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Life cycles and growth rates of *Baetis* spp. (Ephemeroptera: Baetidae) in the laboratory and in two stony streams in Austria

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SUMMARY. Larvae of *Baetis alpinus, B. lutheri* and *B. rhodani* were reared in a stream channel (water temperature range 4.2–11.4°C) in the laboratory. The larval growth was exponential and the mean specific growth rate varied from 1.93 to 2.24% day^{-1} for *B. alpinus,* 1.49 to 3.41% day^{-1} for *B. lutheri* and 0.79 to 3.11% day^{-1} for *B. rhodani*. These variations in growth rate were related to variations in mean temperature and this was the major factor affecting growth in the laboratory.

Non-quantitative samples of the benthos in the Seebach and Unterseebach, two stony streams near Lunz, Austria, were taken at approximately monthly intervals from November 1965 to May 1968. In each year, there were two winter and three summer cohorts for *B. alpinus* from Seebach and two or three winter and one to three summer cohorts for *B. lutheri* and *B. rhodani* from Unterseebach. Over the study period of 30 months, eleven cohorts were recorded for *B. alpinus* and *B. lutheri*, and ten cohorts for *B. rhodani.* The life cycle of a cohort varied from 3 to 8 months in *B. alpinus*, from 2.5 to 9 months in *B. lutheri* and from 2.5 to 8 months in *B. rhodani*. Mean specific growth rate in length varied from 0.82 to 2.97% day^{-1} for *B. alpinus*, 0.96 to 3.33% day^{-1} for *B. lutheri* and 0.65 to 3.01% day^{-1} for *B. rhodani*. The percentage of the variability in growth rate accounted for by variations in mean temperature was 63% for *B. alpinus*, 91% for *B. lutheri* and 82% for *B. rhodani*. Therefore mean temperature was clearly the major factor affecting the growth rates in the field.

An agreement was found between the growth rates of *B. alpinus* in the field and the laboratory. The growth rates of *B. lutheri* and *B. rhodani* were slower in the field than in the laboratory at higher temperatures. The possible reasons for this latter discrepancy are discussed, and the growth rates of the three *Baetis* spp. are compared with those of other species of Ephemeroptera.

Introduction

The mayflies, *Baetis alpinus* Pictet, *B. lutheri* Müller-Liebenau and *B. rhodani* Pictet are widespread and abundant European species. Larvae of *B. alpinus* and *B. lutheri* are found in swift-flowing stony streams, with *B. alpinus* restricted to cold upland streams and *B. lutheri* occurring chiefly in warm lowland streams and lake outflows. The larvae of *B. rhodani* occur in streams and rivers, and are found in plants as well as on stones.

The life cycles of *Baetis* spp. have been described by several workers (e.g. Macan, 1957; Pleskot, 1958, 1961; Thorup, 1963, 1973; Bretschko, 1965; Elliott, 1967; Landa, 1968; Ulfstrand, 1968; Larsen, 1968; Langford, 1971; Thibault, 1971; Benech, 1972a), and some of these workers have found that the

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pattern of larval development can be markedly different from biotope to biotope and even in a biotope from year to year. Some authors have suggested that these variations in the life cycle may be due to the effects of water temperature on egg development and larval growth. Although the effect of temperature on the hatching time of eggs of *B. rhodani* (Bohle, 1969; Benech, 1972b; Elliott, 1972) and *B. alpinus* (Humpesch, 1979) has already been studied in detail, little is known about the effect of temperature on larval growth. There is a paucity of detailed work on growth in Ephemeroptera, one notable exception being the recent study of Brittain (1976).

The aim of the present study was to rear larvae of *B. alpinus, B. lutheri* and *B. rhodani* in the laboratory and to compare their growth rates with those of the same species in two streams near Lunz in Austria.

Description of the streams and sampling sites

Seebach is a calcareous mountain stream and Unterseebach is the calcareous outflow of Lunzer Lake (altitude 650 m; 47° 51′ N, 15° 04′ E). As the hydrography, physical and chemical conditions of the streams have already been described in detail (Kann, 1978; Humpesch, 1971) only a brief account is given here.

The stream bottom at the sampling point on the Seebach consists of large stones (diameter *c.* 40 cm) over smaller stones (diameter *c.* 10 cm) and gravel, with bryophytes on the larger stones. The width of the stream is *c.* 4 m with a depth of 14–18 cm. The modal water velocity, measured at the surface using an Ott current meter, was 80 cm s^{-1} (annual range 40–200 cm s^{-1}). The water temperature is rarely above 11°C or below 3°C, and the oxygen concentration is always > 90% saturation.

