THE RELATIVE GROWTH OF PARTS
IN *PALAEMON CARCINUS*

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(With Seven Text-figures and One Plate.)

INTRODUCTION.

It has been suggested (Huxley, 1927; Shaw, 1928) that in various animals, such as some Crustacea which show disharmonic growth, there exist growth centres correlated with the active growth of specific organs or regions. Also that the growth of neighbouring parts is correlated with the growth of the heterogonic organ. In *Maia squinado* (Huxley, 1927) and *Inachus dorsettensis* (Shaw, 1928) the growth of the appendages posterior to the heterogonic pereiopod was increased and of those anterior decreased. In these previous cases, however, the heterogonic organ was the 1st pereiopod; therefore the appendage whose growth decreased was the 3rd maxilliped, which (a) is very small and (b) belongs to a different type of appendage. The result might thus be accidental since the appendage in each case was so small; if not, the result might be correlated with the different type of appendage, or it might be due to its position on the main axis of the body. In *Palaemon carcinus* the heterogonic cheliped is the 2nd pereiopod, hence the main object of the present experiment was to determine whether the growth of the pereiopod anterior to the cheliped is decreased.

The present work was carried out under the supervision of Professor J. S. Huxley.

MATERIAL AND METHODS.

*Palaemon carcinus* is a very large species of Indian prawn. Specimens of both males and females of varying sizes were very kindly sent to Professor J. S. Huxley by Colonel Seymour Sewell, the Director of the Zoological Survey of India. The only other measurements made of *P. carcinus* were carried out by Kemp and his workers (Kemp, 1913, 1914, 1915 and 1923) and they drew attention to the change in proportion of the chelipeds without, however, proving the simple heterogony relation (Huxley, 1927). Miss I. L. Dean (referred to on p. 161 of Huxley, 1927) analysed the data of Kemp on *P. carcinus* and was able to show that the cheliped showed simple heterogony in both male and female but that the relative growth was greater in the male than in the female. She also showed that the proportion parts of the cheliped was approximately the same in the male and the female when the limb was the same absolute size.
The best method of carrying out the experiment would be to measure parts of the individual prawns at various times during their life. This method, however, could not be adopted owing to the impossibility of keeping the prawns in captivity. The collection of prawns was therefore taken at random but including a large range in size. The total number of prawns measured was 143; of these 80 were female and 63 male.

With the exception of the 3rd maxilliped the appendages were broken off at the breaking joint; this can be done accurately since the limbs are stout. In the case of the 3rd maxilliped, however, it was cut off with scissors at a definite point. The measurements, all of which were linear, were simple to make owing to the large size of the prawns, the length of the carapace varying from 6.6 to 2.4 cm. The measurements made were as follows:

1. **Carapace length.** This was the standard with which all the others were compared. The measurement was made by means of a pair of accurately adjusted dividers and the exact length measured was from behind the right eye to the mid-point of the carapace posteriorly (see Fig. 1). This position posterior to the eye was chosen rather than that from the anterior end of the rostrum because the rostrum was so often damaged.

2. **Third maxilliped.** The chitin of this appendage is thin, hence it was found to be more accurate to cut this appendage off at a definite place by means of scissors than to attempt to break it off at the breaking joint. The position at which it was cut off was the joint between the protopodite and the fused ischiopodite and meropodite. The remainder of the limb, consisting of three segments, was then measured by placing it upon a steel ruler.

3. **Pereiopods.** These appendages were broken off at the breaking joint, which exists near the proximal end of the segment representing the fused basipodite and ischiopodite. They were then measured with a steel ruler.

All appendages were stretched out to their fullest extent upon a steel ruler when measured. All measurements are probably accurate to the nearest ½ mm.

The original data have been deposited at the British Museum (Natural History).

The prawns were divided into classes according to carapace length, six classes of males and five of females. The number of prawns in some classes was obviously insufficient to allow of accurate results. In the females for example the first class possesses only two individuals and wherever the data from this group were used, dotted lines indicate the fact. (Graph B'.)

The results were analysed by means of the following graphs:

C. This graph represents a comparison of the mean relative lengths of appendages in the male and female for all classes together.
A comparison of the relative growth percentage of the appendage per 100 per cent. growth of carapace in male and female.

D. A comparison of the ratio \( \delta/\varphi \) for the absolute size of the appendages, in large and in small crabs of approximately the same carapace length.

