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FREQUENCY CURVES IN HERRING INVESTIGATION

BY

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§ 1. *Chaterine W. M. Sheriff* in a paper[1]) which is accompanied by an introductory note by Prof. *D'Arcy W. Thompson* subjected a number of samples of herring to mathematical analysis. The problem of the first part of her work, as is seen from § 1 of the paper in question, has been to ascertain whether "the examination of a random sample of herring from a single shoal indicates (either as regards length or number of rings) a distribution that is or is not in accordance with the law of probability". That is to say, she has investigated the curves of frequency for the length of the herring and for the number of rings which have been counted on the scales in the samples in question, and the investigation had as its aim to ascertain whether to these empiric curves of frequency can be adjusted such mathematical curves which are called curves of probability or curves of variation.

These curves, among which are for instance the Gauss law of errors:—

$$y = y_0 \, e^{-\frac{x^2}{2\sigma^2}}$$

and the formula worked out by Pearson:

$$y = y_0 \left[1 + \frac{x}{\alpha_1}\right]^{m_1} \left[1 - \frac{x}{\alpha_2}\right]^{m_2}$$

as is well known are of such a character that in many cases by a judicious selection of constants they may be brought into accordance with the empirical curves of frequency, which are commonly styled curves of variation, because they reflect the phenomenon which goes by the name of biological variation or variability.

[1]) Report on the Mathematical Analysis of Random Samples of Herrings. Fisheries, Scotland. Sci. Invest. 1922, I. (Sept. 1922).

The result of this investigation may in short be stated to be that some of the empirical curves may very well be represented by one or another of the said mathematical curves while some of the empirical curves viz. those which are more irregular (bimodal) may be represented by the addition of two mathematical curves of the character just mentioned.

This result has suggested to Miss Sheriff the idea that *"a mathematical analysis favours the hypothesis that a random sample is homogeneous"*. What is meant in this connection by the dangerous term "homogeneous" has not been clearly defined by Miss Sheriff, and it is necessary to refer to Prof. D'Arcy Thompson's introductory note to ascertain what is to be understood by the term, and what biological problems the mathematical analysis is intended to clear up.

Any reader of the introductory note will, I believe receive the definite impression that the mathematical analysis as it has been carried out by Miss Sheriff, is to serve the purpose of solving the question whether the individuals in one herring shoal are generally of equal age, or whether the herring shoals are generally composed of individuals of varying age.

If a shoal of herrings generally contains individuals of the same age only—and D'Arcy Thompson is inclined towards this assumption —then we have to abandon the assumption that the rings seen on the herring scales are annual rings which may be used to estimate the age of a herring. For it is a long since demonstrated fact that the majority of herring samples contain herring with at times extremely varying number or rings on their scales. If the individuals of such samples should prove in spite of this fact to be of the same age, the number of rings would have to be reckoned among the "variable" characteristics, like the length of the herring, the distance from the tip of the snout to dorsal fin etc., and could be no indicator of the age of the herring. Here lies, according to Prof. D'Arcy Thompson, the biological problem which is to be made clearer by mathematical analysis, and in his opinion there would be needed more evidence, more proof than what is found in Miss Sheriff's work, but he also says:—"I think that Miss Sheriff's work helps us already towards a decision:—it is bound to reawaken interest and to promote discussion".

If the analysis thus carried out of the empirical curves of frequency are to be suited to serve as a method to the solution of the said biological problems, the shape of the curves must characterize whether a sample of herrings consists of individuals of equal age only, or whether it comprises individuals of various generations. A closer consideration would lead to the assumption that when a sample of herrings has curves of frequency, the shape of which corresponds to one or another of the mathematical curves of variation or probability then the sample is homogeneous in the sense *that its individuals are of the same age*, whilst the samples, of which the curves lack the regular "normal" shape are not homogeneous, and contain individuals of several generations. If these suppositions are abandoned and the possibility is admitted that even samples of herrings comprising several generations may have curves of frequency of "normal" shape, then it is obviously impossible any longer to decide whether a sample of herrings contains one or more annual groups.

That such a supposition has at least been in Prof. D'Arcy Thompson's mind seems probable from his words in the introductory note:— "A sample from a herring shoal seems to be a very different thing from a random sample of plaice or haddock or cod captured by the trawl. In these latter cases by *mere measurement* of the fish, we can sort them into *groups* and recognise (more or less clearly) in these groups the successive annual broods or generations of fish. Other methods of estimating age (by scales, earbones etc.) tend to tally with and to corroborate these groupings, and to confirm and define the several generations. But measurement (at least in the great majority of cases) shows us but a single "group" in the case of the herring shoal".

The contrast between the multimodal and complex curves for haddock or cod, and the frequently quite uniform appearance and unimodal curves for samples of herring, appear to Prof. D'Arcy Thompson to be a symptom supporting him in the belief towards which he is inclined, viz. "that a herring shoal is (so to speak) one great family party, a vast company of fish all of one age, fish that were spawned together, and that have ever since lived and swum and migrated together". In order to change his belief into a certain decision in one or the other direction, we are asked to go the mathematical way and analyse the curves by mathematical methods, to settle their similarity or their dissimilarity with the theoretical curves of variation: "In all statistical enquiries we need, sooner or later, the control and guidance of the mathematician; and here is a case where we can put a clear issue before him. There are certain mathematical laws (as we have stated) which govern the normal natural variation: which help us to recognize and define a natural group, within which natural varibility has played its part and on which it has left its mark. There are other very different characters which mark a mixed or unnatural assemblage, a heterogeneous group".

It would appear, therefore, that there can be no doubt that Prof. D'Arcy Thompson considers the conformity between the empirical curves of frequency and the theoretical curves of variation to be a criterium in deciding whether a sample of herrings contains one single year group or several. To my mind it appears somewhat singular that he has made no attempt to demonstrate the justification of an assumption which is of fundamental importance for the biological valuation of the results of the mathematical analysis.

