

A NEW APPROACH TO THE STUDY OF GROWTH-GRADIENT IN THE SEGMENTS OF THE SECOND PAIR OF CHELIPEDS OF THE INDIAN FRESHWATER PRAWNS, *PALAEEMON HENDERSONI* DeMAN (CRUSTACEA : DECAPODA PALAEMONIDAE)

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ABSTRACT

The author of the present paper has mentioned (Misra, 1957) that the simple allometry formula should be regarded as only a valuable first approximation of the more general formula on differential growth viz.

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

where  $b$ ,  $a$ ,  $a$  and  $c$  are constants.

In the present paper study of growth-gradient within the five segments, Is., Me., Ca., Pro. and Dac., of the second cheliped of a sample of 90 male and 69 female freshwater prawns of *Palaemon hendersoni* DeMan has been done in the light of this new formula in which it has been shown by the author (*op. cit.*) that the equilibrium constant  $\alpha$  of the simple allometry formula should be replaced by  $\rho$  where,

$$\rho = \alpha + (a+c)x + ax \log_e x.$$

The following points, in particular, have been noted :—

- (i) As anticipated by Huxley (1932), the values of the equilibrium constant  $\alpha$  for the cheliped or its segments are, within the limits of error probably due to the fluctuations of sampling and insufficient size of the data, only the means of the values of corresponding  $\rho$  calculated for different values  $x$  of the carapace length.
- (ii) It is seen that there is a progressive change in the successive values of the growth-coefficient. Thus, the first phase of growth in the male cheliped starts with a high point in Ca., which shifts towards the end of the phase to Me. In the female it shifts from Pro. to Me. The second phase of growth in the male cheliped starts with only one high point (at Pro.) and later another high point, though less steep than the first, develops in Me.
- (iii) The growth-gradient graph, as exhibited by the  $\alpha$  values (which has so far been the method commonly followed) does not indicate the final order of values of the growth-coefficient for the segments of the cheliped. On the other hand, as the  $\alpha$  values are identical with the values of mean  $\rho$ , it can be said to show a pattern obtained by pooling together of the patterns in the various stages of growth during a phase.
- (iv) The values of  $\frac{d\rho}{dx}$ , associated with the values of  $\rho$ , give proper assessment of the significance of the shift and of the existence of the growth-centre within the cheliped.
- (v) It is interesting to note from the present study that the growth pattern in the female cheliped need not be identical with the one in the male (1 Phase). In this connection certain points have been discussed in the present paper to compare the growth behaviour of the male cheliped with that of the female.

INTRODUCTION

Early this century it has been shown by D'Arcy Thompson (1942) and others that with the increase in the body size there takes place a gradual change in the relative sizes of parts in all organic forms, except some of the simplest ones. The

fact, however, that an organic form is the result of the differential growth was successfully established by Julian S. Huxley (1932) who showed by actual quantitative analysis that the relationship,

$$y = bx^k \text{ (now written as } y = bx^a),$$

called the simple allometry formula or equation, between the body size  $x$  and the organ size  $y$  occurs in most of the animals and plants. Huxley and others have demonstrated the immense importance of the simple allometry formula in studying various cases such as those in which the change of proportions in parts of an adult form takes place either with the progressive increase in the body size in species of animals which are related with one another or in an evolutionary course.

Although there has been severe criticism about the applicability of the allometry formula in theory as well as in practice, its importance has undoubtedly to be recognised in certain matters such as the opening of an entirely new approach that the formula has been able to make in explaining the occurrence of growth-gradient patterns in a limb whose rate of growth is different from that of the body. It can be said that it has increased the value of (although very novel but incomplete owing to absence of a definite mathematical expression) the method of Cartesian transformation as suggested by D'Arcy Thompson (*op. cit.*), to explain the inherent commonness in shapes of related forms which apparently look like different species.

Some of the accepted shortcomings of the allometry formula have been pointed out by Huxley (*op. cit.*) himself. Thus, the constant value of  $\alpha$  used in allometry is unable to explain the gradual change in the growth activity that must be taking place within and between parts of region under study, which can be explained properly only by a progressively changing value of the growth-coefficient from point to point along the axis of an organ.

The author of the present paper has already mentioned (Misra, 1957) that the simple allometry formula should be regarded as only a first approximation to the general formula of differential growth, for which the following expression has been derived :

$$y = bx^{(a+ax)}e^{cx}, \quad \dots (1)$$

where  $b$ ,  $\alpha$ ,  $a$  and  $c$  are constants.