The stream bottom at the sampling point on the Unterseebach consists mostly of exposed rocks with some large stones (diameter *c.* 60 cm) over smaller stones (diameter *c.* 10–25 cm) and gravel, with bryophytes on the exposed rocks. The width is *c.* 16 m with a depth of 35 cm. Modal velocity was 90 cm s^{-1} (annual range 40–200 cm s^{-1}). The water temperature is rarely above 21°C or below 2°C, and the oxygen concentration is always > 90% saturation.

Seebach and Unterseebach are moderately shaded by deciduous trees, and leaf packets are found at the sides of the streams.

Materials and methods

Non-quantitative samples of the benthos were taken with a pond net (mesh-size 250 μm, diameter 19 cm) from each site at approximately monthly intervals from November 1965 to May 1968.

All samples were preserved in 75% alcohol and sorted by hand in the laboratory. The length of the larvae (from front of the head to the tip of the abdomen) was measured under a binocular to the nearest 0.5 mm Seven stages of larval development were recognized according to the morphological features (development of gills, wing pads and eyes) that are described in detail in Humpesch (1979). Mature larvae with dark wing pads were in stage VII, and were used as an approximate indication of the flight period.

The water temperature of the Seebach was recorded at a site *c.* 500 m downstream from the sampling site, and temperature readings from Lunzer Lake were used for the Unterseebach. As these temperatures were similar to those recorded at the sampling sites, they were used for the analyses because they were recorded daily at 07.00 hours, whereas temperatures at the sampling sites were recorded only at approximately monthly intervals.

The laboratory experiments were carried out in a stream channel under natural light-conditions in the greenhouse of the Biological Station near Lunzer Lake. Larvae of *B. alpinus* were obtained from Seebach, and larvae of *B. lutheri* and *B. rhodani* from Unterseebach. A single larva was used for each growth experiment and was kept in a cage of wire-netting (mesh-size 0.4 mm, height 8 cm, diameter 8 cm). The cages were put in a rearing chamber which functioned in the same way as a chamber that was originally used for breeding trout eggs (see Einsele, 1956). Because of the mesh-size of the cages, only larvae from stages II and III were reared to

maturity. The water was supplied from a spring, there was a continuous flow through the cages (velocity 8–12 cm s^{-1}), and the water depth in each cage was about 5 cm. Ionic concentration, for example HCO_3^-, Ca^{2+} and Mg^{2+}, and conductivity were slightly higher in the rearing chamber than in Seebach and Unterseebach (see Humpesch, 1971). Oxygen concentration was always > 90% saturation. Water temperature in the laboratory was recorded regularly from March 1967 to February 1968, usually once every three days, but occasionally at 2-h intervals in order to ascertain the diel fluctuation. As the differences between the water temperatures in the field and in the laboratory are discussed in detail in Humpesch (1971, 1979), only a brief account is given here. The annual range of temperature in the rearing chamber was similar to that in the Seebach but was less than the range in the Unterseebach. The daily temperature in the chamber was fairly constant, and varied by only *c.* 0.3°C, whilst daily temperatures in the two streams varied by several degrees.

The nymphs in the experiment were fed on epilithic material on stones from Seebach, because larvae of most species of Ephemeroptera are known to feed on periphytic and epilithic material, including algae and detritus (Brown, 1961; Strenger, 1979). Each cage was provided with one stone, which was changed regularly, usually once a week.

The larvae were inspected every 3 days. After each moult, the exuviae were removed and the length of the larva was measured (front of the head to the tip of the abdomen) under a binocular to the nearest 0.5 mm. The stage of development was also recorded.

Results

Laboratory experiments

The relationship between the body length (L, mm) of a single nymph and the time from the start of an experiment (t, days) was found to be linear on a semilogarithmic scale (e.g. Fig. 1). Therefore growth was assumed to be exponential during each experiment and the relationship between L and t is given by:

$$L_t = L_o \, e^{bt} \qquad (1)$$

Converting to logarithms:

$$\log_e L_t = \log_e L_o + bt \qquad (2)$$

where L_o is the body length of the larva at the start of the experiment, L_t is the body length after t days, and the constant b is the relative rate of growth in length (mm mm^{-1} day^{-1}). Growth of individuals was expressed