Considering the great importance for biology in the method proposed by Miss Sheriff and Prof. D'Arcy Thompson, if it be sound, and considering also the amount of damage it may cause if it be incorrect, there is every reason for a closer examination of the fundamental assumption on which the method is based. That is what I have tried to do, and in the following I will set forth my conclusions.

The investigation has been an attempt to decide the following question. Is it possible that herrings of several age groups may form a shoal, for which the curves of frequency with regard to length as well as to age have such a shape that there may be adjusted theoretical curves of variation with considerable "probability of fit"?

This is the gist of the problem, and that is just what Prof. D'Arcy Thompson considers "statistically improbable" (Nature, Sept. 17. 1914).

The working method of the investigation is as follows:—Presupposing that a sample of herrings actually contains individuals of highly varying ages, e. g. 3 to 15 years, it is ascertained what conditions will then be sufficient for the empirical curves to take such a shape as will allow them to be represented by one of the theoretical curves of variation.

If, then, these conditions are not of such a character that they must be rejected as impossible or exceedingly improbable, if in other words it is possible to imagine them approximatively fulfilled in nature, then it will not, when considering empirical curves, be possible to decide whether they represent a sample of individuals of the same age or of different age groups.

§ 2. It is convenient to investigate first the conditions under which the curves of frequency for the *length* of the herring assume a shape which may be represented by a theoretical curve of variation, even though the sample of herring from which the measurements of length are taken contain several different age groups.

By such an examination one must try to find out what conditions or factors may be imagined to influence the shape of the curve of frequency for a sample of herrings containing several age groups. When that is obtained, it should be made clear what shapes are assumed by the curves of frequency when these factors are combined in various ways. If then it should be found that one or several combinations leads up to curves of frequency of such a shape that they may be represented by theoretical curves of variation, then it would be demonstrated at the same time that even samples with several age groups may have curves of frequency for length of "normal" shape.

The idea would then appear very probable that the phenomenon which is called variation or variability with regard to the *growth* of the herring might be one such co-operating factor. We may safely assume that the individuals of a group of herrings of the same age, *are not equally large*, but some are larger and some smaller. This is as much as to say that the curve of frequency for each separate age group extends over several size groups (when these are not made so large as to be disproportionate). If that is so, it is evident that the curve of frequency for one sample containing several age groups must be influenced by the fact. For the curve for the whole sample is the sum of curves for the separate age groups. The immediate conclusion from this is that the *shape* as well as the *area* (the number of individuals) of these curves of frequency for the separate age groups determine the shape and area of the curve for the whole sample.

Another circumstance which should be taken into consideration is the *growth* of the herring from one year to another. The importance of this fact is made clear if we go to the extreme of imagining that the growth from one year to the next is so great that even the largest herring in one age group is smaller than the smallest herring in the older neighbouring group. In this case there would be no single consecutive curve of frequency for the whole sample, only a number of separate curves, one for each separate age group. It is easy to imagine that still more factors are active, but limiting ourselves to the three factors mentioned viz:—(1) the *shape* of the frequency curves for the separate age groups (the component curves), (2) the *number* of individuals in the separate age groups *(the distribution of age),* and (3) the *growth* of the herrings from one year to the next, and attempting to set forth the part taken by these factors in the final shaping of the total frequency curve of length, we may set to work in the following manner: First certain simple assumptions are granted concerning the three factors, and also concerning the number of age groups and concerning the number of individuals with which we decide to operate. For instance we may assume:—that we will operate with 1000 individuals distributed over 11 age groups, from 3 to 13 years, — that the length-frequency for each separate age group is a "normal" symmetrical curve of the same shape as Gauss' law of errors, and that all these curves *(the component curves),* have the same standard diviation of $\sigma = 1$ cm.;—that the curve for the distribution of age is also such a Gauss curve and that the average length of the individuals increases evenly with $\alpha = 0{,}5$ cm. per year.

On the basis of these assumptions it is possible to construe the frequency curve of length for all age groups taken together (*the total curve*), and in this way we obtain a kind of simplified model for a sample of herrings which have been examined with regard to the age and length of the individuals.

In this simplified model sample, which is graphically reproduced in fig. 1 the total curve of length distribution becomes a "normal"