In the present paper study of the growth-gradient in growth intensity of the lengths of the joints Ischium, Merus, Carpus, Propodus and Dactylus (for which the abbreviations Is., Me., Ca., Pro. and Dac. will be used henceforth) has been made in the light of this new formula, in which it has been shown by the author (*op. cit.*) that the equilibrium constant  $\alpha$  of the simple allometry formula should be replaced by  $\rho$  where,

$$\rho = \alpha + (a+c)x + ax \log_e x \quad \dots (2)$$

In crustacean chelipeds there are seven such joints, but out of these the first two, viz. coxa and basis, are firmly fused with Is. and are of insignificant length when compared to the total size of the cheliped. Therefore, in the present discussion only five joints, mentioned above, are taken for study.

Decapoda crustacea provides interesting material for the study of relative growth and it will not be out of place to mention here that the concept of growth-gradient, growth-potential etc. has been mostly based on researches conducted on crustaceans of this group. The genus *Palaemon*, which is very common in tropical and sub-tropical freshwater, is a Decapod crustacea belonging to the group

**Macrura.** An interesting feature of the species under present discussion, like many other species of *Palaemon*, is the enormous size that the second pair of chelipeds attains in males after a certain age.

#### MATERIAL AND MEASUREMENTS

The material, consisting of 90 male and 69 female prawns of *Palaemon hendersoni* DeMan, was kindly lent to the author by the Director, Zoological Survey of India, and all the specimens on which the present work is based are deposited in the reserve collections of the Zoological Survey.

The lengths are in millimetres, and were taken with sliding calipers fitted with graduated dial reading directly upto the first place of decimal, in the following manner:—

- (i) Length of carapace was measured in a straight line between the orbital edge and the posterior border.
- (ii) Lengths of the segments of the cheliped were measured dorsally in a single straight line.
- (iii) The total length of the cheliped was calculated by adding up the lengths of the individual segments.

Also, only the larger of the second cheliped (which is sometimes dextral and sometimes sinistral) was measured, for basically the chelipeds of the two sides should grow at the same rate and the apparent asymmetry that is sometimes noticed in this species appears to be due to some extraneous factors like autotomy and regeneration.

#### OBSERVATIONS AND DISCUSSION

In females the 69 values of log carapace length, denoted by  $X$ , and of log length of the cheliped or its joint, denoted by  $Y$  (the base of logarithm being 10), were condensed to 12 groups with equal intervals for  $X$ . Table I gives the values of group averages for  $X$  and  $Y$ . A similar table for the male chelipeds has been given earlier by the author (*op. cit.*).

TABLE I

*The values of the group averages X and Y in females*

Group	Average X	Average Y					
		Is.	Mo.	Ca.	Pro.	Dac.	Cheliped
0.55—0.60	0.5911	0.3010	0.2553	0.2304	0.3010	0.3617	0.9912
0.60—0.65	0.6368	0.3212	0.2783	0.2382	0.3081	0.3899	1.0086
0.65—0.70	0.6751	0.3674	0.3148	0.2784	0.3489	0.4089	1.0445
0.70—0.75	0.7376	0.4093	0.3552	0.3151	0.3799	0.4259	1.0779
0.75—0.80	0.7761	0.4353	0.3753	0.3516	0.4148	0.4510	1.1062
0.80—0.85	0.8387	0.4939	0.4346	0.3873	0.4870	0.5330	1.1688
0.85—0.90	0.8710	0.5001	0.4740	0.4203	0.5117	0.5562	1.1944
0.90—0.95	0.9247	0.5677	0.5196	0.4543	0.6147	0.6511	1.2658
0.95—1.00	0.9743	0.5875	0.5629	0.5032	0.6616	0.6949	1.3066
1.00—1.05	1.0263	0.6481	0.6304	0.5598	0.7029	0.7627	1.3652
1.05—1.10	1.0792	0.6982	0.6777	0.6249	0.7554	0.8310	1.4228
1.10—1.15	1.1168	0.7476	0.7191	0.6388	0.7901	0.8661	1.4580

The author (*op. cit.*) has derived values of equation (1) for the joints of the male cheliped. Values for the female joints have similarly been calculated and are as follows :—

$$\begin{aligned} \text{Is.} & \quad y = 1.3792x^{(0.40667+0.05239x)} e^{-0.10477x} \\ \text{Me.} & \quad y = 1.1438x^{(0.43286+0.05178x)} e^{-0.09785x} \\ \text{Ca.} & \quad y = 0.8213x^{(0.57277+0.02915x)} e^{-0.05685x} \\ \text{Pro.} & \quad y = 0.9502x^{(0.58641+0.04392x)} e^{-0.07943x} \\ \text{Dac.} & \quad y = 1.8849x^{(0.27958+0.08056x)} e^{-0.15102x} \\ \text{Cheliped} & \quad y = 6.0652x^{(0.42464+0.05121x)} e^{-0.09154x} \end{aligned}$$

Table II gives the values of  $\rho$  calculated from equation (2).

