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LABORATORY STUDIES ON THE REPRODUCTION AND GROWTH OF THE AMPHIPOD, *GAMMARUS PULEX* (L.)

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SUMMARY

(1) Pairs of *Gammarus pulex* were kept in laboratory incubators at 5, 10, 15 and 20 °C to study brood development time and growth.

(2) The most satisfactory description of the relationship between brood development time (D days) and temperature (T °C) was the power law, $\log_e D = a + b \log_e T$ where $a = 5{\cdot}752$ and $b = 0{\cdot}962$ within the temperature range 5–20 °C. The specific growth rate in length (mm) of young individuals increased with increasing temperature from 0·28 to 0·96% day^{-1} at 5 and 20 °C respectively.

(3) Laboratory data were extrapolated to the field situation to predict the longevity of the species. This was 17–23 months for females, which produced 6 broods throughout the summer and up to 2·5 years for males.

INTRODUCTION

Despite the importance of *Gammarus pulex* (L.) both in terms of numbers and biomass in many waters (Ladle 1972; Westlake *et al.* 1972), production studies of this species have been few (Nilsson 1977; Iversen & Jessen 1977; Welton 1979). The main difficulties are in determining growth rates, as cohorts can rarely be seen in natural populations, and on obtaining data for reproduction, as in many places broods are produced continuously. In consequence, young of all ages are present simultaneously.

Some estimates of growth rates of *G. pulex* are given by Heinze (1932), Mottram (1933) and Hynes (1955), whilst the first main work on growth is given by Nilsson (1974) and growth rates in relation to diet by Willoughby & Sutcliffe (1976). An estimate of brood development time is recognized as being essential for the determination of production of animals with continuous reproduction (Winberg 1971; Edmondson & Winberg 1971; Nilsson 1977). An early estimate is given by Sexton (1924) for 'summer temperatures' only whilst Pinkster, Smit & Brandse de Jong (1977) compared estimates of brood development rates of *Gammarus tigrinus* Sexton with those of *G. pulex*. The relationship between temperature and brood development has been studied for other species, e.g. Kinne (1960) on *Gammarus salinus* Spooner, Steele & Steele (1973) on several marine amphipods whilst McLaren (1966) and Bottrell (1975a, b) give mathematical relationships between these two parameters for Copepoda and Cladocera.

The objectives of the present study on *G. pulex* were to provide information on the growth rate and brood development times of *G. pulex*, neither of which can normally be obtained from field studies, and to use the results to determine times of brood production

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and length of life of animals in the natural situation. To obtain data on reproduction, pairs of animals were observed in laboratory incubators and growth in length was followed from juvenile to adult.

MATERIALS AND METHODS

Specimens of *G. pulex* were kept at constant temperature in illuminated laboratory incubators. Four temperatures were chosen to represent the range found in Dorset chalk streams; these were 5, 10, 15 and 20 °C. The animals were kept in plastic pots, each 75 mm high, having a basal diameter of 50 mm and a top diameter of 65 mm. The experimental containers consisted of one pot placed inside another (Fig. 1). The bottom of the inner pot was removed and replaced with monofilament mesh. This system could then be cleaned by removing the inner pot containing the animals and placing it in fresh river water at the appropriate temperature. For the reproduction experiments, the mesh of the netting was 6 meshes cm^{-1} so that the young could pass through and thus avoid the adults. For the growth experiments, netting with 10 meshes cm^{-1} was chosen so that the animals could not pass through the net. The pots were filled with river water to a height of 45 mm in the inner pot. Each double container was continuously aerated and had a lid to reduce evaporation losses. One or two pieces of flint gravel (up to 30 mm in length) were placed in each pot to provide cover for the animals. Distilled water was used to replace water lost by evaporation so that the ionic concentration was not altered except possibly by excretion by the animals.