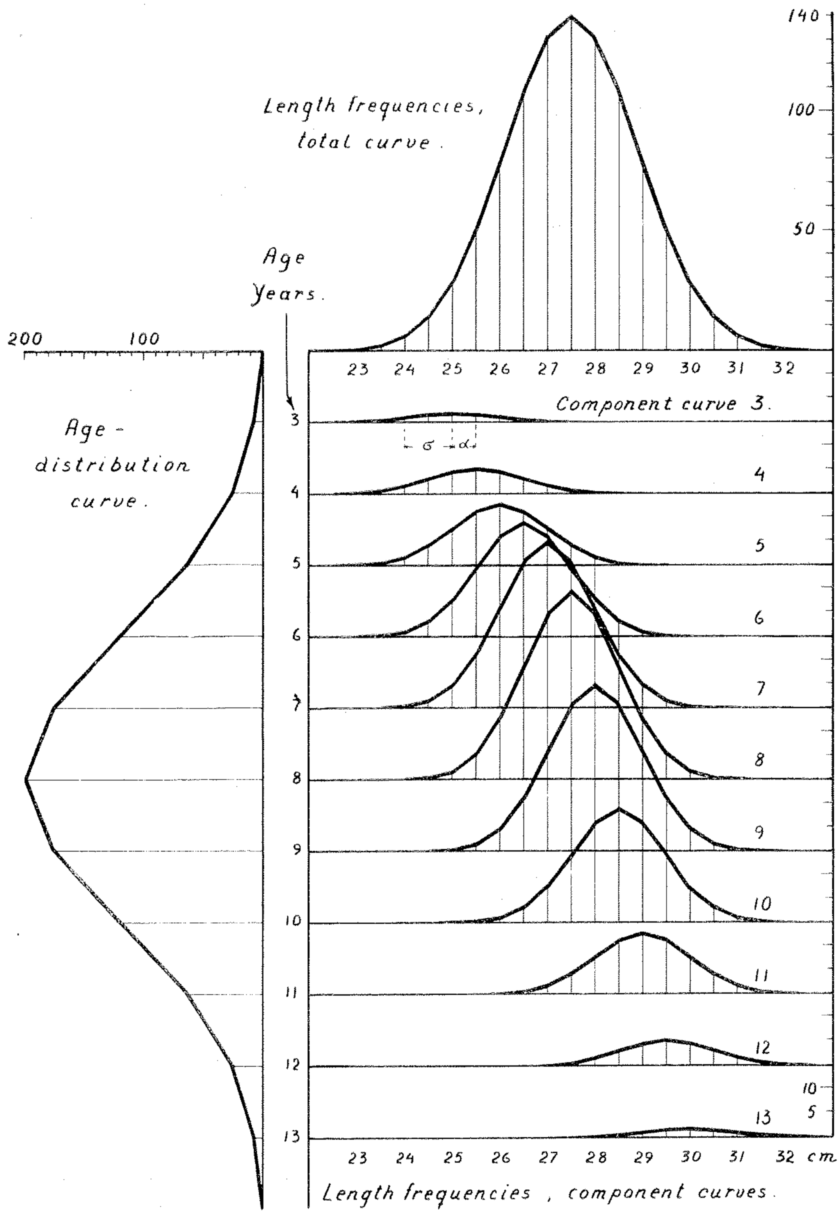

Length frequencies,
total curve.
140
100
50
Age
Years.
200
100
Age-
distribution
curve.
23 24 25 26 27 28 29 30 31 32
Component curve 3.
σ
α
3
4
5
6
7
8
9
10
11
12
13
10
5
23 24 25 26 27 28 29 30 31 32 cm.
Length frequencies, component curves.

Fig 1.

curve shaped like the Gauss' law of errors. This will be evident if we remember that we have to do with an ideal case of *normal correlation.*

By altering the suppositions concerning one factor, leaving the other two intact, we may learn how this one factor reacts on the total curve of length distribution. In the following some of the possible alterations have been made and the resulting changes in the shape of the total curve of length distribution are indicated. These changes in the total curve are easily imagined if we imagine figures like fig. 1, but constructed on the basis of the new suppositions.

(1) If the distribution of age is assumed to be *irregular*, the value of α/σ will decide whether the total curve for length is to be multimodal, complex or unchanged. If α/σ is considerable the total curve will be multimodal, if α/σ has a slight value the total curve remains approximately normal and symmetrical.

(2) If the distribution of age is assumed to be regular, but skew e. g. mode $<$ mean, the total curve will also be regular but skew and with mode $>$ mean.

(3) If the assumption that α is constant, that is to say, that the average length increases with an unchanging amount from one year to the next, is exchanged for the more natural one that the *increase in length diminishes* with the advancing age of the fish, whilst all other assumptions are upheld, then a symmetrical age curve will no longer have a corresponding symmetrical total length-curve, the latter being skew with mode $>$ mean.

(4) If the standard deviation σ for the component curves are not constant, but decreasing or increasing with advancing age, then a symmetrical age curve will have a skew total length curve with mode $>$ mean for decreasing σ and vice versa.

(5) If the component curves are not symmetrical but skew the total-length curve will also be skew in the same direction as the component curves.

(6) If the component curves are not ideal curves as in the figure 1, but possess the irregularities often found in empirical curves, this fact will appear even in the total curve, but not to such a great extent, the irregularities partly counterbalancing each other.

It goes without saying that more possibilities may be imagined than those mentioned here. There is for instance the possibility that the shape of the component curves may alter, but I think it will be evident from what has been said already, that the shape of the total length curve is to a very great extent dependent on the shape of the age curve on the one hand and on the other one the value of the term $\frac{\alpha}{\sigma}$ and that these two factors often decide whether the length curve is to be a regular and simple curve or complex and multimodal.

In a sample where $\frac{\alpha}{\sigma}$ in the whole area is inconsiderable, an irregular age curve will not, as has been mentioned, cause the length curve to be irregular. This case is of importance biologically because the condition may be considered as approximately fullfilled in samples containing older and fullgrown herrings only.

The opposite possibility of $\frac{\alpha}{\sigma}$ being considerable may be expected to be fullfilled in samples containing very young herrings. In such samples the length curve vill be complex or multimodal, even when the age curve is a normal curve of variation.

From the above it will be seen how easily conceivable is a sample of herrings consisting of several age groups, and yet having a total curve of length frequency of a simple shape, (symmetrical or skew). The conditions for the actual existence of such samples are as far as I can ascertain not of a character which allows us to reject them. Indeed the contrary is the case. From the shape of the length frequency curve, when it is simple, we cannot therefore conclude that the sample in question is *homogeneous* in the meaning of the term that it contains individuals of the same age only.