TABLE II

The values of  $\rho$  for the second cheliped and its segments for the 13 values in the male and 12 values in the female of the group average carapace length (denoted as  $x$ )

$x$	$\rho$					
	Is.	Me.	Ca.	Pro.	Dac.	Cheliped
$\delta$ (I Phase)*						
4.9	0.73	0.79	1.04	0.53	0.52	0.76
5.4	0.75	0.83	1.01	0.64	0.62	0.80
6.0	0.77	0.86	0.99	0.74	0.73	0.84
6.7	0.80	0.91	0.95	0.90	0.89	0.91
7.5	0.84	0.97	0.90	1.09	1.09	0.99
8.5	0.89	1.06	0.84	1.36	1.37	1.11
9.4	0.94	1.14	0.78	1.61	1.63	1.21
10.7	1.01	1.26	0.69	1.97	2.01	1.37
$\delta$ (II Phase)						
11.9	0.89	0.64	0.92	1.62	1.50	1.86
13.2	1.01	1.06	1.24	1.92	1.75	1.84
15.1	1.18	1.66	1.70	2.35	2.11	1.82
16.6	1.34	2.21	2.11	2.74	2.43	1.80
18.0	1.48	2.73	2.50	3.11	2.73	1.78
$\eta$						
3.9	0.48	0.53	0.62	0.68	0.43	0.54
4.3	0.51	0.56	0.64	0.71	0.49	0.58
4.7	0.54	0.60	0.66	0.74	0.54	0.61
5.5	0.61	0.66	0.69	0.80	0.64	0.68
6.0	0.65	0.71	0.72	0.84	0.72	0.73
6.9	0.74	0.80	0.77	0.93	0.87	0.83
7.4	0.80	0.86	0.80	0.98	0.96	0.89
8.4	0.90	0.97	0.86	1.07	1.13	1.00
9.4	1.02	1.09	0.93	1.18	1.32	1.13
10.6	1.16	1.24	1.01	1.31	1.55	1.28
12.0	1.34	1.42	1.11	1.47	1.84	1.47
13.1	1.48	1.57	1.19	1.60	2.07	1.62

\* It has been mentioned before by the author (*op. cit.*) that there is a change in phase in growth relationship in the male cheliped.

Values of the equilibrium constant  $\alpha$  of the simple allometry equation and the means of the values of  $\rho$ , as given in Table II, were calculated and the results are shown in Table III.

TABLE III

The values of  $\alpha$  (columns 1) and mean  $\rho$  (columns 2) for the cheliped and its joints (male and female)

	Is.		Me.		Ca.		Pro.		Dac.		Cheliped	
	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)
♂ (I Ph.)	0.84	0.84	0.97	0.98	0.91	0.90	1.10	1.10	1.11	1.11	0.99	1.00
♀	0.83	0.85	0.89	0.92	0.81	0.83	1.00	1.03	1.01	1.04	0.92	0.95
♂ (II Ph.)	1.16	1.18	1.59	1.66	1.64	1.69	2.29	2.35	2.06	2.10	1.82	1.82

It will be seen that, as anticipated by Huxley himself (*op. cit.*), the values of the equilibrium constant  $\alpha$  for the cheliped or for its segments are (within the limits of error due probably to the fluctuations of sampling and insufficient size of data) only the means of the values of corresponding  $\rho$  calculated for different ages, represented by  $x$ , of the prawns.

The values of  $\rho$  enable the existence of the growth-gradient to be seen very clearly. From the records of Table II lines have been drawn in Fig. 1(*a, b, c*) for the cheliped and its segments giving the values of  $\rho$  (along the  $y$ -axis) for different values of the carapace length  $x$  (along the  $x$ -axis) in males and females. (These may be compared with the dotted lines drawn in the same figure to show the distribution of growth potential by the method adopted by Huxley (*op. cit.*), Tazelaar (1930) and others, of taking the centres of homologous regions at equal distances along the  $x$ -axis and the corresponding values of  $\alpha$  along the  $y$ -axis).

