ON THE ORIGINAL VARIATES OF TAXONOMY AND THEIR REGRESSIONS UPON SIZE IN FISHES

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INTRODUCTION

THE CHARACTERS BY WHICH the species, sub-species, populations, or other systematic units are recognized are, of course, the true original variates of taxonomy. The recorded "data" and other symbolic expressions of these characters are secondary and derivative.

The original variates by which systematic units are defined are those of size, form (i.e., shapes, patterns, etc.), counts, color, and physiological properties. Variates of size referring to the absolute dimensions of the whole are of slight value for the identification of a specimen except among the warm-blooded animals, or when used with reference to a definite ontogenetic stage, such as maturation of the gonads. Variates of size that refer to the absolute dimensions of parts are of direct systematic value only when over-all size is a specific constant.

In ichthyology data descriptive of forms far outweigh other features in the space and attention they receive for the purposes of diagnosis and differentiation of systematic units at all levels. Counts occupy second place. Color, as distinct from color patterns which are variates of form, run a very poor third. Absolute size of the whole, but not of the parts, is of some usefulness.

Form and color are the variates by which a trained observer immediately recognizes a familiar species, without close examination. They are commonly also the variates by which he is first made aware of the presence of a previously unknown species. As our knowledge of a group advances, immediate recognition of the unknown becomes more difficult, and closer examination of forms, counts, and colors is required. But the fact that these are the original variates used for systematic identification is not changed by the manner in which they are observed and recorded symbolically so that a knowledge of them can be communicated to other students.

In this discussion we are concerned with the symbolic presentation of the original variates of form. The most direct and most complete symbolic presentation of form, in print, is by pictorial rendering. This method of communicating information about the original variates is, of course, widely used in taxonomy and particularly heavily relied upon in paleontology.

In the even more abstract symbols of the numerical system the original variates of form can be expressed only as proportions. Such ratios, indices, or whatever they may be called are therefore actually the only numerical symbols truly and directly representative of the original morphological variates of taxonomy.

The recording of absolute linear dimensions of parts is a detour commonly taken for practical reasons in developing the proper symbols for the original variates. The detour is not always taken. Many of the proportions recorded in the literature have been directly determined as proportions by setting a pair of dividers to the length of the part (e.g., head) and pacing it off against the length of the whole, to establish that one "goes x times in" the other. And this is still frequently done for rapid identification of a specimen. The basic reason for making the detour of recording absolute dimensions of parts is simply that it reduces the number of manipulations required, because the figures can be recombined to create the symbols for different elements of form without remeasuring the parts. The recorded length of the head serves equally well to create the symbolic expressions for general elements of form such as large-headedness or small-headedness, and for particular form elements such as long-snouted or short-snouted. This use of absolute measurements in order to save time does not in any way make them direct expressions of the original morphological variates of taxonomy, which are forms that can be expressed only in mathematical relationships between dimensions.

A clear understanding of the difference, as well as the relationship, between the true original variates of taxonomy and their descriptive symbols is important in order to secure a proper evaluation, use, and manipulation of these symbols in systematic research.

In the course of ontogeny the forms and proportions characteristic of species and

other systematic units undergo changes, which in fishes apparently continue throughout the life of the individual. The need to find expressions that reflect these ontogenetic changes has therefore received increasing attention among the students of fishes. A simple method of expression previously proposed by the writer (Parr, 1949) as a purely practical measure and further simplified in subsequent applications (Parr, 1952, 1954) has received little or no use by others. A reëxamination and comparison of the intrinsic merits as well as the practical advantages of this and of other methods currently in use among ichthyologists would therefore seem in order.

The writer recognizes that allometry equations, i.e., equations of the form of $y = ax^k$, will often provide approximations which may be mathematically superior to those that are discussed below, and that regressions of this type offer certain advantages for the study of variability as such. But for the practical purposes of taxonomy, such as the identification of specimens by means of keys to the species, it is essential to use functions for which the graphic expressions are readily visualized or can be quickly plotted on simple coordinates, and which can be easily applied to the observed dimensions of a specimen by simple and familiar methods of computation. Diagnostic characters such as "head less than a per cent of the length (L)" are already traditional in fish taxonomy. A refinement such as "head less than $(a - b.L)$ per cent of L" can be easily absorbed into taxonomic tradition and practice, both in the field and in the laboratory. But, in the writer's opinion, an expression like "head less than $a.L^k$" would not be very assimilable in the daily work of identification. Allometric expressions would reduce the usefulness far more than they would enhance the virtues of a synoptic key or a specific diagnosis and would represent refinements of method not warranted by the current lack of refinement of our general knowledge of the taxonomy of fishes. For the purpose of general taxonomic practice, we therefore here consider the adequacy and relative merits only of methods employing other

than the allometric, or the less frequently used exponential, types of regression equations, with full recognition of the true value of such functions in the more rigorous study of large samples bearing upon narrowly defined systematic problems.

Such other methods now in use in systematic ichthyology may be said to fall into one of two separate categories, depending on a basic difference in the first approach to the analysis of the data.

According to the methods widely used in fisheries research and strongly advocated by Marr (1955), the analysis should proceed from a plot of the absolute dimensions of the variable part against the absolute size of the whole and should lead to functions that express the mean regression of these absolute dimensions upon one another. For the sake of brevity this is here designated as the size-on-size approach.

The other methods, here considered, use the ratios of the parts to the whole, or to one another, as the basis of analysis. These ratios, usually given in per cent, are plotted against the length of the whole (e.g., standard length or total length), and functions are developed to express the regression of these ratios upon the size of the whole. This will be referred to as the ratio-on-size approach, or ratio-on-size methods.

In the following discussion y, in all instances, stands for the absolute dimensions of the parts, and x for the absolute dimensions of the whole.[1] When numerical values are applied, both dimensions are expressed in millimeters.

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[1] In ichthyology it is not always clear how the length of the whole is measured. The present writer uses "standard length," i.e., length without caudal fin. "Body length" may be an ambiguous term which the writer uses only when the available data are so described. Even "total length" may express different measurements, e.g., length to the end of middle caudal fin rays, or length to the tip of the longest caudal fin lobe, or length to the median point of a straight line between the tips of the caudal fin lobes. It is unfortunate that such terms are often used without specific definition.

THE RATIO-ON-SIZE approach is the method followed by the present writer in his study of deep-sea fishes. As a first approximation for the description of the changes in proportions with growth, he uses functions of the type previously proposed (Parr, 1949) which are of the general character:

$$100 \, y/x = a + bx, \tag{1}$$

which gives the dimensions of the part (y) as per cent of the whole (x).

Solved for the absolute dimensions of the part, (1) gives

$$y = 1/100 \, (ax + bx^2) \text{ mm.} \tag{2}$$

Because the value of (2) becomes 0 when x becomes 0, (1) and (2) offer the possibility of an approximation to the progress of change throughout the entire ontogeny of the species.

When b in (1) and (2) is negative, as it happens to be in the case of most of the proportions that the writer has found important in
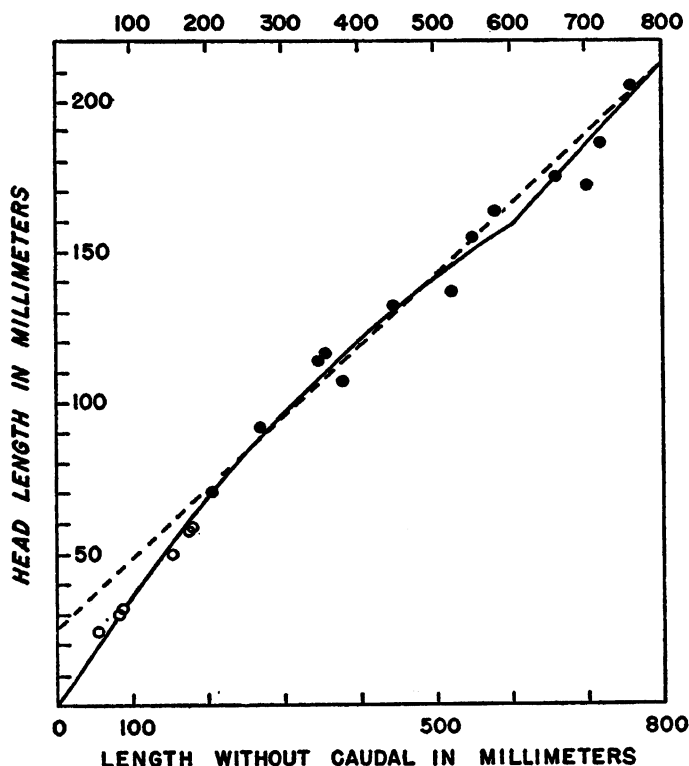

FIG. 1. Length of heads in *Alepocephalus giardi* plotted against length without caudal. Data from Koehler (1896), Holt and Byrne (1908), Collett (1905), and Koefoed (1927) used by Parr (1949). Solid line represents expression used by Parr (1949); broken line, for rectilinear regression ($y = 25 + 0.023\ 57\ x$) based on specimens larger than 200 mm. (solid dots).

In recent work, functions of the type of (1) have been used mainly to define the upper and lower limits of a band within which all the actually observed proportions can be contained (Parr, 1952, 1954).

his own work, the value of (2) reaches a maximum at

$$x = a/2b.$$

If this value of x is less, or only a little

more, than the maximum size attained by the species, a breaking point must be recognized, at least if (1) is used to approximate the progress of change in the average proportions rather than in their upper and lower limits. Figure 1 shows[1] how such a breaking point was recognized in the ratio-on-size plot at $x = 600$ mm., although the maximum value for y is not actually reached until $x = 1090$

whole $(100\ y/x)$ becomes constant in "full-grown" specimens (see Parr, 1949).

