American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 2019 OCTOBER 14, 1960

Negative Growth During Metamorphosis and the Regression of Taxonomic Variates Upon Size in Fishes

By A. E. Parr[1]

Ahlstrom and Counts (1958), in their account of *Vinciguerria lucetia*, have made available for discussion a valuable set of measurements relating to the special and interesting case of metamorphosis involving a period of negative growth, which is known to occur in a few teleosts. Some other instances have also been treated in the literature, but none has been so thoroughly and well documented. The present writer (Parr, 1949, 1956), in his previous discussions of the regressions of taxonomic variates upon size, failed to take this particular type of allometric growth into account, and he must agree with Ahlstrom and Counts that any function that could express in one equation ontogenetic changes of this kind would be too complex to be of any use, at least until electronic computers become everyday equipment in all laboratories. But the fact that an ideal cannot be attained, or a need be met in special instances, does not alter either the ideal or the need. The difficulties encountered in *Vinciguerria*, *Elops*, and some others in no way affect the statement that "one of the primary purposes and needs of taxonomy is to develop expressions that describe a species or other systematic unit as a whole" (Parr, 1956, p. 392), even if our purpose cannot in every instance be immediately achieved today, but must await an "orderly progress of improvement" (Parr, *loc. cit.*)

The continuity of biological processes, including allometric growth,

[1] Senior Scientist, the American Museum of Natural History.

is, of course, actually a continuity in time. Unfortunately, students of the biometrics of deep-sea fishes do not have any direct way of knowing or measuring the lapsed time of ontogeny, or age, of their specimens. So long as the over-all size of the individual increases in a direct relationship to lapsed time, the length of the specimen may at least be taken as a qualitative index of advancing age, and the continuity in time of ontogenetic changes should find reflection in a distorted but not disrupted continuity in reference to over-all size. When, however, temporary inversions occur in the relationship between size and age, as in *Vinciguerria*, the progress of allometric growth plotted against standard length will pass through abrupt changes of direction, which have nothing to do with the fundamental continuity in time of the same growth processes. Even though single functions to express the entire course of ontogeny would not be practical in the case of such growth inversions, the task still remains of determining the type of regression equation that will best, and most logically (or least illogically), serve the needs of taxonomy. On this subject Ahlstrom and Counts have the following to say (*ibid.*, p. 369): "From our study of larval growth in a number of species, we found that a simple size-on-size regression is preferable to a ratio-on-size regression. The regression line will seldom pass through the origin, and for a very simple reason. A body part must have some size at its differentiation. When the head differentiates on an embryo, for example, the embryo is already a millimeter or so in length. It often happens that the head at formation will constitute a different proportion of the standard length than it does subsequently. Whenever this happens, a rectilinear regression of size-on-size will have a y-intercept different from 0. But this line has more validity than one that would pass through the origin, for it will pass through the point representing the size of the part at its initial formation. For this reason, we believe that Parr (*op. cit.*: 378) is mistaken when he states that a regression curve must pass through the origin."

If the comment referred to in the last sentence above had been a general statement, as implied by Ahlstrom and Counts,[1] the present writer would indeed have been mistaken. Actually the generalization of the subject, which Ahlstrom and Counts have ignored, is found

[1] The statement (Parr, 1956, p. 378) referred to by Ahlstrom and Counts simply points out that the value of *y*, representing the length of the head of Alaskan herring, in a *specific* regression equation mathematically and quite unmistakably becomes zero for zero length of specimen, as it also must without mistake in nature.

farther on in the same report (Parr, 1956, p. 394), and reads as follows:

"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 involve 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."

It would seem, at first glance, as though the immediately preceding paragraph had already covered Ahlstrom and Counts's objection before it was made. However, a closer examination of their text suggests a difference of opinion in regard to the first paragraph above, having to do with positive intercepts of the y axis, although the difference is nowhere quite explicitly stated.

Ahlstrom and Counts refer to the fact that many parts do not differentiate sufficiently to be called by their common name (e.g., "head") until the specimen has reached a certain size. However, this is a purely semantic consideration. Any part that becomes recognizable by differentiation must exist and have real dimensions before differentiation, as also stated by Ahlstrom and Counts, but these dimensions cannot be other than zero when the size of the entire specimen is zero.[1] A size-on-size regression curve expressing the allometric growth of that part which becomes the head (including the head, when differentiated) must therefore pass through the origin to be in complete accord with nature.