Reproduction

A mature male and female *G. pulex* in precopula were placed in each of ten pots in all four incubators. The animals were fed on alder leaves (*Alnus glutinosa* (L.) Gaertn) which were collected in the autumn after abscission from trees growing on the banks of the Tadnoll Brook in Dorset (National Grid reference SY 773871), the source of the experimental animals. The leaves were air dried and stored before being fed to the animals; they were 'conditioned' for at least 10 days in the River Frome (National Grid reference SY 866866) to initiate breakdown because studies have indicated that bacteria and/or

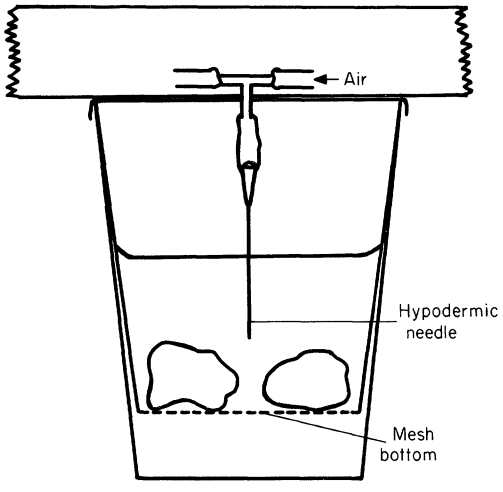

FIG. 1. Diagram of incubator experimental chamber.

fungi are important in the diet of gammarids (Kaushik & Hynes 1971, Bärlocher & Kendrick 1973a, b, Nilsson 1974, Willoughby & Sutcliffe 1976). An excess quantity of leaves was given to each pair so that food did not become a factor limiting growth. The starwort, *Callitriche stagnalis* Scop., was used to supplement the diet. One branch from a growing plant was placed in each pot and replaced when necessary. This provided the animals with *Callitriche* leaves in varying stages of development and decomposition, from growing fresh green leaves at the tip of the stem to yellow decomposing leaves at the base. The pots were examined at least three times a week for the presence of new broods.

GROWTH

From a stock of ovigerous females kept in each incubator, young were removed soon after their release from the female and placed in groups of ten in pots containing river water. Some of the water in which the adults were kept was also transferred because Sexton (1928) concluded that the young did better in a mixture of 'parent' water and 'clean' water. A teat pipette with a wide-bore tube was used to transfer the individuals. Ten young were placed in each pot and fed on fragments of alder leaf and faeces which were collected from the containers of adults. Scorgie (1974) found that young grew well on this diet. The food supply was supplemented by 'conditioned' fragmented leaves.

At intervals, all the individuals from one pot were removed and killed in 70% ethanol. The total body length of each animal was measured to the nearest 0·25 mm by straightening it out with dissecting needles on graph paper under a stereoscopic microscope and measuring from the anterior edge of the head to the posterior edge of the telson, thus providing length and age data for individuals.

Temperature

The temperature of the Tadnoll Brook was measured continuously with a mercury-in-steel thermograph, and the daily median temperatures were calculated, being the mid-points between the maximum and minimum temperatures.

RESULTS

Reproduction

At 5 °C, 16% of the total number of pairs did not produce any broods and no pair produced more than three broods (Table 1). All pairs at 10 °C produced at least one brood, the maximum number of broods produced by one pair being five. The percentage of pairs producing no broods was high at 15 and 20 °C due mainly to mortality of individuals. One pair at 15 °C produced five broods whilst at 20 °C no pairs produced more than three broods. In some cases, when one individual died, a replacement partner was

Table 1. Percentage of total number of pairs producing specified numbers of broods at four temperatures

Number of broods	0	1	2	3	4	5	
Temperature °C							Total number of pairs
5	16	33	41	10	0	0	28
10	0	29	35	18	11	7	28
15	27	25	31	13	2	2	48
20	35	49	14	2	0	0	49

obtained from a precopulating pair. This resulted in two males at 10 °C having two females each and fertilizing a total of five and six broods and one male having three females, also fertilizing six broods. These results are not included in the table.