If functions of the type of (1) are used to define only the changing upper and lower limits of variation, it will often be found unnecessary for practical systematic purposes to take the occurrence of a breaking point into account, when only first approximation is required.
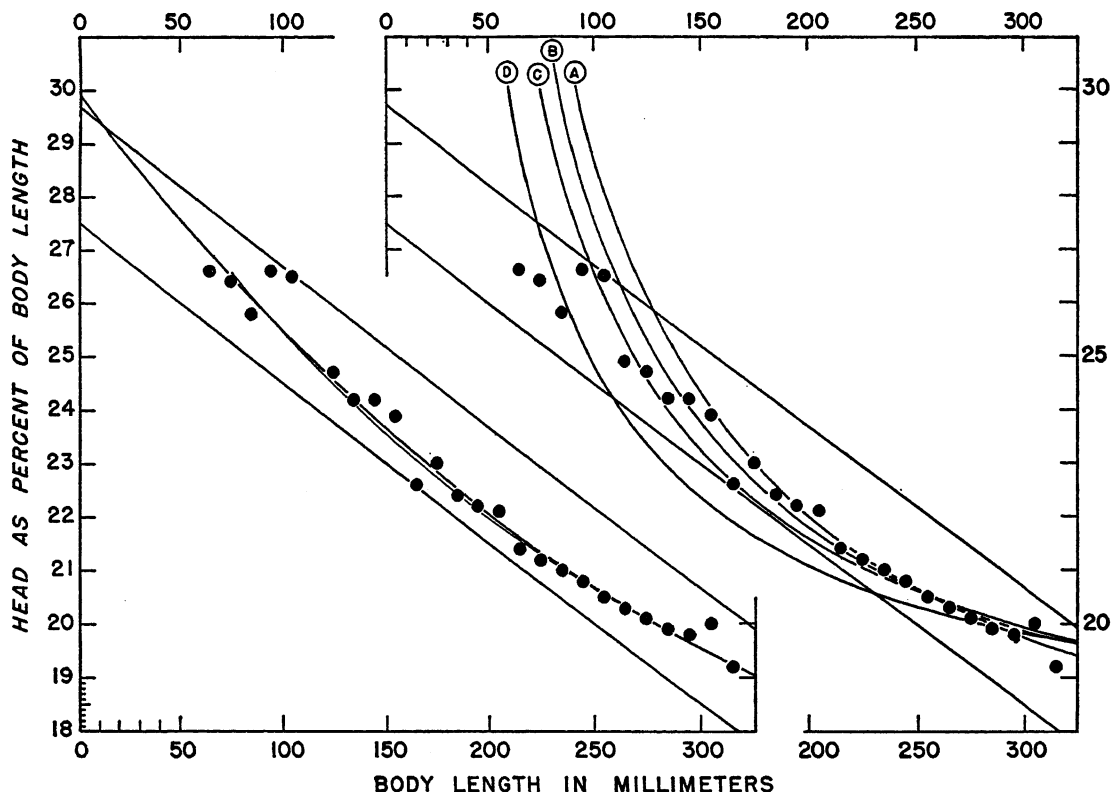

FIG. 2. Ratio-on-size plots of Rounsefell's data on the length of the head in the Pacific herring at entrance to Cook Inlet (see text). Five uppermost dots in left diagram of very unequal weight. The two above the curvilinear regression represent only one specimen each; the three below, a total of 24. Curve passes through mean of all five. Curves A to D in diagram at right correspond to rectilinear regressions in left diagram of figure 3.

mm., according to the function of type (1) represented by the curve from $x = 0$ to $x = 600$.

When such a breaking point must be recognized in the upper size range, an adequate first approximation for the proportions of the larger specimens will often be found if it is assumed that the ratio of the part to the

Because deep-sea fishes are too rare in collections to provide adequate samples for a satisfactory testing of methods, the writer has not made use of his own data for the purposes of this discussion. Fortunately, there are abundant examples already available for use in the published reports of other investigators.

Rounsefell (1930) gives extensive tables for various proportions of the Alaskan herring. His measurements of the heads are

[1] The figure also shows that Marr's assumption (Marr, 1955, p. 28) of a rectilinear regression of size on size in these data is not correct.

chosen as representing a feature of general systematic importance in all groups of fishes. Rounsefell's records of the heads in the herring population at the entrance to Cook Inlet (totals for Shuyak Strait, Halibut Cove, and Lower Kachemak Bay in Rounsefell, 1930,

of these calculated averages against the whole. Finally, curvilinear regressions for ratio-on-size were calculated from the rectilinear regressions of size-on-size and used in the final presentation. Rounsefell's curves should therefore actually be considered under
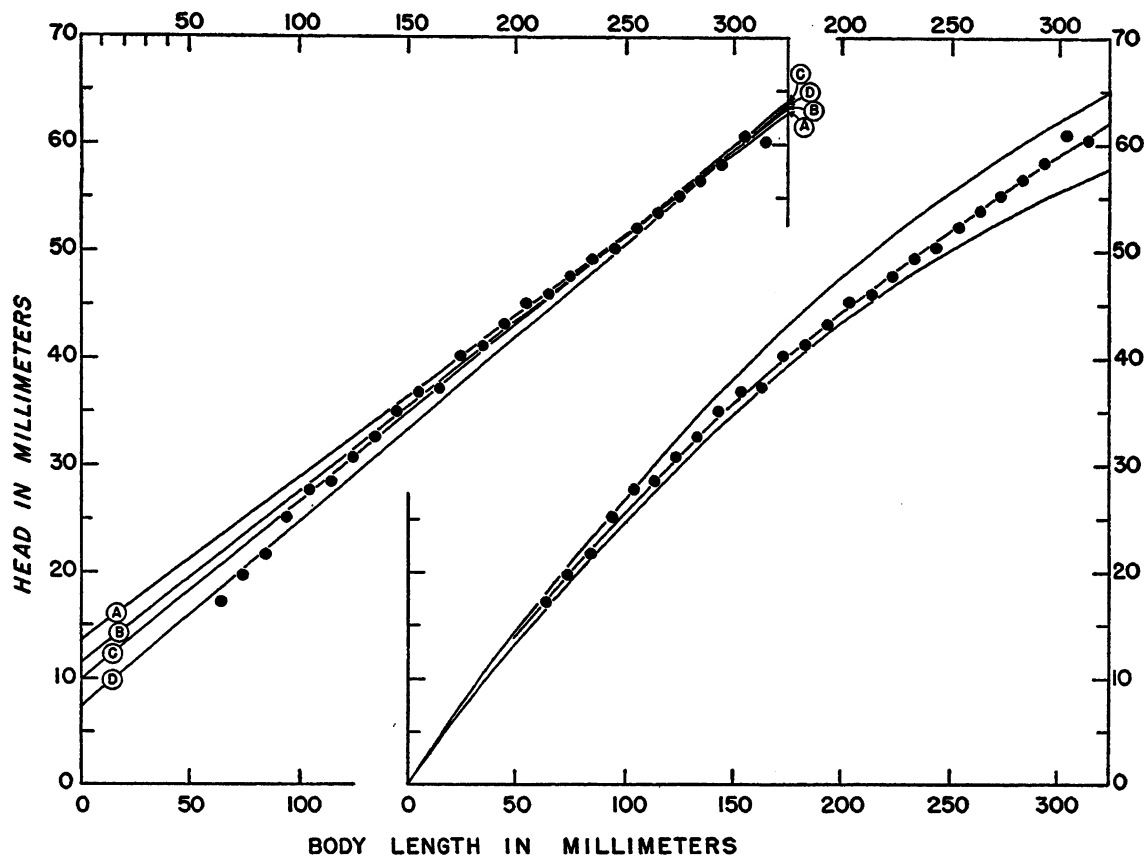

FIG. 3. Size-on-size plots of same data as in figure 2. Straight lines A to D in left diagram correspond to curves A to D in right diagram in figure 2. Outer converging curves in right diagram express rectilinear limits, and middle curve represents curvilinear regression, in the left diagram of figure 2.

p. 268) have been selected for study, because data over a wide range in size, and particularly data including small specimens, are essential for a real test.

Rounsefell based his own studies on ratios and presented his results in ratio-on-size plots. But for the development of curves to fit his data it would appear that he first determined average ratios of parts to the whole (100 y/x) for each 10-mm. interval in over-all length. These averages were used for the calculation of average absolute dimensions of the parts for each interval. Rectilinear regressions were then fitted to a size-on-size plot

the heading of the size-on-size, and not the ratio-on-size, method of approach.

In the left diagram of figure 2 the present writer has applied the ratio-on-size approach to Rounsefell's data as above identified. The first approach to a description of the data is made by fitting to the upper and lower limits of variation the following two rectilinear functions:

$$100 \ y/x = 29.7 - 0.03 \ x \qquad (3)$$

and

$$100 \ y/x = 27.5 - 0.03 \ x. \qquad (4)$$

For comparisons between species, these

limits might suffice. But it is obvious from figure 2 that a curvilinear function would provide a closer fit, as would seem desirable in population studies.

To obtain a second approximation, the writer therefore first drew a fair curve by inspection. This is shown as a thin line in figure 2. With this as a guide he then fitted a function[1] of the general type of

$$100 \ y/x = a + bx + cx^2. \qquad (5)$$

The actual function arrived at is

$$100 \ y/x = 29.9 - 0.048 \ 9 \ x + 0.000 \ 048 \ x^2. \quad (6)$$

[1] This procedure provides a short cut that can save a lot of time in arriving at a second approximation likely to prove serviceable for most taxonomic purposes. This is particularly true if functions of the type of (5) are needed to define only upper and lower limits of variation rather than means or averages.

Functions of the type of (5) will have a minimum or maximum value at

$$x = -b/2c,$$

which is of concern in this connection if b and c are of different sign. Formula 6 has a minimum value at

$$x = 509 \ mm.,$$

well beyond the maximum size of the species.

Solving (5) for y shows that the value of y in this second approximation becomes 0, at 0 value of x, as it also does in the first approximation (1) and as it must in nature.

In the right-hand diagram in figure 3 the convergence upon 0 of the limits of variation in absolute dimensions, calculated from functions (3) and (4) of the first approximation, is shown by the outer curves, with the curve calculated from (6), of the second approximation, shown between.

As mentioned above, Rounsefell actually used the size-on-size method of arriving at the curvilinear regressions shown in his illustrations of ratios-on-size. Rounsefell did not, however, claim that his data on the Alaskan herring actually formed rectilinear regressions in a size-on-size plot. In the series here selected from Rounsefell's data, as the record most suitable for a test of method of presentation, rectilinearity is definitely contra-indicated in the size-on-size regression, as shown by the left diagram in figure 3.

Figure 3 also indicates four different rectilinear functions selected at random, to show the lack of fit of any such function that might be chosen.[1] In the right-hand diagram of figure 2 it is clearly shown that no rectilinear expression that might be selected for the regression of size on size will give an acceptable and usable fit for these data.

Other material for an evaluation of the size-on-size method of approach may be obtained from the data on the yellowfin tuna of Hawaii independently collected and published by Godsil and Greenhood (1951) and by Schaefer (1952). The size of the head is again selected as our first example.

Godsil and Greenhood choose functions of the general type of

$$y = a + bx + cx^{-1} \qquad (7)$$

to express the regression of size on size. This function is discontinuous at $x = 0$. As x approaches 0 from the positive side, y attains infinite positive or negative values according to the sign of c. Curve B in figure 4 expresses Godsil and Greenhood's function for the heads of the Hawaiian samples, namely:

From function (7) the regression of ratios on size may be calculated to be

$$100 \; y/x = 100 \; (ax^{-1} + b + cx^{-2}). \qquad (10)$$

Curves expressing function of the type of (10) derived from (8) and (9) are entered as A and B in figure 5. The comparison is of particular interest in view of Godsil and Greenhood's statement that, although the Palmyra sample regressions have a consistently lesser slope, a comparison of the four samples available from the central Pacific does not warrant positive conclusions. But, if curves as different as A and B in figure 5 can leave any doubts about whether or not they represent different populations, not to say different species, then serious doubts must surely arise as to whether such curves can legitimately be used to represent any systematic data at all.

Investigators using functions of the general type of (7) or (10) are, of course, always careful to point out that these are intended only to provide a fit within the size range of the data available. They also generally leave out the left portion of such graphs as those shown in figures 4 and 5 (as indicated by the broken line in fig. 4), thereby withholding from proper attention the very real shortcomings of the method employed.

