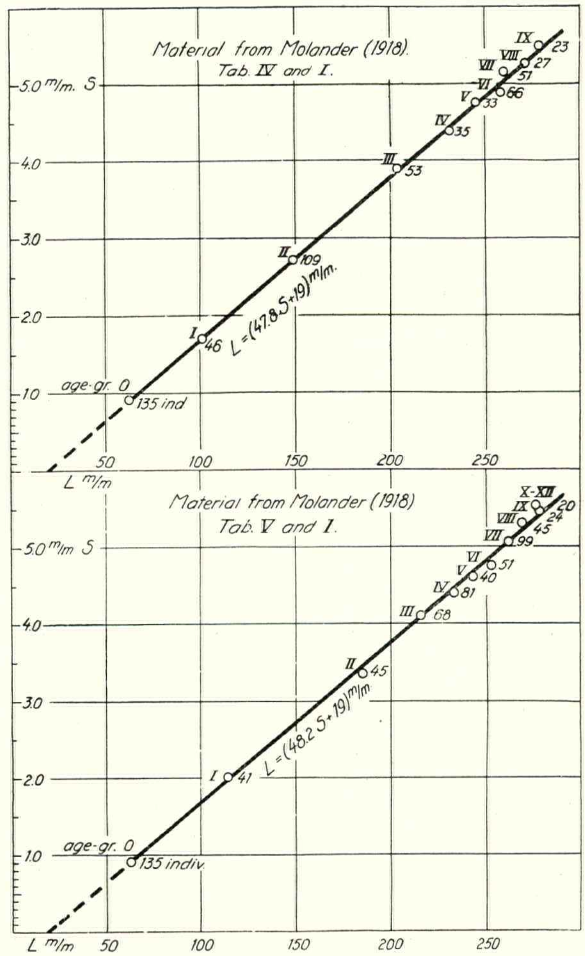

Fig. 1.

function line, which is being sought for, really runs straight from the point $s = 0$, $\mathrm{L} = 30$—50 mm., which is a tacit assumption that $a = 30$—50 mm. can justifiably be introduced into the equation. It can be proved from Molander's own material that this assumption does not hold good, and it emerges both from this material and from my own observations that the function line (equation 1) which runs in a straight line in the area of the growth calculations (from the 1st winter ring and onward) also maintains this straight course for a while below this area. The position of Molander's observations in this respect is shown in Fig. 1, where they are used to determine the course of the mean-point line. In the uppermost section of the figure material from Molander's Table IV is used, in the lowest section material from his Table V. In these two tables are recorded the number of individuals in each size-group (cm.) within each age-group, and for each individual group the mean value of scale size is indicated in

$^1/_{10}$ mm. It is therefore possible to find $\overline{L}$ and $\overline{S}$ for each age-group, and each table, consequently, furnishes a number of mean-points.

Plotting these mean-points in a co-ordinate system shows that in the case of both samples the points are arranged fairly obviously along a straight line represented by the equation $\overline{L} = (48\ \overline{S} + 19)$ mm. In estimating the validity of these results the following information from M o l a n d e r's commentary must be taken into account:— (1) Three scales from each fish have been measured. This will, to some extent, eliminate accidental variation in the scale size and thus be advantageous; (2) The scales have been taken at random (3 scales, no matter which), that is to say, the measurements do not refer to definitely localized scales. This circumstance gives rise to doubts concerning the suitability of the data for constructing a mean-point line; (3) The measurement employed for S is the distance from the basal line to the edge of the scale perpendicularly on the basal line. This measurement is slightly less than that which I have used. The resulting difference exerts no influence on the constant b in equation (1), but on the other hand the constant a is strongly affected. A calculation shows that a difference of 0·2 mm. between M o l a n d e r's and L e a's measurements of S reduces the value of a in M o l a n d e r's material from about 20 mm. to about 10 mm. In Norwegian herring the difference between the two measures is of the order of 0·13 mm., and if the difference was of a similar order in M o l a n d e r's scale material it implies a reduction of a to about 14 mm., thus bringing M o l a n d e r's Swedish and my Norwegian material into satisfactory agreement, considering the amount and quality of the material.

T h e a b o v e a l s o p r o v i d e s a n e x a m p l e o f t h e w a y i n w h i c h e v e n a v e r y s m a l l d i f f e r e n c e i n o b s e r v a t i o n a l t e c h n i q u e m a y c a u s e a p p a r e n t d i s h a r m o n y i n t h e r e s u l t s a n d i t e m p h a s i z e s t h e n e c e s s i t y f o r p r e c i s e d e f i n i t i o n s i n w o r k o f t h i s k i n d.

After the two mean-point lines had been established a new mean-point was marked off which was calculated from data in M o l a n d e r's Table I. This table is of great interest because it refers to a sample of very small herring from 53 to 81 mm. in length, with an average of 63 mm. M o l a n d e r records certain observations which indicate that the herring in Swedish waters do not acquire scales until they are about 50 mm. long. The sample in question, therefore, is only about 13 mm. further advanced in length than the scaleless herring. Nevertheless, the mean-point for this sample is on exactly the same line as the mean-points for the larger and older group (and this is also the case in my material of a similar kind).