The predifferentiation dimensions will, of course, be represented only by extrapolation from postdifferentiation measurements, until more knowledge and better techniques become available.

It is characteristic of all ratio-on-size regression equations of the type (A) used by the present writer, namely,

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

that the absolute dimensions of the part (y) becomes zero at zero length of the whole (x). To that extent, at least, logic is on the side of this form of expression. It is also true of size-on-size regression equa-

[1] If one wishes to be quite technical about it, one must, of course, recognize that a specimen actually starts not from zero but from the size of the egg cell.

tions of the type (B) used by Ahlstrom and Counts, viz.,

$$y = a + bx$$

that they all (unless $a = 0$) give impossible (positive) or unreal (negative) values for the part when the size of the whole approaches zero, and sometimes even for very large specimens (Parr, 1956, pp. 380, 384, 385, 394).

However, if the practical advantages of the size-on-size regressions and the practical disadvantages of the ratio-on-size analysis were great enough, one might have to sacrifice logic for practical usefulness within clearly defined limits. The complexities of Ahlstrom and Counts's abundant and detailed data offer an interesting opportunity to test and compare the alternative methods and check the claims that are made for each.

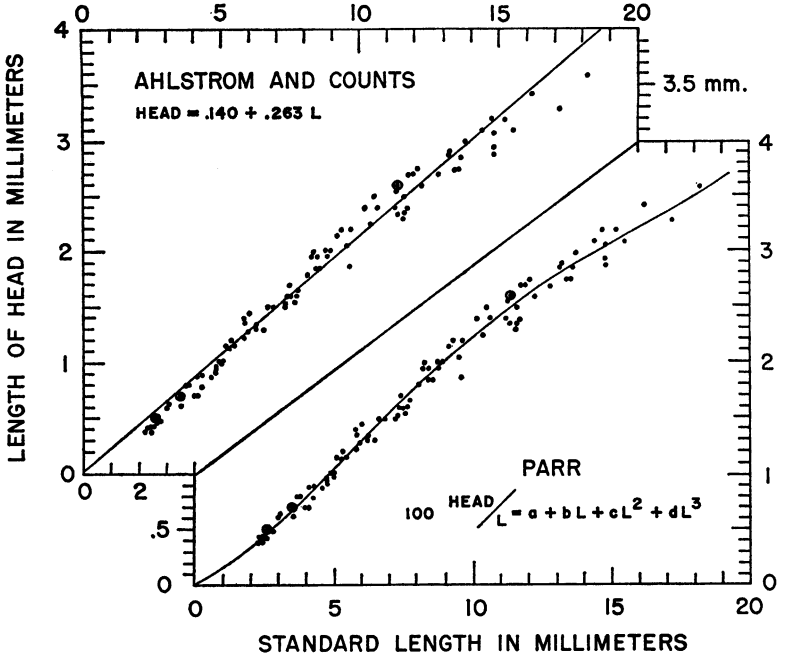

FIG. 1. Length of head in larval *Vinciguerria lucetia*, in millimeters, plotted against standard lengths in millimeters, according to Ahlstrom and Counts's measurements. *Above:* Ahlstrom and Counts's regression ($y = 0.140 + 0.263x$). "This line has more validity for it will pass through the point representing the size of the part at its initial formation" (Ahlstrom and Counts, 1958, p. 369). *Below:* Same data fitted with a regression curve of the type of $100y/x = a + bx + cx^2 + dx^3$, namely, $100y/x = 12.3 + 2.675x - 0.218x^2 + 0.005\ 09x^3$. This line passes through all the points represented by the data.

Figure 1 compares, in size-on-size presentation, Ahlstrom and Counts's size-on-size regression of type (B) with a ratio-on-size regression of type (A) fitted to the same data by the present writer. Figure 2 compares the same two functions in a ratio-on-size plot which clearly reveals the complete incompatibility between the size-on-size regression of Ahlstrom and Counts and the trends shown by the actual evidence of the data. Where one is convex the other is concave, and so on.