But the systematists have both the right and a need to insist that the continuous processes of ontogenetic changes be expressed in continuous curves and functions. Among other tests to be met is the test that the function must not indicate a part larger than the whole at any size of the whole, as indicated by functions of the type of (7) and (10).

$$y = 65.843\;326 + 0.210\;717\;727\;3\;x - 13\;398.266\;35\;x^{-1}. \qquad (8)$$

As an interesting comparison, Godsil and Greenhood's function for the Palmyra samples, likewise from the central Pacific, is entered as curve A, which expresses

As a practical illustration it is evident from figure 5 that neither curve A nor curve B could be used as a test of identity for specimens as large as 400 to 500 mm., or only

$$y = 54.970\;266\;41 + 0.211\;003\;668\;5\;x + 139.745\;79\;x^{-1}. \qquad (9)$$

[1] In seeking a rectilinear expression as a convenience for roughly describing obviously curvilinear data, the present writer does not believe that fitting by mathematical calculations, such as the method of least squares, has any particular meaning. A personal evaluation of the particular sections of the curvilinear series for which closeness of fit is most important seems a more sensible

procedure under such circumstances. Is it the slope between end points of the series, or the tangential slope at some point between, or the slope of a cord that will be most significant and most revealing for the purposes intended? These are questions of personal judgment rather than mathematical solution.
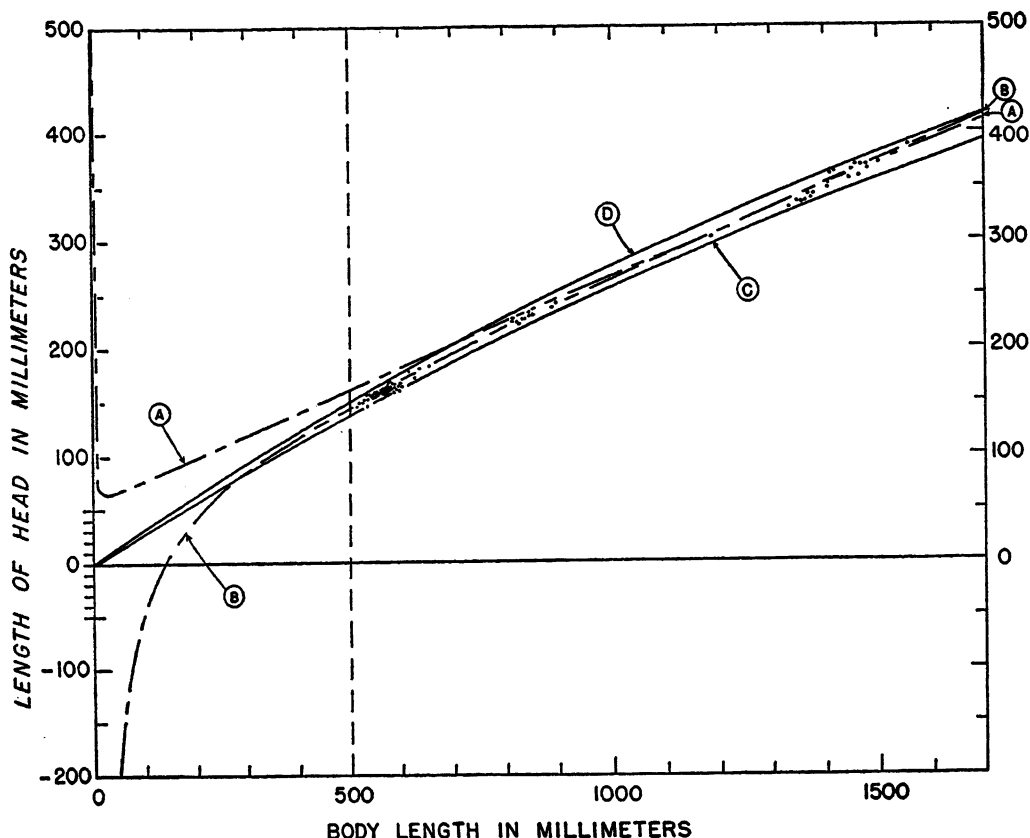
FIG. 4. Size-on-size plot of Godsil and Greenhood's data on the length of the head of the Hawaiian yellowfin tuna. Curve B expresses Godsil and Greenhood's regression (8). Curves C and D converging upon 0 correspond to rectilinear limits E and F in figure 5. Broken curve A represents Godsil and Greenhood's regression for Palmyra sample. (See text.)

slightly less than the smallest specimens in the actual samples.

One of the most objectionable features of (10), and therefore also of (7), is the occurrence of a maximum or minimum value of 100 y/x at $x = -2c/a$. If a and c are of opposite sign, and if (10) is used to fit data showing diminishing values of 100 y/x with increasing value of x, then a maximum value of 100 y/x will occur between x equal to 0 and x equal to the length of the smallest specimen of the series to which (7) or (10) has been fitted. In other words, the maximum must, in these circumstances, occur within the ontogenetic size range of the species, a condition that in most instances is quite unacceptable from the systematist's point of view. According to (8) the maximum occurs at a length of 407 mm.

For purposes of comparison, the writer has entered, by visual fitting, in figure 5 a median and two symmetrically converging upper and lower limits, which express first approximations of the general type of (1) and, specifically:

$$100 \ y/x = 32 - 0.004 \ 4 \ x \qquad (11)$$

and

$$100 \ y/x = 30.65 - 0.004 \ x \qquad (12)$$

and

$$100 \ y/x = 29.3 - 0.003 \ 6 \ x. \qquad (13)$$

Figure 5 also shows a second approximation to the data of the general type of (5) and, specifically:

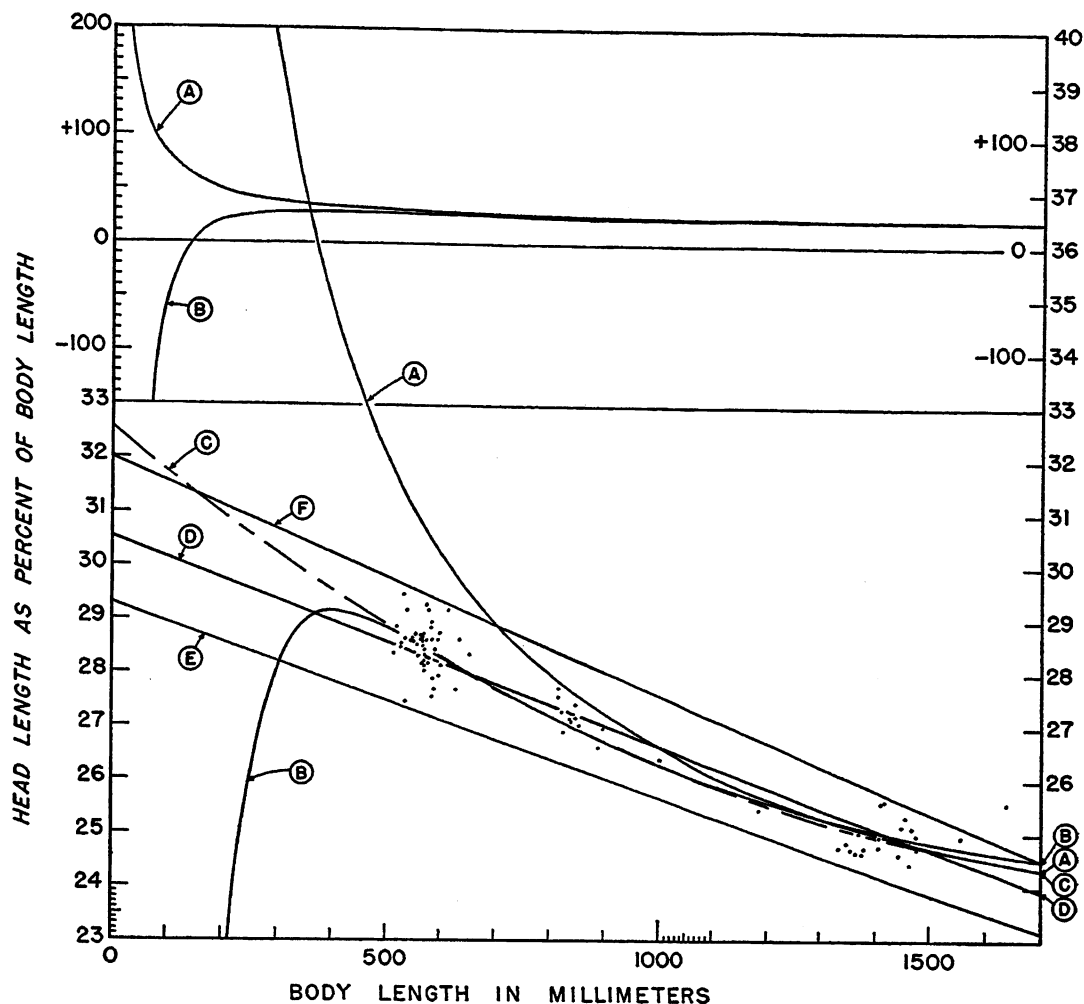$$100 \ y/x = 32.54 - 0.008 \ 22 \ x + 0.000 \ 002 \ x^2. \quad (14)$$

FIG. 5. Ratio-on-size plot of same data as in figure 4. Curves A and B derived from Godsil and Greenhood's regression for Hawaiian (B) and Palmyra (A) samples. Rectilinear regressions D, E, and F, and curve C fitted by the present writer (see text). Curves A and B shown above on reduced scale of proportions given at left.

Over the significant part of the range of the data, i.e., 500–1500 mm., (14) differs from Godsil and Greenhood's (8) by only 0 to about 0.16 per cent of the length (x), with an average difference of about 0.053 per cent of x, or less than 1 mm. in absolute dimension. In formulating (14) the writer disregarded an isolated, single measurement of a large head in one of the largest specimens (see fig. 5). If this were taken into account and a function of type (10) were fitted specifically to Godsil and Greenhood's (8), it would be

$$100 \ y/x = 32.64 - 0.008 \ 63 \ x + 0.000 \ 002 \ 3 \ x^2 \quad (15)$$

instead of (14). Over the significant range of the data function (15) differs from (8) only by 0 to about 0.032 per cent of the length, with an average difference of only about 0.013 2 per cent, or less than 0.2 mm. The fit could be made even closer if decimal points were added to the constants in (15). Terms of higher powers can also be added when needed.

