THE RATE OF EYE-GROWTH AND ITS VARIATION IN *GAMMARUS CHEVREUXI*

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(With Two Text-figures.)

THE eye of *Gammarus chevreuxi* has served several times as an object for genetical observations. We have accordingly thought it useful to undertake a more detailed study of certain quantitative features of its development.

For this purpose we picked out from a wild stock, kindly supplied by Mrs Sexton from the Plymouth Laboratory, several mating pairs, which have been cultivated under rigorously standard conditions in a constant temperature chamber at 23° C. In these conditions the interval between two moultings was constantly seven or eight days, so that the biological age of the animals could be expressed in terms of moulting periods. The moment of reaching sexual maturity coincides with the sixth moult, after which the first pairing immediately takes place. We have thus considered the first mating of the young as a sign of sexual maturity, and the moult which immediately preceded it, as the sixth moult. But we have also made notes at earlier and later moults. In the instars after reaching sexual maturity the determination of moulting-time was easier, because the appearance of the brood coincides with the moulting of the female.

The growth of the eye was studied either by counting the eye facets, or both by counting the facets and by measuring the eye surface area in different instars. Counting was effected in animals slightly narcotised with chloretone, under a microscope, in incident light concentrated with a lens. Drawings of the eye area were made by means of an Abbé drawing apparatus under standard low power and each eye was drawn three times at the same time. The area was measured with a planimeter and the average has been calculated from the three measurements. This method of course involves a considerable error, as the eye surface is not a plane. But it is probable that this error is systematic and that it did not affect our results to any important degree.

The number of eye facets has been determined in 954 instances. The average values are summarised in Table I. When plotted against the age, they give an

S-shaped curve (Fig. 1). This type of curve, well known for developmental processes in general, thus holds good also for the growth of the eye in *Gammarus chevreuxi*. It is not possible to determine from our counts the moment when this curve becomes asymptotic to the abscissa, because even in the oldest individuals, so far as we have observed them, the eye facet number continues to increase, although at a very low rate. It is probable that eye-growth in *Gammarus chevreuxi* never ceases and that the eye continues to grow until death as does the whole body in this form.

Table I.

Stage	No. of individuals	Number of facets						Standard deviation	Coeff. of variation
		Minimal	Maximal	Average			Mean for both sexes		
				Males	Females	Both sexes			
Hatching	286	13	18	—	—	15·8	16	1·098	6·9
Moult 1	159	15	29	—	—	20·4	19	3·763	19·8
„ 2	140	15	40	—	—	26·4	24	3·733	26·7
„ 3	71	18	48	—	—	32·0	—	7·127	22·3
„ 4	46	18	59	—	—	38·2	38	9·302	24·5
„ 5	36	22	68	—	—	48·3	53	10·640	20·1
„ 6	100	48	85	68·9	62·2	65·3	63	6·733	10·7
„ 7	24	52	94	78·7	70·4	74·6	75	9·244	12·3
„ 8	24	68	96	87·8	74·3	81·0	—	8·209	10·1
„ 9	26	69	100	89·7	76·4	83·0	—	8·870	10·7
„ 10	24	77	110	99·4	83·2	91·0	—	10·000	11·0
„ 11	9	81	113	107·3	87·0	—	—	—	—
„ 12	5	83	112	107·5	92·0	—	—	—	—
„ 13	4	90	109	109·0	91·3	—	—	—	—

The curve of eye-growth shows a distinct sexual difference, in that it inflects sooner in females than in males. This difference is very marked at the moment of reaching sexual maturity, and it is probable that it is foreshadowed before this. However, it is not possible to divide the young into two distinct groups as to eye facet number, as the sexual differences are covered by the large individual variations.

The eye surface area has been determined in 67 instances and eye facets have been counted at the same time. To discover the relation between eye area and facet number in the earliest developmental stages, young have been taken out from the brood pouches of two females, kept alive in watch-glasses, and the required values have been determined on them. When area values in relative units, which are square centimetres of the drawn surfaces, are plotted against facet number, the curve of Fig. 2 is obtained. Values for males, females, young and embryos are all grouped around a single average curve, showing that there are no sexual differences in the relationship between eye facet number and eye area and that the area depends on the facet number only. The closest fit may be expressed by the following equation:

$$F = \frac{18 \cdot 6}{A^{0 \cdot 584}},$$

where F is the facet number and A the area in relative units. From this formula and from the curve itself it is evident that eye facet number increases at a lower rate than eye area. In other terms, not only the whole eye area increases with age, but the area of a single facet increases as well.

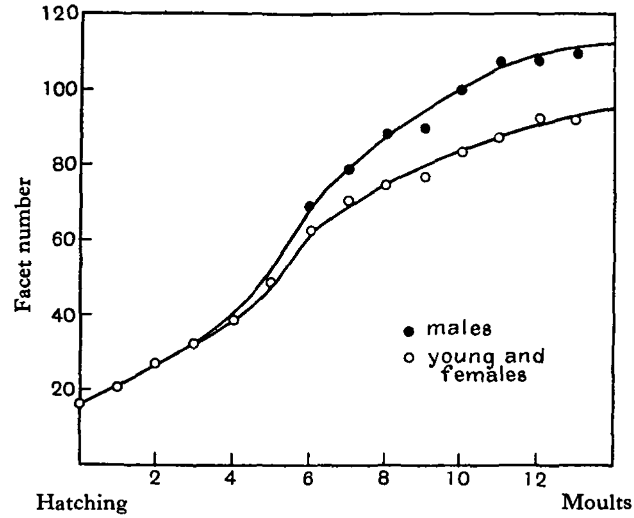

Fig. 1. Growth curve of the eye in *Gammarus chevreuxi*.