Brood development time

The brood development time was defined as the time between copulation and the release of the brood from the brood pouch since copulation usually occurs immediately after release of a brood (Della Valle 1887–9; Sexton 1928). Times between the release of the successive broods were taken as an indication of this brood development time. The time of copulation was regarded as that when precopula was terminated. The relationship between brood development time (D days) and temperature (T °C) is shown in Fig. 2. An analysis of variance was first carried out to subdivide the total variation in the development times into that due to the difference between the rearing temperatures and the variation within a temperature. The proportion of the total variation in $\log_e D$ due to differences in temperature was 59·03% and this was the maximum proportion (as measured by R^2, where R = multiple correlation coefficient) that any regression equation relating $\log_e D$ to T could explain. Regression analyses were then used to try and explain the between T variations in $\log_e D$ by its regression on some function of temperature T. The following exponential relationship was examined first:

$$\log_e D = a + bT \qquad (1)$$

where a and b are constants (values in Table 2). Note: $V = 1/D$ = rate of development is used instead of D by some authors in their analysis. Any regression involving $\log_e V$ as the dependent variable is identical (except for a change of sign of the regression coefficient) to the corresponding regression involving $\log_e D$.

Equation (1) suggests that the proportional decrease in development time with increasing temperature is constant. As stated by Bottrell (1975), this is equivalent, over the range considered, to the Vant' Hoff or Q_{10} rule with Q_{10} constant and roughly equivalent

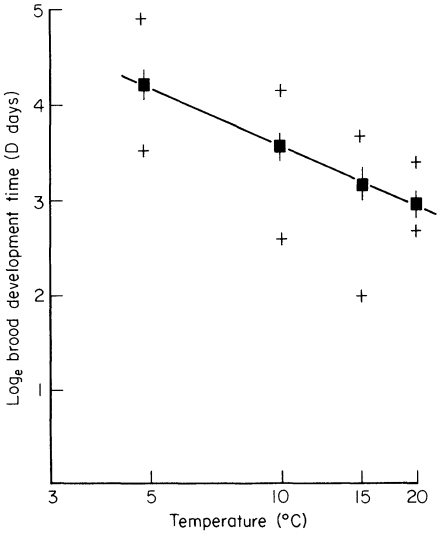

FIG. 2. Relationship between $\log_e$ brood development time (means ± 95% CL) and $\log_e$ temperature. + minimum or maximum individual values.

TABLE 2. Summary of the regressions relating brood development time (D days) to rearing temperature (T °C)

Eqn	a ± 95% CL	b ± 95% CL	∝ ± 95% CL	R_T^2	R^2
1	4·490 ± 0·932	−0·088 ± 0·032	—	93·8	55·34
2	5·752 ± 0·408	−0·962 ± 0·116	—	99·3	58·62
3	5·819 ± 2·108	−0·982 ± 0·640	0·195 ± 5·831	99·3	58·63

R_T^2 = % of between T variation in $\log_e D$ explained by the regression. R^2 = % of total variation in $\log_e D$ explained by the regression. All four regressions are highly significant ($P = < 0{\cdot}001$).

to the Arrhenius law with constant μ. The values of Q_{10} for each of the three successive pairs of temperatures were 3·64 for 5–10 °C, 2·33 for 10–15 °C and 1·56 for 15–20 °C. Therefore Q_{10} decreases over the range 5 to 20 °C. This agrees with the comments of McLaren (1963) on the inadequacy of assuming a constant Q_{10} and using a semi-logarithmic relationship for development time and temperature over the 'naturally-occurring range of temperatures'.

The relationship was made linear by regressing $\log_e D$ against $\log_e T$:

$$\log_e D = a + b \log_e T \tag{2}$$

where a and b are constants (values in Table 2). This power-law regression gave an excellent fit to the data accounting for 99·3% of the between T variation in $\log_e D$ values. There was no visible curvature in the relationship between $\log_e D$ and $\log_e T$ and the inclusion of a $(\log_e T)^2$ term (Bottrell 1975) did not give any significant improvement in fit ($P > 0{\cdot}5$); and the use of $(\log_e T)^2$ instead of $\log_e T$ was slightly worse ($R^2 = 58{\cdot}0\%$ instead of $R^2 = 58{\cdot}62\%$).