It is seen that there is a progressive change in the successive values of the growth-coefficient. Thus, the first phase of growth in the male cheliped starts with a high point in Ca., which shifts towards the end of the phase to Me. In the female it shifts from Pro. to Me. The second phase of growth in the male cheliped starts with only one high point (at Pro.) and later another high point, though less steep than the first, develops (in Me.).

Also, the order of the values of  $\rho$  changes from (Dac., Pro., Is., Me. and Ca.) to (Ca., Is., Me., Pro. and Dac.) in the first phase of growth of the male cheliped, thus almost reversing itself. In the female the order changes from (Dac., Is., Me., Ca. and Pro.) to (Ca., Is., Me., Pro. and Dac.). Hence the final order of values of the growth-coefficients is identical in the two cases. This is interesting, for, as shown by the  $\alpha$  values in the above table and as pointed out by Huxley (*op. cit.*) and others, the growth pattern in the female cheliped is generally comparable with the one in male cheliped of most of the species of this genus in its first phase of growth. It will thus be seen that the growth-gradient, as exhibited by the  $\alpha$  values, does not indicate the final order of the values of the growth-coefficient for the segments of the cheliped. On the other hand, as the  $\alpha$  values are identical with the values of the mean  $\rho$ , it can be said to show a pattern obtained by pooling together of the patterns in the various stages of growth during a particular phase.

In the second phase of growth of the male cheliped the order of the values of  $\rho$  changes from (Me., Is., Ca., Dac. and Pro.) to (Is., Ca., Me., Dac. and Pro.).

Thus, it is seen that although the final order of values of the growth-coefficient may be the same in male (I Phase) and female chelipeds, the flow of the growth potential, before the final order is reached, has been different in the two cases. It may be noted here that Ca. decreases from a small positive allometric to a marked negative allometric joint in the first phase of growth in the male cheliped, while in the female it is just the opposite, i.e. it increases from marked negative allometry to a small positive one.

To study more clearly the difference in the growth behaviour of the male (I Phase) and the female chelipeds it will be interesting to calculate the values of  $\frac{d\rho}{dx}$  ( $= 2a+c+a \log_e x$ ). This has been done in Table IV.

TABLE IV

The values of  $\frac{d\rho}{dx}$  for various values of the group average carapace length ( $x$ )

$x$	$\frac{d\rho}{dx}$					
	Is.	Me.	Ca.	Pro.	Dac.	Cheliped
♂ (I Phase)						
4.90	0.037	0.057	-0.043	0.181	0.187	0.074
5.45	0.040	0.063	-0.047	0.198	0.204	0.082
5.98	0.042	0.068	-0.051	0.212	0.219	0.088
6.68	0.045	0.074	-0.055	0.229	0.237	0.096
7.49	0.048	0.081	-0.060	0.247	0.255	0.104
8.54	0.052	0.088	-0.065	0.267	0.276	0.114
9.43	0.055	0.092	-0.069	0.282	0.292	0.121
10.69	0.058	0.100	-0.074	0.302	0.312	0.130
♂ (II Phase)						
11.92	0.087	0.305	0.232	0.219	0.182	-0.012
13.25	0.092	0.321	0.244	0.230	0.191	-0.013
15.07	0.096	0.342	0.259	0.244	0.202	-0.014
16.64	0.100	0.358	0.270	0.255	0.211	-0.014
18.05	0.104	0.371	0.280	0.263	0.218	-0.015
♀						
3.90	0.071	0.076	0.041	0.068	0.120	0.081
4.33	0.077	0.082	0.044	0.073	0.128	0.086
4.73	0.081	0.086	0.047	0.077	0.135	0.090
5.46	0.089	0.094	0.051	0.083	0.147	0.098
5.97	0.094	0.098	0.054	0.087	0.154	0.102
6.90	0.101	0.100	0.058	0.093	0.166	0.110
7.43	0.105	0.110	0.060	0.096	0.172	0.114
8.41	0.112	0.116	0.064	0.102	0.182	0.120
9.43	0.118	0.122	0.067	0.107	0.191	0.126
10.62	0.124	0.128	0.070	0.112	0.200	0.132
12.00	0.130	0.134	0.074	0.118	0.210	0.138
13.09	0.135	0.133	0.076	0.121	0.217	0.143

Fig. 2 (a, b, c) has been drawn to show the change in the value of  $\frac{d\rho}{dx}$  (taken along the  $y$ -axis) for the values of the carapace length  $x$  (taken along the  $x$ -axis).