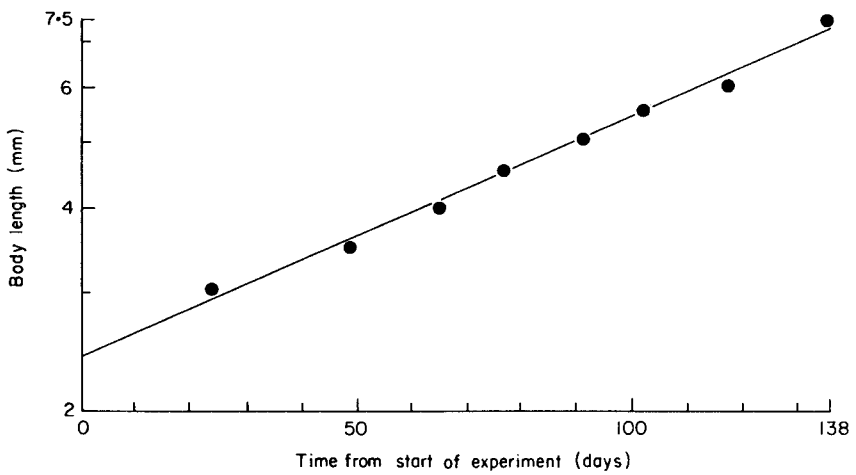

FIG. 1. Semi-log plot of body length in a larva of *Baetis rhodani* at a mean water temperature of 5.8°C, SE ± 0.7 (range 4.4–8.7°C).

TABLE 1. Growth of individual larvae of *Baetis* in the laboratory. For each experiment is shown the larval stages; the length (mm) at the beginning and end of each experiment; number of moults; dates of experiments (†1966, *1967, ‡1968); length of experiment in days; water temperature (T, °C mean ± SE) and the temperature range. Specific growth rate (G, % length day^{-1} ± 95% CL) is also given with r^2 values (proportion of the variance in length due to the regression of length against time)

Species	Larval stages	Length	Moults	Dates	Days	Mean T	Range of T	Mean G	r^2
B. alpinus	♂ III–VII	3.0–8.5	6	2 Apr–24 May*	52	6.5 ± 0.4	4.2– 8.6	1.93 ± 0.53	0.96
	♂ II–VII	2.0–8.5	8	19 May– 8 Jul*	50	8.8 ± 0.4	6.6–11.0	2.75 ± 0.54	0.96
	♂ III–VII	2.5–6.0	6	30 Aug– 5 Oct*	36	8.8 ± 0.2	7.7–10.2	2.52 ± 0.55	0.99
	♀ III–VII	3.0–8.0	5	21 May– 4 Jul*	44	9.3 ± 0.3	8.5–10.7	2.24 ± 0.11	0.93
B. lutheri	♂ III–VII	3.0–7.5	6	25 Mar–22 May†	58	6.8 ± 1.2	4.6– 8.7	1.49 ± 0.30	0.98
	♂ II–VII	2.0–8.5	7	14 May– 2 Jul*	49	9.0 ± 0.2	8.2–10.7	2.82 ± 0.78	0.94
	♂ II–VII	2.5–7.0	6	5 Jul – 4 Aug*	30	10.1 ± 0.2	8.8–11.0	3.41 ± 0.86	0.97
B. rhodani	♀ III–VII	3.5–7.5	7	12 Jan –12 Apr†	90	5.2 ± 0.5	4.4– 7.1	0.91 ± 0.20	0.97
	♂ III–VII	2.5–7.5	9	21 Dec– 8 May†	138	5.8 ± 0.7	4.4– 8.7	0.79 ± 0.05	0.99
	♂ III–VII	3.0–7.5	6	27 May– 7 Jul‡	41	8.7 ± 0.1	8.2– 9.5	2.29 ± 0.30	0.99
	♂ III–VI	2.5–7.0	7	7 Oct –23 Nov*	47	8.7 ± 0.3	7.4–10.9	2.18 ± 0.26	0.99
	♀ III–VII	3.0–8.5	6	22 May– 8 Jul*	47	9.7 ± 0.4	8.5–11.2	2.12 ± 0.48	0.97
	♀ III–VII	3.0–8.0	6	16 Aug–18 Sep*	33	11.1 ± 0.1	10.4–11.4	3.11 ± 0.43	0.99