Bělehrádek (1935) and McLaren (1963) suggested using the more general equation:

$$\log_e D = a + b \log_e (T - \propto) \tag{3}$$

where a and b are constants and $\propto$ is the 'biological zero'. The general iterative approach suggested for non-linear regression by Snedecor & Cochran (1968) was used to obtain the values of the constants in Table 2. As $\propto$ is approximately zero, its inclusion does not give any significant improvement in fit ($P > 0{\cdot}5$). In summary, the power-law relationship (eqn 2) provides the best description of the data.

In order to calculate the maximum number of broods produced annually by one female *G. pulex*, it was necessary to divide the daily mean temperatures of the river into four groups, which equate with the four temperatures used in the laboratory. Doing this on temperature data for the Tadnoll Brook, where the experimental animals were found, gives the number of days in each category (Table 3). If the mean brood development time at temperature T is $\bar{D}_T$ with standard error S.E. $(\bar{D}_T)$, then the expected number of broods produced over N_T days at this temperature is $B_T = N_T/\bar{D}_T$ and from the first term expansion for the variance of the reciprocal of a variable (Bulmer 1965), we have $SE(B_T) \simeq N_T\, SE(\bar{D}_T)/D_T^2$. The total number of broods produced in 1 year is then estimated by $B = B_5 + B_{10} + B_{15}$ (no days in the 20 °C group) with $SE(B) = \sqrt{(\mathrm{Var}(B_5) + \mathrm{Var}(B_{10}) + \mathrm{Var}(B_{15}))}$. The estimated maximum number of broods produced was $\simeq 10$ in both 1973 and 1974 although the temperature regime was quite different in the 2 years studied resulting in 5 broods being theoretically produced in the 10 °C category in 1973 but 7 broods in 1974 (Table 3). There was a compensating difference in the 15 °C category

TABLE 3. Partition of annual brood production of *G. pulex* between four temperature ranges of the Tadnoll Brook, calculated from the number of days on which the mean temperature fell with each range

Temperature range (°C)	2·5 — 7·4	7·5 — 12·4	12·5 — 17·4	Total
Mean temperature (°C)	5	10	15	
Number of days (1973)	86	182	97	365
Number of days (1974)	50	268	47	365
Mean brood development time (days) $\bar{D}_T \pm 95\%$ C.L. ($\bar{D}_T$)	69·7 ± 10·4	36·5 ± 2·7	23·9 ± 2·1	
No. of broods produced 1973 $B_T \pm 95\%$ C.L. (B_T)	1·23 ± 0·19	4·99 ± 0·38	4·06 ± 0·35	10·28 ± 0·43
$B_T \pm 95\%$ C.L. (B_T) 1974	0·72 ± 0·11	7·34 ± 0·54	1·97 ± 0·19	10·03 ± 0·55

with 4 broods produced in 1973 but only 2 in 1974. No provision has yet been made for biological factors such as a female's sustained reproductive ability or the number of broods actually produced by females kept in the incubators.

The development time calculated is not, of course, for a single stage of the life cycle, but for development of the eggs and young up to release from the brood pouch. The rate of development is not necessarily the same for both eggs and young but as it is extremely difficult to differentiate between the two stages when they are beneath the oostegites, the assumption that they both develop at similar rates has been made in this study.

Observations made in the incubator indicated that development proceeded rapidly at 20 °C, although this temperature seems to be approaching the upper limit for reproduction with only 65% of the pairs producing broods. During 1973 and 1974 the temperature range in the Tadnoll Brook was 4 to 17 °C which is inside the lower and upper limiting temperatures for reproduction.

Growth

The overall growth of many animals has been shown to follow a sigmoid curve and during the earliest stages it is generally accepted that growth is exponential. Exponential growth curves were fitted to the four sets of data by the linear regression of log length (Y) against days of growth (t) (Table 4, Fig. 3).

$$\log_e Y = \log_e A + bt \qquad (4)$$

where $A = e^a$ = mean length of newly released individuals and b = specific growth rate and $100b$ is the growth rate as % day^{-1}.