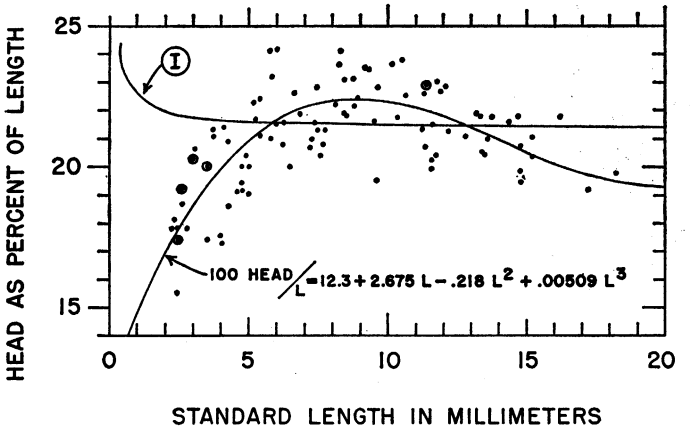

FIG. 2. Length of head in larval *Vinciguerria lucetia* as per cent of standard length, plotted against standard length in millimeters to show the derivation of the regression represented by the lower curve in figure 1, and to compare its validity with the regression used by Ahlstrom and Counts (curve I).

It should be clearly understood that the expression "incompatible with the data" as used herein is in no sense meant to imply any error in Ahlstrom and Counts's computation of linear regressions by the method of least squares. On the contrary, it is the author's confidence in the accuracy of Ahlstrom and Counts's handling of their data which makes their findings so very useful for an evaluation of the method used by them and by many others. It is the method of presentation by rectilinear size-on-size regressions that is incompatible with the data, not the mathematical derivation of the functions from the measurements. It is also the entire method of size-on-size analysis which is again up for comparison with the ratio-on-size approach.

While Ahlstrom and Counts list separate regression functions for head length, and a number of other dimensions, for each of the five stages into which they divide the ontogeny of *Vinciguerria*, they do not offer a graphic presentation of the entire ontogeny of any feature. In the case of the head length only larval stages are illustrated in this

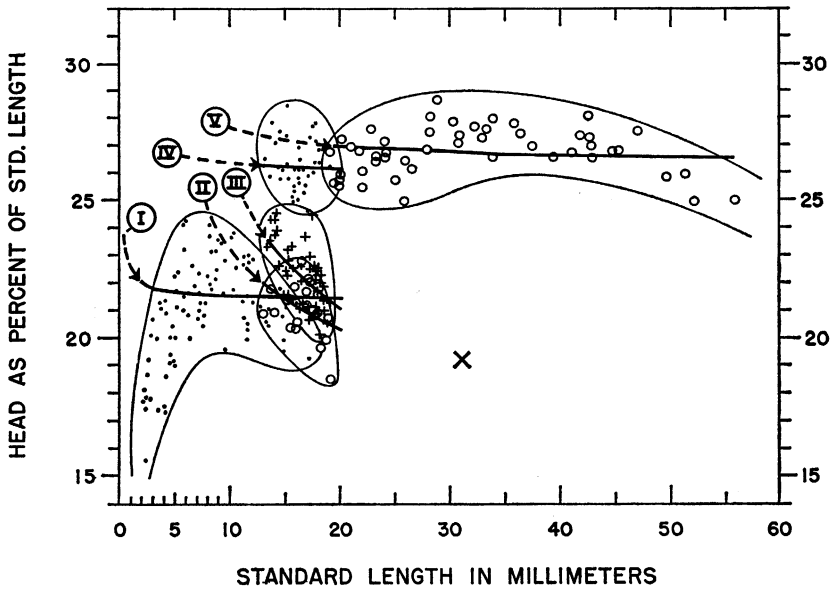

FIG. 3. All measurements of the heads of *Vinciguerria lucetia* according to Ahlstrom and Counts converted to percentages of standard lengths. Larval, prometamorphic, midmetamorphic, postmetamorphic, and juvenile and adult measurements, according to the terminology of Ahlstrom and Counts, have been differentiated by the use of dots, rings, crosses, dots, and rings in that order. The regressions used by Ahlstrom and Counts are shown as curves I–V, which have been extended in broken lines for easier identification.

manner. Figure 3 shows all the measurements of the heads of *V. lucetia* in a ratio-on-size plot. Ahlstrom and Counts's five regression functions are shown in relation to the areas occupied by the measurements for each of the five ontogenetic stages. The outlines of each of these five areas are indicated for identification with figure 4.