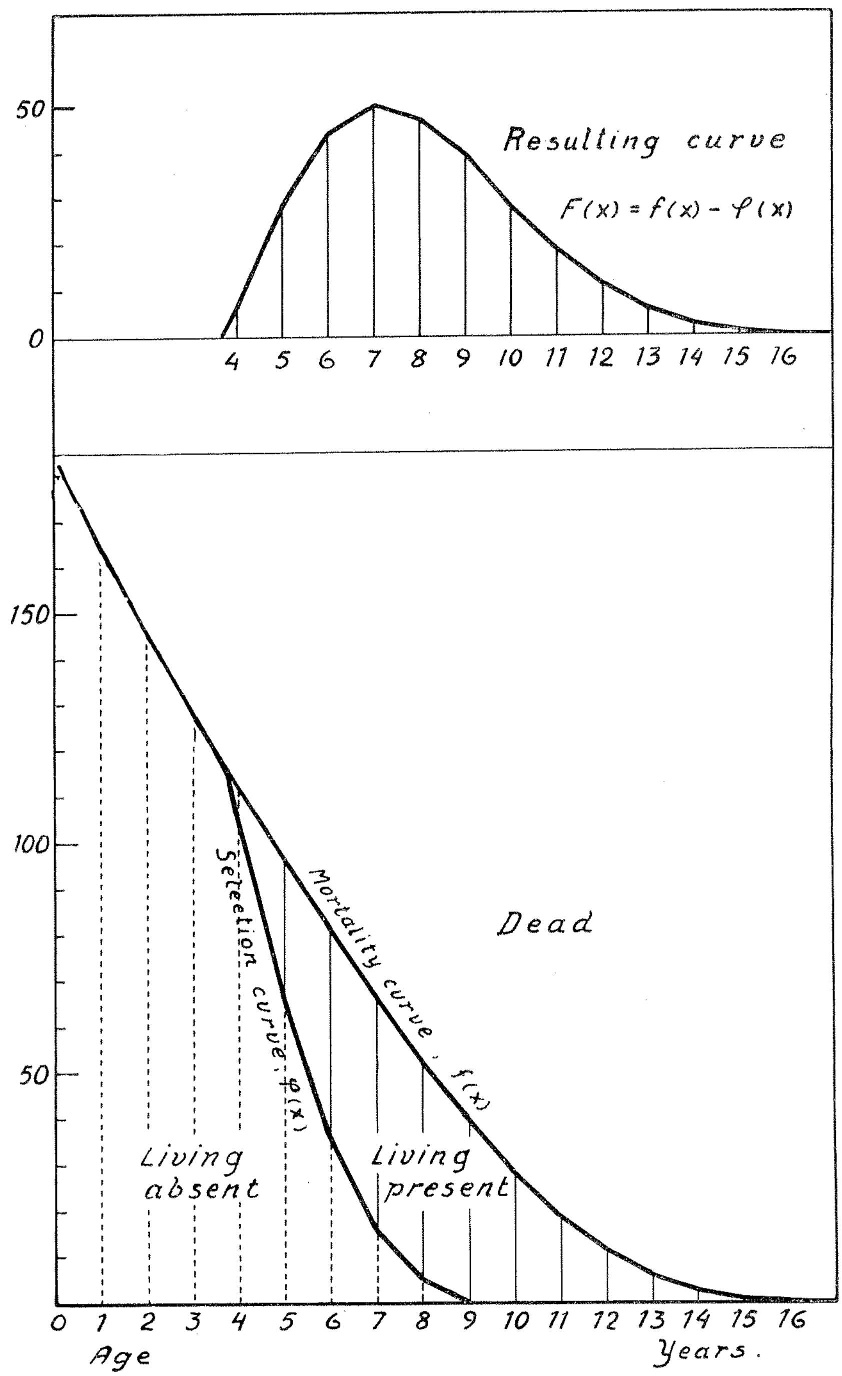
§ 3. The task before us has thus been reduced to an investigation as to whether the *age distribution curve* for a sample (shoal) of herrings may be imagined to have such a shape that it corresponds to a theoretical curve of variation.

Personally I find myself able to imagine such a case with the utmost ease. I think the fact may be considered to be established that no sample of herring examined up to date possesses the characteristic of being representative with regard to distribution of age of the whole population to which it belongs, i. e. that all generations of the total population are represented in their correct proportion in any one sample of herrings. Experience also shows that the facts are the same with regard of the shoals of herring from which the samples are taken. The herring shoals and the herring samples *represent only a selection* of a population of herring. If that is so, there is no difficulty in imagining that this selection may have taken place in such a manner that the curve of of age distribution in the herring sample obtains a shape so similar to that of a theoretical curve of variation, that the latter may be said to represent the empirical curve.

In order to illustrate this, it is expedient to employ a method similar to the one adopted with regard to the curves of length frequency, and to construct a model population with known characteristics. This model population may at a stated time every year receive an addition of a stated number of newborn individuals, which addition just compensates for the decrease by death in the number of the popopulation which decrease in the course of time has been running steadily according to some law. At the time when the additional newborn individuals arrive a census is taken, the number of individuals of each year-group being counted.

The result of the census is illustrated graphically (see Fig. 2 at the bottom). On an abscissa ordinates are erected at fixed intervals. To the ordinate farthest to the left is given a height which is proportionate to the number of newborn individuals (0-year old herrings), the height of the second ordinate corresponds to the number of 1-year old herrings and so on. The final points of the ordinates are then connected by lines, producing a curve which might have been called the curve of age distribution for the total population, but which in the graph is termed the mortality curve f (x) because if the dead herrings are also included it forms the boundary line between the individuals already dead and those still living of all year groups. In the area above (to the right of) the mortality curve, are the dead herrings, whilst in the area below (to the left of) the same curve are found the living fish. The curve is regular in shape, as the causes of death are supposed to operate in a regular way.

This hypothetical population of herrings has the characteristic in common with a real population that the qualities and the course



50
0
Resulting curve
F(x) = f(x) − φ(x)
4 5 6 7 8 9 10 11 12 13 14 15 16
150
100
50
Dead
Mortality curve, f(x)
Selection curve, φ(x)
Living absent
Living present
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Age
Years.

Fig. 2.

of life of the individual are not exactly the same for all. Some individuals grow more quickly, others more slowly than the majority of their age, and there are also differences in the development of sexual functions. Thus it would happen that some few individuals become adult as early as at the age of four years, whilst the main part of their contemporaries are still unripe. Among the five years old herrings a comparatively large consignment would be adult, among the six years old more than half, among the seven and eight years old the great majority and among older herrings all individuals.

If the herrings in each age group could be arranged in series according to sexual development and placed alongside the ordinates in such a manner that the fully developed individuals were at the top, we might on the ordinates for the year groups 4—8 mark off a point dividing the fully developed fish from the sexually undeveloped. The part of an ordinate above this point would represent the number of developed individuals in that year group, whilst the part below would represent the as yet undeveloped herrings. If these dividing points are connected by lines, we optain a curve which in Fig. 2 is called the curve of selection $\varphi(x)$ because the individuals to the right of the curve represent a selection among the living herring, viz. the sexually developed fish of all year groups.