as specific growth rate, G, % day^{-1}, where $G = 100b$. Values of G are given in Table 1, which shows that the growth rate varied with the mean temperature. For *B. alpinus*, G was highest at a mean temperature of 8.8°C. For *B. lutheri* and *B. rhodani*, the values of G were highest at the highest mean temperature of 10.1°C and 11.1°C respectively. The relationship between mean specific growth rate and mean water temperature (T, °C) for the three *Baetis* species together and *B. rhodani* alone was well described by the linear regression equation:

$$G = a + bT \qquad (3)$$

where a and b are constants. The values of the constants, with 95% confidence limits, were $a = -1.13 \pm 1.14$ and $b = 0.40 \pm 0.13$ for the three *Baetis* species together (solid line in Fig. 2), and $a = -1.20 \pm 1.14$ and $b = 0.38 \pm 0.13$ for *B. rhodani* alone (broken line in Fig. 2). The values of a and b for the three *Baetis* species combined were not significantly different from those obtained for *B. rhodani*. However, the proportion of the variance of the mean growth rate due to regression (r^2) was higher for *B. rhodani* ($r^2 = 0.94$) than for the three *Baetis* species together ($r^2 = 0.80$). Therefore 94% of the variability of G for *B. rhodani* was accounted for by variations in mean temperature, and this was clearly the major factor affecting growth in the laboratory. The two regression lines were a good fit to the data and the F-values from the variance ratio were highly significant ($P < 0.01$).

The number of moults observed between stages III and VII was five to seven for *B. alpinus*, six for *B. lutheri* and six to nine for *B. rhodani* (Table 1). The moulting frequency of the larvae varied throughout the year: the interval between moults was 14–30 days from late autumn to winter, about 14 days from late winter (February) to early spring (April), and 3–8 days from spring to early autumn.

Life cycle and growth in the field

The life cycles of the three *Baetis* species are illustrated by Figs 3 and 4, in which the catches from the monthly samples are expressed as a frequency distribution over the seven developmental stages. The presence of mature larvae indicated that the flight period was from March to September for *B. alpinus* (Fig. 3); April to September 1966 and April to July, and September 1967 for *B. lutheri* (Fig. 4); May to July and September 1966, and April to June and September 1967 for *B. rhodani* (Fig. 4). Larvae in stage I were collected throughout most of the summer, autumn and winter, but were absent in spring before and after the onset of emergence.

The cohorts were separated according to the hatching time of the eggs and the exponential growth of the larvae. As females

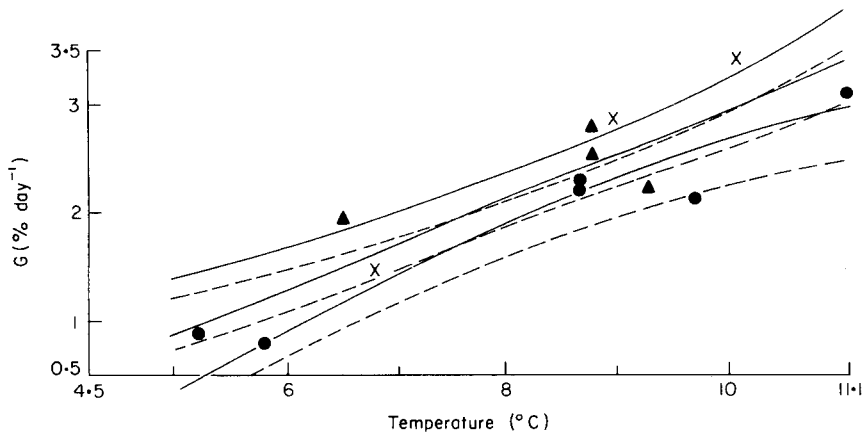

FIG. 2. Relationship between mean specific growth rate ($\bar{G}$, % length day^{-1}) in the laboratory and mean water temperature (T°C) for three *Baetis* species (solid line and ▲ *B. alpinus*, X *B. lutheri*, ● *B. rhodani*) and for *B. rhodani* alone (broken line and ●); 95% confidence limits are given for each regression line.