From figure 3 it may be seen that none of the five regressions obtained in rectilinear form by the size-on-size approach, using the method of least squares, is compatible with the data. It is particularly noticeable how curves I–IV fail to represent, or even remotely approach, the true axes of the configurations in which the data for each stage are contained. It is also noticeable how curve V reverses the curvature actually shown by the data. But most conspicuous of all is how all the five curves together fail to give a coherent, intelligible and even remotely possible picture of ontogeny. If each regression is to be taken as the norm for its stage (and, if not, what does it represent?), then each must lead on to

the next. That is, succeeding curves must have intercepts within, or, allowing for some rounding of corners, in reasonable proximity to the areas covered by the actual measurements. This is true only of the relationships between curves I and II, not of any of the other intercepts. The location of the intercept between II and III is indicated by a large X, and curves IV and V have no real intercept at all, that is, they meet only at a negative length of —55.5 mm. According to these regressions, the postmetamorphic growth can therefore not lead to the juvenile condition. But this is obviously not an acceptable way of describing allometric growth during metamorphosis, even in first approximation only.

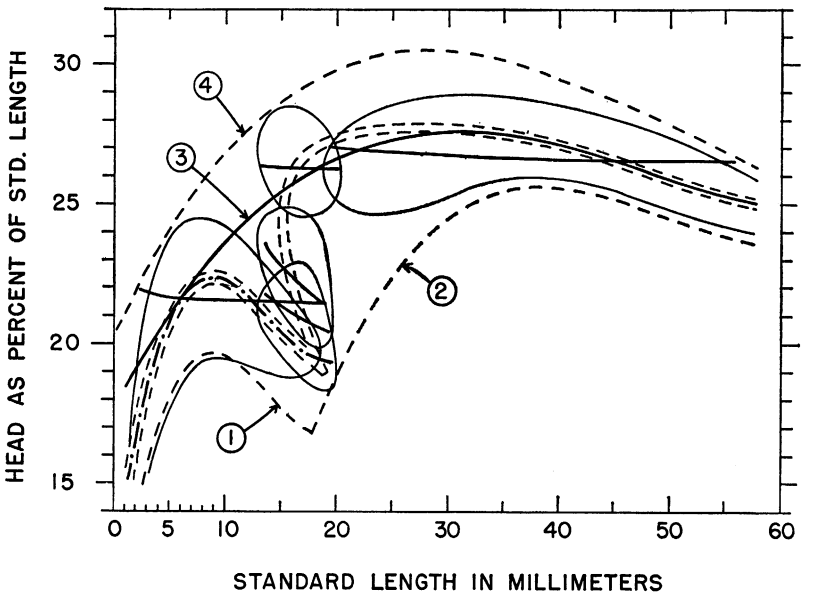

FIG. 4. Length of head in *Vinciguerria lucetia* as per cent of standard length plotted against standard lengths in millimeters. Scatter areas containing the measurements of each of the five ontogenetic stages recognized by Ahlstrom and Counts shown by their outlines taken from figure 3. Heavy dot and dash for juvenile regression ($12.3 + 2.675L - 0.218L^2 + 0.005\ 09L^3$) used in figures 1 and 2. Heavy solid line (3) for adult regression ($17.65 + 0.755L - 0.017\ 64L^2 + 0.000\ 117\ 6L^3$). *Lower boundary:* Curve 1 = $9.5 + 2.675L - 0.218L^2 + 0.005\ 09L^3$. Curve 2 = $-15 + 2.665L - 0.056\ 25L^2 + 0.000\ 375L^3$. *Upper boundary:* Curve 4 = $20.4 + 0.816\ 7L - 0.02L^2 + 0.000\ 133L^3$. The five regressions used by Ahlstrom and Counts are also shown, together with the band contained between two broken lines that may approximately indicate the actual ontogeny.

