Contributions to the Study of Relative Growth in *Gammarus chevreuxi*.

By

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With 18 Figures in the Text.

Introduction.

The following two sections represent two preliminary communications to the study of relative growth in a small Crustacean admirably adapted for use as a laboratory animal in all studies involving growth and development.

It is not proposed to discuss the significance of the results in detail at the present moment. For this, more data will be necessary. But one or two points may be mentioned.

One of the results of work on relative growth has been to show (Huxley, 1927) that in Crustacean appendages, showing disharmonic (heterogonic) growth, there exist *growth-centres* where the growth-rate is at a maximum. In the appendages so far studied the growth centre appears to be not at but close to the distal end (propodite). A distal growth-centre for heterogonic organs also exists in the antlers of deer, in the legs of mammals (unpublished work of J. Hammond, to whom we would like to express our thanks for allowing us to mention the fact), and in the abdomen of female Inachus (unpublished observations of Miss M. E. Shaw).

The studies of the present paper do not throw further light on this particular aspect of the problem. They do, however, throw some light upon the problem of growth-centres in the main trunk-region of the animal. For instance, the facts concerning the growth of the fifth free segment (see later) indicate that in females there is here a growth-centre (presumably part of a larger region of rapid growth) associated with the development of ovary and brood-pouches in this segment. In the two sexes the whole relative rate of growth of trunk (including head) and appendages is also different, the partition of growth-potential being more in favour of the appendages in the male, of the trunk in the female.

Another general fact appears to be that excess growth of appendages as a secondary sexual male character is predominantly in *length*, even in parts which (like gnathopod propodite) are broad and massive. All appendages (as would be expected, since they are outgrowths from the body) grow more in length than in breadth in both sexes ; and apparently it is natural that this tendency should be still the underlying one in the sexual heterogonic growth of secondary sexual characters.

Finally, when a part shows marked enlargement in one sex, it appears often to show relative decrease in the opposite sex, instead of remaining constant (isogonic) in its growth as might perhaps be expected. This appears to be the case with the ♂ fifth free segment, the ♀ uropod, and the ♀ gnathopods. Even in details, the growth-processes appear often to be reversed in the two sexes when the organ is an enlarged sex character in one sex (see under gnathopods).

It is hoped that by the accumulation of studies such as these a detailed knowledge of the growth-centres in the body, or, we may say, the partition of growth-potential in different species, may be gradually acquired. If so, it would pave the way for interesting biochemical studies in growth.

PART I.

By

B. W. Kunkel.

(*A*) Foreword, Material, and Methods.

The work done recently on heredity in the brackish-water Gammarus, *G. chevreuxi*, especially that which indicates that certain eye mutations are in the nature of retardations in the development of normal characters (Ford & Huxley, 1927), has made the study of the growth-changes of this animal seem highly desirable. On Professor Huxley's suggestion, therefore, while working in his laboratory at King's College, London, in 1925, I undertook to study the changes in bodily form of this species under normal circumstances. It gives me great pleasure at this time to express my appreciation of the many courtesies and suggestions of Professor Huxley in connection with this study.

The material used in the study consisted of some two hundred wild specimens from Plymouth, England, where the species was first found, together with about fifty which had been reared in the laboratory at Oxford. These latter were used to fill out certain gaps in the material procured at Plymouth. In order to measure the appendages it was found necessary to dissect them off carefully and mount them in glycerine to render them transparent. The gnathopods especially showed so strong a tendency to be bent medially that without dissection they were greatly foreshortened and so incapable of accurate measurement. It was found most convenient to project the magnified image of the appendages on a glass plate over which co-ordinate paper ruled to millimetres could be moved about freely. The paper was sufficiently thin to allow the image to show through readily. At the magnification used, namely, 61 diameters, it was impossible to read the measurements closer than one millimetre apparent—i.e. about 17 μ absolute.

The following measurements were made: breadth and length of the second joint of the peduncle of the first antenna; breadth and length of the propodite of the first and the second gnathopods and of the first pereiopod. In addition to these measurements, the joints of the flagellum of the first antenna were counted. This last-named character was exceedingly irregular, probably because of the frequency with which the flagellum is injured and joints of the flagellum autotomized. For the sake of brevity, the second peduncular joint of the first antenna will be referred to simply as "the antenna" and the propodites of the gnathopods and pereiopod will be referred to simply as "the gnathopods" and "pereiopods" respectively.

It is fully realized that the method of studying growth of an organism by measuring a population, as has been done in the present study, is open to certain objections from which the study of successive ecdyses of the same individual is free. Mrs. Sexton's (1924) paper, however, shows that Gammarus can be examined in this way only with the greatest difficulty, because of the tendency of the animal to eat its own skin very shortly after shedding it.

The propodite of the first pereiopod was selected as the index of the size of the individual throughout because of its uniformity in the two sexes and because of the fact that in the course of growth the pereion does not suffer the conspicuous changes which the cephalon does.

The growth in total size of the female Gammarus ceases much earlier than that of the male. This has been observed already in *G. chevreuxi* in the paper referred to above by Mrs. Sexton, and in other species by a number of observers. After sexual maturity is reached, the female's growth becomes very slow, while that of the male continues high. I did not meet with any male as large as Mrs. Sexton reported, but even so, in my largest male the pereiopod attained a length 164% of that of the largest female in my collection.

In general, the sexual differences could not be determined at as early a stage as Mrs. Sexton has shown in the careful drawings of successive moults of the same individual. The characteristic curved hairs of the second antenna of the male do not appear generally as early as she has figured them. The smallest individuals whose sex I could be sure of had a pereiopod length when projected of 11, and the flagellum of the first antenna in one case had only ten segments, which would correspond with Mrs. Sexton's fourth stage ; but generally when the sex could be determined in so small an animal, there were from fourteen to sixteen flagellar segments, which would indicate a fifth or sixth stage.

(*B*) Results :—1st Antenna ; Gnathopods ; 1st Pereiopod.

The changes in the relations of certain dimensions with age can be expressed in several ways. One of the simplest is by plotting the ratio of

TABLE I.

Ratios to Pereiopod Length, expressed as %.

Pereio-pod length mm.	Ant. length. no.	sex ? %	no.	sex ♀ %	no.	sex ♂ %	Gn. 1 length. sex ? %	sex ♀ %	sex ♂ %	Gn. 2 length. sex ? %	sex ♀ %	sex ♂ %
·08	6	83·3					80			96·7		
·098	11	72·8					84			84·5		
·11	6	76					85·2			85·2		
·13	6	85·7					91·5			91·5		
·15	6	77·8					83·5			83·5		
·16	10	84					90			90		
·18	11	84·2	3	82	2	91	89·7	91	103	89·7	95·5	106
·197	4	87·5	1	83	3	86	91·7	100	102·7		100	91·7
·21			1	77	4	86·5		92	102		100	102
·23			1	100	7	90			97			104·4
·25			5	90·6	2	90		100	100		101·2	106·5
·26			2	94	7	89·9		100	102·3		100	102
·28			5	87·2	2	91		102·4	103		104·5	104·8
·29			9	95·7	5	95·6		99·8	122·4		103·6	117·5
·31			6	89·3	3	96·7		98·3	119·7		95·7	128
·33			10	90	7	97·9		100·2	116·4		100	127·9
·34			2	88	1	86		95	124		93	138
·36			3	91	4	101·2		95·3	136·2		104·7	150·5
·38			2	95·5	6	105·5		98	138·3		102·5	150·8
·39			1	96	5	101·6		100	142·2		104	155·8
·41			2	84	8	106·5		92	150·2		94	166·5
·43					7	107·9			153·3			163·3
·44					9	109·8			149·1			162·4
·46			1	64	7	108·1		75	146·9		75	162·4
·48					4	107·5			148·2			166·7
·49					5	105·6			143·8			158·6
·51					2	108			148			162
·525					3	103			139·7			151·5
·54					1	115			145			164
·56					8	107·5			144·1			158·2
·57					1	108			146			157
·59					2	108·5			140			154·5
·61					2	104			135			170
·62					2	116			145			166
·64					2	106			136			155
·66					2	110			146·3			149
·67					1	112			146			151

the part in question to the standard against the standard itself. The ratios of length of antenna and of first and second gnathopods to length of pereiopod are shown in Table I, and have been plotted against pereiopod length in Figs. 1 and 2. In spite of the size of the groups upon which these graphs are constructed, they exhibit certain irregularities whose significance has not yet been interpreted. It is obvious that in the early stages, before sexual differentiation is apparent, there is an elongation