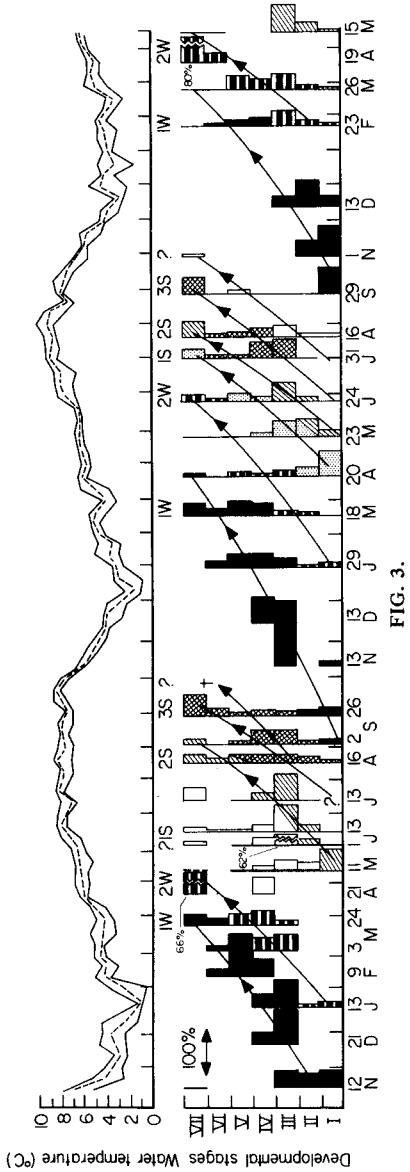
Developmental stages Water temperature (°C)
100%
66%
62%
1966

FIG. 3.

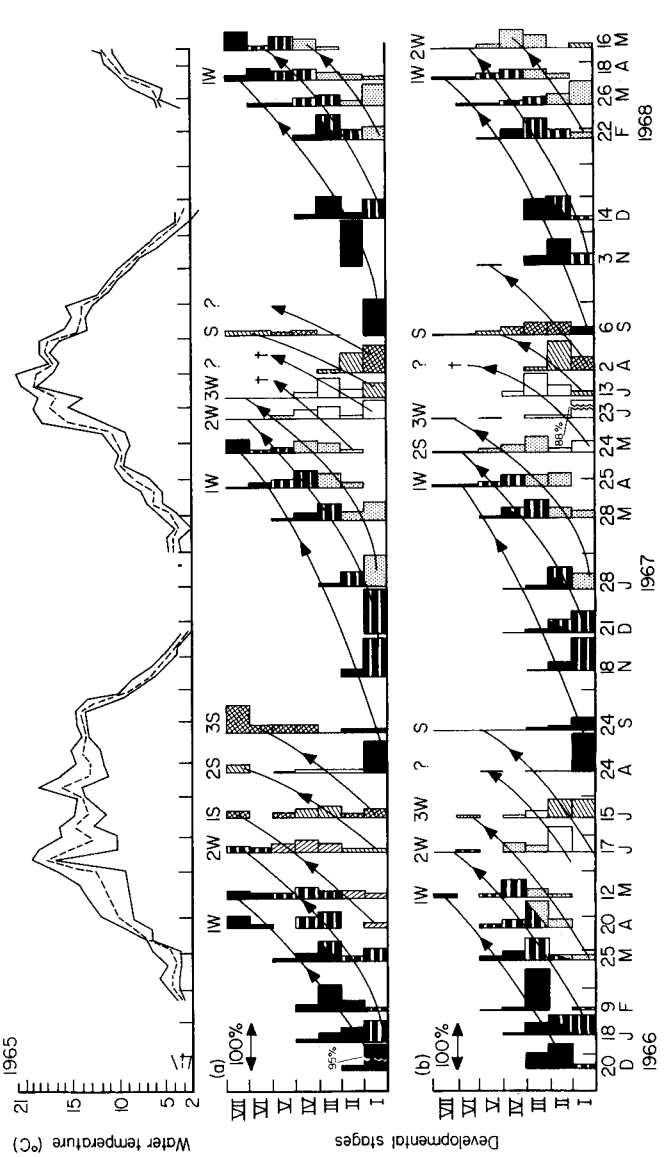
Water temperature (°C)
1965
Developmental stages
(a)
(b)
100%
95%
98%
1967
1968

FIG. 4.