The specific growth rate, (Table 4) increases with temperature, and the growth rate at 10 °C, denoted by b_{10}, is significantly greater than b_5 ($t = 7{\cdot}1$); b_{20} is significantly greater than b_{10} ($t = 2{\cdot}28$) but not b_{15} ($t = 1{\cdot}89$) and there is no significant difference between b_{10} and b_{15}, each at the $P = 0{\cdot}05$ level of significance.

As the mortality of newly-released animals was high, some pots were set up with larger juveniles, the sizes within each group not differing by more than 1 mm. Size classes of individuals between 3 and 6 mm were used. The size groups were obtained by placing individuals in sieves of various mesh sizes and taking groups either passing through or being retained. Representatives of the smallest and largest were then picked out by eye and measured until a group of individuals of approximately the same size were obtained. Groups of these juveniles were then reared at each of the four temperatures. After varying periods of time, individuals were removed and measured.

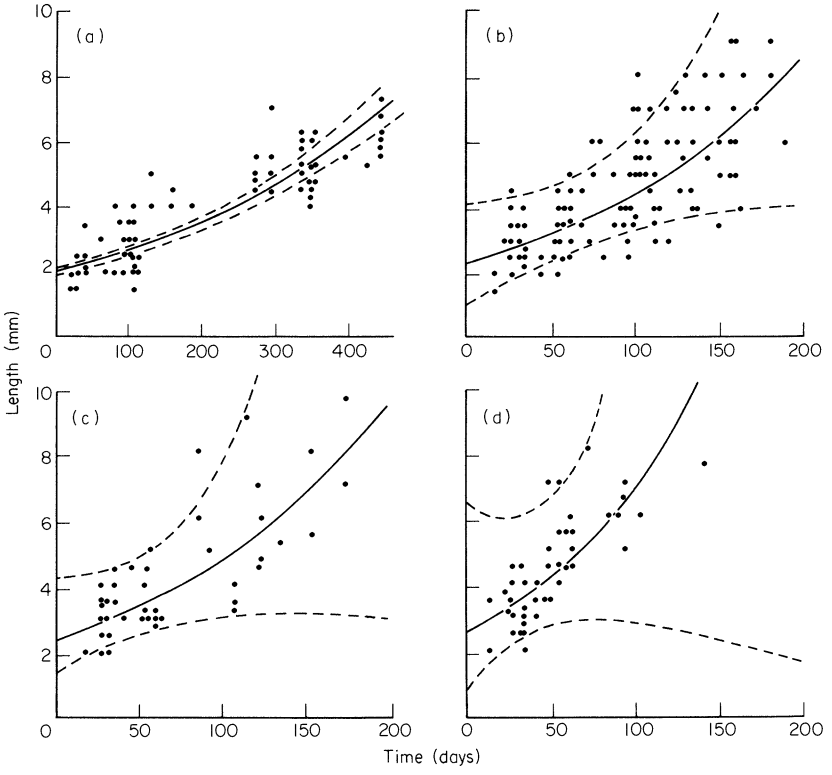

FIG. 3. Relationship between growth in length and time at four temperatures; (a) 5 °C, (b) 10 °C, (c) 15 °C, (d) 20 °C. ● individual values, – – – 95% CL of the fitted line.

TABLE 4. Summary of the linear regression of log length against days of growth for newly-released *G. pulex* reared at four temperatures

Temperature °C	n	a	95% CL(a)	b	95% CL(a)	s^2	r^2%
5	123	0·732	0·056	0·00275	0·00028	0·0374	76·4
10	138	0·833	0·099	0·00645	0·00099	0·0699	54·9
15	79	0·880	0·096	0·00685	0·00066	0·0563	57·8
20	49	0·951	0·148	0·00960	0·00259	0·0541	53·9

n = sample size; a, b, 95% C.L.(a), 95% C.L.(b) are the regression coefficients and their 95% confidence limits; s^2 = error mean square; r^2 = proportion of variation in log length explained by the regression. All regressions are significant at $P < 0{\cdot}001$.