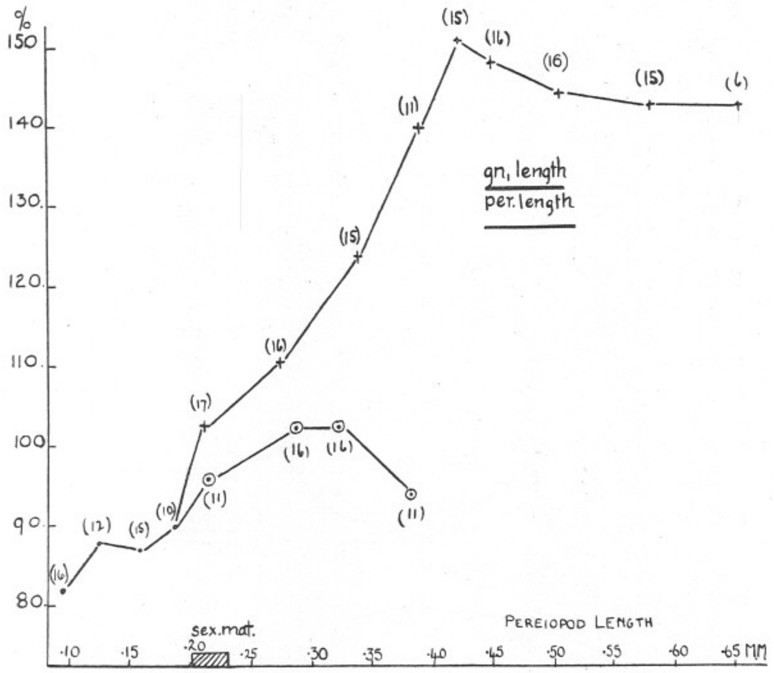


FIG. 1. Ratio of the length of the first gnathopod to the pereiopod expressed as % plotted against the pereiopod length. The figures in parentheses indicate the number of individuals in each class. The young in which the sex was indeterminate are indicated in all the diagrams by a ●, the males by a +, and the females by a ⊙.

of the antenna and the two gnathopods which is more rapid than that of the pereiopod ; furthermore, that of the antenna is more uniform than either of the gnathopods, in which appendages the sexual differences are more marked. In the female, from the time sexual differences are evident, there is practically no further relative elongation of the antenna, as is indicated by the nearly horizontal position of this portion of the curve. The antenna of the male, on the other hand, increases more rapidly in length relatively to the pereiopod, until the latter attains a length of about 0·44 μ, which is beyond the maximum size attained in the female.

From this time on, although actual growth does not cease, the male antenna simply keeps pace with the pereiopod, maintaining a proportion of 106 to 109% of the latter.

The changes in the length of the first gnathopod with reference to the pereiopod are similar, but rather more irregular. During adolescence there is a gradual increase, as in the case of the antenna. While the latter

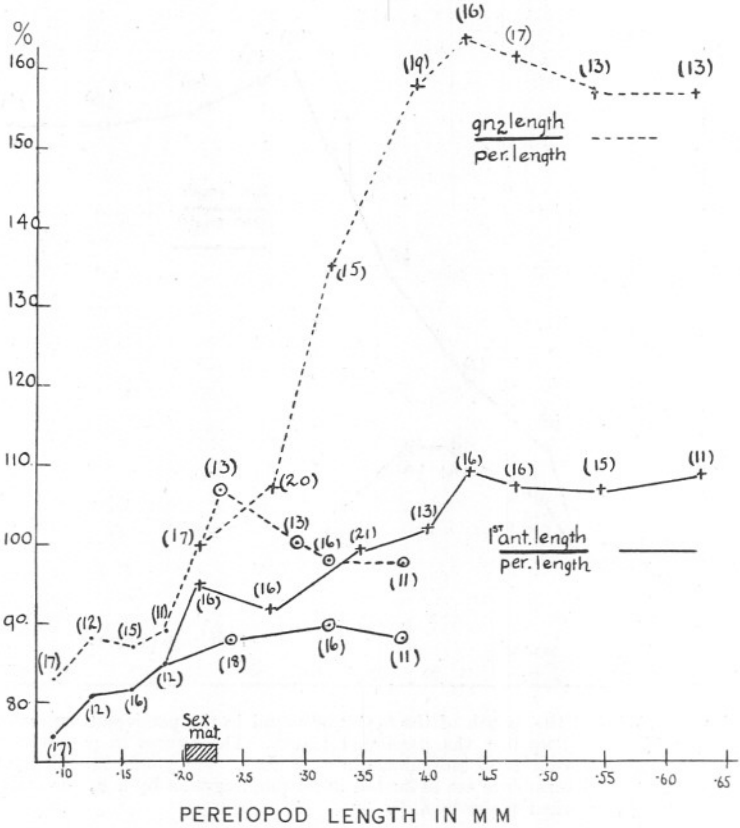


FIG. 2. Ratios of the length of the antenna and of the second gnathopod to the pereiopod expressed as % plotted against the pereiopod length. The graph of the antenna is represented by a solid line, that of the second gnathopod by a broken line.

increases from 75% to 85%, the elongation of the first gnathopod is from 83% to 90%. The gnathopod of the mature female elongates for a short time more rapidly than the pereiopod, then for a very brief period at the same rate, and then when older it lags markedly behind the pereiopod. The changes in the length of the first gnathopod of the male are quite different from those of the female. From the size at which sexual differences are first discern'ble, up to about the size finally attained by the female, elongation is very rapid. In very large males, however, the growth falls somewhat behind that of the pereiopod, until the gnathopod proportional length finally becomes constant at 143% of the pereiopod. In comparing the growth changes of the male gnathopods and the antenna, it would seem as if the former gained a certain momentum of growth and then lagged behind the pereiopod, while the antenna during the period in which the gnathopods are growing so rapidly, grows at a lower rate but maintains its relative size, instead of falling behind like the more markedly heterogonic appendages when comparative old age has been reached.

The changes in length of the second gnathopod with reference to that of the pereiopod are more marked than those of the first gnathopod, and of the same character, but a little less regular. During immaturity, before the sexes can be distinguished, there is a slight irregularity similar to that of the first gnathopod, but more marked. In general, the second gnathopod-length shows a more marked relative increase during this period than does the first, the relative growth-rate being highest just before maturity.

The second gnathopod of the female shows at first a very rapid relative rate of elongation, and at about ·225 mm. pereiopod-length actually surpasses that of the male. This is followed, however, by a longer period, during which the relative length of the gnathopod grows less, until finally the ratio becomes constant at about 97%. The second gnathopod of the male exhibits essentially the same changes in elongation that the first gnathopod does. There is a very rapid rising of the curve from 100% to a maximum of 164% during the time between the attainment of sexual maturity and the time that the body-size of the largest female is reached. In the largest males there is a slight relative retardation of the gnathopod and then a constant ratio of 157% is maintained. The second gnathopod is thus relatively longer than the first in large males, but smaller in small males. *Per contra*, the female second gnathopod is relatively longer than the first in small animals, but then decreases more rapidly, though not to a finally lower level.