In other words, functions of the type of (5) can be fitted to a function of type (7), over the range of data actually fitted by (7), with an accuracy far exceeding anything that the data will permit. This would seem to leave no reason for selecting a function of type (7),
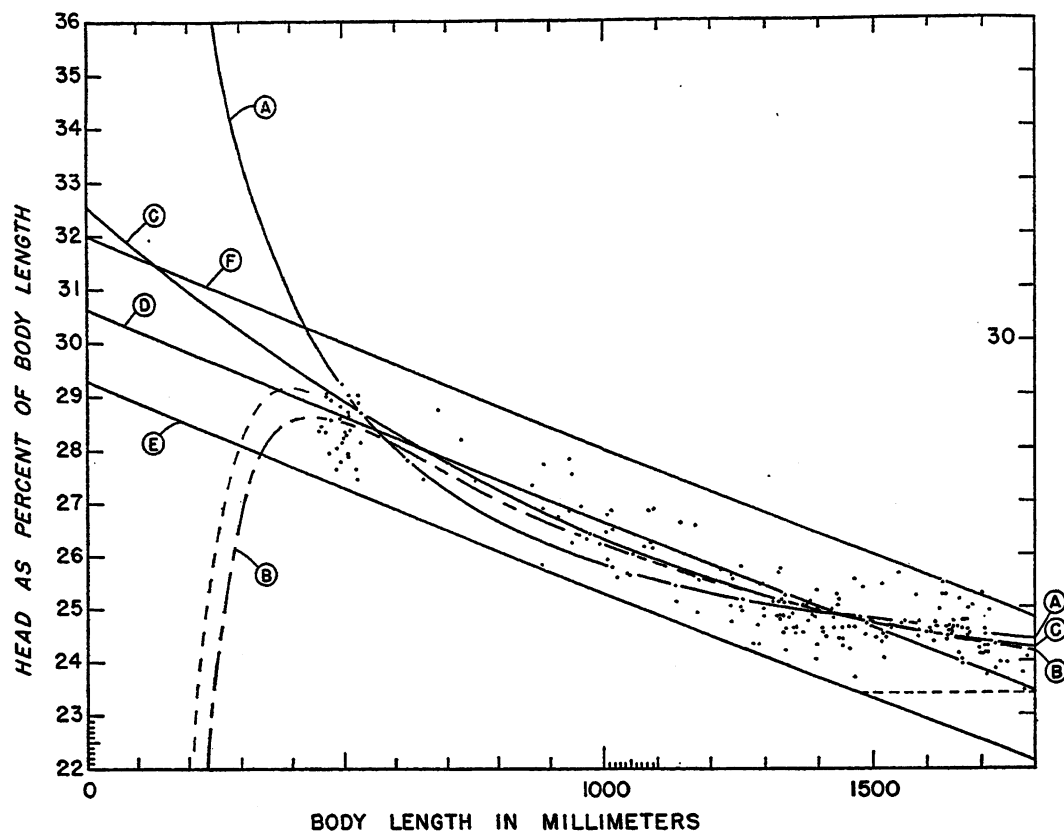
FIG. 6. Ratio-on-size plot of Schaefer's data on the length of the heads in the Hawaiian yellowfin tuna. Curves *A* and *B* express Schaefer's regressions (18) and (19) in the present text. Rectilinear regressions *D*, *E*, and *F*, and curve *C* fitted by the present writer (see text). Lower limit of variation in large specimens marked by broken line at right. Broken curve at left for Godsil and Greenhood's regression.

which cannot possibly fit the actual ontogeny of the species, in preference to a function of type (5) which does offer such a possibility.

It should also be noted that functions of type (10), calculated from type (7) as well as function (17) below, approach a constant value of 100 *b*, for high values of *x*. This might, in a way, be taken as confirmation of the writer's statement (p. 376) that, when a breaking point must be recognized in the use of functions of type (1) as first approximations, it will often be possible to do so by the use of a constant in first approximation of the value of 100 *y/x* for higher values of *x*.

Schaefer (1952) reëxamined the Hawaiian population of yellowfin tuna on the basis of entirely new data, using the size-on-size method of analysis, and functions of the rectilinear type:

$$y = a + bx \qquad (16)$$

to fit the data. For ratio-on-size this gives

$$100 \ y/x = 100 \ (ax^{-1} + b). \qquad (17)$$

The value of (17) becomes infinite as *x* approaches 0. Functions of type (16) or (17) can therefore not approximate the true ontogeny of the species any more than can functions of type (7).

Schaefer's function for the heads of the tuna is

$$y = a + 0.225 \ 67 \ x. \qquad (18)$$

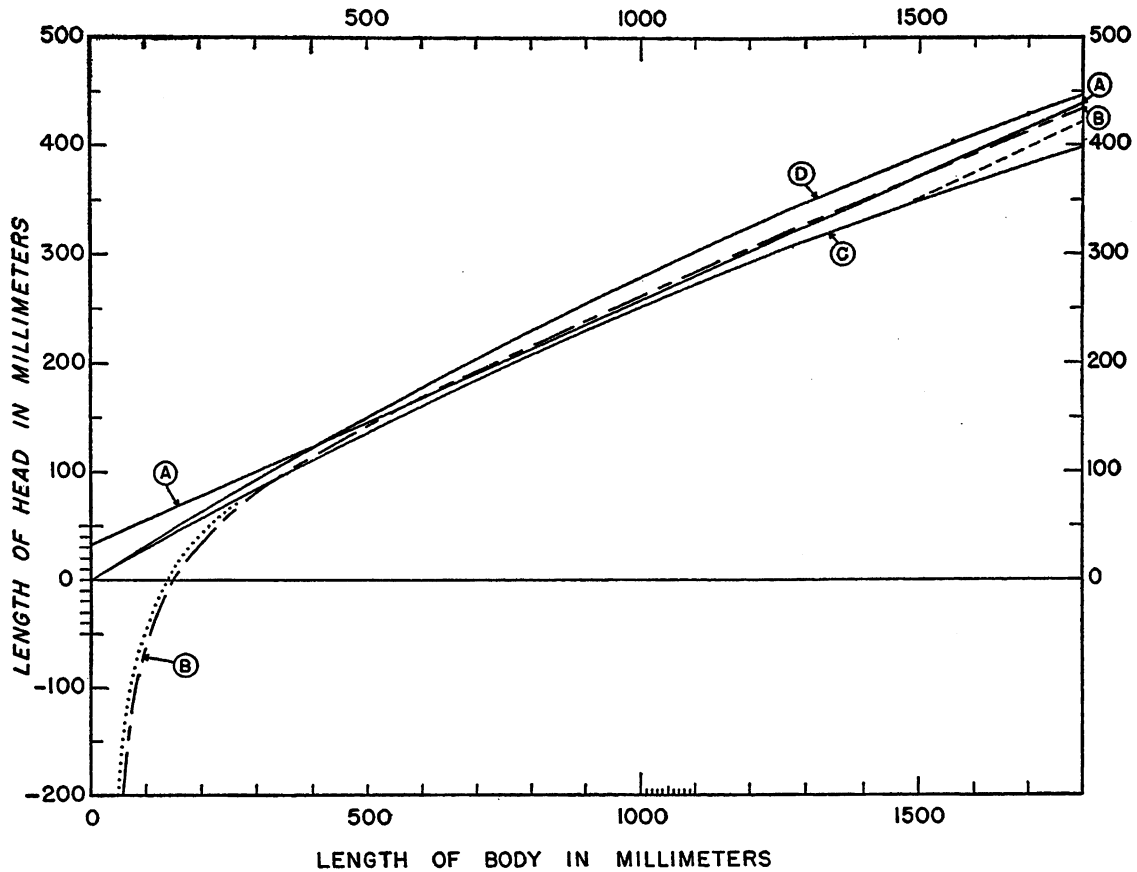The value of *a* is not given but can be de-

FIG. 7. Size-on-size plot of regressions of Schaefer's data shown by ratio-on-size in figure 6. *A* represents the rectilinear, *B* the curvilinear, regressions of Schaefer. *C* and *D* represent the present writer's rectilinear limiting regressions of ratio-on-size in figure 6. Curve *C* of figure 6 would fall between *C* and *D* in this figure but is not shown. For dotted curve at left and broken line at right, see legend of figure 6.

termined graphically as approximately 33. Schaefer also states that a function of type (7) used by Godsil and Greenhood would provide a better fit, and he gives it as follows:

$$y = 69.54 + 0.208\ 05\ x - 15\ 419\ x^{-1}. \quad (19)$$

In figure 6, curves expressing (18) and (19) are compared with a curve, *C*, expressing (14) of the type of (5), already fitted to Godsil and Greenhood's data (see above).

Over the significant range of the curves, from 600 to 1700 mm., the values of (14) differ from those calculated from (18) by 0 to about 0.66 $x/100$, with an average of about 0.29 $x/100$. From (19), which is better fitting according to Schaefer, the values of (14) differ only from 0 to less than 0.22 $x/100$, with an average difference of only about 0.085

$x/100$, or less than 1 mm. The maximum difference in the latter comparison does not exceed 1.5 mm.

On the other hand, the difference between the values calculated from the two functions (18) and (19), proposed by Schaefer, range from 0 to about 0.395 $x/100$, with an average of about 0.202 $x/100$, or nearly 2.5 mm., and with a maximum difference of more than 3.5 mm. This difference is characterized by Schaefer himself as "slight." The difference between (14) and (19) is less than half as large, as shown in the preceding paragraph.

An interesting fact brought out by Schaefer's new data is that the convergence of the limiting functions (11) and (13) fitted to Godsil and Greenhood's data was unwarranted. And it is even more interesting to note from
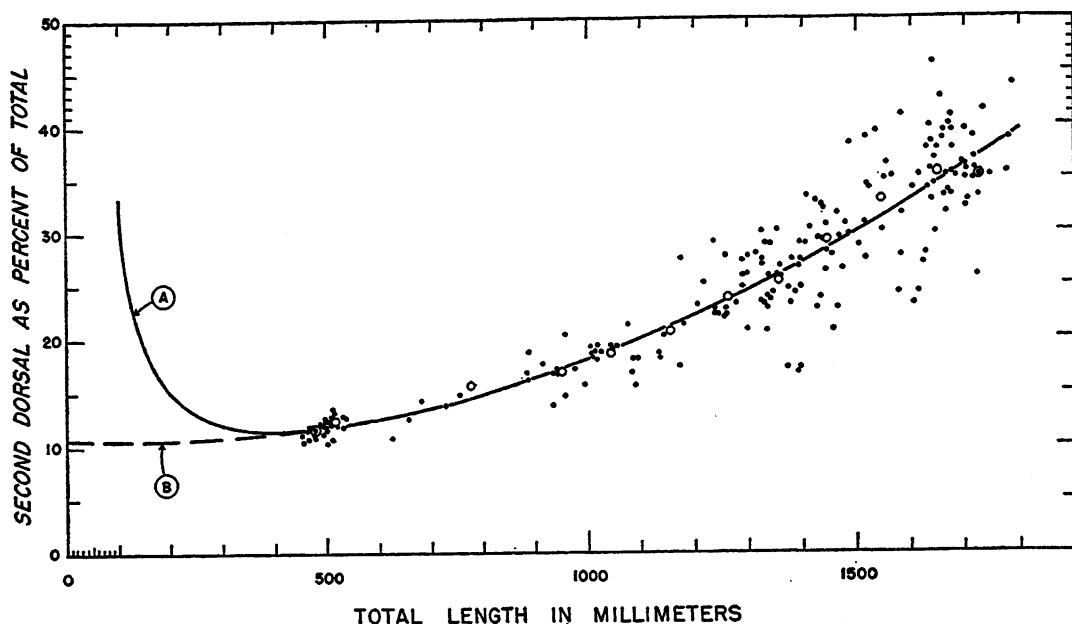
FIG. 8. Ratio-on-size plot of Schaefer's data on the length of the second dorsal fin in the Hawaiian yellowfin tuna. Solid curve (A) expresses Schaefer's regression; broken curve (B) represents regression proposed by present author. Open rings indicate averages, used also in figure 9. A single average for 600–900-mm. interval, other averages by 100-mm. intervals.

figure 6 that the new limits are excellently fitted by simply changing the coefficients of slope in the limiting functions (11) and (13) to the same coefficient as that of the median function (12) previously fitted to Godsil and Greenhood's data by first approximation according to (1). No other change is required, and the new limiting functions become simply:

$$100 \ y/x = 32 - 0.004 \ x \qquad (20)$$

and

$$100 \ y/x = 29.3 - 0.004 \ x. \qquad (21)$$

This confirms the present writer's general experience with the scarcer data on deep-sea fishes that the limiting functions of variability in the ratio-on-size plots tend to run parallel. In second approximation parallelism between curves may be looked for. With this minor emendation, both the first and the second approximations to the first set of data

on the yellowfin tuna of Hawaii, according to (1) and (5), have proved entirely satisfactory as approximations of the new data as well. While the changes required in such approximations as (8), (18), and (19) may not be very great over the same size range, they become quite drastic when the range is extended towards smaller sizes, especially in such cases as (8) and (19), both of which have maximum values between 400 and 500 mm. in length. Even specimens between 350 and 450 mm. in length would be beyond possibility of fit by these functions.