Our model population has thus by means of these curves been divided into three groups (if the dead herrings are included). Among these we will consider the group of sexually full-grown herrings. Concerning the individuals of this group we will assume that at a fixed time they appear on the spawning grounds of the population in order to propagate the race and that they are very well mixed.

Then fishing is started with apparatus which does not act selectively in any way, and large random sample is taken out, the individuals of which are examined with regard to age by means of a neverfailing metod. How will the age distribution curve of this sample appear? It will have the appearance of the graph at the top of Fig. 2, and this curve is obtained by placing on an abscissa those parts of the ordinates in the figure below that lie between the curve of mortality $f(x)$ and the of selection $\varphi(x)$. When the final points are connected by lines, a curve appears which looks very much like a skew curve of variation, but the general formula of which is

$$F(x) = f(x) - \varphi(x) \quad ^{1})$$

where $f(x)$ is the function which in Fig. 2 represents the curve of mortality, whilst $\varphi(x)$ represents the curve of selection.

The curve obtained in this way is not a probability curve or curve of variation, like the Gauss' law of errors and Pearson's curves. It has been constructed on quite different premises. And it is assumed that the individuals in the sample belong to several age-groups. In spite of this the shape of the curve is very similar to a curve of variation (as will be demonstrated later on) so much so that curves of frequency empirically determined may be represented equally well or better by this theoretical curve than by theoretical curves of variation.

The theoretical curve of frequency $F(x)$ for the sexually mature individuals of the model population, as will be seen, has the characteristic of being, in the area of 9—16 years, practically identical with the mortality curve for the total population.

Now it is quite conceivable that shoals of herring exist in which the distribution of age is the result of selection in several directions. For instance, the herrings which have started their sexual development for the first spawning, but which are not sexually adult and ready for spawning, may have a tendency to swim together in shoals.

Such a group of the total population will then have a distribution of age limited on one side by the characteristic of total immaturity. The distribution of age will be the result of a *double selection.* In exactly the same manner as we constructed the curve of selection $\varphi(x)$ in Fig. 2 we may construct another $\psi(x)$, which in the graphic representation of the model population divides the sexually totally immature individuals and those in which development has started towards the first spawning. Such a case is illustrated in Fig. 3 where the uppermost graph to the left indicates the distribution of age in such a sample of double selection, whilst the uppermost curve to the right indicates a distribution according to a one-sided selection of a

[1]) The selection curve is presumed to follow the mortality curve until the selective influences become active, when it breaks off and takes its own course.

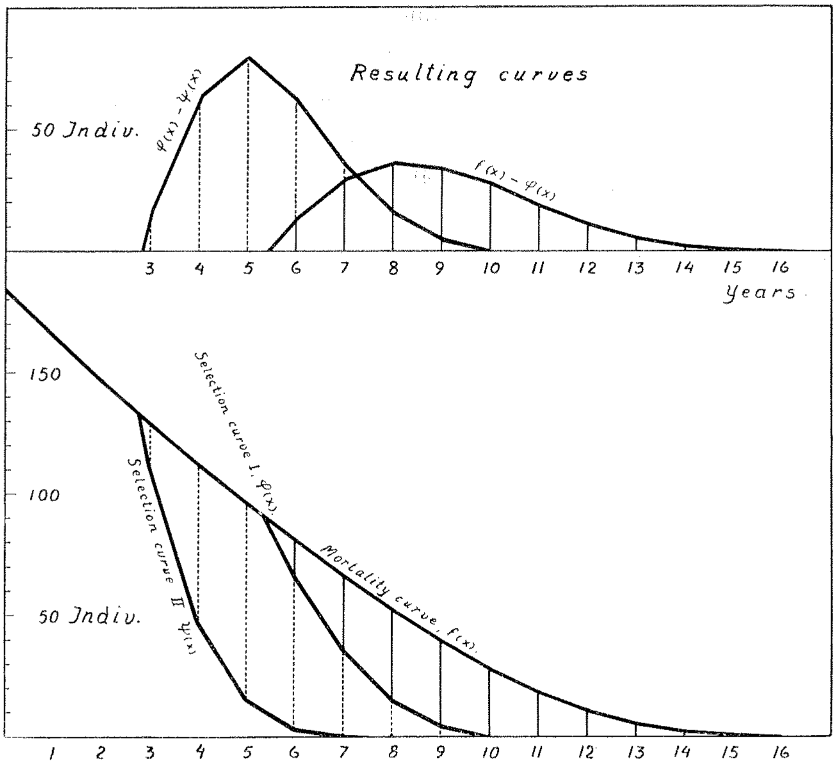


Fig. 3.

similar character as the curve in Fig. 2. Mathematically the distribution of the double-sided selection is expressed by the formula:

$$\varphi\,[x] - \psi\,[x] \qquad ^{1)}$$

and it will be seen that even this function has a shape which may quite conceivably be represented by a theoretical curve of variation, in the cases where it is not, as in the graph, the result of a mathematical construction but of empirical determination, and possesses accidental errors arising from that circumstance.

The conclusion from this investigation is, that the distribution of age in herring shoals may conceivably be represented in a form resembling theoretical curves of variation, *if the shoals have been formed by selection* within a total population with certain stated characteristics. In the hypothetical instance assumed in the above, the total distribution of age is a mathematical function of age, and in the same

[1]) See footnote p. 15.

manner the selection curves are functions of age. Viewed biologically this would mean that the renewal of the population by birth as well as destruction by death go on in the same manner without variation from one year to another, and also that the physiological processes determining selection (and which are exemplified by the sexual development) go on uniformly year after year.

Such ideal circumstances cannot be expected in nature, nor are they necessary for our argument.

Renewal by birth may fluctuate from one year to another, or vary, within certain limits with no other effect than that the theoretical distribution becomes somewhat uneven or taking a somewhat altered shape. For instance, if the replenishment by birth decreases during a number of consecutive years, while all other circumstances remain as presupposed in the model population, then the resulting curve F (x) in Fig. 2 will take a somewhat different form and may be conceived as represented ty the function

$$F\ [x] = f\ [x] - \varphi\ [x] - \omega\ [x]$$

where ω (x) is supposed to be a term introduced to account for the effects of this new selective influence.