A better index of growth than the increase in a single dimension of a flattened structure is the increase in its area. Accordingly the product of length and breadth has been calculated for the joints measured. This will not be far from being proportional to the actual area of the surface; and for brevity's sake is hereafter referred to as "the area" of the joint in question. The areas of the projection of the antenna and of the gnathopods, thus found, were then plotted against the area of the pereiopod, on a double logarithmic graph. Table II gives the data upon which graphs in Figs. 3, 4, and 5 have been constructed. The graph illustrating the growth of the antenna shows that the antenna area increases at a rate only slightly greater than that of the pereiopod area. In the simple heterogony formula, $y = bx^k$, k expresses the ratio of the two growth-rates considered, and is here between 1·1 and 1·2. The general tendency is for the relative growth-rate to be higher at first (k=1·2 to 1·3) during adolescence and early maturity, and then to decrease, earlier in females than in males, to a rate actually below that of the pereiopod area (k=about 0·8 and 0·9 in females and males respectively). In other words, the breadth of the antenna cannot be increasing relatively as fast as that of the pereiopod. This is brought out in Fig. 4. The slight irregularities

TABLE II.

Ratios of Breadth to Length, expressed in %.

	Per.						Ant.			Gn. 1.			Gn. 2.		
Per length mm.	No.	Sex ind. %	No.	♀ %	No.	♂ %	Sex ind. %	♀ %	♂ %	Sex ? %	♀ %	♂ %	Sex ind. %	♀ %	♂ %
·08	6	23·3					60·3			80			63·3		
·098	11	33					65·4			62			71·5		
·11	6	29					59·5			75·3			71·7		
·13	6	25					55·8			66			69		
·15	6	23·8					54			63·2			64·3		
·16	10	21					52·7			69·1			61·2		
·18	7	20·5	4	22·5	3	21	51·7	50·2	48·3	68·1	65	63	66·7	59·5	63·3
·197	4	21	1	25	3	25	48·2	50	52·5	70	58	58·7	66·7	58	57
·21			1	23	4	23		50	51·5		67	64·2		54	60·2
·23					7	23			43			65·4			62·4
·25			5	24·2	2	23·5		43	48		55·2	66·5		62·2	59·5
·26			2	19	7	22·4		43·5	48·1		62·5	64·2		59·5	60·3
·28			5	22·8	3	20		46·8	39·7		62·6	60·7		58	55
·29			9	20·9	5	21·2		38·8	43·8		61·8	61·7		58·8	62
·31			5	19	3	19·7		39·6	41·2		63·9	62		62·6	62·7
·33			10	20·5	7	20		40·2	39·7		65	61·9		59·7	58·7
·34			2	22·5	1	19		38	44		61·5	54		61·5	57
·36			3	21·3	4	21·7		43·3	36		65·3	58·2		64	60
·38			2	19·5	6	20·3		38·5	35·3		64·5	54		55·5	56·7
·39			1	21	5	20·2		39	34·6		58	55		56	56·6
·41			2	20	8	19		38	33·9		63	52·4		62	56·1
·43					7	18·4			35·1			50			57
·44					9	19·3			32·9			48·9			55·2
·46			1	18	7	18·4		44	32·6		62	49·9		62	57·3
·48					4	19			34·2			49·5			56·2
·49					5	19·4			33·4			48·6			55·4
·51					2	19			40			47			54·5
·525					4	19			32			51·7			59·2
·54					1	18			29			46			54
·56					8	20·2			33			49·5			58·4
·57					1	20			34			51			60
·59					2	18			32			44·5			54·5
·61					2	19			29·9			47			58·5
·62					2	18			29·5			48			57·5
·64					2	19			33			51			57
·66					3	19·3			29			50·7			57·7
·67					1	17			26			47			66

are essentially the same as those exhibited in the growth in length with respect to the pereiopod length.

The increase in the area of the first gnathopod relative to that of the pereiopod is shown in Fig. 4. It is comparable to what had been found in a number of secondary sexual characters, as has recently been pointed out by Huxley (1926). During adolescence, before the sex can be determined,

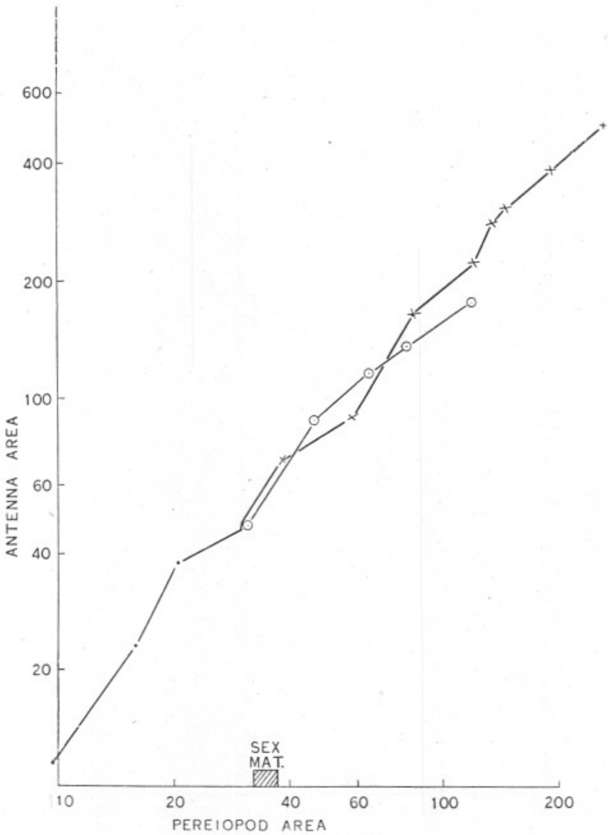


Fig. 3. The area of the antenna is plotted against the area of the pereiopod, on a double logarithmic grid.

the gnathopod area increases more rapidly than that of the pereiopod, so that the slope of the graph is greater than 45 degrees ; k, as read from the tangent of the angle made by the graph with the x axis, is nearly 1·4. The rate is on the whole greater at first, less (k=about 1·2) later. In the female, this decrease is gradually accentuated, k being at first close to 1·0, dropping later to 0·8. On the other hand, in the male the gnathopod increases much more rapidly from soon after the moment of sexual differentiation up to the time that the maximum female size is reached. During this period k is almost equal to 2·0. At the close of this period, the increase of the area of the gnathopod slows down to a little below that of the pereiopod.

The second gnathopod area (not figured) increases with somewhat greater uniformity than that of the first gnathopod, as well as at a greater

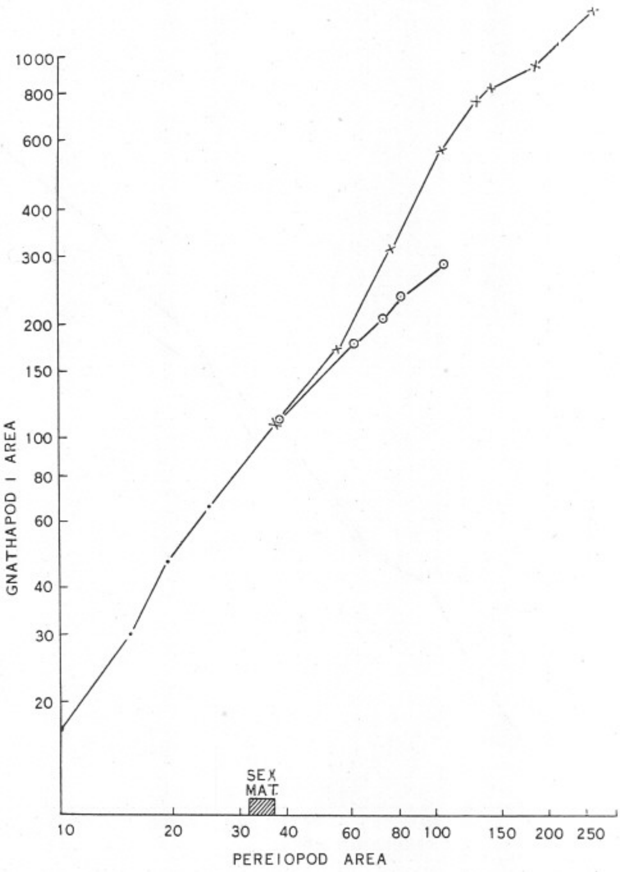


FIG. 4. The area of the first gnathopod is plotted against the area of the pereiopod, on a double logarithmic grid.

rate. During adolescence the gnathopod increases in area faster than the pereiopod. Throughout the period of sexual differentiation the female exhibits great regularity, the graph being a straight line and k being a little over 1·1. This is peculiar in view of the irregularities in length percentages ; presumably the area is much more constant than the length or breadth taken singly. This is corroborated by Fig. 5. The second gnathopod of the mature male grows very rapidly in respect to the pereiopod. Up to approximately the time when the maximum size of the female is reached, k averages a little over 2·0, with a maximum value of nearly 2·5. In very old males, however, the gnathopod and pereiopod areas increase at about the same rate.