Figure 4 shows the present author's attempts to find more satisfactory ways of describing what actually takes place. The configurations of measurements and Ahlstrom and Counts's five regressions are repeated from figure 3, as is the regression developed for juvenile heads in figure 2. An interpretation of what apparently occurs is indicated by the band contained between two broken lines. As stated already, the author agrees that it would complicate matters too much, at least at present, to try to describe in a single equation the course followed by this band. A regression function which satisfactorily describes the juvenile to adult heads and also has a junction with the larval regression is represented by curve 3. In certain other data involving shrinkage during metamorphosis the author has found indications that it might not be too difficult to combine larval ontogenetic changes before metamorphosis begins with allometric growth after metamorphosis is completed in a single equation of the form of

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

This would treat the metamorphosis itself as a detour from the underlying basic process of differentation and might possibly be a useful fiction to employ for descriptive purposes. The other data available are, however, not nearly so satisfactory as those presented by Ahlstrom and Counts, and the present author has not been able to find a joint early larval-juvenile function of the type indicated above of less than the fourth power, which even these data would scarcely justify.

In his own work the present writer has become increasingly convinced of two things. On the one hand we have no adequate methods of workable simplicity for establishing norms for allometric growth, notably because of the difficulties encountered in trying to find a measure of variance that takes proper account of changes in size and is also applicable to curvilinear functions (see Parr, 1956, p. 386). On the other hand suitable definitions of specific limits of variability are even more useful in most of the everyday work of taxonomy than norms and variances would be. With this in mind a search was made for the narrowest envelope that could conveniently be used to contain the measured lengths of the heads in *V. lucetia.* The result is the three curves 1, 2, and 4 between which all the measurements are contained. In a description this would read as follows: Heads larger than ($9.5 + 2.675L - 0.218L^2 + 0.005\,09L^3$) and also larger than ($-15 + 2.665L - 0.056\,25L^2 + 0.000\,375L^3$) per cent of L, but less than ($20.4 + 0.816\,7L - 0.02L + 0.000\,133\,1^3$) per cent of L. This statement and the curves it represents are in complete accord with the facts and not in

disharmony with the trends indicated by the data, although these trends can certainly not be said to be clearly reflected in detail. Figure 5 shows the limiting curves in a size-on-size comparison with the data and with other forms of presentation.