The examples that are presented above are concerned with proportions that diminish with increasing total length. It may be of interest to consider a case in which the proportions increase with growth. Schaefer (1952) gives measurements of the length of the second dorsal fin in the Hawaiian yellowfin tuna, to which he has fitted the following equation:

$$\log y = 7.649 \ 65 - 5.595 \ 55 \log x + 1.266 \ 13 \ (\log x)^2. \qquad (22)$$
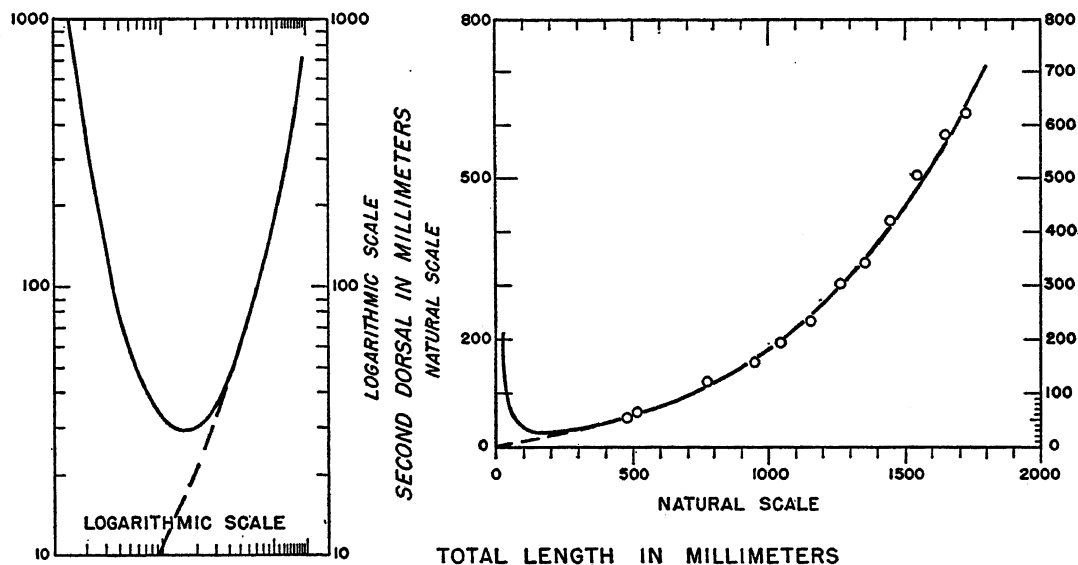
FIG. 9. Size-on-size plots of length of second dorsal fin in Hawaiian yellowfin tuna, according to Schaefer's data. Both dimensions on logarithmic scale at left; both on natural scale at right. Curves as in figure 8.

As x approaches 0, (22) approaches infinity; (22) also has a positive minimum value between 150 and 200 mm.

Using the ratio-on-size approach, the present author arrives at the following regression:

$$100\ y/x = 10.77 - 0.003\ 35\ x + 0.000\ 010\ 7\ x^2.\quad (23)$$

According to (23), the value of 100 y/x reaches a minimum of 10.508 per cent at a length of 156.5 mm. This minimum is only slightly less than the value of (23) at $x=0$. Because (23) does not give minimum values of y for positive values of x, a minimum value for 100 y/x would indicate only that the second dorsal fin begins its growth at a slightly slower rate than the growth rate of the body. This is certainly not an impossibility and may even be a reasonable assumption under the circumstances indicated by these measurements.

As indicated by figures 8 and 9, it is quite impossible to distinguish graphically between curves representing (22) and (23), in any form of presentation, over the entire range of the available measurements. The elaborate treatment of the data[1] and the physically impossible assumptions required by (22) are therefore completely unnecessary in order to obtain an equally good fit by using the ratio-on-size approach to arrive at a simple polynomial regression, such as (23).

[1] In its generalized form (22) can be written as follows:
$$\log y = a - b \log x + c\ (\log x)^2$$
By solving for y we obtain:
$$y = 10^a\ x^{c\ \log x - b}$$

A KNOWLEDGE OF THE variability of morphometric characters is essential for a proper evaluation of their systematic significance. The ontogeny of variability may also be a subject of independent interest. To the extent that variability undergoes change in the course of ontogeny, it may be safely assumed that the change is a continuous process. The systematist is therefore also entitled to an expression of variability which does, at least, offer the possibility of providing a continuous approximation to the actual state of affairs throughout the life of the species. This condition is not fulfilled by the expressions of variance customarily used in the size-on-size presentation and analysis of morphometric data.

The usual expressions of variance are based on the squares of individual deviations. In the size-on-size comparisons, the deviations are measured in units of absolute dimensions, e.g., millimeters. Such expressions of variance as those implicitly or explicitly used by Godsil and Greenhood (1951) and by Schaefer (1952), e.g., "mean square," therefore express variability as a constant, absolute linear dimension regardless of the size of the individual. To assume that actual variability during ontogeny would remain constant in the absolute sense of such expressions would be contrary to all experience and all logic. For example, a variance of heads equivalent to ±6.5 mm., established on data from specimens of 600 to 1600 mm. in length, can obviously not apply to specimens of 100-mm. length. If the mean size of the head at 100 mm. is 30 per cent of the length, this variance alone would cover a range of from 23.5 to 36.5 per cent of the length, with the total range of variability even much wider. This would be range enough for several species or even genera and bears no relation to facts of experience.

It seems obvious that, for the needs of the systematist concerned with the species as a whole, variability must be expressed as a function of the length (x) equally applicable at all stages of ontogeny. The experience illustrated in figure 6, of finding all individual variations in a ratio-on-size plot confined within parallel lines, suggests a very simple solution, namely, that variability may, in first approximation, be assumed to have a constant ratio to the length, as already noted by students of other groups (see Imbrie, 1956, p. 239). If individual deviations from the curve that expresses the mean ratio of the part to the whole are measured as proportions (e.g., per cent) of the whole, standard methods of computing variance would lead to expressions of variance as a constant function of the whole (n per cent of x) instead of an absolute constant, which would probably provide a fair fit for the actual ontogenetic changes of variability.

When the size-on-size regression of the part upon the whole is not rectilinear and a second approximation is needed for the description of variability, the method of determining dispersion around a regression line proposed by Klauber (1943) and further discussed by Imbrie (1956) should prove useful. According to this method, a measure of the dispersion of y (D_{yx} in Imbrie's expression of the formula) would be obtained when the standard deviation of y from the regression line is expressed as per cent of the mean value of y ($\bar{y}$) for the entire series, which thus makes the measure of dispersion a direct function of y and an indirect function of x, of which y is regarded as a dependent variable, thus[1]:

$$D_{yx} = \frac{100\sqrt{\dfrac{\sum (dy)^2}{N}}}{\bar{y}}.$$

A further refinement might be obtained by computation of a standard variation (SV), as distinct from a standard deviation, directly from the individual measurements by determining the percentage deviation of each value of y (y_L) from the mean value $\bar{y}_L$) indicated by the regression equation for the same total length (value of x), thus:

$$SV = \sqrt{\frac{\sum\left(\dfrac{100\,(y_L - \bar{y}_L)}{\bar{y}_L}\right)^2}{N}}.$$

[1] N freedoms are used in this discussion merely for the purpose of defining measures descriptive of the data available. The actual number of freedoms (N-m) to be used in the computation of probable errors, etc., may depend on the form of the regression line.

SV and D_{yx} would in most instances approximate each other very closely.

Philosophically the concept that in taxonomy we are concerned with forms and their symbolic description might be carried one step farther. It may be argued that form is only a perceptual, as distinct from a conceptual, symbol of the distribution of matter in space, and that the basic dimensions of reference should therefore be the quantity of matter, not any particular linear distance. The thought is not without practical significance. It would lead to the treatment of all linear dimensions, including total length, as dependent variables.

In various forms of life that lack a linear main axis uniquely defined by morphological characteristics, as in many invertebrates, such treatment of the data serves a very useful purpose and has already been incorporated in Imbrie's D_d, or coefficient of relative dispersions about a reduced major axis (Imbrie, 1956, p. 241). If the actual size of, say, a shellfish is uniquely determined only by its volume or its weight, it follows that no linear dimension that can be selected in the absence of an unambiguously defined main axis can be regarded as more directly representative of total size than is any other linear measurement. If total size attained is considered the independent variable of the ontogenetic process, this therefore means that all linear dimensions of the shellfish must be treated as dependent variables in relation to the total mass. This, in turn, means that all linear dimensions must be regarded as equally independent with respect to one another. Thus interpreted, Imbrie's Coefficient analyzes the mathematical relationship between dependent variables without direct reference to the independent variate of total size, and therefore without directly implying comparisons between the dimensions of a specimen of a given size and the dimension it might have had if it had reached another size. Although such comparisons may be, and undoubtedly often will be, involved indirectly, they do not in themselves form the actual basis of computation of the coefficient.

The reasoning here advanced will, in principle, apply to all forms of life. But the degree of freedom from implication of total size in arriving at Imbrie's Coefficient will differ according to the morphology of the organism. In the presence of a well-defined main axis, as in fishes, the dimensions of this axis are, in a sense, more directly representative of actual total size (total matter) than are any other linear dimensions that are likely to be considered (except girth and, to a slightly less extent, depth of body). Therefore it becomes less logical to assign to total length, and to other linear dimensions, equal independence with reference to one another, and more likely that such assignments will automatically involve comparisons with hypothetical dimensions at an actual size not attained by the specimen and, in many cases, even beyond any actual size attainable by the species. For these reasons the author prefers Klauber's coefficient of relative dispersion from a regression, as further defined by Imbrie, or the standard variation suggested here on page 386, in dealing with organisms having a well-defined and morphologically fixed main axis, using total length as a dimension representative of the total size attained by growth, which may be considered the independent variable of the growth process with reference to ontogenetic changes in proportions.