Table V gives the mean values of  $\frac{d\rho}{dx}$  (as given in Table IV) for the male and the female segments.

TABLE V  
The mean values of  $\frac{d\rho}{dx}$  for the segments of the male and the female chelipeds

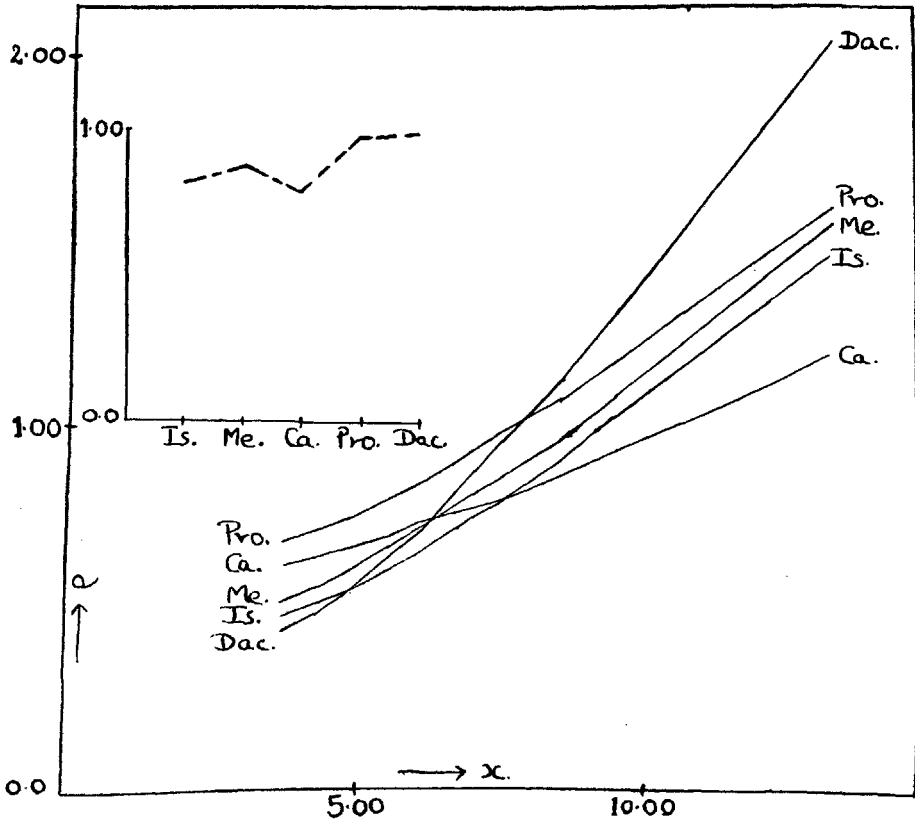
	Is.	Me.	Ca.	Pro.	Dac.	Cheliped
♂ (I Phase)	0.047	0.078	-0.058	0.240	0.248	0.101
♀	0.103	0.107	0.059	0.095	0.168	0.112
♂ (II Phase)	0.096	0.339	0.257	0.242	0.201	-0.014

These reflect clearly upon the significance of the shift of the growth-centre and also on the existence of it, as discussed earlier in this paper. From these it is seen that:

- (i) In the distal region of the cheliped consisting of the chela (Pro. and Dac.) the relative growth rate tends to increase faster in the male (I Phase) than in the female; and it is just the opposite in the basal region (Is. and Me.) where the growth-coefficients for the male segments increase at lesser rates than what they do for the female ones.
- (ii) In general it is seen that the differences in the change of rates of growth between the male segments (I Phase) are much more marked than between the female segments. This reveals an important fact that the growth-gradient in the female cheliped is more stable than in the male cheliped.
- (iii) The rates at which the growth-coefficients increase in value follow different orders in male (I Phase) and female joints. Thus in the male it is (Ca., Is., Me., Pro. and Dac.) and in the female it is (Ca., Pro., Is., Me. and Dac.); Ca. in the former case actually loses its rate of growth. In male (II Phase) the order is (Is., Dac., Pro., Ca. and Me.).
- (iv) Although the growth-centre is elsewhere, Dac. gains its final size at a faster rate than any other segment of the cheliped, both in the male (I Phase) and in the female. It thus forms the region of greatest activity in the cheliped. In the male (II Phase) it is Me. which gains its growth at the fastest rate of all the segments of the cheliped.