Changes in the form of the appendages with growth are shown in Fig. 5, which is constructed from the data shown in Table II. These changes in form are indicated by the ratio of the breadth to the length of the appendages in question. These ratios in the diagram have been plotted

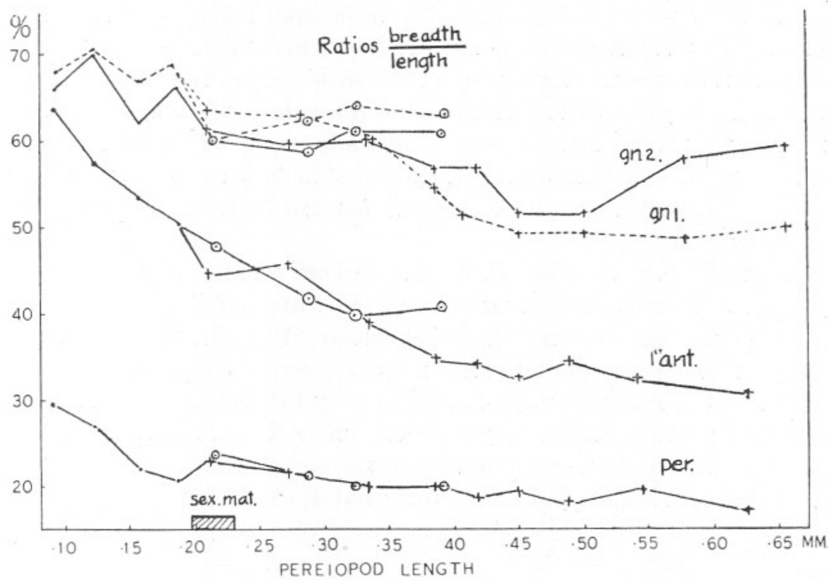


FIG. 5. The ratios of the breadth to the length, expressed as a %, are plotted against the length of the pereiopod. The graphs of the pereiopod, antenna, and second gnathopod are shown with solid lines, that of the first gnathopod by a broken line.

against mean pereiopod length. In the very early stages the pereiopod becomes rapidly more slender, but before sexual maturity is reached the form becomes more established and from that time on in both sexes the increase in slenderness is slighter (somewhat over 20% decrease in the relative breadth). The total decrease of the relative breadth is under 40% of its original value. The antenna of the male shows in general an increase in slenderness, more marked at first, but evident in even the oldest males. The total decrease of relative breadth is over 50% of its original value, and the decrease after maturity is over 30% of its value at maturity. In females there is a similar increase in slenderness until they become fairly old, when the ratio becomes constant. The male ratio never becomes constant, but there is a definite slowing up of the decrease in this sex, as in the females.

The changes in the form of the gnathopods are less regular than in the antenna or the pereiopod. During immaturity there is an increase of slenderness, but with marked oscillations. This cycle is repeated before the period of sexual differentiation is reached, but the general tendency is definitely toward an increase of slenderness. In the female, both gnathopods during the period of sexual maturity tend to increase in relative breadth, the first more so than the second. In mature males, there is first a period of slight, and then one of rapid increase of slenderness, followed by constancy of ratio in the first, but marked increase of relative breadth in the second gnathopod of large males. It is interesting to note that in females the second gnathopod is throughout the slenderer, while in males the reverse is the case except for a short period after the attainment of maturity. The second gnathopod of males then grows relatively more rapidly both in length and breadth than any of the other appendages measured.

The maximum decrease (between extreme points) of the relative breadth of the male first gnathopod is slightly over 30% of its maximum value, of the male second gnathopod under 27%. In the female the corresponding figures are 15% and under 17% respectively. The decrease from initial to final values are as follows :—♂ first, 20% ; ♂ second, just over 10% ; ♀ first, under 8% ; ♀ second, under 9%. It is interesting to note that in spite of the massiveness of the second gnathopod propodite of old males, it is always slenderer than that of old females.

PART II.

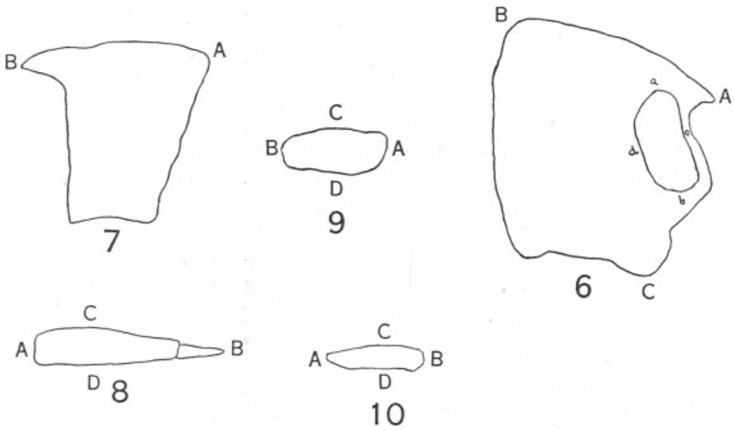
By

J. A. Robertson.

(*A*) Foreword and Methods.

It was suggested to me by Professor J. S. Huxley that some investigation of the comparative rates of growth of various appendages of *Gammarus chevreuxi* would be of interest, especially in view of the knowledge recently acquired of its genetic constitution. Since Professor B. W. Kunkel had already investigated the growth of the first antenna, first and second gnathopods, and the first pereiopod in this species (see Part I of this paper), it was decided that further measurements of head, eye, second antenna, uropod, and fifth body-segment would render the account of the growth-phenomena more comprehensive. I accordingly undertook the latter measurements, together with those of the first pereiopod as a standard whereby the two sets of results might be compared; the only other measurement common to the two investigations is the record of the number of flagellar joints in the first antenna.

The measurements were made by means of a screw-micrometer-eyepiece, and the combination of lenses was such that one division of the screw-vernier equalled ·00213 mm. The readings for each animal



FIGS. 6–9. Camera lucida drawings of parts of one animal.

FIG. 6. *Head.*
AB=Head length.
AC=Head depth.
ab=Eye length.
cd=Eye breadth.

FIG. 7. *Fifth Body-segment.*
AB=Fifth segment length.

FIG. 8. *Uropod, last two joints.*
AB=Uropod length.
CD=Uropod breadth.

FIG. 9. *Second antenna, first large joint.*
AB=Second antenna length.
CD=Second antenna breadth.

FIG. 10. Freehand drawing of a first pereiopod propodite (approximately same scale).
AB=Pereiopod length. CD=Pereiopod breadth.

separately, and also in the tables of sums and means (or averages), were expressed in terms of unit divisions of this screw-vernier. I measured 121 animals.

The actual measurements taken were the length and depth of the head (Fig. 6), the length of the fifth body segment (Fig. 7), the lengths and breadths of the last two joints of the uropod (Fig. 8), of the first large joint of the second antenna (Fig. 9), and of the propodite of the first pereiopod (Fig. 10). The length and width of the eye was taken in some cases, but since the stock was of the genetic constitution known as "colourless," in which the ommatidia are unpigmented and frequently scattered, these measurements were not sufficiently numerous or accurate to warrant inclusion in the results. The number of joints in the flagellum

TABLE III.

The Mean Absolute Values for the Various Measurements Taken, Arranged in Classes According to First Pereiopod Propodite Length.