If Y_0 denotes the length of an individual at the start of the experiment and Y_t the length after t days, then:

$$\log_e(Y_t/Y_0) = bt. \tag{5}$$

Thus regressions through the origin of the logarithm of the ratio of the final to initial length against days of growth enable one to estimate the specific growth rates of these larger juveniles, even though their lengths at the start of the experiment vary (Fig. 4, Table 5). The specific growth rates b, again increase with temperature of rearing. However, the growth rates are all slower than the corresponding rates for newly released individuals (Table 5).

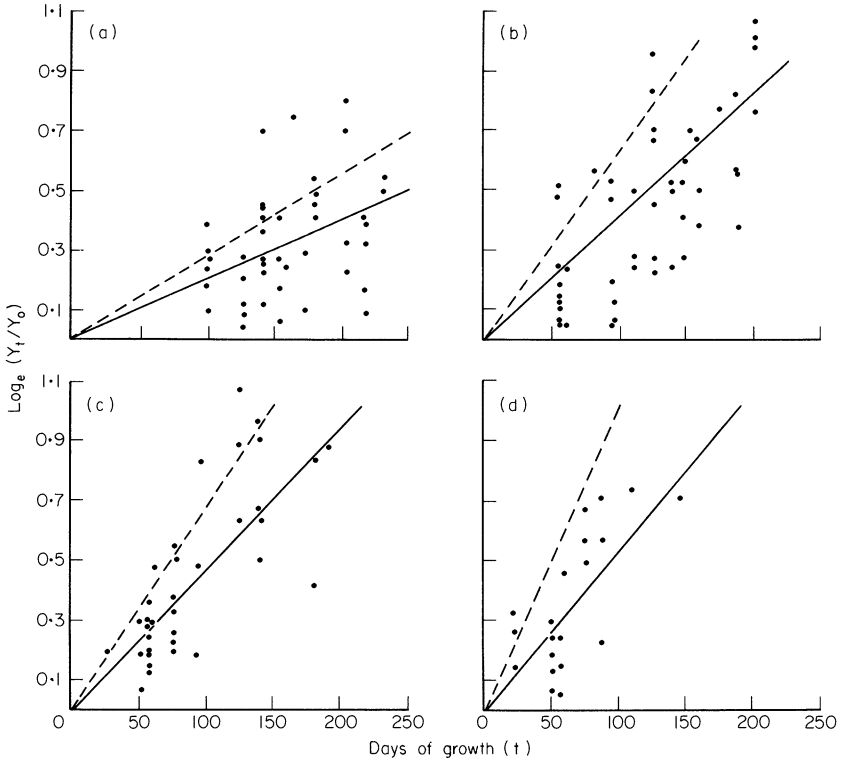

FIG. 4. Plots of the logarithm of the ratios of the final to initial lengths, $\log_e(Y_t/Y_0)$ against days of growth (t) for the additional juvenile *G. pulex* for each of four temperatures. (a) 5 °C, (b) 10 °C, (c) 15 °C, (d) 20 °C. ● individual values, — mean specific growth rate (from Table 5), – – – mean specific growth rate for newly-released individuals (from Table 4).

TABLE 5. Summary of the linear regressions of the logarithm of the ratio of the final to initial length of additional *G. pulex* against days of rearing for each of four temperatures (see Eqn 5)

Temperature °C	n	b	95% CL(b)	s^2	r^2%	t
5	50	0·00201	0·00404	0·0286	14·2	1·20($P > 0·2$)
10	64	0·00406	0·00094	0·0353	54·6	3·40($P < 0·01$)
15	53	0·00470	0·00104	0·0231	64·0	2·54($P < 0·05$)
20	24	0·00531	0·00250	0·0266	48·6	2·43($P < 0·05$)

n = sample size; b, 95% C.L.(b) = regression coefficient and 95% confidence limits: s^2 = error mean square, r^2 = proportion of variation in the dependent variable explained; t = value of t test between the specific growth rates of young and older individuals.

DISCUSSION

Gammarus pulex is usually regarded as a detritivore, eating allochthonous leaf material and presumably its associated microflora. In this study, under laboratory conditions, *G. pulex*, apart from eating the decaying leaves of *Callitriche stagnalis*, also ate the fresh green leaves. Few references are made in the literature to amphipods eating living material. Moore (1975) showed that *G. pulex* ingested living algae whilst Marcus, Sutcliffe & Willoughby (1978) found that the isopod *Asellus aquaticus* (L.) ate fresh growing leaves of *Elodea canadensis* Michx.

