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AN APPLICATION OF THE ALLOMETRY EQUATION TO THE STUDY OF GROWTH IN
CALLINECTES SAPIDUS RATHBUN

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SEVERAL investigators have demonstrated the application of the allometry equation $Y = a X^b$ to problems dealing with the relative growth of a body part in relation to the whole body (Huxley, 1932; Miller and Hoy, 1939; Newcombe, Sandoz and Rogers-Talbert, 1949; Newcombe, Campbell and Eckstine, 1949). The application of this relative growth equation to a set of data is dependent upon the existence of a straight line relationship when the data are plotted on a double logarithmic grid. The growth coefficient b expresses the ratio of the percentage growth rates of the dimensions being studied and may be obtained by measuring the slope of the line through the logarithmic plotting by inspection or else by the method of least squares which is used in this paper. The constant a indicates the ratio

$$\frac{Y}{X^b}$$

and has been called the "initial growth index" (Huxley and Teissier, 1936).

Growth studies of the Blue Crab, *Callinectes sapidus* Rathbun in the Chesapeake area by Newcombe, Sandoz and Rogers-Talbert (1949), conducted at the Virginia Fisheries Laboratory, have shown that as the crab grows it changes in form; hence there are disproportionate rates of growth in respect to the several linear dimensions studied. The dimensions examined include: width (W), the shortest distance between the ends of the 9th pair of antero-lateral spines of the carapace; length (L), the perpendicular distance across the carapace from a point im-

mediately posterior to the rostrum to a point just above the first segment of the abdomen; eye to spine (E), the distance between the first and ninth antero-lateral spines of the right margin of the carapace; the propodus (C) of the right chela represented by its maximum length; and the distance between the preorbital spines (interocular width) F (figure 1).

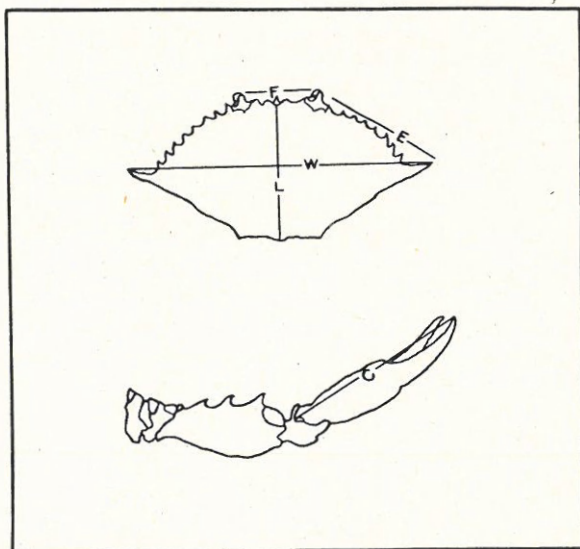


FIG. 1. Outline drawing of the Blue Crab, *Callinectes sapidus* Rathbun, showing the dimensions measured. W = width; L = length; E = distance between the 1st and 9th antero-lateral spines of the right margin of the carapace (eye to spine distance); C = length of the propodus of the right cheliped; and F = distance between the preorbital spines (interocular width). (after Newcombe, Sandoz and Rogers-Taibert, 1949).

In addition to a description of several growth dimensional ratios, the number of moults was estimated by direct use of a curve obtained by plotting a series of initial and final width measurements, that is, widths before and after shedding (figure 2). Knowing the average width of the first instar to be 2.47 mm, obtained by measuring large numbers of first stage post-larval crabs reared from megalops by my associate, Mildred D. Sandoz, it was

readily possible to estimate from the curve the width of the different instars and their approximate number (Newcombe, 1949).