Average Measurements in Millimetres.

	Group by Pereiopod length in Micrometer divisions.	No. of Individuals in group.	Head L	Head Depth (Anterior border).	2nd Antenna 1st large joint L	2nd Antenna 1st large joint B	1st Antenna No. of joints in flagellum.	Uropod L (last 2 segments).	Uropod B (penult. segment).	1st Pereiopod propodite L	1st Pereiopod propodite B	5th Body segment L
Indeterminates. Taken together.	34–59	5	·285	·238	·098	·049	6·80	·193	·040	·092	·026	·133
	72–85	7	·462	·412	·211	·084	14·1	·330	·075	·167	·043	·324
	(34–59 and 72–85 together)	12	·388	·340	·164	·070		·272	·060	·136	·036	·243
	86–102	7	·511	·448	·232	·086	15·1	·422	·080	·200	·044	·360
♂, ♀ and indeterminates	103–122	20	·574	·509	·285	·106	17·3	·492	·101	·243	·052	·435
	123–146	26	·692	·595	·338	·117	21·1	·631	·122	·288	·057	·531
Females.	(72–85 omitted from graphs)	[1]	[·679]	[·574]	[·311]	[·113]	[20·0]	[·601]	[·102]	[·179]	[·055]	[·575]
	147–175	7	·784	·682	·379	·129	21·6	·709	·136	·336	·064	·653
	176–210	5	·955	·805	·464	·150	28·0	·794	·152	·426	·084	·876
Males.	147–175	16	·790	·679	·477	·151	25·2	·860	·149	·345	·072	·586
	176–210	6	·859	·730	·533	·163	27·8	1·02	·162	·405	·081	·634
	211–252	10	1·02	·937	·683	·199	29·9	1·34	·194	·494	·100	·788
	253–362	11	1·19	1·02	·814	·234	33·0	1·53	·221	·601	·111	1·04

of the first antenna was also recorded, but in several cases the flagellum was broken. The lengths of the longest hairs on the first large joint of the second antenna, and on the uropod, were also taken, but discarded owing to the prevalence of curling, which rendered accurate measurement impossible.

The animals were arranged in groups according to the length of the propodite of the first pereiopod, the two sexes and indeterminate (indistinguishable) animals being separated. It is impossible to take age as the criterion for grouping, since temperature, nutrition, and genetic factors all have a profound effect upon the rate of growth, and careful standardisation of these conditions was not feasible with the means at my disposal at the beginning of this investigation. Since, however, *relative* growth was being investigated, and relative appendage-size seems to be almost or wholly a function not of age but of total size, this does not matter. Each group had a pereiopod length 20% greater than the previous one. It was found necessary, in order to compare significant numbers of animals, to combine some of these groups. Tables giving the sums, and means (averages) of these groups (in terms of unit divisions of the screw-vernier) for each measured character were compiled, and from them a table giving the ratios of the various parts, expressed as percentages of the "first pereiopod length" (propodite) of the group taken as standard. A table giving the ratios of various characters to each other was also drawn up. Finally, a table of means (averages) reduced to absolute measurements in millimetres was obtained. (Table III.) Since the numbers of sexually distinguishable animals in some of the earlier groups were small in comparison to the number of indeterminates, the last two groups of indeterminates were recombined with the corresponding sexed individuals and indiscriminately called indeterminates. Thus the last two groups of indeterminates in the graphs (with the exception of Fig. 13) include some distinguishable males and females. The single female falling into the first group of its sex was so atypical in its proportions that it was omitted from the graphs.

From the data provided by the tables referred to, three types of graphs were constructed; firstly, average-graphs (Figs. 11–13) in which the average measurement under consideration was plotted as ordinate against the average pereiopod propodite (or other) measurement of the group in the abscissæ. These graphs gave the *absolute size* attained by the organs of the three classes (males, females, and indeterminates) at the same stages of pereiopod growth. Secondly, a graph showing the proportions of the lengths of various organs to the pereiopod length (expressed as percentages of the latter) was drawn; from this the growth-changes in the *relative proportions* of the various organs can be most readily observed. The percentages were plotted in the ordinates and the pereiopod-lengths of the groups in the abscissæ (Fig. 14); had the curve for the pereiopod propodite length been drawn it would, of course, have been a straight line of 100%. Finally, a series of log-log graphs (Figs. 15–18) were constructed, in which the logarithms of the size-averages of

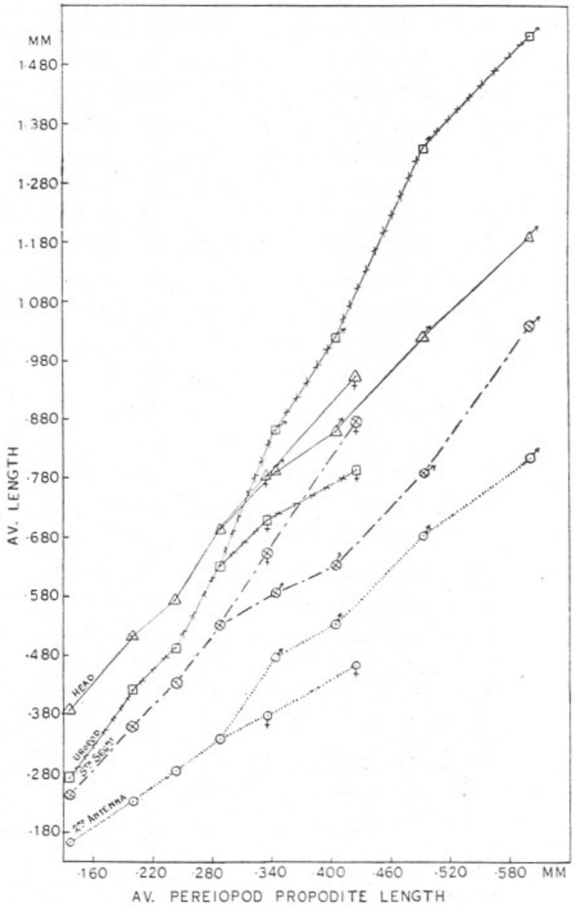


FIG. 11. The mean absolute lengths of the head, uropod (last two joints), fifth body segment, and second antenna (first large joint), plotted against mean absolute length of the first pereiopod propodite.

various organs (in the ordinates) were plotted against the logarithm of some other average measurement (in the abscissæ) as standard. In this way the relative *rates of growth* of the various organs in their different dimensions could be compared (see below).

From these three types of graphs, showing respectively the actual progress of growth and absolute size attained, the relative proportions, and the comparative rates of growth found in the various organs examined, some understanding of the quantitative relations of the processes at work in the different parts may be extracted.

The formula for simple heterogony put forward by Professor J. S. Huxley ('27); viz. $y=bx^k$, where y=organ measurement, x=standard

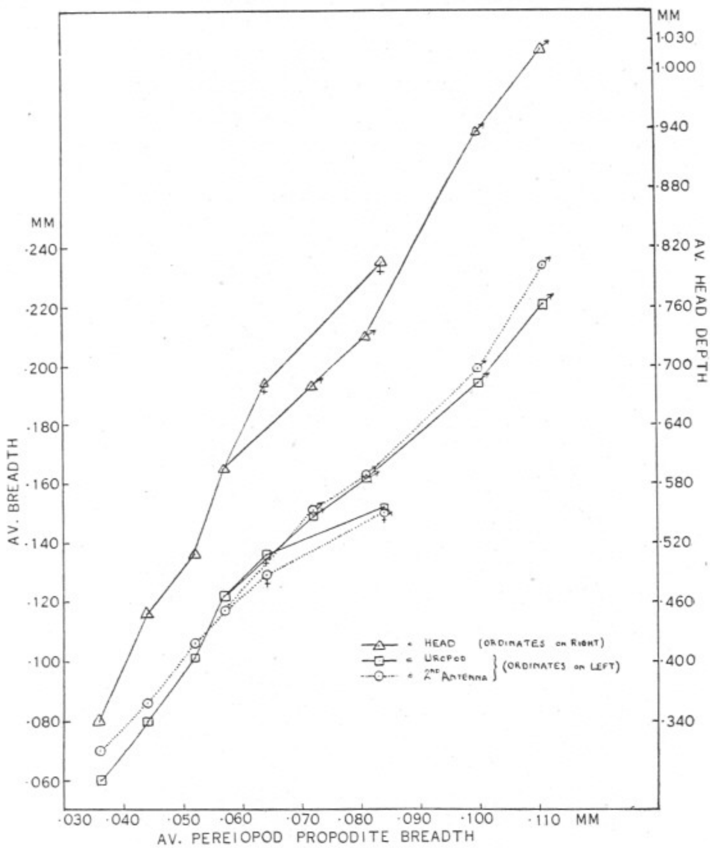


FIG. 12. The mean absolute depth of the head, and breadths of the uropod (last two joints) and second antenna (first large joint), plotted against mean absolute breadth of the first pereiopod propodite.