It should also be noted that Imbrie's Coefficient has been introduced with particular reference to the measurement of dispersion around a size-on-size regression, for which purpose it provides an admirable tool, except in the particular case of a great disparity between the variates in regard to their degree of independent variability. Imbrie's Coefficient is not, however, always adaptable to the measurement of dispersion around a ratio-on-size regression, for which it was not primarily designed. The difficulties arise from the facts that positive y intercepts are quite normal, and maxima or minima fairly frequent features of ratio-on-size regressions. As a result, d_x for data that refer to a small specimen may often have to be measured from an imaginary starting point corresponding to negative values of x (e.g., for a point above the curve at low values of x in fig. 2). For deviations above a maximum (see fig. 13) or below a minimum the value of d_x would become infinite. For deviations below the ratio-on-size regression curve, in the region in which the curve attains a maximum, two

different values of d_z would be obtainable (see fig. 13), and it is not certain that the least of these two values could always be considered the significant one.

Taking for granted the fact of common ex-

mean variance over the size range of the material. Other things being equal, a sample with heavier representation of specimens in the upper part of the size range should show a larger variance than another sample of the
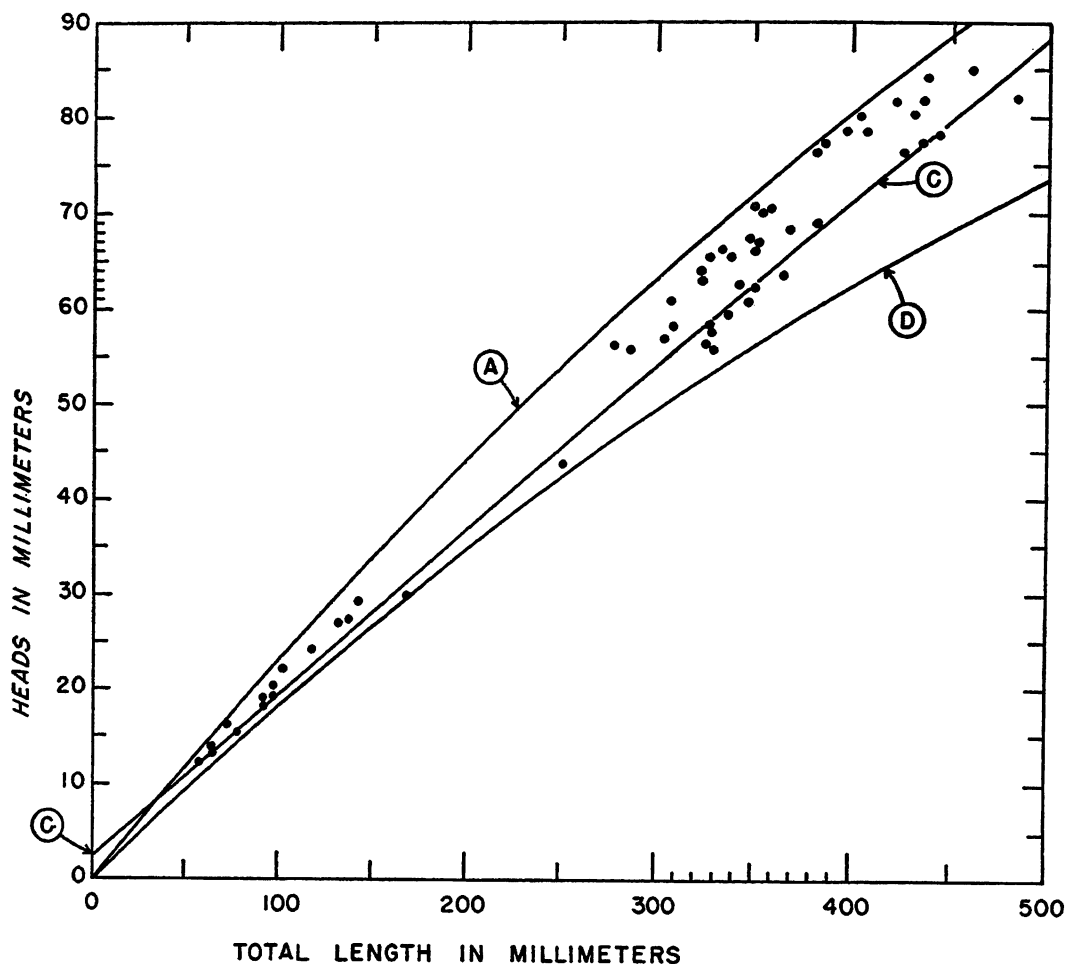
FIG. 10. Size-on-size plot of mean sample lengths of the heads in the Australian mullet calculated from Kesteven's tables. Line C represents Kesteven's regression. Curves A and D represent corresponding limiting regressions in figure 11.

perience that the limits of variability in absolute terms must diminish with diminishing absolute size, one will find that the significance of variances calculated on the basis of the squares of individual deviations measured in absolute dimensions is even more limited than is shown above. Such measures of variance cannot be taken to represent the

same range but with a different size distribution. Nor can the variance be taken to represent the variance of either the mean or the median size of the material. Owing to the use of the squares of the individual deviations, a sample with a preponderance of specimens near the two ends of the size range will give a larger calculated variance than another

sample of the same range and the same mean (or the same median) size in which the specimens are preponderantly clustered around the mean (or around the median). In other words, variances calculated in this manner can be taken to be representative only of the

plot for the graphic presentation and study of morphometric data. In such a plot the significance of individual deviations in the smaller specimens is completely obscured by the two facts that the absolute limits of variability for each species or population must
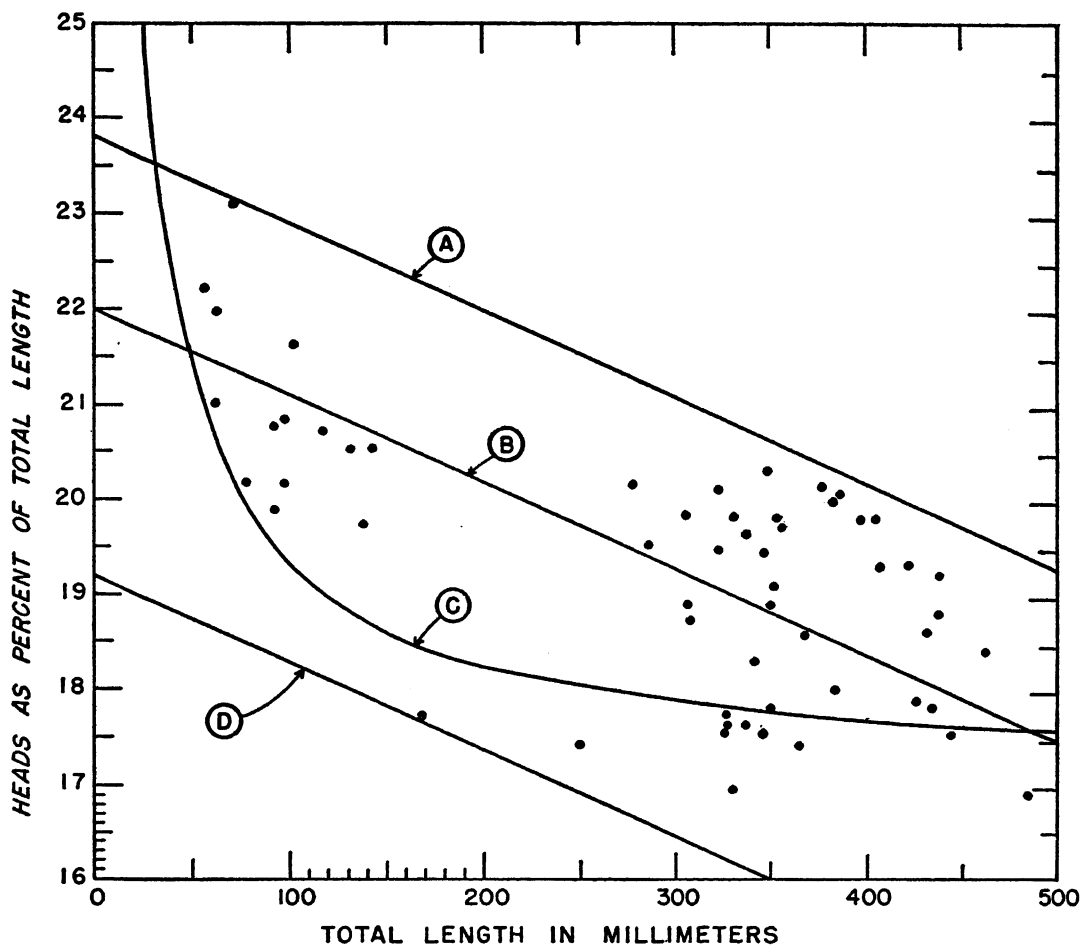

FIG. 11. Ratio-on-size plot of lengths of heads of Australian mullet according to Kesteven's tables 3A and 3B. Curve C expresses Kesteven's regression. Compare with figure 10.

particular size composition of the sample, in the sense that they are valid only for comparisons with other samples of the identical size composition, and not merely of the identical size range, or identical mean, or median size. The use of variances so restricted seems of very slight purpose.

The discussion of variability leads to another objection to the use of the size-on-size

diminish with diminishing absolute size, and that the regressions of a part upon the whole must converge upon the zero point of the coordinate system in all species and populations, making even the interspecific differences indistinguishable. A comparison between the ratio-on-size plot in figure 6, which shows a uniform spread of correlation points through the size range, with the size-on-size

plot in figure 7, in which the same data would be confined between the converging curves C and D, will serve to illustrate this point.

A still better illustration of the advantages afforded by the open scale of the ratio-on-size plot may be obtained from the data on the length of the head of the Australian mullet given by Kesteven (1942). Kesteven used the size-on-size plot and rectilinear regressions of type (16), describing the length, of the head specifically as

$$y = 0.172\ x + 2.16 \text{ (here expressed in mm.). (24)}$$

Figure 10 shows both the justification of Kesteven's use of (24) as a first approximation, represented by line C, and also its shortcomings. Figure 10 is based on the mean lengths and mean values of 100 y/x for each sample, given in Kesteven's tables 3A and 3B. Even in Kesteven's figure 3, where all the individual measurements are entered on a very small scale, a very slight curvilinearity is revealed by close scrutiny. The subtlety of the deviation from actual rectilinearity in the size-on-size regression is also revealed, if one should not say concealed, in figure 10 of the present paper. But the ratio-on-size plot of the same data in our figure 11 makes it abundantly clear that first approximations of the form of (1) are more serviceable for the description of these data, and the wide dispersal of the correlation points may even suggest a possibility of heterogeneity of material (populations). The distribution of the data in the ratio-on-size plot is contained between lines D and A (fig. 11), expressing:

$$100\ y/x = 19.2 - 0.009\ x \qquad (25)$$
and
$$100\ y/x = 23.8 - 0.009\ x. \qquad (26)$$

The coefficient of slope (0.009) used in (25) and (26) was obtained by first drawing a fair line through the scatter diagram, shown as line B in figure 11.

The values of y computed from (25) and (26) are entered in figure 10 as the limiting curves A and D for comparison with the data and with Kesteven's rectilinear regression, represented by C.

