AN EXPRESSION FOR THE GROWTH-COEFFICIENT α IN THE LAW $y=bx^{\alpha}$ OF CONSTANT DIFFERENTIAL GROWTH RATIO, EXPRESSING THE GROWTH RELATIONSHIP BETWEEN THE BODY SIZE x AND THE ORGAN SIZE y, IN VARIOUS ORGANIC FORMS

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Introduction

Although almost all organic forms are the results of differential growth, this problem did not receive the notice of scientists till Julian S. Huxley (1932) and others, from their study on a vast number of species of animals, ventured to show an entirely new method of approach to its study. Huxley gave a detailed application of the quantitative expression to the general law of differential growth, to describe adequately a wide range of growth phenomena in animals and plants, in the form of the formula, which is known popularly as the allometry formula or equation,

$$y = bx^{\alpha},$$

where x and y represent respectively the body and the organ sizes; and b and α are two constants, known respectively as the 'initial growth index' and the 'equilibrium constant' or the 'growth-coefficient'.

There are, however, certain shortcomings in the allometry formula, which do not allow it to explain with great perfection many problems of relative growth. Thus the constant value of α, as given in this formula, does not properly explain the existence of growth-gradient within a limb. The growth-coefficient on the other hand should progressively change from point to point along the axis of an organ in order to fully justify the idea of a growth-gradient.

In the present paper an expression, depending on the size of the body, has been derived for the growth-coefficient.

Discussion

Huxley's assumption that,

$$\frac{1}{y}\frac{dy}{dt}\Big/\frac{1}{x} = \text{a constant } \alpha \qquad \ldots \quad (1)$$

where x and y denote the sizes of the body and the organ respectively, t being the time factor, may be regarded as a first approximation to the more general assumption that,

$$\frac{1}{y}\frac{dy}{dt}\Big/\frac{1}{x}\frac{dx}{dt} = f(x) \qquad \ldots \quad (2)$$

where $f(x)$ is a function of the body size. The form of $f(x)$ is to be derived now. This may be done as follows :

On integration with respect to x the equation (2) leads to,

$$y = c' \, e^{\int \frac{f(x)}{x} dx} \quad \dots \quad (3)$$

where c' is an arbitrary constant and e is the base of natural logarithms.

Similarly, integration of equation (1) leads to the well known equation,

$$y = bx^{\alpha},$$

or, on taking the logarithms,

$$\log_e y = \log_e b + \alpha \log_e x \quad \dots \quad (4)$$

Further, on arranging a sample data, giving the n values of the pair (x, y), arranged in order of magnitude of x, beginning with the smallest x, $(n-1)$ sets of values of the pair (x, y) are obtained on taking these two by two. Thus the first set will consist of the first and the second pairs, the second set of the second and the third pairs, and so on. On fitting the equation,

$$y = bx^{\alpha},$$

for each of these sets, $(n-1)$ values of the pair (b, α) are obtained. Hersh (1931, 1934) has shown that the relation holding between these values of b and α is of the form,

$$b = Be^{-r\alpha} \quad \dots \quad (5)$$

where B and r are constants.

Next, a curve may be fitted between the values of x and α. A sample of 90 males of the Indian freshwater prawns, *Palaemon hendersoni* DeMan was studied for this purpose. (The material was kindly lent to the author by the Director, Zoological Survey of India. It is deposited in the reserve collections of the Z. S. I.). It was seen that the relationship between α and x, within the limits of fluctuations due to sampling, is linear. Whether or not this straight line shows the best functional relationship between α and x can be decided only on a vast and extensive application of this analysis on different types of data; but in any case it may be taken to hold good at least as a first approximation, since a straight line is a type of relation which is always of importance and usefulness, being one of the simplest functions to fit and to explain.

The relationship between α and x is then expressible in the form,

$$\alpha = a_0 + a_1 x \quad \dots \quad (6)$$

where a_0 and a_1 are constants.