measurement, and b and k are constants, may be applied in this paper. I have calculated the values of k in Table III, these being equal to the tangents of the angles made by the log-log graphs with the abscissæ; k expresses the ratio of the two growth-rates concerned. Thus, where $k=1$ the compared rates of growth are equal; where $k > 1$ the organ in the ordinates is growing faster (positive heterogony), and when $K < 1$

the standard in the abscissæ has the higher relative growth-rate (negative heterogony). The values of k given are approximate; they do not pretend to accuracy beyond the first decimal place.

Such statistical data as do not actually appear in this paper are deposited for reference at the British Museum.

(*B*) Results and Description of Graphs.

Appendages.

(*a*) *First Antenna.* The number of joints in the flagellum is smaller in females than in males of the same pereiopod-size group.

(*b*) *Second Antenna, first large joint.* (i) It can be seen from Figs. 11

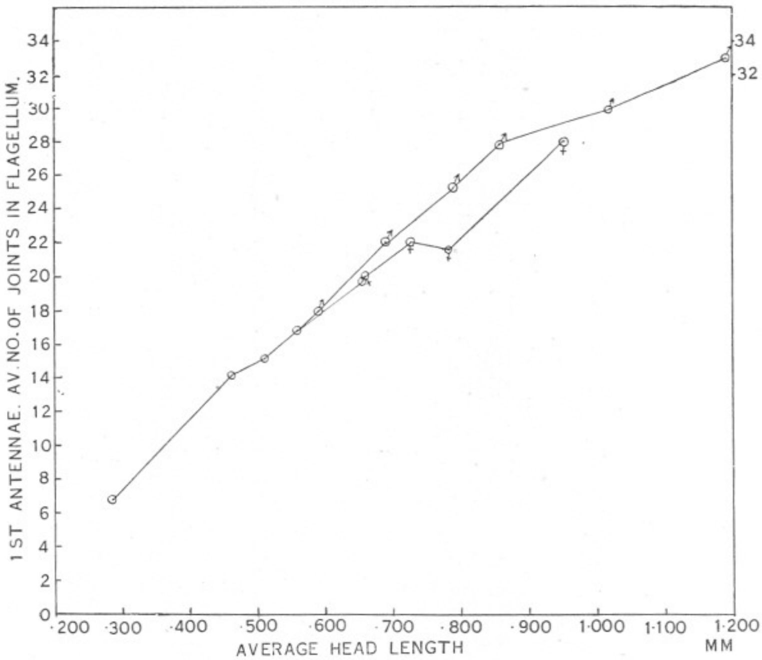


Fig. 13. The mean number of joints in the flagellum of the first antenna, plotted against mean absolute head-length.

and 12 that the actual size attained both in length and breadth is always greater in males than in females of corresponding groups.

(ii) From Fig. 14 it may be seen that the proportions remain more or less unaltered in the indeterminates and females, though in the latter a slight tendency to relative decrease is observable, while in the males a relative enlargement occurs early and remains fairly constant.

(iii) The relative rate of growth *in length* in indeterminates and females is slightly less than that of the fifth segment, being especially noticeable in the case of the females. (Fig. 15 : k=·91 and ·62 respectively.) The relative rate is very nearly the same as that of the pereiopod in the indeterminate (k=·94), but lower in the females (k=·72). In males the relative rate is very markedly greater than that of fifth segment at first (Fig. 15 : k=3·7), but tends to equal it later, while its rate is about twice as high as that of the pereiopod (k=2·0).

The relative rate of growth *in breadth* (Fig. 18) is somewhat higher in indeterminates than that of the pereiopod, decidedly lower in the females, and somewhat higher again in males (k=1·1, ·81, 1·1 respectively).

(iv) In males, females, and indeterminates the rate of growth in length is somewhat greater than that in breadth (Fig. 17 : k=1·35) ; i.e. the joint in question is becoming longer and relatively narrower with growth.

(*c*) *Uropod, last two joints.* (i) From Fig. 11 it can be seen that the actual length attained in corresponding groups is very much greater in males than in females, but in breadth (Fig. 12) the males are only slightly larger than females. This difference in length between the sexes is much more marked than the divergence found in the second antenna, but the sex-differences in breadth are very similar in the two appendages and their curves follow each other remarkably closely.

(ii) The relative (length) proportions of the indeterminates (Fig. 14) show a variable tendency to enlargement ; this is continued as a definite and considerable increase in the males, which is progressive, until a slight decrease occurs in the last group. The females show a decided decrease in proportion relative to the pereiopod propodite length.

(iii) The relative rate of growth *in length* (Figs. 15 and 16) in indeterminates about equals that of the fifth segment (k=1·06) and is slightly greater than that of the pereiopod (k=1·12). The relative rate *in breadth* is markedly higher than that of the pereiopod (k=1·5 to 1·6 ; Fig. 18). The length-rate in females is decidedly lower than that in either fifth segment (k=·63) or pereiopod (k=·74) ; the breadth-rate is also markedly lower than that of the pereiopod (k at first=1·05, but much lower later ; Fig. 13). In males the relative rate in length is very much greater than that of the fifth segment at first (k=2·8), but tends to equal the rate of the females later (k<·63), resembling the second antenna in this peculiarity ; the length-rate is considerably greater than that of the pereiopod (k=1·4), and though it falls off in the last groups this does not occur to so great an extent as it does relative to the fifth segment. Fig. 18 shows that the *breadth* growth-rate in males is somewhat lower than that of the pereiopod (k=·82) ; it should be noted that the males and females have lower relative rates than have the indeterminates in this respect (cf. Table IV).

(iv) Fig. 17 shows that in indeterminates and females the rate of growth in length is slightly greater than that in breadth (k=1·1 to 1·2), whereas, in males, the length-rate is markedly higher (k=1·6). Thus, the male uropod tends to become relatively longer and thinner than that of an indeterminate or female.

(*d*) *First Pereiopod, propodite.* (i) In Fig. 15 it can be seen that the

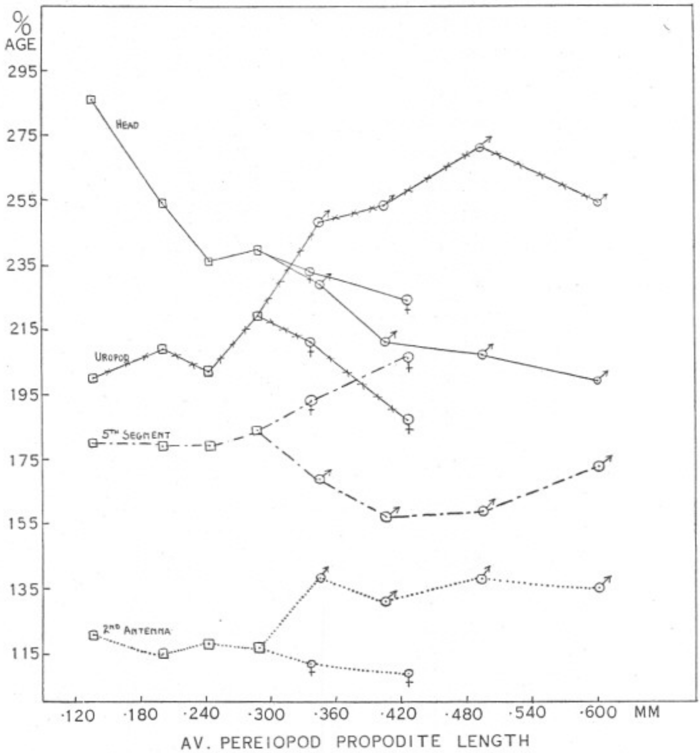


FIG. 14. Ratios of lengths as percentages of pereiopod propodite lengths (standard).