The decrease in brood development time with increasing temperature found in the present study agrees with previous work on gammarids (Kinne 1961; Steele & Steele 1973; Nilsson 1977 and Kock-Kallnbach & Meijering 1977). The power-law relationship between brood development time and temperature has also been described for egg incubation period of species of Plecoptera (Brittain 1977, 1978) and Ephemeroptera (Elliott 1972; Newell & Minshall 1978; Humpesch 1980).

From these experiments, the theoretical maximum number of broods which could be produced by one female *Gammarus* in a year is 10. However, the maximum number produced by one female in the laboratory was five, perhaps indicating that the number of broods is more likely to be around this figure. In experimentation on laboratory populations, Nilsson (1977) found that all female *G. pulex* died after producing 3–4 broods. The number of broods produced in marine gammarids depends on the species and the habitat (Steele & Steele 1972; Steele & Steele 1969, 1970). *G. setosus* Dementieva produced only one brood per year in the Arctic, whilst *G. oceanicus* Segerstrale, *G. duebeni* Lillj. and *G. obtusatus* Dahl, with more southern distributions, produce several broods per year.

Heinze (1932) quoted 16–17 days for brood development of *G. pulex* in summer conditions although no temperature range is given. Hynes (1955) used this information to determine that the number of broods produced in the Shotwick Stream was 5–6 (plus possibly one from the previous autumn) allowing 3 weeks per brood from early March, when the first young appeared, to mid-June or early July. At this time there was a sharp fall in the mean size of adult females in this stream which he considered to be due to the deaths of the large females. It may, however, have been accentuated by recruitment from the immature stock.

Pinkster, Smit & Brandse-de Jong (1977) gave figures for the brood development time of *G. pulex* of 40 days at 10 °C, 25–30 days at 15 °C and 18–21 days at 20 °C. These are supported by the times observed in this study of 36·5 ± 1·3, 23·9 ± 1·0 and 19·2 ± 0·2 days at 10, 15 and 20 °C respectively. Sexton's (1924) estimate of 16–17 days at summer temperatures is slightly faster than the time at 20 °C in the present study. Nilsson's (1977) results of 65 days at 5 °C, 36 days at 10 °C and 21 days at 15 °C are also similar (69·7 ± 4·9 days at 5 °C in the present study).

Early works (Heinze 1932; Mottram 1933; Hynes 1955) gave little information on growth, quoting only times to reach maturity. Experiments at room temperature (15–20 °C) by Mottram (1933) and Hynes (1955) gave 100 days and 120 days respectively to reach maturity which Hynes (1955) said was attained at 6 mm. In the present study, the time taken to grow to this size was 133 days at 15 °C and 87·5 days at 20 °C. Times taken to reach maturity at similar temperatures in other species vary considerably. *Gammarus tigrinus* matures at 4 mm taking only 27–29 days to reach this size (Pinkster, Smit & Brandse-de Jong 1977). *Gammarus duebeni* maturing at 7–8 mm takes 150–210 days (Hynes 1955) whilst Kinne (1953) states that this species matures at 11–12 mm taking 170–180 days. *Gammarus zaddachi* Sexton takes 40–50 days to reach maturity at a size of 7–9 mm (Kinne 1961). Thus *G. pulex* in the present study matures at a faster rate than *G. duebeni* but slower than *G. tigrinus* and *G. zaddachi.* Nilsson (1974) in his laboratory study of *G. pulex* gave growth curves in terms of wet weight of individuals and degree-days (presumably above 0 °C). At a mean temperature of 10 °C, his animals grew to a wet weight of 43 mg (average weight of males and females) which is the weight at approximately 12 mm length. At the start of the experiment his animals were *c.* 1·9 mg (4 mm). Using Eqn (4) and Table 4 the times taken to grow to 4 mm and 12 mm in the present study were 86 and 256 days respectively, a difference of 170 days which compares very favourably