In this paper interest centers on the application of a

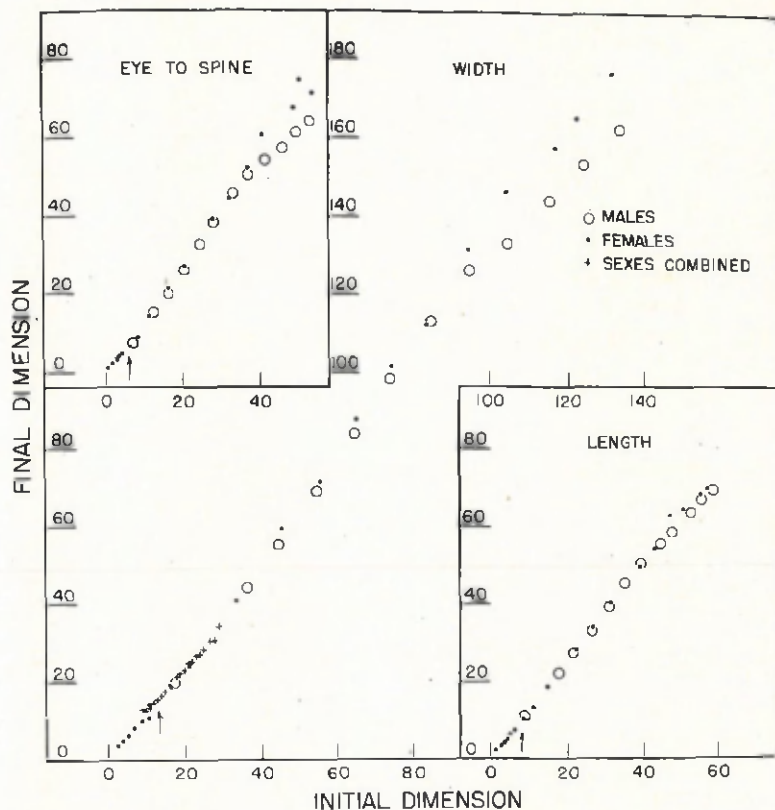


FIG. 2. Relation of initial to final dimensions (before and after moulting) in *Callinectes sapidus* Rathbun. Sexes combined in groups to the left of the arrows and in the plus groups, the latter serving as a check on the former in regard to slope of line of best fit. (From Newcombe, Sandos and Rogers-Talbert, 1949).

method for analyzing the intensity of dimensional growth throughout the size range of the species. Also, there is provided a mathematical basis for determining the theoretical number of instars characteristic of the species which may be extended to related forms. For these pur-

poses, the allometry formula has been employed (Brody, 1945 p. 608; and Huxley, 1932). The application of this parabola to the data presented by Gray and Newcombe (1938a, 1938b) and Newcombe *et al.* (1949) together with the information about relative growth rates thereby revealed, is discussed here.

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RESULTS AND DISCUSSION

Huxley's applications of the allometry equation to diverse types of growth data have contributed greatly to the meaning of differential growth processes. He recognized *heterogonic growth* and *isogonic growth* depending upon whether the rate of growth of a body part is different from or similar to that of the body. In this analysis the problem is whether or not the rate of growth of a particular dimension, e.g. width, remains the same throughout life. The percentage increment of width in the case of a crab 20 mm wide may be 32, and that of one 80 mm wide may be the same or it may be different. Hence, it is desirable to obtain a mathematical expression of the size range or ranges over which the percentage increments are the same as well as to establish the sizes at which proportionality and rates of growth undergo changes.

The data on which these analyses are based are from Gray and Newcombe (1938b); and Newcombe *et al.* (1949) (figure 2). By plotting the logarithms of the initial dimensions against the logarithms of the final dimensions (measurements before and after moulting), it has been possible to break down the growth curve into parts or "stanzas" that have similar growth rates and to correlate the size at which a break occurs with related growth or physiological behavior (figure 3). The constants of the allometry equations established from these data may be

used as a basis for measuring the significance of possible differences in growth rates of the same dimension in different parts of the size range or of different dimensions within the same size range of the species.