□ Indeterminates. ♂ Males. ♀ Females.

rate of growth in length is approximately equal to that of the fifth segment in the indeterminates (k=1·0), in the females it is slightly lower (k=·77), but in the males is considerably higher at first (k=1·8), approaching the female rate later. In this respect the male pereiopod resembles the male second antenna and uropod, but in this case the sex difference in comparative growth-rates is not so pronounced.

(ii) Fig. 17 shows that the rate of growth in length is slightly higher, for all classes, than that in breadth (k=1·2 for ♂, ♀, Indets.). This positive heterogony in length is less marked than in the case of the second antenna.

Body Segments.

(*e*) *Head.* (i) The actual size attained both in length and depth in corresponding groups is slightly greater in females than in males (Figs. 11 and 12). This is the reverse of the relationship in the appendages.

(ii) From Fig. 14 it can be seen that the proportionate size of the head decreases rapidly at first among the indeterminates, then becomes more stable, and finally the decrement is continued more gently in both males and females. In the former the decrease is greater than in the latter, presumably owing to the faster growth of the male appendages, the pereiopod included.

(iii) The relative *length* growth-rate is markedly less, in indeterminates

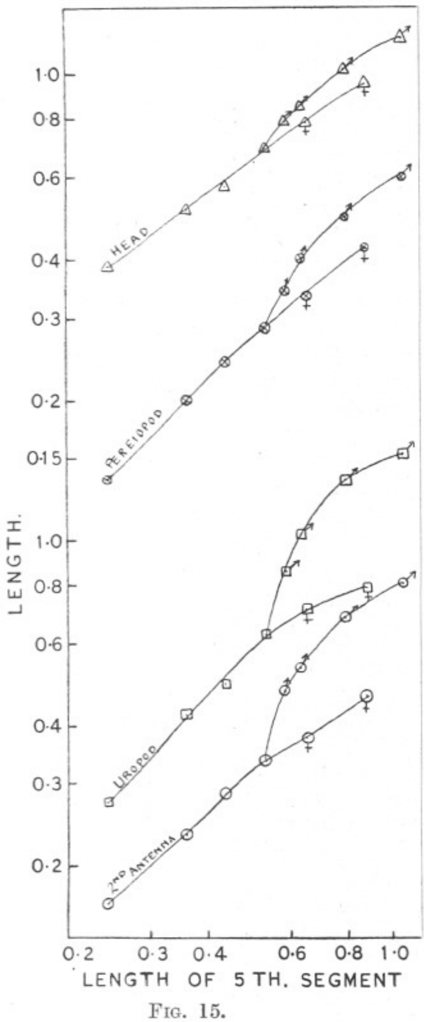


FIG. 15.

FIG. 15. The mean lengths of head, first pereiopod propodite, uropod (last two joints), and second antenna (first large joint), plotted against the length of the fifth body segment, on a double logarithmic grid.

FIG. 16. The mean lengths of uropod (last two joints), and fifth body segment, plotted against first pereiopod propodite length, on a double logarithmic grid.

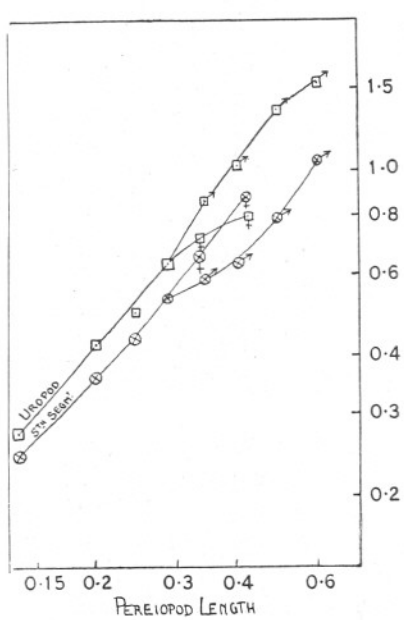


FIG. 16.

and females, than that of the fifth segment (Fig. 15 : k=·71 in both classes), and also of the pereiopod (k indet.=·74, k ♀=·82). The relative *breadth* growth-rate is somewhat higher in indeterminates (k=1·2), and though higher at first in the females (k=1·2), later becomes lower than the breadth-rate of the pereiopod (Fig. 18).

In males the *length*-rate is somewhat higher than that of the fifth segment at first (k=1·3), but approximates to the female rate later ; on the

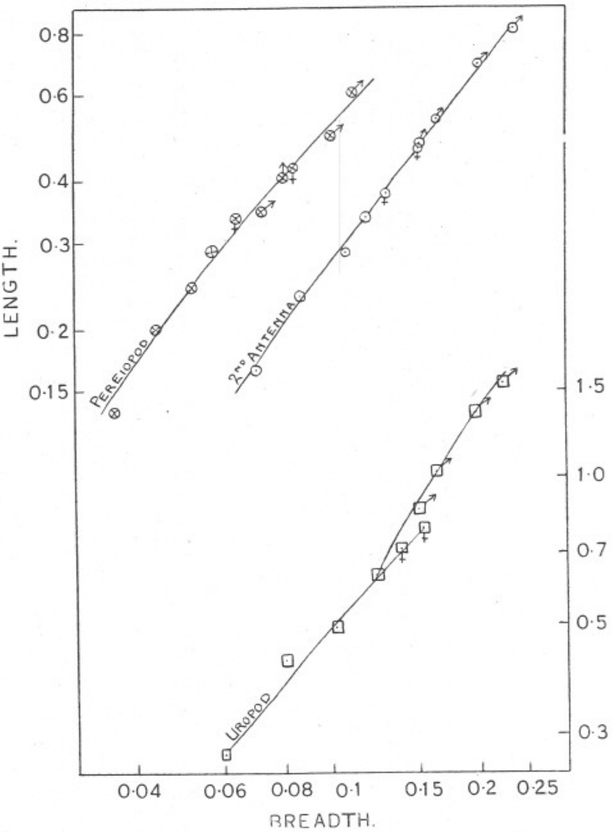


FIG. 17. The mean lengths of first pereiopod propodite, second antenna (first large joint), and uropod (last two joints), plotted against their respective breadths, on a double logarithmic grid.

other hand, the male length-rate is even lower than that of indeterminates and females in comparison to that of the pereiopod (k=·72). The relative rate in *breadth* is very markedly lower in the males at first (k=·6), but later becomes somewhat higher than the corresponding rate in the pereiopod.

N.B.—That the head, in Fig. 15, shows males with a higher rate of growth relative to the fifth segment than females, is the reverse of the usual relation in body-segments ; this appears to be due to the fast growth of the fifth segment in females pulling their line down towards the abscissæ (probably associated with the growth of the brood pouches) ; such an occurrence is not found in the male, since its fifth segment is not particularly fast-growing ; when the growth-rate is compared with that of the pereiopod (Table IV) the relations are quite different. (For values of k see Table IV.)

TABLE IV.

Approximate Values of the Exponent k in the Heterogony Formula.