The important points to note in the comparison between figures 10 and 11 are: (A) the manner in which the band confining the data in figure 10 contracts towards small values of x, with the result that the true significance of individual variations emerging from the ratio-on-size plot (fig. 11) is nearly lost sight of in the size-on-size presentation, and with the further consequence (B) that only the ratio-on-size plot was able to reveal clearly the actual unsuitability of a rectilinear regression of type (16), represented by (24), which seemed quite reasonable in the size-on-size plot.

The measurements of the heads of the Pacific mackerel from the Viscaino region published by Roedel (1952) have been selected as an illustration of a fairly common situation in which the near-rectilinearity of the data in a size-on-size plot is deceptively close. Although the series covers the widest size range found in Roedel's material, it still lacks data from the lowest two-fifths of the full size attained by the species. The data therefore lack evidence from the size groups in which the curvilinearity of the size-on-size regression would be most clearly revealed. The nearly rectilinear arrangement of the data available furthermore points to a very low y intercept for which Roedel has given the value of 5.13 in his regression:

$$y = 5.13 + 0.254\ 2\ x. \qquad (27)$$

A low y intercept in a rectilinear approximation to data from the larger specimens implies a relatively slight curvature of the true size-on-size regression. This fact, combined with the lack of revealing data from small specimens, makes the use of rectilinear expressions particularly tempting. On the basis of the size-on-size plot shown in the lower portion of figure 12 there would scarcely be any justification for questioning the validity of Roedel's regression (27). But, even with such subtle differences and inadequate data, we again find the deficiencies of the rectilinear size-on-size approximation clearly revealed when the data are replotted on the open scale of the ratio-on-size diagram shown in the upper part of figure 12. Although it is possible that the slope of the regression for smaller sizes may be steeper, it seems beyond question of doubt that (27), represented by curves C in figure 12, cannot possibly describe the mean course of ontogeny below about 120–150 mm. in length. Nor can there be any doubt that functions of type (1), e.g., as rep-
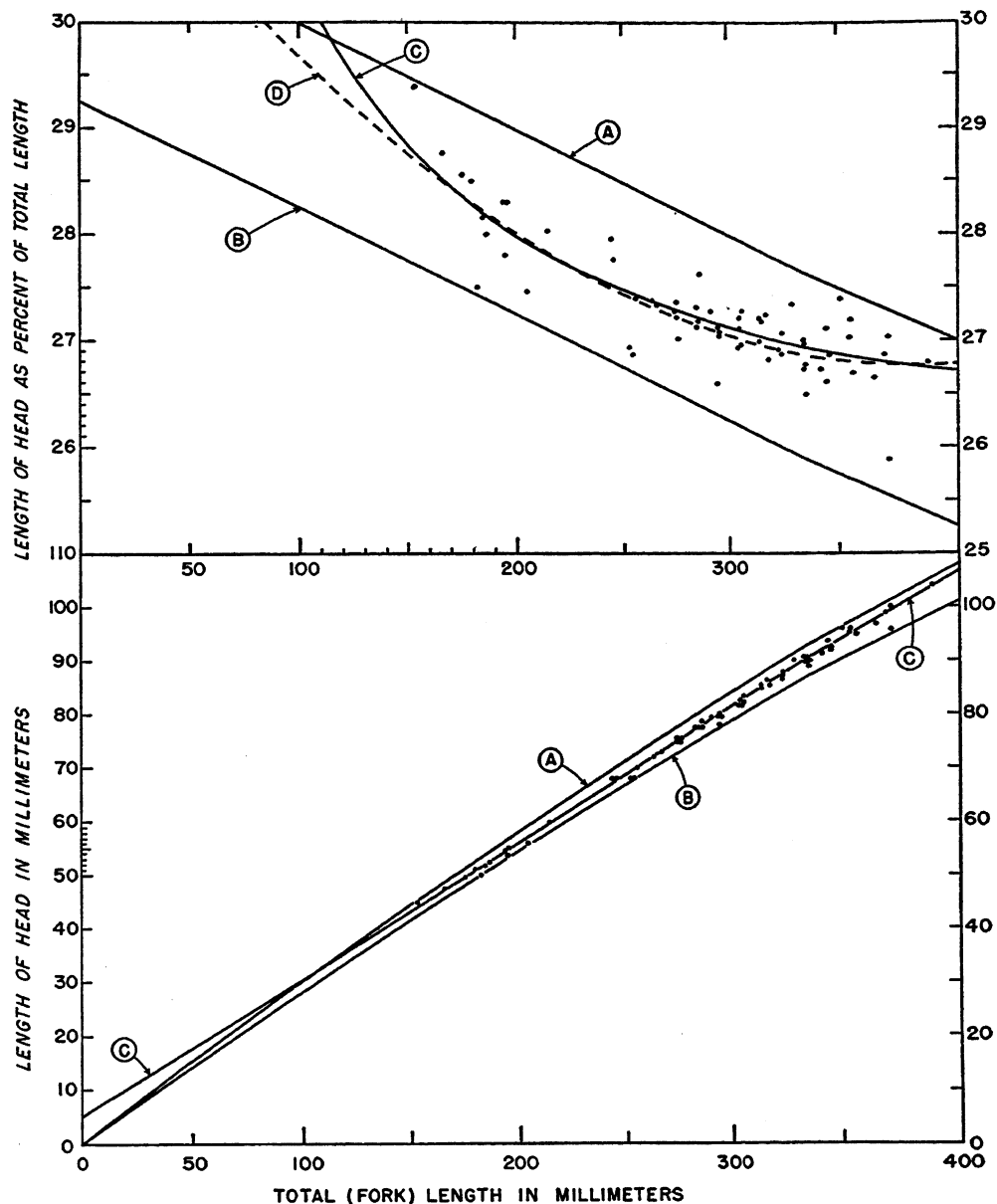
FIG. 12. Ratio-on-size plot (above) and size-on-size plot (below) of the lengths of the heads of the Pacific mackerel in the Viscaino region according to Roedel (1952). Head lengths and total lengths averaged for 10-mm. intervals for each sample separately. Curves C express Roedel's regression. Other curves represent first (A and B) and tentative second (D) approximations suggested by the present writer. (See text.)

resented by the limiting curves A and B in figure 12, or of type (2), very tentatively represented by curve D,[1] offer a much better and

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[1] The regressions expressed by these lines are:
Curves A: $100\,y/x = 31 - 0.01\,x$
Curves B: $100\,y/x = 29.25 - 0.01\,x$

more credible description of the data available.

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Curve D: $100\,y/x = 32.05 - 0.027\,2\,x + 0.000\,035\,x^2$. The departure of the size-on-size plot of D, for small values of x, from the band defined by A and B could not be visibly rendered on the scale of the lower diagram in figure 12.

ONE OF THE MAIN purposes of the preceding sections is to show that the practice of fitting limited series of data by functions that cannot possibly fit the species represented by the data is not an acceptable procedure in systematic research. It is shown by several examples that the apparent justification of such functions depends on the lack of material

so that these first approximations, in the literal sense of time, can become starting points for the ultimate development of accurate descriptions, by gradual refinement, rather than having to be discarded and replaced. When the morphometric characteristics of a systematic unit are described in a manner that involves physically impossible
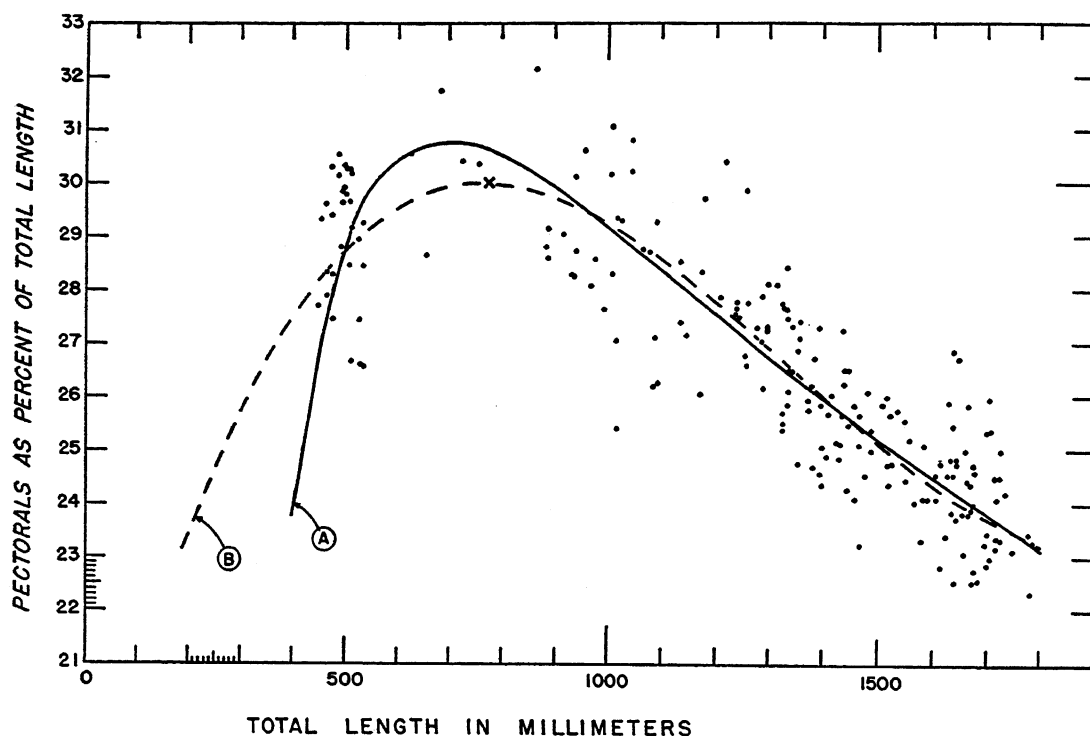

FIG. 13. Ratio-on-size plot of lengths of pectoral fins in yellowfin tuna of Hawaii, according to Schaefer's measurements. Curve A expresses Schaefer's regression; B, the present author's own regression. Cross indicates mean of nine measurements between 550 and 900 mm. total length.

rather than on the evidence of the data actually available, which can also be described in other ways.