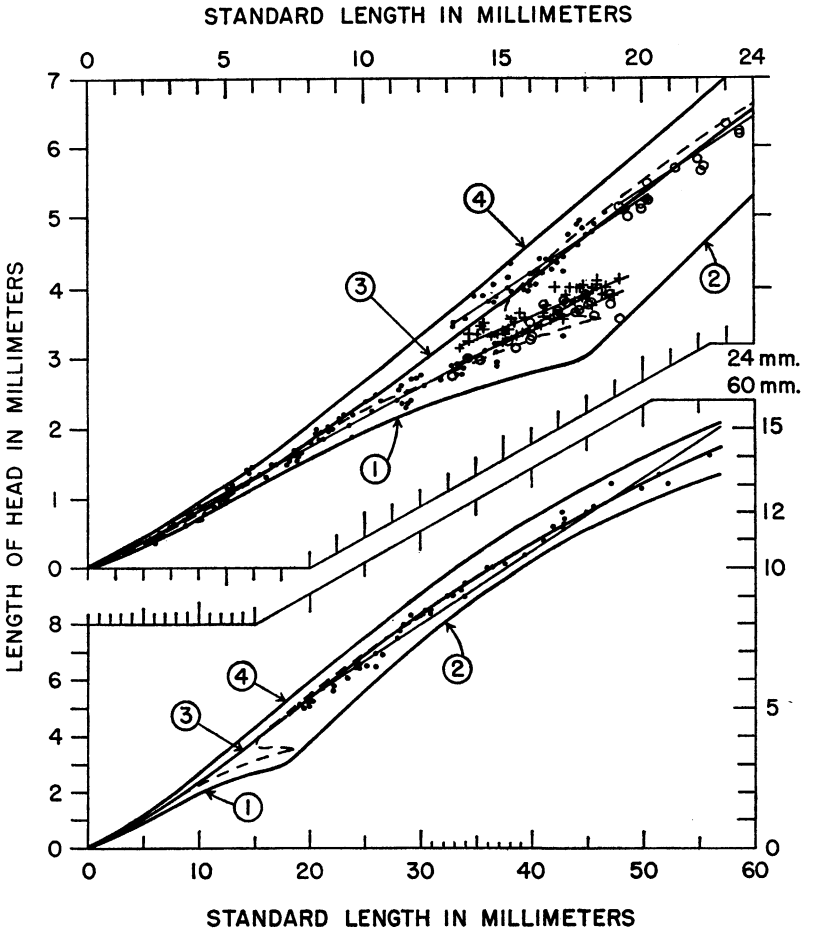

FIG. 5. Length of head in *Vinciguerria lucetia* in millimeters plotted against standard lengths in millimeters. For identification of curves, see legend to figure 4. Broken lines represent band of probable ontogeny shown between broken lines in figure 4. *Above:* Enlarged section from hatching through completion of metamorphosis. Five regressions used by Ahlstrom and Counts represented by the straight lines. *Below:* Complete ontogeny. Only juvenile to adult measurements entered individually, with rectilinear regression used by Ahlstrom and Counts.

The final test of taxonomic validity and usefulness is, of course, to be sought in comparisons between related, but distinct taxonomic units.

Ahlstrom and Counts give the measurements of 26 larvae of *Vinciguerria poweriae* (*ibid.*, p. 402), and of 34 larvae of *V. nimbaria* (*ibid.*, p. 407). They also list rectilinear size-on-size regressions for this material on page 405 and a graphic size-on-size comparison between the head lengths of *V. poweriae* and *V. lucetia* larvae in their figure 28 (p. 406).

The accompanying figure 6 gives the measurements of the larval heads of all three species in a ratio-on-size plot, with curves A, B, and C representing Ahlstrom and Counts's regressions for each species. This figure gives an excellent illustration of the superior analytical powers of the ratio-on-size presentation as compared with a size-on-size plot. The fact that one of the published measurements, here indicated by an arrow, if not incorrect or abnormal, cannot pertain to any of the three species here considered can scarcely escape notice in a ratio-on-size diagram, as it so easily does in a size-on-size plot. But the most significant revelation of figure 6 is again that of incompatibility between the

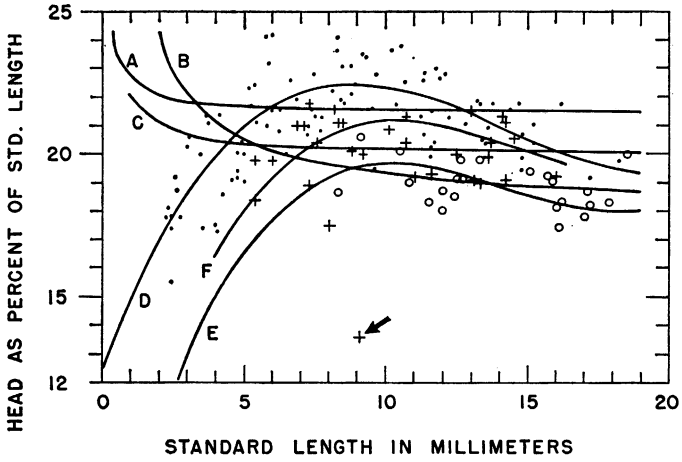

FIG. 6. Lengths of larval heads, as per cent of standard lengths, in *Vinciguerria poweriae* (circles) and *V. nimbaria* (crosses) plotted against standard lengths in millimeters for comparison with *V. lucetia* (dots). Ahlstrom and Counts's regression functions are represented by curves A (*V. lucetia*), B (*V. poweriae*), and C (*V. nimbaria*). Curve D represents regression fitted to meaurements of *V. lucetia* by the present author. Curves E and F, analogous to curve D, suggest types of regressions for *V. poweriae* (E) and *V. nimbaria* (F).

data and the rectilinear size-on-size regressions. To be of any usefulness, a regression function for larval heads must allow some, although not unlimited, extrapolation, when the data for different taxonomic units do not cover the identical size ranges. If the rectilinear regression for *V. poweriae* (B) is used for such purposes (which Ahlstrom and Counts, of course, do not do), it would carry the startling implication that the species that has been shown merely to have the smallest heads among the three species above 8 mm. in length should be expected to have larger heads than the other two below about 5.5 and 3.5 mm., respectively, in length. It is not, in this connection, the details of extrapolated head lengths for each species separately that are of particular importance, but the fact that the relationships between the three regression functions supposedly representative of each species together give a completely unwarranted, incredible, and misleading picture of the actual morphometric relationships of the forms compared.