B and B'. The relative lengths of the appendages were plotted against the carapace length. These graphs thus indicate the growth changes in the proportion of the various limbs in male and female.

A. The logarithm of the mean size of the cheliped in the different classes was plotted against the logarithm of the corresponding mean carapace length. Similar graphs were also constructed for the other pereiopods; these are described and discussed later, but are not included in the paper since graphs D and D' illustrate the chief points. The value of \( k \) from the heterogonic growth formula \( y = bx^k \) (where \( y = \) length of the part in question, \( x = \) the standard measurement) can be obtained from these graphs and thus the relative growth rate could be numerically compared.

RESULTS.

The greatest range in carapace size occurred amongst the males; they were both smaller and larger than the females. The females tended to group themselves into a few large classes of which the middle classes were the largest.

Growth of the cheliped.

In graph A, by plotting the logs of the mean cheliped length of the classes in male and female against the logs of the mean carapace length, a close approximation to a straight line was obtained in the female and to two straight lines meeting at

Text-fig. 2. Graph A. Logarithmic plot of means for male and female cheliped length against carapace length.
an angle in the male. The value of \( k \) in the male was approximately 1.8 over its whole length. It will be seen, however, that the slope of the line changes in places. The slope of the line through the first three points represents stages at which the carapace length is from 2.66 to 3.8 cm. in length and the value of \( k \) is here only about 1.4; the latter part of the slope, however, is much steeper and here the value of \( k \) is 2.15. The more gradual slope of the curve probably corresponds to the growth of the cheliped preceding sexual maturity which then resembles the rate of growth of the female cheliped. This difference of growth of the heterogonic chela at distinct periods was also shown in the growth of the chela propus of *Inachus* (Shaw, 1928, Text-fig. 3, p. 149). The growth of the cheliped in the female is heterogonic, but not so markedly as in the male, the value of \( k \) being 1.48. In the female only five points were obtained and these seemed to fall naturally nearly in a straight line.

There was a suggestion of dimorphism in the male chela since a bimodal frequency curve was obtained, the modes occurring at 10 and 31.2 cm. length of cheliped. For a possible explanation of the fact, see Shaw, 1928, p. 148.

**Growth of the pereiopods.**

**Male.** A log. log. graph representing the relative growth of the pereiopods and the 3rd maxilliped in the male was constructed. The curves representing the growth rates of \( p_1 \) and \( p_3 \), that is of the pereiopod anterior and that posterior to the cheliped, are roughly parallel between the first four points. This corresponds to the stage at which the carapace length is 2.6 to 4.15 cm. long. After this period, when the carapace length is from 4.15 to 6.4 cm., the growth rate of \( p_3 \) is greater than that of \( p_1 \); hence the curves cross. This point is better illustrated in graph B in which the relative appendage lengths in the various classes of males are plotted against the absolute length of the carapace. Note that the crossing of curves representing the relative growths of \( p_1 \) and \( p_3 \) does not occur in the corresponding curves in graph B' for the females. The values of \( k \) for the whole curves are: \( p_1, 1.01; p_3, 1.07; p_4, 1.05; p_5, 1.04 \); the value of \( k \) grades off slightly from \( p_3 \) to \( p_5 \). This grading is more marked when \( k \) is calculated for the later parts of the curves, the values then being \( p_1, 1.08; p_3, 1.21; p_4, 1.17; p_5, 1.13 \).

**Female.** A log. log. graph corresponding to the above was constructed for the females. In this case the growth of \( p_3 \) does not exceed that of \( p_1 \) at any time, hence the curves do not cross. The values of \( k \) are: \( p_1, 1.09; p_3, 1.07; p_4, 1.03; \) and \( p_5, 1.10 \). The graded effect for the values of \( k \) from \( p_3 \) to \( p_5 \) is again noticeable. The \( k \) value of \( p_1 \), however, is here the greatest whereas in the males it is the least.

The values of \( k \) in the 3rd maxilliped are 0.93 male and 0.95 female, both showing slight negative heterogony.

The differences in growth between the pereiopods of the male and female are well shown in Pl. II, figs. 1, 2 which are photographs of the pereiopods of a male and female of the same carapace length. Fig. 1 represents the chelipeds, the larger cheliped being of course that of the male. In fig. 2 the pereiopods are placed in pairs, the left one of each being the male pereiopod, the right the corresponding
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one of the female. From left to right the pairs are the 5th, 4th, 3rd and 1st pereiopods. The 1st pereiopods appear to be of the same length, actually, however, that of the female is slightly longer than that of the male. In the remaining three pairs it is obvious that in each case the male pereiopod is of greater length.