The validity of the straight mean-point line

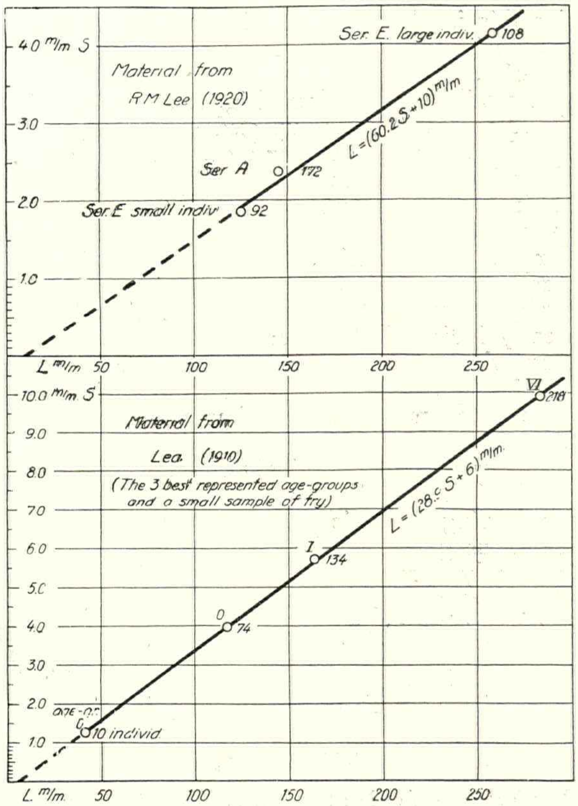

Fig. 2.

(equation) thus extends far down towards the length at which scales first appear on the herring, a circumstance of great importance for justifying the use of the growth equations. This finding also serves to show the untenability of all the views which have been advanced in connexion with the circumstance that the herring does not acquire scales before metamorphosis.

Fig. 2, uppermost section, shows the results of an analysis corresponding to the foregoing which has been carried out with the observations to be found in L e e's work (1920) and the lowest section is based upon data from L e a (1910) analysed in the same way. In L e e's work the individuals are not grouped according to age and no mean-points can therefore be calculated for age-groups. But as a part of the material (Table 2) forms two distinct size-groups and as in addition there is one more sample, 3 mean-points of a somewhat more complex significance can be calculated. It should be borne in mind when considering these mean-points that when two points (or more) lie on the same straight line, so also does the point, the co-ordinates of which are the mean values of the co-ordinates of the individual points; in other words, if the mean-points of the unknown age-groups in such compound groups lie on a straight line this is also the case with the more complex mean-points which can be calculated from the material.

As will be seen from Fig. 2 the mean-points lie as well as can be expected on a straight line and the constant a has, for Lee's data, a value of about 10 mm., and is thus also of the same order of size as in the Norwegian and Swedish material (after correction for a difference in measurement). For Lea's material, which deals with the earshaped scale situated behind the gill-cover, the straight course of the mean-point line is very clearly indicated. The constant a is about 6 mm. long, whereas b has a value entirely distinct from that in Lee's and Molander's data, since both scale and measurement dimensions are quite different.

There should accordingly be reason to expect that it will be possible to arrive at a growth-formula for herring in which the effect of the heteromorphous growth in the two dimensions L and S is largely compensated. The conditions for the attainment of this goal are that adequate material is collected once and for all for as many herring populations as possible, and that this material is measured in the same way and dealt with by calculation according to the same principles.

Literature.

Buchanan-Wollaston, H. J. 1934. The Theory of Variation, Correlation and Regression. Its Relevance in Researches on Proportional Growth. Rapp. et Proc.-Verb., Vol. LXXXIX, Copenhagen.

Dahl, K. 1910. Alder og Vekst hos Laks og Ørret i Norge. Landbruksdept. Oslo, 1910. Engl. Edit. Salm. and Trout Assoc. London, 1911.

Graham, M. 1929. Studies of Age-Determination in Fish. Fishery Invest., Ser. II, Vol. XI, No. 2. London.

Hodgson, W. C. 1929. Investigations into the Age, Length and Maturity of the Herring of the Southern North Sea. Fishery Invest., Ser. II, Vol. XI, No. 7. London.

Huntsman, A. G. 1918. The Growth of the Scales in Fishes. Transact. Roy. Canad. Inst. Toronto.

Huxley, Julian S. 1932. Problems of Relative Growth. London.

Lea, E. 1910. On the Methods used in Herring Investigations. Publ. de Circ., No. 53. Copenhagen.

Lea, E. 1929. The Herring's Scale as a Certificate of Origin. Rapp. et Proc.-Verb., Vol. LIV. Copenhagen.

Lee, R. M. 1912. An Investigation into the Methods of Growth Determination in Fishes. Publ. de Circ., No. 63. Copenhagen.

Lee, R. M. 1920. A Review of the Methods of Age and Growth Determination in Fishes. Fishery Invest., Ser. II, Vol. IV, No. 2. London.

Meek, A. 1916. The Scales of the Herring and their Value as an Aid to Investigation. Dove Mar. Lab. Rep., New Ser. V. Newcastle.

Molander, A. R. 1918. Studies in the Growth of the Herring. Sv. Hydrogr.-Biol. Komm. Skr. Gothenburg.

Runnstrøm, S. 1936. A Study on the Life History and Migrations of the Norwegian Spring-Herring. Rep. Norw. Fish. and Marine Invest., Vol. V, No. 2. Bergen.

Segerstråle, Curt. 1921. Lämna årsringarne i fjällen hos vora vanliga sötvattenfiskar en tilförlitlig bild av fiskens tillväxt under olika ålders-stadier? Acta Soc. Faun. Flor. Fenn., 48, 6.

Thompson, H. 1926. Haddock Biology III. Fisheries, Scotland, Sci. Invest., II. Edinburgh.

Watkin, E. Emrys. 1925. Investigations on Cardigan Bay Herring. Rep. Mar. and Fr. Water Invest. Univ. Coll. Wales, Aberystwyth, Vol. I.

Winge, Ø. 1915. On the Value of the Rings in the Scales of the Cod as a Means of Age-Determination. Meddel. Komm. Havunders. Fisk., IV, 8. Copenhagen.