Growth rates of linear indices of body size. Growth

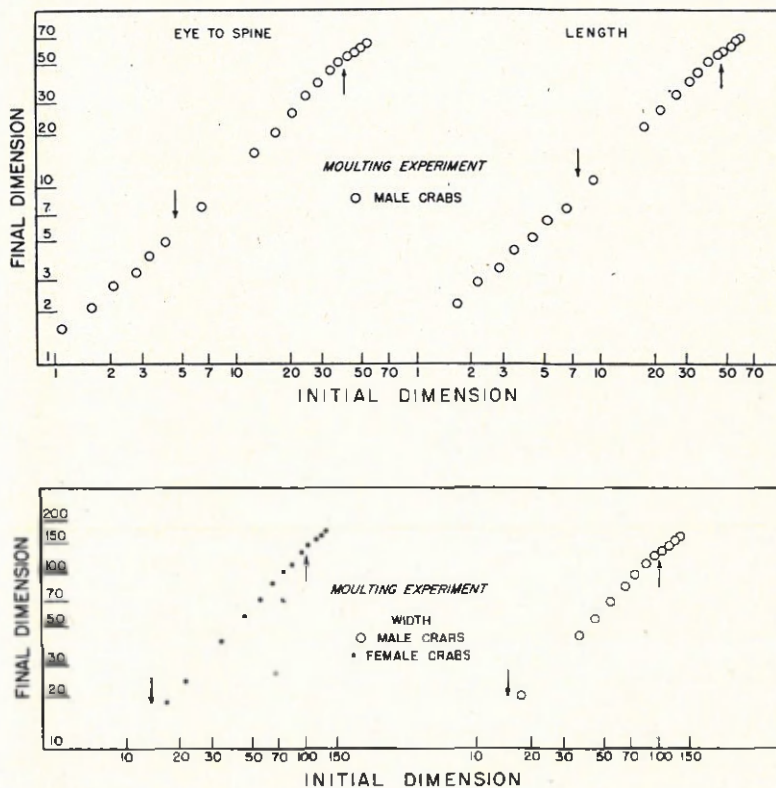


FIG. 3. Growth trends for width, length and eye to spine dimensions as shown by plotting initial size (before moulting) against final size (after moulting) on a double logarithmic scale.

rates of individual linear indices of body size during the different moultings are in some instances described by a single straight line on a double logarithmic grid. In others, displacements are clearly evident and two or even three straight lines are required (figures 2 and 3). The changes may be abrupt, i.e. during one moult, even though

the regression indicates a gradual change. For example, an individual female crab becomes sexually mature in its last instar but that stage is not reached at the same size in all crabs, hence the composition of the data yields a curvilinear regression. A comparison has been made of the b values for the W, L, E, F, and C dimensions in the group range I-VII (table I). The difference between the values of b for L and C, namely 0.93 and 0.79 was found to be significant at the 5 percent level but not at the 2 percent level. In the remaining nine comparisons of pairs of b values, not a single difference was significant at the 5 percent level.

An index to the growth trend is provided by the data of table I. In groups VIII to XV and XVI, the b values for males and females, respectively, are positively allometric and significantly different at the one percent level. A slight displacement is seen to take place in both sexes at a width of about 95 mm. The slope is greatest in the males in every instance. The least noticeable bend in the line is for length (L) while the most conspicuous one is for the eye to spine distance (E) (figure 3). Weymouth and MacKay (1936) associate a comparable change, interestingly at a similar size, with sexual maturity in *Cancer magister*. The slight bend in the logarithmic plotting, near the upper extremity of the regression, is believed to be an index of sexual maturity in *Callinectes sapidus*. This possibility is discussed by Newcombe *et al.* (1949).

The value of b for width in groups I-VII is 0.854 whereas for groups VIII to XV and XVI, males and females, b values are 1.097 and 1.137, respectively. As a partial check on the value of b , namely 0.854, for the first groups, specimens representative of each millimeter group between widths of 9 and 29 mm were brought to the laboratory and held until they moulted (see plus marks on curve in figure 2). These crabs were subjected to laboratory conditions only for short periods as compared with those of groups I to VII that were reared in the labora-

tory from the megalops stage. However, the a and b values for the series 1.68 and 0.88, respectively, were found to be essentially the same as those of the laboratory reared crabs, namely 1.67 and 0.85 (table I). These data suggest that the factor of laboratory rearing is not sufficiently significant to account for the difference in slope between 0.854 and 1.097 in the males and 1.137 in the females of the next larger group. Also, they seem to indicate that the change in growth increment is a gradual one taking place at widths of around 20 mm.