Text-fig. 3. Graph B. ♂. Mean relative length of 3rd maxilliped, cheliped and pereiopods 1, 3, 4 and 5 plotted against mean carapace length.

Graph C. In this graph the mean relative length percentages of the various appendages were plotted for the male and female. The greater relative size of the male cheliped is well shown in this graph. It can also be seen that the 3rd pereiopod is greater than the 1st in the male, but that in the female the 1st is larger than
the 3rd. The relative values from $p^3$ to $p^5$, those which occur posterior to the cheliped, are graded, the 5th having the greatest value and the 3rd the smallest. In both *Inachus dorsettensis* and *Maia squinado* the reverse holds good (Huxley, 1927, abb. 5, p. 163 and Shaw, 1928, Text-fig. 9). This difference is due to the fact that the absolute lengths of the most posterior pereiopods in the case of *M. squinado* and *I. dorsettensis* are the smallest and those anterior largest; the reverse is the case in *P. carcinus*. In *M. squinado* the difference between the relative values of the pereiopods in males and females decreases from $p^1$ to $p^4$, in *P. carcinus* this occurs to a slight extent only.

**Graph D.** The two curves shown on this graph represent the ratio of large class $\frac{\varphi}{\varphi}$ per cent. and of small class $\frac{\varphi}{\varphi}$ per cent. for the 3rd maxilliped and the five pereiopods. The most obvious difference between the curves is the fact that the value of the ratio $\frac{\chi\text{eliped}}{\chi\text{eliped}} \frac{\varphi}{\varphi}$ per cent. in the mature classes is far greater than it is in the immature classes. The difference between the ratios of the 1st and 2nd pereiopods is obvious, but in the small class ratios the difference between them is
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The ratio $p^3/p^1$ per cent, being slightly greater than the corresponding one for $p^1$. This difference is accentuated in the large class ratios, showing that the difference in size between the 3rd and 1st pereiopods increases in the male with size.

Graph E. In this graph the total percentage growths for the 3rd maxilliped and the pereiopods in males and females were calculated per 100 per cent. growth of carapace. The growth of the male appendages could thus be compared with the growth of those of the female. In the 3rd maxilliped and the 1st pereiopod the growth is greater in the female than in the male, but in all other appendages it is greater in the male. There is a slight graded effect between the rates of growth of the 3rd, 4th and 5th pereiopods which is more marked in the male than in the female. The difference in growth between $p^1$ and $p^3$ in the male and female is best shown by this method of presenting the facts.
Table I. ♂.
Mean absolute measurements in cm.

<table>
<thead>
<tr>
<th>Reference number of class</th>
<th>Carapace length classes</th>
<th>Average carapace length</th>
<th>No. in class</th>
<th>3rd max. length</th>
<th>Pereiopod length</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1st</td>
</tr>
<tr>
<td>I</td>
<td>6-0</td>
<td>6.29</td>
<td>17</td>
<td>4-6</td>
<td>10-07</td>
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<tr>
<td>II</td>
<td>5-5-6-0</td>
<td>5.86</td>
<td>11</td>
<td>5-26</td>
<td>9-4</td>
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<tr>
<td>III</td>
<td>4-5-5-5</td>
<td>5.23</td>
<td>7</td>
<td>3-82</td>
<td>8-44</td>
</tr>
<tr>
<td>IV</td>
<td>4-0-4-5</td>
<td>4.16</td>
<td>5</td>
<td>3-06</td>
<td>6-42</td>
</tr>
<tr>
<td>V</td>
<td>3-5-4-0</td>
<td>3.79</td>
<td>7</td>
<td>2-75</td>
<td>5-71</td>
</tr>
<tr>
<td>VI</td>
<td>3-0-3-5</td>
<td>3.3</td>
<td>9</td>
<td>2-42</td>
<td>4-98</td>
</tr>
<tr>
<td>VII</td>
<td>2-5-3-0</td>
<td>2.66</td>
<td>7</td>
<td>2-07</td>
<td>4-13</td>
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Table II. ♀.
Mean absolute measurements in cm.