with Nilsson's time of 160 days. However, in a further study, Nilsson (1977) quotes growth in terms of degree-days and number of segments of the first antenna. Using his equation relating these two parameters, the number of degree-days taken to reach 15 and 25 segments of antenna 1 were 1396 and 2824 respectively, i.e. it took 1528 degree-days or 153 days at 10 °C. The weights of an animal at these two sizes were found from Nilsson's equation (0·6 mg and 6·1 mg) and converted to lengths. The times taken to grow to these two lengths (4·4 mm and 10·2 mm) in the present study were 101 days and 231 days at 10 °C, i.e. it took 130 days at 10 °C to grow from the smaller to the larger size. Thus the growth rate in the present study was slightly faster than that quoted by Nilsson (1977) for an equivalent animal (130 days cf. 153 days).

At 15 °C the growth is 0·69 mm% day^{-1} (equivalent to 1·01 μg% day^{-1}) for animals fed on decaying alder leaves and *Callitriche*. This compares with 1·69 μg% day^{-1} given by Willoughby and Sutcliffe (1976) for animals kept at the same temperature and fed on decaying elm and oak leaves. The mean specific growth rate varied with diet from nil to 1·69 μg% day^{-1} (Willoughby & Sutcliffe 1976), thus the value found in this study is similar although perhaps lower than for a comparable diet.

Extrapolation of laboratory data to the field situation

Using the temperature data for the Tadnoll Brook, split into the ranges used in Table 3 but on a monthly basis, the growth eqn (4) and data given in Table 4, the size of an animal released from the brood pouch in June (the time of maximum brood release) is shown throughout its life (Fig. 5). The timings of brood release are also shown, determined from brood development times at each temperature. Young, produced in June, overwinter as immature animals and mature the following March/May at a size of 6–7 mm. Females then produce broods throughout the summer at approximately monthly intervals until the end of October when they have reached *c.* 10 mm in length. No larger mature ovigerous females were found to overwinter (Welton 1979), therefore, it is probable that females die at this time having produced six broods. The life span then is between 17 and 23 months for females (respective sizes at these times, 10 and 12 mm, the largest size found in the Tadnoll Brook) and up to 2·5 years for males growing to 16 mm.

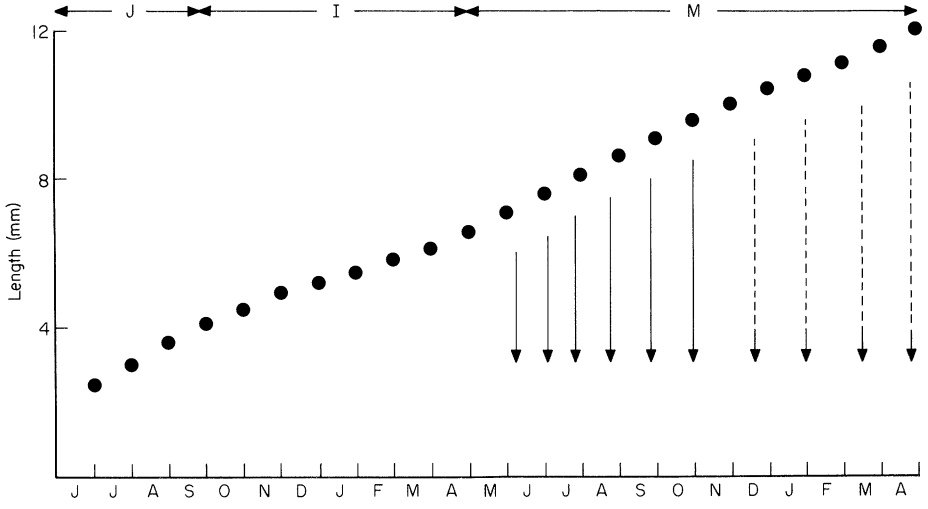

FIG. 5. Life history of a female *G. pulex* showing timings of maturity and brood production. J juvenile, I immature, M mature, ↓ brood produced, ⇣ possible brood produced.

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