In a similar manner, mortality may fluctuate or vary within certain limits without the resulting curve F (x) loosing its similarity with the curve in Fig. 2.

Finally the physiological functions determining selection (and many such are conceivable) may not act so regularly as presupposed in the case assumed.

The chief point is, however, whether circumstances similar to the hypothetical ones obtaining amongst the model population, may be conceived to exist in an approximate form in nature. I can see no obstacle to this. It is not an absurd idea that renewal by birth and reduction by death may go on at a comparatively even and measured pace. We are practically safe in assuming that the shoals represent a selection of the total population and we are fairly safe in assuming that this selection is not without a plan, but that it goes on according to some scheme or some rule. Everyone who has seen shoals of herrings in nature, or caught them by means of non-selective implements will easily arrive at the idea that the shoal keeps together *qua* shoal because it forms a kind of organism, because the individuals or the shoal have something in common, whether that something be size, swimming power, a uniform appetite, sexual development or some other characteristic which they all share. The idea will also easily occur to the observer, that this "organism" will be of a more or less stable construction, according to the homogeneity in the several directions possessed by the units of the shoal, the individual herrings, and the conception will be completed by the idea that the "organism" is alive, that is to say that it is renewed by the addition of fresh units from the population as in their development these gain the stage represented by the shoal, and that it is reduced by shedding off of units the development of which removes them from the common characteristics of the majority.

§ 4. It now remains to be demonstrated, that functions of the type indicated in the foregoing section may really represent empirical curves of frequency, which at the same time fulfil the condition for a theoretical curve of variation.

This demonstration may be carried out in such a way that an empirical curve of frequency is procured, to which a theoretical curve of variation may be adjusted with great probability of fit. It should then be investigated whether the said empirical curve may be represented by a theoretical curve of the character indicated in the preceding section.

As empirical material for this investigation was chosen a series of frequencies for the number of scale rings, given in § 2 of Miss Sheriff's treatise. This series is the result of an analysis of a sample of herring (No. 625) carried out by Miss P. Gullaksen, and appears as follows:

No. of rings on the scales	4	5	6	7	8	9	10	11	12	13	14	15	16	Total
No. of individuals	5	32	46	49	51	40	29	18	11	5	2	1	1	290

This series was chosen because, as Miss Sheriff has shown, it corresponds uncommonly well with a theoretical curve of variation, of Pearson's Type I and with the formula:

$$y = 53.18 \left[1 + \frac{x}{3.93}\right]^{2.48} \left[1 - \frac{x}{17.59}\right]^{11.10}$$

The correspondence is so close that the calculated probability of fit is 0.999 which is practically unity. To Prof. D'Arcy Thompson this correspondence must be an important fact indicating that the individuals of the sample are of the same age. For me who consider that the number of scale rings is an indicator of age, not absolutely infallible but very useful, the series seems to represent a distribution of age according to a one-sided selection, symbolized by the formula

$$\mathrm{F}\,[x] = \mathrm{f}\,[x] - \varphi\,[x].$$

In accordance with this formula, the right part of the empirical series must be part of the total distribution of age in the whole population to which the shoal (the sample) belongs, whilst the central and left part of the series is the result of a selection of some kind or other [1]).

The right part of the series may thus serve to determine the nature of and the constants for the function of mortality f (x).

By a graphic differentiation of the curve which may be drawn based on the frequencies for the numbers of scale rings, viz. 9—16, it was evident that the formula for the derived function of f (x) might be estimated as:

$$\frac{\mathrm{d}\,y}{\mathrm{d}\,x} = -y\left[\mathrm{a} + \mathrm{k}\,\mathrm{b}^{x}\right]$$

$$\text{or} \quad -\frac{\mathrm{d}\,y}{y\,\mathrm{d}\,x} = \mathrm{a} + \mathrm{k}\,\mathrm{b}^{x} \qquad (1)$$

where x means the number of rings and y means the number of individuals.

This equation is well known from the studies concerning human mortality. It is the expression for what is termed the force of mortality in cases where the mortality follows Makehams law [2]).

[1]) In this selection may also be included the action of the implement employed, viz. a common trawl.

[2]) See f. inst. E. F. Spurgeon, Life Contingencis, London 1922, p. 192.

As will be known the formula is the mathematical expression for the hypothesis that the force of mortality depends upon two complexes of causes, one (symbolizied by a) acting with the same power in young and old lives, independent of age, while the other complex (symbolizied by b) acts with progressively increasing power with increasing age.

By integration of (1) one arrives at Makehams formula:

$$\frac{dy}{y} = - \left[a + k\,b^{x}\right] d\,x$$

$$\text{Log } y = - ax - \frac{k\ b^{x}}{\text{Log b}} + C \qquad (2)$$

If we insert in (2)

$$- a = \text{Log S}, - \frac{k}{\text{Log b}} = \text{Log G and C} = \text{Log K},$$

we obtain the equation valid for all systems of logarithms:

$$\log y = \log K + x \log S + b^{x} \log G \qquad (3)$$

which gives:

$$y = K\ S^{x}\ G^{b^{x}} \qquad (4)$$

which is the formula constructed by Makeham for describing mortality in human populations.

The empirical frequencies for the number of rings 9—16 being considered as belonging to a curve of the above type, the constants were determined and the curve was calculated for the area of 3—17 years.