One of the primary purposes and needs of taxonomy is to develop expressions that describe a species, or other systematic unit, as a whole. The task can be approached only if we induce from the available data functions combining a fair fit for these data with a fair possibility of their being serviceable approximations also beyond the range of the data,

mathematical assumptions, it means that the description is offered with full knowledge that it cannot actually be valid for the taxonomic unit concerned and cannot offer a basis for the development of systematic definitions by an orderly progress of improvement. Regardless of abstract mathematical merits, it also seems questionable in logic to use physically impossible assumptions for the comparison of physical realities, even over the range covered by the data.
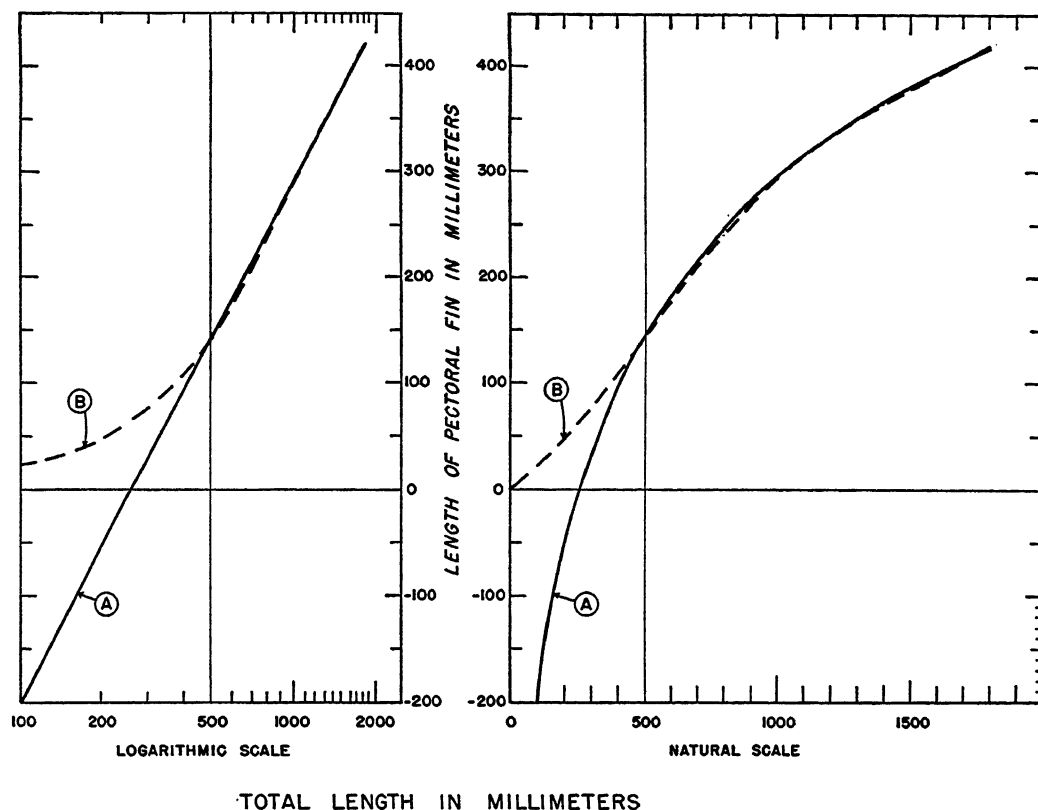
·TOTAL LENGTH IN MILLIMETERS

FIG. 14. Curves representing Schaefer's (*A*) and the present author's (*B*) regressions for lengths of pectoral fins in Hawaiian yellowfin tuna plotted against logarithms of total length (at left) and against total lengths on natural scale (at right).

DESCRIPTION OF DATA

In suggesting that serviceable functions for first and second approximations to the accurate description of fishes may commonly be found in binomial or short polynomial series fitted to ratios plotted against absolute length, the author is fully aware that such expressions may not be suitable in all instances.

It is true, of course, that rectilinear functions could always be used to define the limits of the occupied area of a scatter diagram and could in that sense always be claimed to offer a first approximation. But the designation would scarcely have any justification in some cases. It may also be true that a sufficiently extended polynomial function might be made to fit almost any distribution of morphometric data likely to be encountered. But the advantage of simplicity would then be lost,

and other functions would become preferable in most instances.

The usefulness and superiority of the linear and quadratic functions are shown by various examples given above, taken from data previously fitted by other methods that involved physically impossible assumptions. It may be of interest to examine a case in which quadratic functions would provide merely first approximations of limits, and in which cubic functions must be sought for a second approximation.

Schaefer (1952) has provided a very interesting series of measurements of the lengths of the pectoral fins of the yellowfin tuna, to which he fitted the following function:

$$y = 491.9 \log x - 1184. \tag{28}$$

In common with the functions examined

above, (28) also involves physically impossible assumptions. As x approaches 0, y approaches negative infinity. The indicated length of the pectorals becomes 0 at the very substantial size of 255 mm.

Figure 13 shows a ratio-on-size plot of Schaefer's data in which a curve (A), calculated from Schaefer's regression (28), has been entered for comparison with curve B suggested by the present writer as an expression of the following equation:

A positive y intercept (positive value of a) is normal and natural in the ratio-on-size regression, which makes the choice of a reasonable fit much easier.

A positive y intercept in a size-on-size regression indicates the assumption of a physical impossibility under all circumstances and should therefore not be permissible in systematic research.

A negative y intercept of either a ratio-on-size, or a size-on-size, regression will also in-

$$100 \ y/x = 16.89 + 0.039\ 495\ 5\ x - 0.000\ 036\ 119\ 4\ x^2 + 0.000\ 000\ 008\ 965\ x^3. \qquad (29)$$

It will be seen that the curves representing (28) and (29) do not differ significantly, within the size range of the data, except in the region of maximum curvature from 550 to 900 mm. in total length.[1]

Over this part of the size range the recorded measurements are so few (only nine out of a total of 204) and so widely scattered (from 28.6 to 32.8 per cent) that the distribution of the individual correlation points does not offer much guidance for a choice between the two curves. But if the average total length (774 mm.) and the average pectoral length (232.222 . . . 2 mm.) are calculated for all of the nine specimens, the average relative length of the pectorals (30.003 per cent of total length) agrees almost precisely with (29), which gives $100 \ y/x = 29.978$ at $x = 774$ (a difference of only 0.025) as shown by the cross in figure 13. The value for $100 \ y/x$ calculated from Schaefer's regression (28) is 30.616, which differs from the mean of the nine specimens by 0.613.

Again we find, even in this more complex case, that the accurate description of the data does not require physically impossible assumptions, and that a better fit is actually obtained from a short polynomial series not involving physical impossibilities.

There are dangers of physically impossible assumptions inherent in almost any type of regression that might be used. The dangers are less and more easily guarded against when simple regressions are derived from a ratio-on-size plot than when an attempt is made to fit a size-on-size presentation of the data.

volve physical impossibilities except when the data refer to characteristics that actually do not appear until a certain size has been reached (e.g., scales in fishes, calcification in many vertebrates). In the latter case the x intercept [$f(x) = 0$] should agree with the size at which the feature makes its first appearance.

Physically impossible assumptions are involved whenever x, or a product of x, forms the entire denominator of any term in a size-on-size regression, and if x, or a product of x, with an exponent of x greater than 1 forms the entire denominator of any term in a ratio-on-size regression.

Fractions in which the denominator is an algebraic sum formed by x, or a product of x and a constant, e.g., $a/(k+mx^n)$, may be useful in ratio-on-size regressions, in which such fractions do not involve physical impossibilities unless they make the entire regression negative as x approaches 0. In size-on-size regressions fractions of this type imply a y intercept other than 0, unless the enumerator is a product of x or the zero value of the fraction is canceled by the zero value of other terms in the regression.

The regression functions must, in all instances, be tested for the possible occurrence of maxima or minima at values of x lying between 0 and a value somewhat larger than the maximum length attained by the species. Such maxima or minima may be justified (see fig. 13) but should always be critically examined and may often invalidate a chosen regression.

ILLUSTRATION OF DATA

The purpose of illustrations, whether published or used merely as a tool of research, is

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[1] In the size-on-log size and size-on-size plots shown in figure 14 even the difference in the 550–900-mm. range seems almost imperceptible.

to help make available for visual comparison as many of the significant characteristics of the data as possible. The value of a graphic presentation must therefore be measured by what it reveals, not by what it contains mathematically but successfully conceals visually.

In the preceding sections of the present paper many examples are given of the superior resolving power of the ratio-on-size plot as compared with the size-on-size diagram. An even more striking example is provided by Schaefer's data on the pectoral fins.

From the ratio-on-size plot in figure 13 we learn that the yellowfin tuna goes through a long-finned stage only to revert to a short-finned form when fully grown. This is information of considerable interest to students of evolution, to practicing taxonomists, to students of the dynamics of fish locomotion, to physiologists, and to ecologists. It gives rise to many questions. Does the curve express a simple growth process, or growth combined with deterioration from use, accelerated by a change in the mode of life at a length of about 600 to 800 mm.? Does the scarcity of data from the 550–900-mm. range suggest reduced availability to the fisheries

at this size, which, in turn, might relate to a change in mode of life at this size? Does the change in the curve relate to increasing calcium demands from maturing gonads, or to changed nutrition related to migration or change of habits, or to increased physical strain on the fins due to increased locomotion or changed dynamic properties of the larger body, or to any combination of these factors, or to none of them?

Turning to figure 14, we now see that none of these interesting questions could arise from a visual inspection of the plot of pectoral length against the logarithm of total length used by Schaefer, and here shown at the left. In this form of presentation the basic information about the change in the appearance of the fish is completely concealed from the eye. Even in the simple size-on-size plot shown at the right the change of form at mid-size is not visually revealed. The fact that the information is contained in, and could be mathematically deduced from, the curves has nothing to do with the value of these graphs as visual presentations of the morphological characteristics of the species and their ontogenetic development.

SUMMARY

DURING ONTOGENY THE proportions characteristic of a species, race, or population undergo changes which, in fishes, apparently continue throughout the life of the individual.

The processes of ontogeny are continuous. It is therefore not only necessary but should also be possible to use mathematical functions that will provide continuous approximations of the actual morphometric characters through all stages of growth.

Beyond the fitting of the data available, such functions must be of a form that will not at any point within the size range of the species indicate integral parts of the whole[1] larger than the whole itself, or other conditions contrary to logic and experience. These requirements are easily met by polynomial series of low degrees fitted to the regression upon the whole of the ratio of parts to the whole or to one another.

For the general purposes of fish taxonomy, adequate first approximations can often be obtained from linear (first-degree polynomial) functions of the general form:

$$100 \ y/x = a + bx$$

In other instances, and for purposes of second approximations, one may use functions of the forms of:

$$100 \ y/x = a + bx + cx^2$$

or

$$100 \ y/x = a + bx + cx^2 + dx^3.$$

Many of the methods of fitting the data currently used and recommended in ichthyological research rest upon or lead to physically impossible assumptions. As a result, the regression functions developed by these methods are usually incapable of expressing the course of ontogeny beyond, or even to, the limits of the data available, which generally do not include a substantial lower portion of the size range of the species. As a further result, these functions are therefore also unsuitable as a basis for the continued development of our knowledge of the species as a whole, by an orderly process of gradual refinement and improvement instead of seriatim substitutions and abandonments.

That functions using low-degree polynomial series for the regressions of ratios upon the whole will fit actually available ichthyological data equally well or better than functions with physically impossible assumptions, previously applied to the same data, is demonstrated by many examples.

The absolute dimensions of variability are related to, and limited by, the absolute dimensions of the part and thus indirectly of the whole. Variability, measured in units of absolute length, must therefore also undergo a continuous process of change during ontogeny. Variability can accordingly not be expressed by absolute constants but must be described by continuous functions. It is suggested that individual deviations be measured, in first approximation, as per cent of the whole, or, in second approximation, as per cent of the average size of the deviating part at the given length of the whole. Variances or other expressions of variability calculated from such measures of deviations will then take the form of continuous functions capable of fitting the entire course of ontogeny.

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[1] Organs such as produced fin rays that are not integrated in the measured size of the specimen may, of course, exceed its recorded total length.

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