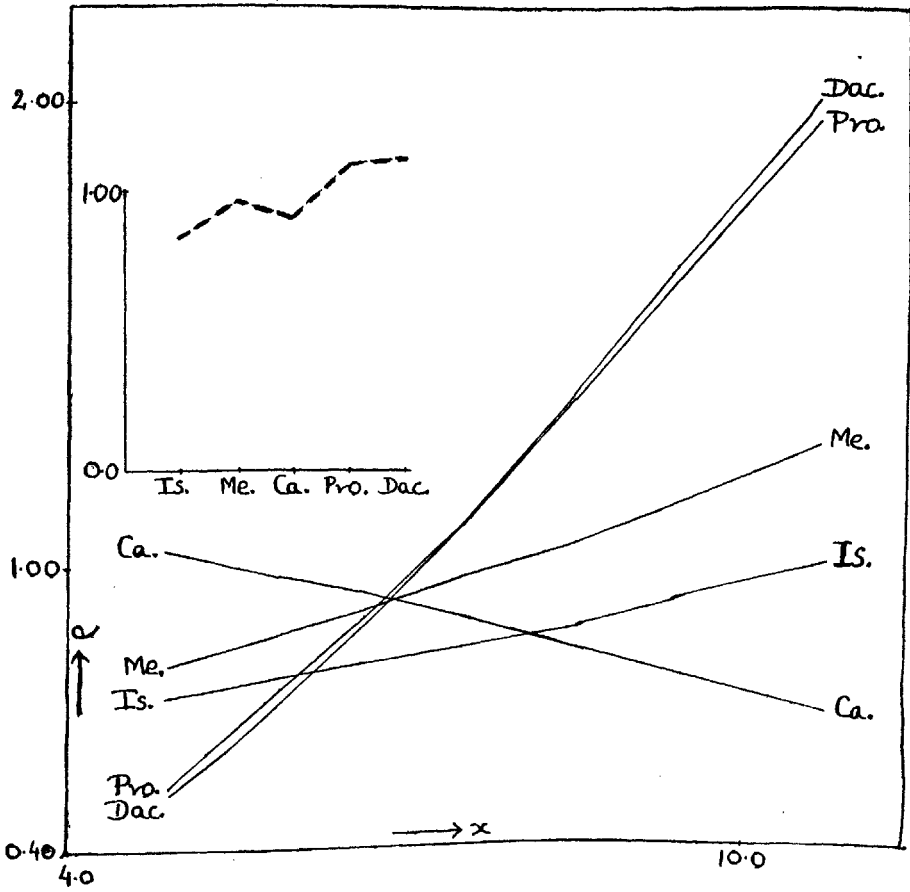
#### REFERENCES

- Clark, W. E. Le Gros, and Medawar, P. B. (Edited by). (1945). *Essays on Growth and Form*. Clarendon Press, Oxford.
- Huxley, Julian S. (1932). *Problems of Relative Growth*. Methuen & Co. Ltd., London.
- Misra, R. K. (1957). An expression for the growth-coefficient ' $\alpha$ ' 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. *PNISIBS*, 23B, 42-47.
- Tazelaar, M. A. (1930). The relative growth of parts in *Palaemon carcinus*. *Brit. Jour. Exper. Biol.*, 7, 165.
- Thompson, D'Arcy W. (1942). *Growth and Form*. Cambridge Univ. Press.