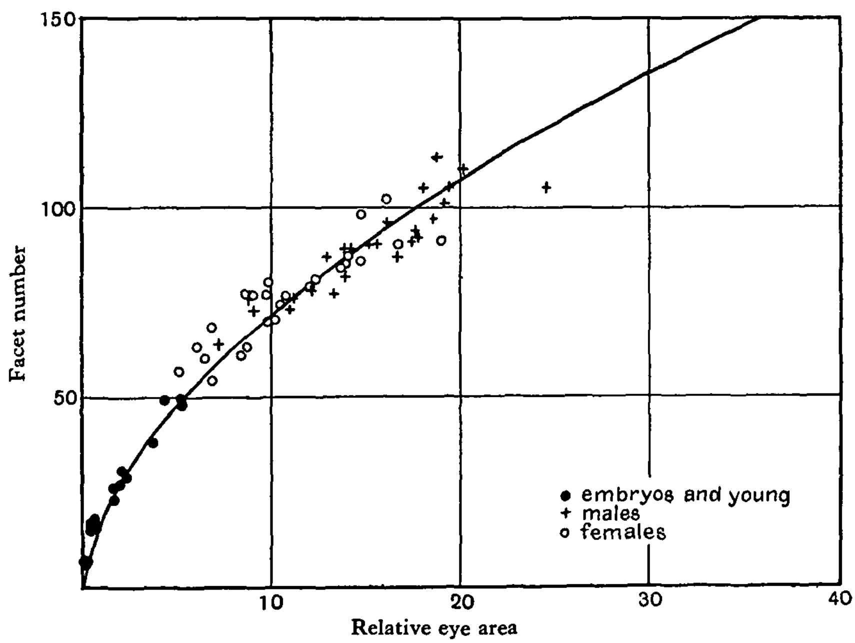

Fig. 2. Relationship between facet number and area of the eye.

The eye facet number at any period of development shows a distinct variability. From our data we have calculated the standard deviation and the coefficient of variability in successive instars from the hatching up to the tenth moulting. The curves of variation are not all quite symmetrical, but in most cases the mean values differ only slightly from the corresponding averages. Therefore in the more advanced instars, where we could not determine the mean directly from the distribution of deviations, we have taken the average values instead of the m[illegible] Table I gives the values of standard deviation and coefficient of variability.

As it is not possible to make a clear distinction between males and females before they reach sexual maturity, the standard deviation and the coefficient of variability had to be calculated regardless of sex. In spite of the fact that sexual differences in the facet number become important in later stages, when sexual maturity has been reached, the error introduced by calculating the data for both sexes together is not too great. At the sixth moult the coefficient of variability is 9·2 for males, 8·1 for females and 10·7 for both sexes. We have therefore calculated the coefficients of variability for both sexes together for the stages after reaching sexual maturity, in order to make the values comparable.

In a more important way than with sex, the coefficient of variability of eye facet number changes with age. It is small at the moment of hatching, but increases rapidly during the next three moulting periods, to drop with the same rapidity after the fifth moult. Between the sixth and tenth moults it remains practically unchanged. It is thus evident that its changes could not be accounted for by sexual differences. The most probable explanation seems to lie in the unequal slope of the individual eye-growth curves. The average number of eye facets at the adult stage is reached by some individuals quicker than by others, and when a cross-section is made through this bundle of individual curves at the moment at which the eye development is quickest, the range of variations must be larger than when the same cross-section is made before or after that moment. It may therefore be expected that the greatest degree of variability should coincide with the most rapid phase of eye development, when the curve bends upwards, and the decrease of the coefficient of variability is to be expected as soon as the curve begins to bend towards the upper asymptote.

It is probable that these individual variations in the rate of the eye-growth are of a hereditary character. Similar hereditary variations in the rate of eye pigmentation have been observed by Huxley and Ford in a mutant of the same species. Our observations however could not be carried on for a sufficiently long time to demonstrate this for eye-growth. Only in one case a distinctly "slow"[1] male was crossed with a normal female and the result was 5 normal and 2 "slow" young in one brood, 5 normal and 1 "slow" in a second brood, which together gives a relation of 10 normal : 3 "slow." Unfortunately we have not been able to get further examples of such Mendelian segregation with "slow" as a recessive character. The chief obstacle was the low viability of "slow" individuals, which could only rarely be reared to sexual maturity.

REFERENCES.

HUXLEY AND FORD (1925). *Nature*, pp. 861–3.
FORD, E. B. and HUXLEY, J. S. (1927). *Brit. J. Exp. Biol.* 5, 112.

[1] We have designed as "slow" any individual which had 14 or less eye facets at hatc[illegible]; male with the same or lower facet number than an average female of the same age; and a female whose facet number was at least 15 per cent. below the average.