Considering the character of the growth trend in the upper groups, the allometry equation indicates that the males grow less in proportion to their width than the females beyond a width of about 90–100 mm. The change in allometry indicated by figure 3 is more noticeable in the males. In addition to the above treatment of the data, the upper two parts of the curve have been fitted to a single straight line, b values for males and females being 1.020 and 1.100, respectively. The difference is significant at the 1 percent level.

The application of the allometry equation is equally satisfactory for analyzing the growth rates of the length and eye to spine dimensions. Comparing the b values for length in the different groups, it is seen that the slope is similar and the relationship could be expressed by one equation with $a = 1.263$ and $b = 0.991$ for males and with $a = 1.228$ and $b = 1.006$ for females (table I). These differences fail to show significance. However, in view of our understanding of the changing width increments with increasing moults and on a basis of the arithmetic relations shown in figure 2, we recognize trends similar to but less conspicuous than those pointed out in the discussion of width, the essential difference being one of magnitude. In groups VIII to XV and XVI, the values of b are practically identical, namely 1.029 and 1.049 in males and females, respectively, but on a basis of the figures there is a biologically significant difference in slope from the pre-

TABLE I

CONSTANTS OF DIFFERENTIAL GROWTH RATES OF SEVERAL DIMENSIONS OF *Callinectes sapidus* RATHBUN AS EXPRESSED BY THE EQUATION
 $Y = \text{INITIAL SIZE OF THE DIMENSION I.E. SIZE BEFORE MOULTING AND } Y = \text{FINAL SIZE AFTER MOULTING.}$
 t VALUES FOR DIFFERENCES IN b VALUES ARE GIVEN

Dimension	Male Specimens				Female Specimens				σ and φ	
	Group	Interval of initial dim.	a	b	Group	Interval of initial dim.	a	b	t	P
W Width	I-VII	2.5-11.0	1.67	0.854	9.0-29.0	1.68	0.881		
	VIII-XV	17.6-95.4	0.86	1.097	VIII-XVI	16.8-94.6	0.75	1.137	3.15	< .01
	XVI-XXII	104.8-153.2	2.31	0.869	XVII-XX	104.5-131.5	2.23	0.896	0.24	> .05
	VIII-XXII	17.6-153.2	1.14	1.020	VIII-XX	16.8-131.5	0.86	1.100	3.56	< .01
L Length	I-VII	1.7-6.5	1.35	0.931						
	VIII-XV	9.2-44.6	1.14	1.029	VIII-XVI	8.9-43.2	1.03	1.049	0.29	> .05
	XVI-XXI	47.9-63.5	1.73	0.909	XVII-XX	47.2-57.2	1.09	0.451	4.68	< .01
	VIII-XXI	9.2-66.5	1.33	0.978	VIII-XX	8.9-57.2	1.03	1.050	1.75	> .05
E Eye to Spine	I-XXI	1.7-66.5	1.26	0.991	I-XX	1.7-57.2	1.23	1.006		
	I-VII	0.7-4.1	1.37	0.898						
	VIII-XV	6.5-37.0	1.04	1.072	VIII-XVI	6.1-37.0	0.86	1.139	2.32	.02 < P < .05
	XVI-XXI	42.0-61.5	2.15	0.860	XVI-XX	41.7-54.0	2.99	0.781	0.55	> .05
C Propodus of chela	VIII-XXI	6.5-61.5	1.25	1.003	VIII-XX	6.1-54.0	0.92	1.113	3.89	< .01
	I-XXI	0.7-61.5	1.35	0.980						
F Betto. eye Spines	I-VIII	1.3-5.6	1.54	0.795						
	I-VIII	1.8-7.7	1.45	0.876						

ceding group. In the larger group it is likely that the changing logarithmic slopes represent small but biologically significant changes in the growth rates involved. From a biometrical standpoint the difference between $b = 0.978$ and $b = 1.050$ for groups VIII to XXI and XX, respectively, is not significant at the 5 percent level. However, observation of the data shows that the downward slope for the males is demonstrable.