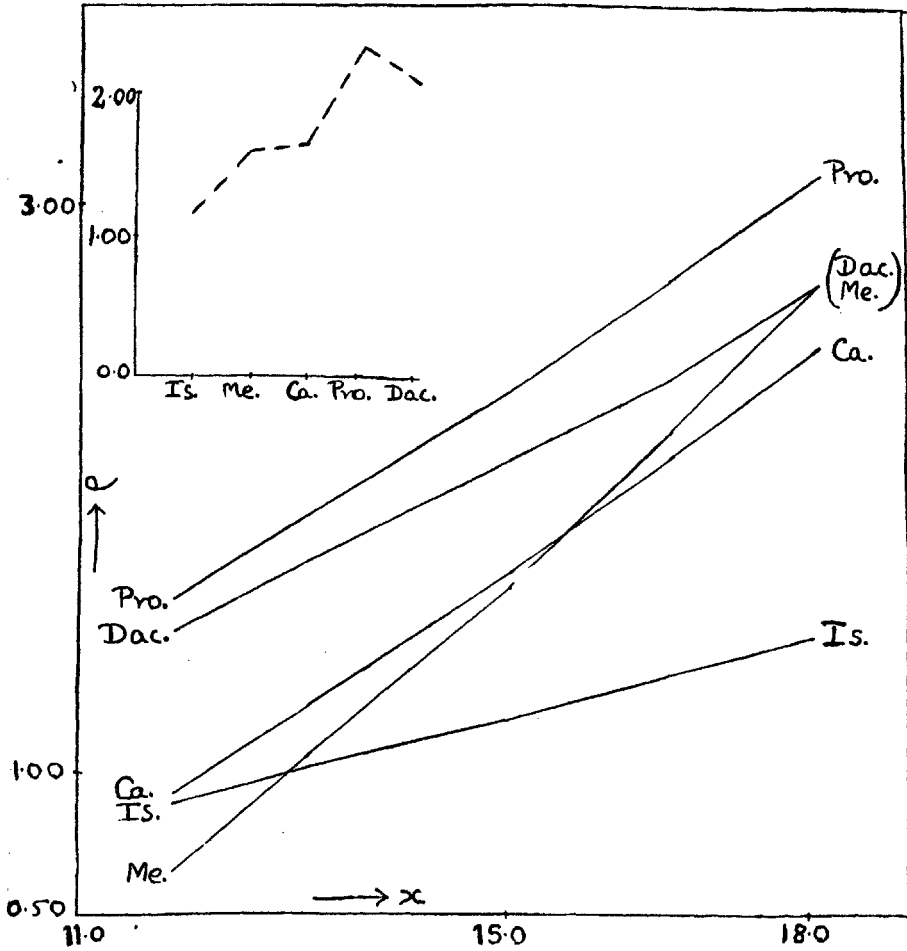


Text figure. 1(a). Showing growth-gradient within the cheliped (female).