<table>
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<tr>
<th>Reference number of class</th>
<th>Carapace length classes</th>
<th>Average carapace length</th>
<th>No. in class</th>
<th>3rd max. length</th>
<th>Pereiopod length</th>
</tr>
</thead>
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<td>4-15</td>
<td>9-05</td>
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<td>9</td>
<td>3-82</td>
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<td>III</td>
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<td>15</td>
<td>3-42</td>
<td>7-22</td>
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<td>2-12</td>
<td>6-15</td>
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<tr>
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<td>37</td>
<td>2-8</td>
<td>5-76</td>
</tr>
</tbody>
</table>

Tables I and II show the various classes in ♂ and ♀ and their respective mean measurements.

\[
\frac{\triangle}{\bigtriangleup} \frac{\text{Large } \delta\delta}{\text{Large } \varphi\varphi} \text{ per cent.}
\]

\[
\bigcirc \ldots \bigcirc \frac{\text{Small } \delta\delta}{\text{Small } \varphi\varphi} \text{ per cent.}
\]

Text-fig. 6. Graph D. Ratio \(\delta\delta/\varphi\varphi\) for various appendages and abdomen in large and small crabs.
DISCUSSION.

Even though the data were in some respects incomplete several points seem to emerge clearly.

There is undoubtedly a correlation between marked heterogony in an appendage and the growth rate of neighbouring appendages. The correlation is of the following nature: that the growth of appendages immediately posterior to the heterogonic organ is increased, that of appendages immediately anterior is decreased, irrespective of whether they are of the same type as the heterogonic organ (e.g. pereiopod and chela) or of different type (e.g. maxilliped and chela).

The existence of this correlation is well brought out by the fact that the difference in growth between \( p^1 \) and \( p^3 \) is greatest where the heterogonic growth of the cheliped is greatest. In Graph B this is well shown; where the carapace length is from about 4.2 to about 6.3 cm. it will be seen that \( p^3 \) grows more rapidly than \( p^1 \); this coincides with the carapace length at which the growth of the cheliped is greatest.

Text-fig. 7. Graph E. The relative growth percentage of 3rd maxilliped, cheliped and pereiopods 1, 3, 4 and 5 per 100 per cent. growth of carapace in \( \delta \) and \( \varphi \).
There is at present no explanation that I can suggest for this curious fact. Elaborate experiments on the effect of regenerating appendages on the growth of neighbouring appendages will be necessary before this can be adequately discussed. It may be pointed out, however, that a mere "drainage" effect of the very rapidly growing chela on neighbouring parts does not seem to fit the facts. Either there is an effect of the rapidly growing organ on neighbouring organs which is of different sign up and down the main axial gradient of the body or else we must think in terms of the total distribution of what may be called "growth potential" along the body axis, which would then be different in male and female; the size of the chela in male and female would then be an effect rather than a cause of the different growth rates of neighbouring parts in the two sexes. In any case, however, the empirical fact of the difference in growth rate of appendages in front of and posterior to a heterogonic appendage would seem to be of quite general occurrence.

**SUMMARY.**

Linear measurements of certain appendages and the carapace of *P. carcinus* were made and plotted in various ways. The following conclusions were drawn:

1. The cheliped shows heterogonic growth in both male and female, but more markedly in the male, the values of $k$ being: male 1.8 and female 1.48.

2. The pereiopods in both male and female are slightly heterogonic. The relative growth rates are graded from $p^3$ to $p^5$, that of $p^3$ being slightly greater than that of $p^5$.

3. Of the ordinary pereiopods the rate of growth of $p^1$ is the smallest in the male, but the largest in the female.

4. The difference between the rates of growth of $p^1$ and $p^3$ in male and female is greatest where the rate of growth in the heterogonic organ, the cheliped, is most excessive in the male.

5. The growth of the 3rd maxilliped is slightly negatively heterogonic, the value of $k$ in the male being 0.93 and in the female 0.95.

Hence there seems to be a correlation between the marked heterogony in the cheliped on the growth rate of neighbouring appendages. In those immediately posterior to the cheliped the growth rate is increased and in those anterior decreased.

**REFERENCES.**


**DESCRIPTION OF PLATE II.**

**Fig. 1.** Chelipeds (2nd pereiopod) of a male and female of about the same carapace length. (Reduced by about §.)

**Fig. 2.** From left to right, ♂ and ♀; 5th, 4th, 3rd and 1st pereiopods from individuals of the same carapace length. Note that the 3rd, 4th and 5th ♀ pereiopods are shorter than those in the ♂, whereas the 1st is slightly longer than that of the ♂. (Reduced by about §.)
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(pp. 165-174).