The nature of the function $f(x)$ can now be easily derived as follows :

Differentiation of equation (4) with respect to t leads, after slight rearrangement of terms, to

$$\frac{1}{y}\frac{dy}{dt} \Big/ \frac{1}{x}\frac{dx}{dt} = \frac{x}{b}\frac{db}{dx} + \alpha + x \log_e x \frac{d\alpha}{dx} \quad \dots \quad (7)$$

Next, differentiation of equations (5) and (6) with respect to x gives

$$d\alpha/dx = a_1$$

and $$\frac{1}{b}\left[\frac{db}{dx} = -r \, d\alpha/dx\right.$$

$$= -ra_1$$

Substituting the values of $d\alpha/dx$ and $\frac{1}{b}\, db/dx$ in equation (7), it is seen that,

$$\frac{1}{y}\frac{dy}{dt}\Big/\frac{1}{x}\frac{dx}{dt} = -ra_1\,x+\alpha+\,a_1\,x\log_e x$$

$$= a_1\,x(1-r)+a_0+a_1\,x\log_e x, \text{ from equation (6)}$$

Comparison of the right hand members of this equation and equation (2) gives,

$$f(x) = a_1\,x(1-r)+a_0+a_1\,x\,\log_e x$$

Hence,

$$f(x)/x = a_1(1-r)+a_0/x+a_1\,\log_e x$$

leading to,

$$e^{\int \frac{f(x)}{x}\,dx} = x^{(a_0+a_1x)}\,e^{-ra_1x}$$

Thus equation (3) may be written as,

$$y = c'\left[x^{(a_0+a_1x)}\;e^{-ra_1x}\right]$$

Fitting the regression equation between $\log_e y$ and $\log_e\left[x^{(a_0+a_1x)}\;e^{-ra_1x}\right]$

gives finally a relation which may be expressed as,

$$y = bx^{(\alpha+ax)}\,e^{cx} \qquad \ldots \quad (8)$$

where b, α, a and c are constants.

(Equation (8) reduces to $y = bx^{\alpha}$, when $a=c=0$).

The growth relationship between the body size x and the organ size y is thus established.

The growth-coefficient is, therefore, given as,

$$\text{The growth-coefficient} = \frac{1}{y}\frac{dy}{dt}\Big/\frac{1}{x}\frac{dx}{dt}$$

which, from equation (8) $= \alpha+(a+c)x+ax\log_e x$

This may be defined as ρ.

This expression for ρ thus shows that the growth-coefficient is not independent of the body size for a range of values of x, however small. On the other hand it is a function of the body size.

Verification of the Law

The 90 values of the log. carapace length, X, and the log. length of the second cheliped (or its segments Ischium, Merus, Carpus, Propodus and Dactylus), Y, in the male prawns of *P. hendersoni* DeMan were condensed to a smaller number, 13, of classes, with equal intervals. Table I shows the values of group averages for X and Y.

Table I

(Showing the values of the group averages X and Y)

Group*	Average X	Average Y					
		Is.**	Me.	Ca.	Pro.	Dac.	Ch.
				(First Phase)			
0.65—0.70	0.6902	0.3802	0.3010	0.2553	0.3424	0.3802	1.0334
0.70—0.75	0.7364	0.4150	0.3520	0.3323	0.3979	0.4232	1.0846
0.75—0.80	0.7764	0.4589	0.3867	0.3602	0.4370	0.4705	1.1236
0.80—0.85	0.8245	0.4928	0.4347	0.3918	0.4780	0.5120	1.1632
0.85—0.90	0.8745	0.5301	0.4773	0.4355	0.5260	0.5631	1.2078
0.90—0.95	0.9315	0.5729	0.5181	0.4830	0.5809	0.6244	1.2599
0.95—1.00	0.9745	0.6191	0.5807	0.5376	0.6533	0.6801	1.3145
1.00—1.05	1.0290	0.6685	0.6393	0.5792	0.7324	0.7671	1.3815
				(Second Phase)			
1.05—1.10	1.0763	0.7295	0.6944	0.6320	0.7995	0.8338	1.4431
1.10—1.15	1.1220	0.7750	0.7489	0.7012	0.8889	0.9132	1.5108
1.15—1.20	1.1781	0.8393	0.8342	0.7897	1.0205	1.0393	1.6166
1.20—1.25	1.2211	0.8926	0.9016	0.8496	1.1160	1.1166	1.6903
1.25—1.30	1.2565	0.9367	0.9859	0.9367	1.2133	1.2055	1.7737

* Groups have been formed according to X.

** Abbreviations : Is.—Ischium; Me.—Merus; Ca.—Carpus; Pro.—Propodus; Dac.—Dactylus and Ch.—Cheliped.

(It will be seen that there is a change of phase in the growth relationship at about the value 1.05 of X).