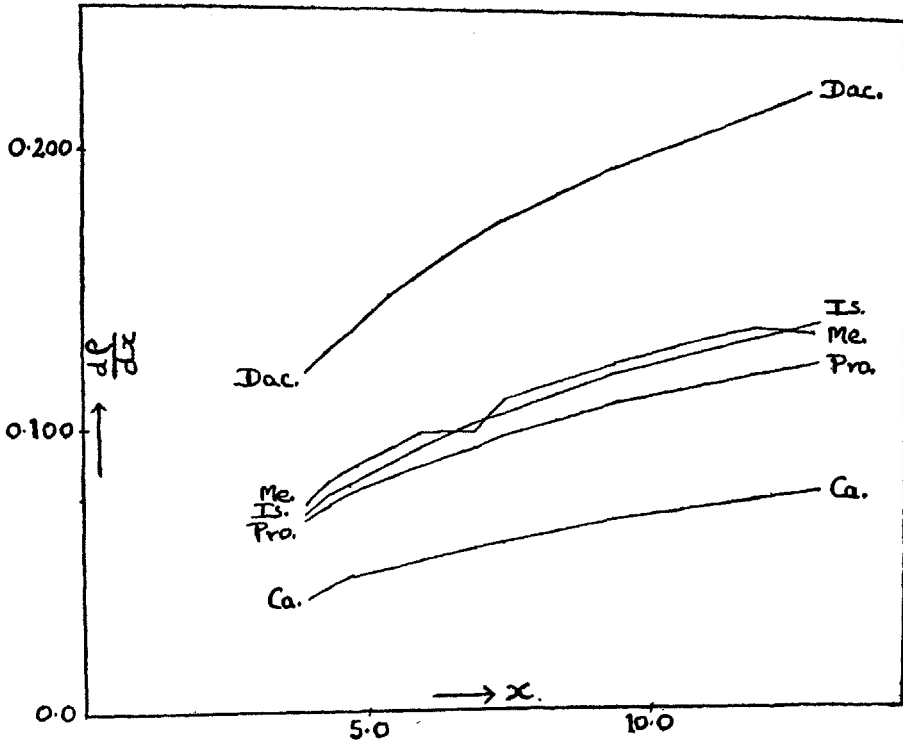




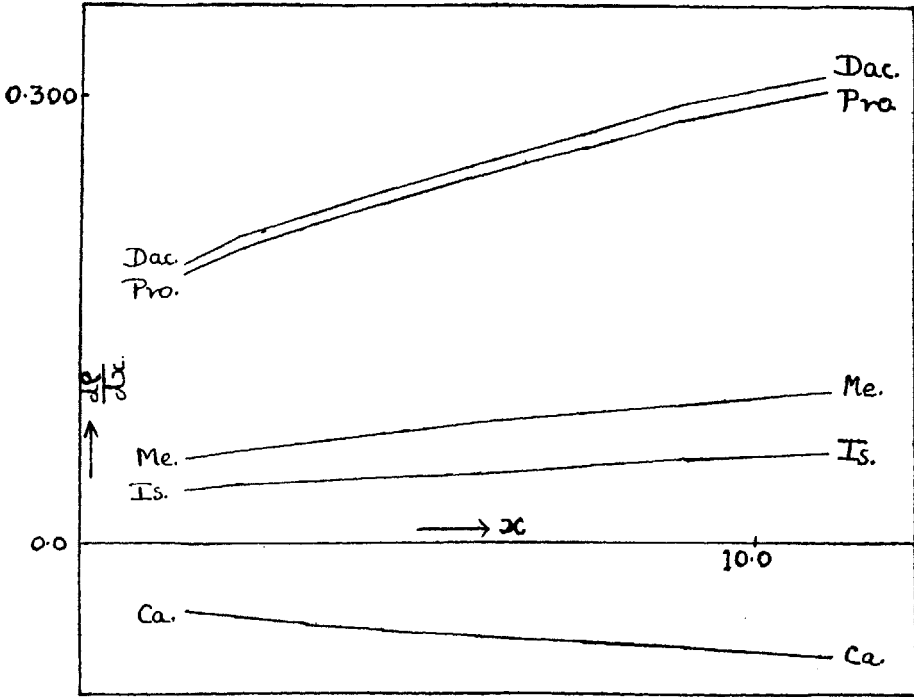
Text-figure. 1(b). Showing growth-gradient within the cheliped (male, I Phase).



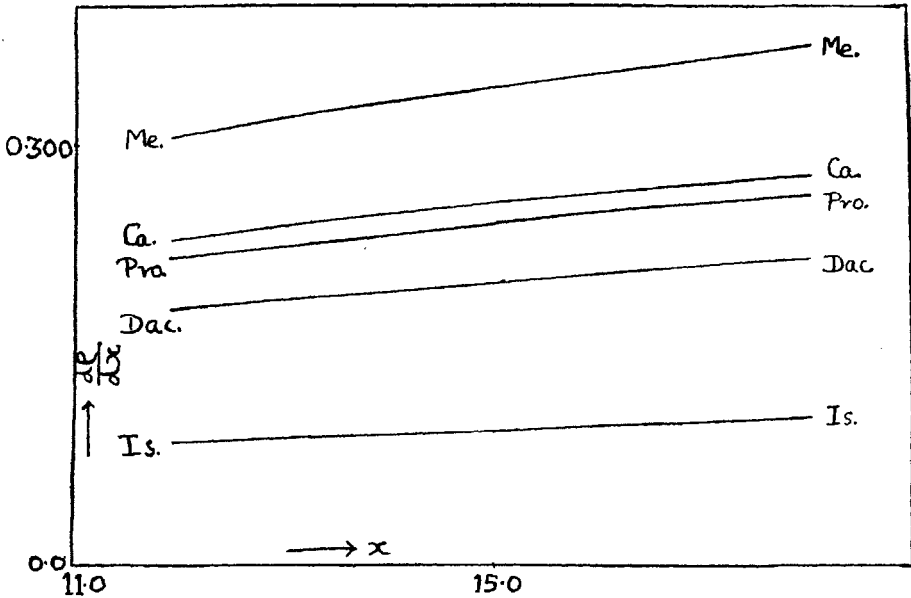
Text figure. 1(e). Showing growth-gradient within the cheliped (male, II Phase).



Text figure. 2(a). Showing the graph of  $\frac{dp}{dx}$  ( $y$ -axis) against the carapace length  $x$  ( $x$ -axis) ; female.



Text figure. 2(b). Showing the graph of  $\frac{d\rho}{dx}$  (y-axis) against the carapace length  $x$  (x-axis) ; male, I phase.



Text figure. 2(c). Showing the graph of  $\frac{d\rho}{dx}$  (y-axis) against the carapace length  $x$  (x-axis) ; male, II Phase,