All that the data actually show is that the larval heads are generally largest in *V. lucetia* and smallest in *V. poweriae* at all sizes for which measurements are available. The measurements also strongly suggest that the true curves of allometric growth are probably somewhat flatter in *V. poweriae* and *V. nimbaria* than in *V. lucetia.*

In the absence of sufficient data to establish independent regressions for the rarer species, differences and similarities can be stated only as deviations from or agreements with the dimensions indicated by the regressions established for the better-known members of the same genus or, at most, of closely related and morphologically similar genera. In the simplest case, this actually means using as first approximations to the biometrics of the scarce material regression curves that are entirely congruent with those of the nearest related species. That is, we imply that the differences are entirely due to differences in the value of a in functions of the type of $(a + bx + cx^2 + dx^3)$.

When somewhat more information is available, we may be able to use modifications of the form of the regression functions of related species, which we may call analogous functions, for our first approximation. For example, it has generally been found possible to use rectilinear functions to describe the ratio-on-size regressions of head lengths among the juvenile to adult specimens of Alepocephalidae and Searsidae, thus: $100y/x = a - bx$. The numerical value of b has also been found to be inversely related to the size of the head in the adult, large-headed forms showing low values of b, and vice versa. If we have a single specimen of a new species with a length of the head that falls midway between the head lengths of two other species of which the

regression functions for this dimension are ($a_1 - 0.03x$) and ($a_2 - 0.04x$), it is therefore logical to use ($a_3 - 0.035x$) as a first approximation for the new species. In other words, instead of using parallel lines, as described in the preceding paragraph, we now use a regression line that divides the angle between neighboring regressions on the two sides.

Whenever additional material has become available, it has confirmed the "common sense" practice of using congruent or analogous curves for first approximations in taxonomic comparisons.

In the cases of the heads of larval *Vinciguerria poweriae* and *V. nimbaria* curves analogous to the curve of *V. lucetia*, but somewhat flattened, have been devised and entered in figure 6 as E and F, with E representing ($4 + 3.75x - 0.285x^2 + 0.000\ 665x^3$) and F representing ($5.5 + 3.75x - 0.285x^2 + 0.000\ 665x^3$). It will be noticed that these functions differ from the function for D ($12.3 + 2.675x - 0.218x^2 + 0.005\ 09x^3$) in all their constants, and are therefore analogous only with the latter, but also that they differ among themselves only by the values of a (respectively, 4, 5.5) and are therefore congruent with each other, the data being insufficient to justify the suggestion of other differences between the two less known species.

The author confidently leaves it to the reader and to the future to determine whether curves D, E, and F, or curves A, B, and C offer the most valid and taxonomically most useful means of describing allometric growth in the three species in first approximation.

SUMMARY

The problem of describing allometric growth during metamorphosis involving periods of shrinkage in over-all size is examined on the basis of measurements of three species of *Vinciguerria* published by Ahlstrom and Counts. The opinion of these authors that it is not at the present time practical to seek the ideal solution of a single equation for the entire cause of ontogenetic changes is confirmed. But it is shown that the superior resolving power of the ratio-on-size method of analysis will give a much clearer picture of the morphological changes taking place also during period of negative growth than does the size-on-size presentation. Examples are given to show how the ratio-on-size method clearly reveals inconsistencies between data and descriptions that easily develop in a concealed or inconspicuous manner by the use of the size-on-size approach. Rectilinear size-on-size regressions are in most cases incompatible with the import of the data on allometric growth in fishes.

REFERENCES

AHLSTROM, E. H., AND R. C. COUNTS
1958. Development and distribution of *Vinciguerria lucteia* and related species in the eastern Pacific. Fish. Bull. Fish and Wildlife Serv., Washington, vol. 58, pp. i–iv, 363–416 (Fish. Bull. no. 139).

PARR, A. E.
1949. An approximate formula for stating taxonomically significant proportions of fishes with reference to growth changes. Copeia, 1949, no. 1, pp. 47–55.
1956. On the original variates of taxonomy and their regressions upon size in fishes. Bull. Amer. Mus. Nat. Hist., vol. 100, pp. 369–398.