The following values of equation (8) have been derived from the contents of Table I :

(First Phase)

Ischium $$y = 0.8987\, x^{(0\cdot67854+0\cdot02704x)}\, e^{-0\cdot06006x}$$

Merus $$y = 0.7644\, x^{(0\cdot78821+0\cdot05575x)}\, e^{-0\cdot14321x}$$

Carpus $$y = 0.2882\, x^{(1\cdot05783-0\cdot03945x)}\, e^{+0\cdot09836x}$$

Propodus $$y = 2.3217\, x^{(0\cdot40589+0\cdot15517x)}\, e^{-0\cdot37601x}$$

Dactylus $$y = 2.6564\, x^{(0\cdot38025+0\cdot15969x)}\, e^{-0\cdot38597x}$$

Cheliped $$y = 4.7731\, x^{(0\cdot73874+0\cdot07066x)}\, e^{-0\cdot17922x}$$

(*Second Phase*)

Ischium $y = 2.2187\, x^{(0\cdot81015+0\cdot03874x)}\, e^{-0\cdot08604x}$

Merus $y = 88.8581 x^{(-1\cdot08553+0\cdot15950x)}\, e^{-0\cdot40973x}$

Carpus $y = 13.5650\, x^{(-0\cdot44531+0\cdot11665x)}\, e^{-0\cdot29084x}$

Propodus $y = 3.0040\, x^{(0\cdot27779+0\cdot10663x)}\, e^{-0\cdot25838x}$

Dactylus $y = 2.5010\, x^{(0\cdot38496+0\cdot08817x)}\, e^{-0\cdot21310x}$

Cheliped $y = 0.2271\, x^{(1\cdot92861-0\cdot00620x)}\, e^{+0\cdot01573x}$

Table II shows the observed (in columns a) and the calculated (in columns b values of the carapace length, x, and the lengths, y, of the cheliped and its five segments; rounded of to the first place of the decimals and expressed in millimeters.

TABLE II

(*Showing the observed, in columns* 'a', *and the calculated, in columns* 'b', *values of the group average lengths, for x and y, expressed in mm. and rounded of to the first place of decimals.*)

Average x	Average y											
	Is.		Me.		Ca.		Pro.		Dac.		Ch.	
	(First Phase)											
	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)
4.9	2.4	2.4	2.0	2.0	1.8	1.8	2.2	2.3	2.4	2.5	10.8	11.1
5.4	2.6	2.6	2.2	2.2	2.2	2.1	2.5	2.5	2.6	2.7	12.1	12.1
6.0	2.9	2.8	2.4	2.4	2.3	2.3	2.7	2.7	3.0	2.9	13.3	13.0
6.7	3.1	3.1	2.7	2.7	2.5	2.5	3.0	2.8	3.3	3.2	14.6	14.4
7.5	3.4	3.4	3.0	3.0	2.7	2.8	3.4	3.3	3.7	3.5	16.1	16.0
8.5	3.7	3.8	3.3	3.4	3.0	3.1	3.8	3.8	4.2	4.1	18.2	18.4
9.4	4.2	4.1	3.8	3.8	3.4	3.4	4.5	4.5	4.8	4.8	20.6	20.6
10.7	4.7	4.7	4.4	4.4	3.8	3.7	5.4	5.6	5.8	6.0	24.1	24.2
	(Second Phase)											
11.9	5.4	5.4	5.0	5.1	4.3	4.4	6.3	6.4	6.8	6.9	27.7	27.2
13.2	6.0	6.0	5.6	5.6	5.0	4.9	7.7	7.7	8.2	8.2	32.4	33.0
15.1	6.9	6.9	6.8	6.6	6.2	6.0	10.5	10.2	11.0	10.6	41.4	41.8
16.6	7.8	7.8	8.0	8.0	7.1	7.2	13.1	13.1	13.1	13.2	49.0	50.0
18.0	8.6	8.7	9.7	9.8	8.6	8.7	16.3	16.6	16.0	16.3	59.4	57.8

Note : In the above Table the sum of the lengths of the five segments for some groups may differ from the length of the corresponding cheliped because of rounding the resulting figures to the first place of decimals. Figures correct up to the second place of decimals are retained by the author.

SUMMARY

1. It has been established that the allometry equation, $y = bx^{\alpha}$, expressing the growth relationship between the body size x and the organ size y in an organic form, is only a first approximation of the following more general relationship between x and y :—

$$y = bx^{(\alpha+ax)}e^{cx},$$

where b, a, α and c are constants.

2. The existence of such a relationship between the carapace length x and the length y of the second pair of chelipeds (or their segments) has been verified from data on 90 male species of the Indian freshwater prawns, *Palaemon hendersoni* DeMan.

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