TABLE II

WIDTHS OF INSTARS OF MALE AND FEMALE BLUE CRABS CALCULATED FROM ALLOMETRY EQUATIONS BY STARTING WITH THE WIDTH OF INSTAR I, NAMELY 2.47 MM. THE SIZES OF INSTARS II-VIII (SEXES COMBINED) WERE OBTAINED FROM THE EQUATION $F.W. = 1.67 I.W.^{0.834}$, THOSE OF THE REMAINING ONES FROM $F.W. = 0.859 I.W.^{1.40}$ FOR FEMALES AND $F.W. = 1.14 I.W.^{1.02}$ FOR MALES.

Instar No.	Instar width		Instar No.	Instar width	
	males	females		males	females
I	2.47	2.47	XI	24.92	20.67
II	3.65	3.65	XII	30.29	24.05
III	5.05	5.05	XIII	36.97	28.41
IV	6.66	6.66	XIV	43.30	34.11
V	8.43	8.43	XV	55.73	41.73
VI	10.30	10.30	XVI	68.85	52.07
VII	12.25	12.25	XVII	85.43	66.45
VIII	14.19	14.19	XVIII	106.4	86.90
IX	17.05	15.90	XIX	133.2	116.7
X	20.57	18.01	XX	167.4	161.4

The values of a and b for the eye to spine (E) dimension over the range of groups I-VII are quite similar, but not the same as those for the length and width dimensions. These dimensions adhere to the allometry equation and for purely prediction purposes may be regarded as similar. The b values of groups VIII to XV and XVI show sex differences that are significant at the 5 percent level while those for groups VIII to XXI and XX show differences at the 1 percent level (table I). The equation for males that covers the entire range is $F.E. = 1.349 I.E.^{0.980}$.

The growth equation may now be used as a means for estimating the theoretical numbers of instars for the species. Thus, starting with an initial width of 2.5 mm, the mean width of the 1st instar, the width of the 2nd in-

star obtained by substitution in the equation given in tables I and II, is 3.65 mm, that of the fourth is 5.05 mm, and so forth. On this basis there appears to be 20 instars, the widths of which are given in table II. Weymouth and MacKay (1936) conducted extensive growth studies on the Pacific Edible Crab, *Cancer magister*, and concluded that in British Columbia waters the males and females passed through 17 and 16 post-larval instars, respectively.

It is of interest to compare the variation in values of a and b . Huxley (1927) compared the growth constants of numerous forms and concluded that a is by far the most variable. Hersh (1931) found that for each sex in *Drosophila*, a decreased in geometrical progression, as b increased in arithmetical progression demonstrating a uniform relation between the two with definite biological meaning. Throughout the series of a and b values compared here, there is an inverse relation between the magnitude of these two constants. No attempt, however, has been made to evaluate the meaning or uniformity of the relation.

CONCLUSION

1. The allometric growth formula, $Y = a X^b$, is a suitable expression for comparing the rates of growth of the several linear dimensions of the Blue Crab, *Callinectes sapidus* Rathbun.

2. During the first seven or eight post-larval moults the relative growth rates of the five dimensions studied do not differ significantly among themselves except in one instance. Values of the growth constant b for increase in body length and in the length of the propodus of the right chela, namely 0.93 and 0.79, respectively, are significantly different at the 5 percent level but not at the 2 percent level, t being equal to 2.67.

3. The allometry expression indicates that rates of growth of the width and eye to spine dimensions show sex differences that are significant at the 1 percent level,

whereas growth in length is quite similar in males and females.

4. Application of the allometry method suggests that negative heterogeneity starts at a width of about 95–100 mm in male crabs. This trend of growth appears to be significant and indicative of the average size at which sexual maturity is reached in male Blue Crabs.

5. The allometry equation is a valuable means for analyzing growth trends in respect to particular body dimensions and also for estimating the theoretical number of instars that characterize a particular species.

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