	Part.	Indeterminates.	Females.	Males.
Lengths vs. length of 5th segment (Fig. 15)	Head	·71	·71	1·3 at first (about =♀ later)
	1st Pereiopod	·95–1·0	·77	1·8 at first (about =♀ later)
	Uropod	1·1	·63 but considerably lower later	2·8 at first (but less than ·65 later)
	2nd Antenna	·9	·6	3·7 at first (but about=♀ later)
Lengths vs. length of pereiopod (Fig. 16)	Uropod	1·1	·75 but considerably lower later	1·4 (tendency to become lower later)
	5th Segment	1·0	1·3	·5 (but increases to about = ♀ later)
Lengths vs. length of pereiopod	Head	·75	·8–·85	·72
	2nd Antenna	·95	·7–·75 somewhat higher later	2·0 at first (about = indeterminates later)
Lengths vs. respective breadths (Fig. 17)	1st Pereiopod	1·2 all classes (approx. ; somewhat higher at first and somewhat lower later)		
	Uropod	1·1 (approx.)	1·1 (approx.)	1·6 (tendency to become lower later)
	2nd Antenna	1·3–1·4 (approx.) all classes		
Breadths vs. breadth of pereiopod (Fig. 18)	Head	1·2	1·2 at first, considerably lower later	·6 (later about= indets.)
	Uropod	1·6	1·0, much lower later	·8–·85 (tendency to become higher later)
	2nd Antenna	1·1	·8 at first, considerably lower later	1·1 at first (then lower, then gradually higher)

(*f*) *Fifth Body-segment.* (i) Inspection of Fig. 11 reveals the interesting fact that the actual length attained in corresponding groups is very much greater in females than in males. This is the reverse of the relation holding in appendages and similar to that for the head, but more marked. It seems possible that this considerable growth in the females is correlated with the formation of the brood-pouch, for the third pereiopod (attached to fifth segment of body) carries a brood-plate (Sexton, '24).

(ii) The indeterminates maintain their original relative proportions; in the females there is a marked increment, while the males decrease at first, become stable, and finally increase in proportion once more (Fig. 14).

(iii) Fig. 15 shows that the growth-rate *in length* of the fifth segment is somewhat faster than that of other organs in the females; in indeterminates it varies, but is on the whole equal to or slightly lower than the rate of females. In the males the fifth segment lags markedly at first, but later its rate approaches or surpasses those of the other organs (cf. Table IV).

From Fig. 16 it can be seen that the indeterminates have a length growth-rate of the fifth segment about equal to that of the pereiopod ($k=1{\cdot}05$), in the females it is higher ($k=1{\cdot}3$), while in the males the rate is very much lower at first ($k={\cdot}5$), but eventually becomes decidedly higher. This curve should be compared with that of the uropod in the same graph, since it shows distribution of positive and negative heterogony to opposite sexes in the two cases. In both the length growth-rate of the indeterminates *approximately* equals that of the pereiopod (somewhat higher in the uropod). Positive heterogony occurs in the male uropod and female fifth segment, while the female uropod and male fifth segment (at first) show negative heterogony with respect to the pereiopod.

(*C*) Conclusions.

From the above data we may, with some degree of confidence, draw the following conclusions :—

1. It appears that in each group (classified by pereiopod propodite length) the male appendages and female head and body-segments show the greater absolute size (Figs. 11, 12, and 13), and therefore the greater proportionate length (Fig. 14), and the higher relative rate of growth (Figs. 15, 16, and 18). The relative increase of the female fifth segment is considerably greater than that of the female head.

2. The greatest divergence between the sexes is shown by the length of the uropod among the appendages, and by the fifth segment among the body-measurements (Figs. 11, 14, 15, and 16).

As regards breadth, however, the uropod does not show greater sex-divergence than other appendages (Figs. 12 and 18).

3. (i) In the appendages selected, there is positive heterogony in males relative both to fifth segment and to pereiopod, while in females there is negative heterogony. These facts, or at least the positive heterogony in the male, would be expected, since both the appendages measured show positive secondary sexual characters (curved sensory hairs) in the male.

(ii) In the case of the fifth segment at least, the length of body-segments shows in the females positive and in the males negative heterogony relative to pereiopod length (Fig. 16): this again is to be expected

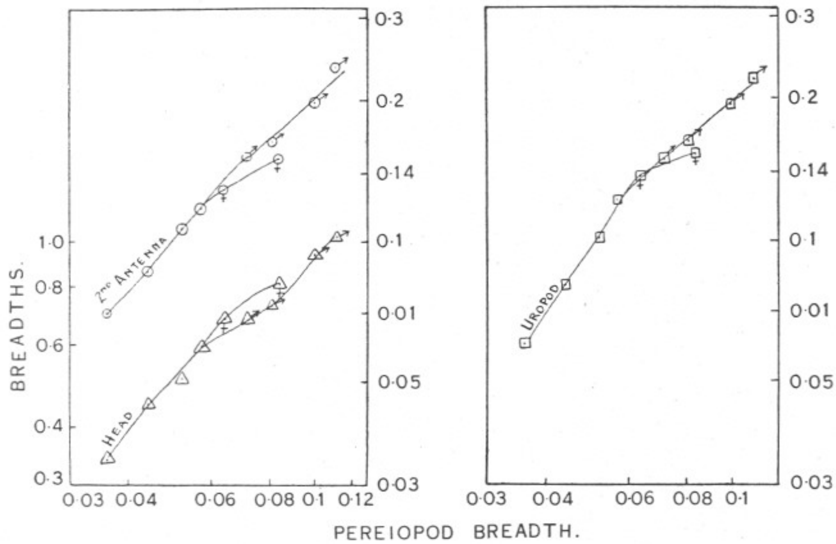


Fig. 18. The mean depth of head, and breadths of second antenna (first large joint), and uropod (last two joints), plotted against the breadth of the first pereiopod propodite, on a double logarithmic grid.

in the female, on account of the presence of the secondary sexual character of brood-pouches on this segment. As regards head-length, the female has a higher comparative growth-rate than the male (Table IV), with respect to the pereiopod, although both are negatively heterogonic. On account of the great growth of the fifth segment in females, the growth-rate of the head relative to fifth segment-length is higher in males.

It appears that the head is comparatively little affected by onset of sexual maturity, unlike the male appendages or the female fifth segment which undergo acceleration of growth, but, as might be expected, its growth is more like that of the fifth segment than that of the appendages.

(iii) The distribution of positive and negative heterogony to opposite sexes in the case of the uropod and fifth segment (Fig. 16) illustrates and confirms the foregoing conclusions (1, 2, and 3).

4. (i) When breadth is compared with breadth, the relative rate of growth in breadth (Fig. 18) is highest in the indeterminates, the breadths of the various appendages being here decidedly positively heterogonic with respect to the pereiopod breadth. The females appear to become gradually lower in rate, whereas the males tend to show a variable drop in rate at first, and a later partial recovery.

(ii) When appendage-length is compared with appendage-breadth, the relative rate of growth in length is higher than that in breadth (Fig. 17); this is particularly observable in the case of the male uropod (which shows extreme positive heterogony of length as compared to other organs). In this case the length growth-rate is accelerated in the male at maturity, differing in this respect from the first pereiopod and second antenna, where the males' curve simply continues that of the indeterminates and females.

(iii) From (i) and (ii) above it can be seen that the various appendages tend to become relatively longer and narrower with growth, and that this alteration in proportions appears to be most conspicuous in those organs which show most marked positive heterogonic growth in length relative to other parts.

The results here given agree in substance with those obtained by Professor Kunkel; in particular an inspection of his Figs. 1 and 2 reveal curves for first antenna, and first and second gnathopods, coinciding in general form with mine for second antenna and uropod, respectively, in Fig. 14. He also finds that a change of proportions occurs with growth in the appendages he measured, and that this change is a relative elongation and narrowing of the part concerned—a result in complete agreement with my conclusions.

The work upon *Gammarus chevreuxi* detailed above was begun in the biological laboratory of Stowe School, continued at the Department of Zoology in Birmingham University, and finished during a visit to the Zoological Department, King's College, London.

It is a great pleasure to record my gratitude to Professor J. S. Huxley, who was responsible for the inception of the work, for its direction while in progress, and for the preliminary introduction; and also for the help I received in some of the laborious statistical work at the hands of a friend.

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