Then the frequencies for the ring groups 4—8 were marked off from the curve downwards along the ordinates respectively in the same manner as shown in Fig. 2. As a result there appeared an empirical representation of the supposed function of selection $\varphi(x)$, for which the problem was to determine a probable theoretical term. A study of its empirical form indicated that a type of curves similar to Makeham's might be applied:

$$\frac{d\,\varphi(x)}{d\,x} = - y\,k_1\ b_1^{\,x} \qquad (5)$$

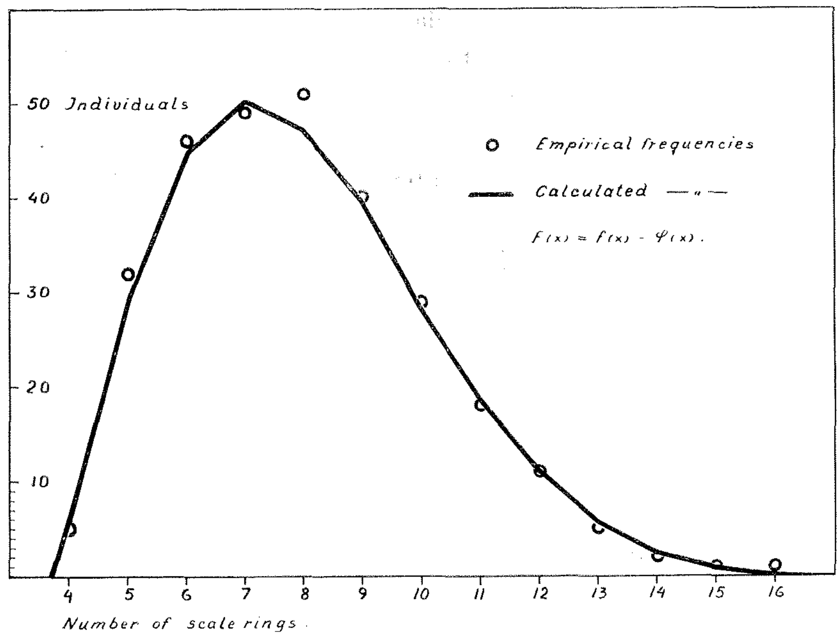


Fig. 4.

which when integrated can be given the following form:

$$\varphi(x) = K_1 \ G_1 \ {b_1}^{x} \qquad (6)$$

This formula has also been employed for the description of mortality in human populations. It is the formula constructed by Gompertz, of which the Makeham formula may be considered to be a modification.

The constants in our special case were calculated and thereby the resulting functions of frequency F (x) were determined.

The result is given in Fig. 2, which is not a figure with functions chosen hap-hazard, but the result of an analysis of the said empirical series of frequency.

How well the functions thus found represent the empirical facts appears when we consider Fig 4, where the function has been compared with the empirical frequencis. In reality, the latter are better represented by the function F (x) than by the curve of variation, which has been adjusted to it by Miss Sheriff, as will be seen from the following table:

No. of Rings on Scales	Frequencies			Squares of Differences Empir.—Calculated	
	Empiric	Calculated			
		Sheriff	Lea	Sheriff	Lea
4	5	6.9	6.9	3.61	3.61
5	32	28.1	29.7	15.21	5.29
6	46	46.3	45.0	.09	1.00
7	49	53.1	50.6	16.81	2.56
8	51	49.5	47.4	2.25	12.96
9	40	38.9	39.9	1.21	.01
10	29	27.3	28.6	2.89	.16
11	18	17.3	19.0	.49	1.00
12	11	9.9	11.4	1.21	.16
13	5	4.9	6.0	.01	1.00
14	2	2.2	2.7	.04	.49
15	1	.9	1.0	.01	.00
16	1	0	.2	1.00	.64
Sum of Squares of Differences:				44.83	28.88

I desire to state that the constants of the function have not been determined by any systematic method (method of least squares or method of moments) and that therefore a still better adjustment might be obtained. This, however, is quite superfluous.

With regard to the two functions of wich F (x) is a difference, one, (viz. f (x) = curve of mortality in Fig. 2) is as before said, Makeham's formula of mortality.

In a similar way as this formula is employed when studying human populations to describe the mortality, it has been used in our analysis as a mathematical expression for what has been assumed to be part of the distribution of age in a population of herrings upon which mortality has acted. It would hardly present any great difficulty to conceive that mortality expresses itself in a similar way in a population of herrings as in a human population.

The second function (φ (x) = curve of selection in Fig. 2) as has been stated, has a form similar to f (x). Biologically it expresses a devevelopment from one physiological stage to another, e. g. with regard to sexual development. The formula implies that this development is completed within a certain period or, that there is variation with regard to the time required by the several individuals of one age to reach a certain stage in their development.

Even this assumption does not appear either impossible or improbable; on the contrary it appears to me to be so plausible that one is forced, beforehand, to adopt it as a possibility.

The two functions of which the difference is F (x) in the cases investigated have the following numerical form:

$$\log f(x) = 2.29757 - 0.03847x - 0.03136 \cdot 1.30709^{x}$$

$$\log \varphi(x) = 2.61603 - 0.1854 \cdot 1.33625^{x}$$

Both are functions of time, which is represented by x. As has been stated they do not differ greatly in their theoretical form. This is easily understood when we remember that $\varphi(x)$ is to some extent a function of f (x), the function of mortality.

§ 5. From the above it will be seen that empirical curves of frequency, of which the similarity to theoretical curves of probability or variation cannot be doubted, may arise from and represent processes which have nothing to do with variation and variability in the sense given to these terms by Prof. d'Arcy Thompson. The curve of frequency for the length of the herrings in a random sample may easily show sufficient degree of similarity to a theoretical curve of variation even though the individuals in the sample belong to several age groups, and the curve of frequency for the number of rings on the scales, may also have a form, which is so like a theoretical curve of variation that it might be mistaken for one, without this fact arguing against the assumption that the rings are annual rings, and that consequently the curve of frequency represents the distribution of age in the shoal from which the sample comes.

But if that is so, the results of Miss Sheriff's analyses justify the conclusion that the rings on the scales are annual rings as little as they justify the assumption of the contrary. The method does not carry us any further towards the solution of this problem, in one or the other direction. It is not a method for an investigation to determine the nature of the scale rings, as it does not suit the problem to be solved.

The problem concerning the rings on the scales of the herrings is *per se* a problem concerning the *rate of formation of rings in the course of time*. In its most rigorous form the question is whether in the course of one year, one ring (that is to say one growth zone and one narrow transparent ring) is formed on the scales of all herrings, or whether on the scales of some herrings no rings are formed, one ring or more rings that is to say whether the rate of formation is invariably one ring per year or not. If observations and investigations are made with regard to this problem, the methods used must be suited to the nature of the problem. This means that it is necessary to consider the factor of time, just because the question is concerned with the alterations occuring in the scales in the course of time. It must be made possible to establish a relation between the observations and the course of time, to have them arranged alongside an axis of time.

In the investigations which have already been carried out with regard to the problem before us, time has been introduced in two ways, indirectly and directly.

In an indirect way time was introduced in the investigations based on the method indicated by Dr. C. G. Joh. Petersen for determining the age of fish, by measurements of the length of fish and the construction of curves of frequency of length.

As mentioned by Prof. D'Arcy Thompson, it is often possible, especially when dealing with young fish, to distinguish between the successive annual broods because the difference in length between the individuals of the various generations is so great that the curve of frequency becomes multimodal. This great difference in length is due to the circumstance that there is supposed to be an interval of about one year between each period of spawning. The co-ordinate axis on which the ordinates for the curve of length frequency are erected, is in a manner of speaking changed into a time axis in that the areas corresponding to the various periods of spawning are marked off from the various modes of the curve of frequency. A comparison between the results of the analysis of age by measurements, with those of an analysis by sorting the individuals according to the number of scale rings, will offer the possibility of a decision on the analysis carried out by examining the scales.

This method is justified as far as it goes and when used with caution[1]). With regard to herrings it is hardly possible to distinguish more than the three youngest generations by means of this method of measurement.

In other investigations time has been introduced into the observations quite directly.

One kind of investigation consists in studying the growth of herring scales throughout the seasons of the year, by means of samples taken at short intervals, so that it is finally possible to draw up a consecutive curve for the growth, and to mark off the interval of time within which the formation of a fresh zone or growth commences[2]).

In investigations of another character use has been made of curves of frequency which are obtained by classifying the individuals with regard to the number of rings on their scales. In several cases it has been observed that these curves have a characteristic shape for a certain kind of herring. Such has been very markedly the case in the curves obtained by an examination of the samples from shoals of grown herrings appearing every year to spawn near the West Coast of Norway. In the year 1908 a preponderance was observed in the samples of individuals with 4 rings, and the assumption had some justification that there were more individuals with 4 rings than with 5. If this assumption holds, and if the same shoals or the same group of herrings returned the next year, and *if the rings on the scales are annual* it might be expected that i 1909 many individuals with 5 rings would be found in the samples. This also happened. These facts gave good basis for the assumption that the group of herrings with 5 rings formed a considerable part of the millions of herrings present off the coast, and that the rings on the scales really were annual rings. If the latter assumption be correct, the individuals with 5 rings should have been born in 1904, and it might be supposed that many fish with 6 rings would be caught in 1910, with 7 rings in 1911 etc.

This supposition has been affirmed in the most striking manner by the investigations carried out every year up to the present time, not only so, however, but other characteristics of the curves of fre-

[1]) See Publications de Circonstance, No. 53, p. 21.
[2]) See Publ. de Circ., No. 61, p. 37—41.

quency for the number of rings on the scales have "behaved" in the manner requisite if the rings are anual. The whole of the long series of investigations which have been carried out from 1907 till now forms one large system of affirmations of the assumption that the scale rings are annual rings[1]).

Whilst in investigations of the character just mentioned the chief object for examination was the characteristic peculiarities in the shape of the curves of frequency for number of rings, and their alterations in the course of time, use has been made in a third kind of investigation of special features in the arrangement of rings on the scales of the herring. In 1910 it was found that the scales in a considerable number of the individuals with 6 rings (in samples from the West Coast of Norway) exhibited the characteristic that the 3rd growth zone was much narrower than the 4th growth zone lying outside it. Investigations proved that this was so practically only within the 6-ring group, and that the characteristic might consequently be used as a distinguishing mark for the group. The hypothesis of annual rings demands that this characteristic in the year 1911 should be found in individuals having seven rings, in 1912 in those with eight rings etc., in other words that it should not disperse over other groups. — Investigation has demonstrated the fulfilment of this requirement as completely as may be expected i. e. as completely as the technique of observation permits of a demonstration[2]).

All these investigations and others which have not been enumerated here, decidedly point towards on single conclusion, as far as Norwegian herrings are concerned, viz.:—the rings on the scales are annual rings which are formed with a wider growth zone during the summer half of the year (the summer zone) whilst the narrow transparent ring which separates two summer zones is formed during the winter season, and may therefore be styled the winter ring.

These investigations vary with regard to the kind of observations

[1]) Hjort, Fluctuations in the Great Fisheries etc., Rapports et Procès-Verb., Vol. XX, 1914. For later years data are published in „Aarsberetning vedk. Norges Fiskerier, Bergen 1916—1921.

[2]) See Lea, Report on Age and Growth of the Herring in Canadian Waters. Canadian Fisheries Expedition, 1914—15. 1918 (M. S. dispatched from Norway June 7th, 1916).

made on the herrings and their scales, but they are uniform in one principle viz, that the observations are arranged in connection with a scale of time, a principle considered by me as absolutely indispensable and which has been completely neglected in the work organised by Professor D'Arcy Thompson.

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He also has directed my attention to a publication from the Norwegian Statistical Bureau (Norges Officielle Statistik IV, 118, 1905), where frequency curves, essentially similar to those given here (figs. 2—4) are derived for married persons of a human population in exactly the same manner as in this paper. These curves seem to me rather interesting in this connection, not so much because of the analogies which are doubtless present as for the fact that the two curves of which it is a difference have rather different aspects from those adobted for the construction of figs. 2 and 3, the mortality curve, f. inst. being curved the other way over a considerable range and having an inflection point at one of the higher ages (as well as one at very young ages).

It appears as if the two functions may be varied within rather wide limits without the resulting difference curve loosing its resemblance with common variation curves.

2/7 — 1924.

Einar Lea.