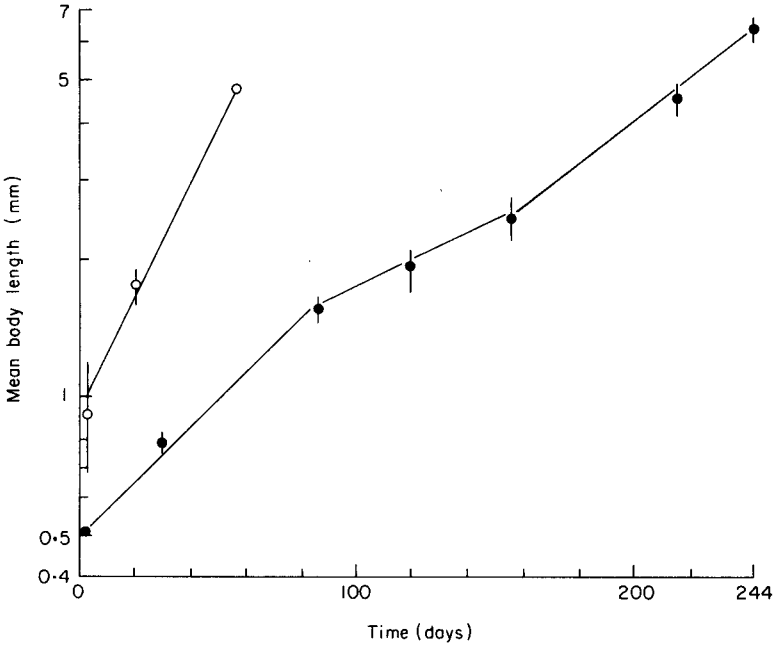

FIG. 5. Growth of typical summer (○) and winter (●) cohorts of *Baetis rhodani* in Unterseebach. Each point is the geometric mean ± 95% CL for body length (in mm).

and eggs of *B. lutheri* could not be separated from those of *B. rhodani*, *Baetis* eggs which were found in Unterseebach were called *Baetis* spp. The hatching time of these was similar to that found for *B. rhodani* by other workers (Bohle, 1969; Benech, 1972b; Elliott, 1972). The hatching time of *B. alpinus* is given in Humpesch (1979). In each year, there were two winter and three summer cohorts for *B. alpinus* from Seebach (Fig. 3) and two or three winter and one to three summer cohorts for *B. lutheri* and *B. rhodani* from the Unterseebach (Fig. 4). Therefore, over the study period of 30 months, eleven cohorts were recorded for *B. alpinus* and *B. lutheri* and ten cohorts for *B. rhodani*. Measurements of body length for each cohort in each month were converted to logarithms, the geometric mean lengths were calculated and these were plotted on a semilogarithmic scale against time (days from onset of hatching). The relationship was always linear for the summer cohorts (e.g. Fig. 5), but there were marked changes in the growth rate of winter cohorts and therefore the data for the latter were divided into periods over which exponential growth was constant (Fig. 5).

The relationship between mean length and time from the start of each period of growth was defined in eqn 1 in which the constant b is the relative rate of growth in length. Values of b were calculated for each cohort or for the growth periods in the life cycle of a cohort, using eqn 2. F-values from the variance ratio for all regressions were highly significant ($P < 0.01$). Growth of each cohort

FIG. 3. Life cycle of *Baetis alpinus* in Seebach from November 1965–May 1968. Values of mean temperature (and range) are given every 10 days at the top of the figure. Catches of larvae are expressed as a frequency distribution over the seven development stages; cohorts are distinguished by different shadings and are numbered as 1W, 2W, 1S, 2S and 3S in each year.

FIG. 4. Life cycle of (a) *Baetis lutheri* and (b) *Baetis rhodani* in Unterseebach from December 1965 – May 1968. Values of mean temperatures (and range) are given every 10 days at the top of the figure. Catches of larvae are expressed as a frequency distribution over the seven development stages: cohorts are distinguished by different shadings and are numbered at 1W, 2W, 3W and 1S, 2S, 3S or S in each year.

TABLE 2. Growth of cohorts of *Baetis alpinus* and *B. lutheri* in the field, showing the period over which larvae were caught and measured; water temperature (T, °C mean with range) and mean specific growth rate (G, % length day^{-1} ± 95% CL). n is the number of larvae which were measured; r^2 is the coefficient of determination for regressions of ln length against time. All regressions were highly significant ($P < 0.01$). W = winter, S = summer cohort

Cohort		Period	Days	Mean T	Range of T	n	Mean G	r^2
Baetis alpinus								
1965–66	1W	12 Nov–24 Mar	1–132	3.6	0.5– 5.6	175	1.38 ± 0.17	0.59
1966	2W	13 Jan –11 May	1–118	4.5	0.5– 7.0	54	1.50 ± 0.39	0.54
1966	2S	11 May– 2 Sep	1–114	7.6	5.3– 8.8	598	2.10 ± 0.10	0.75
1966	3S	16 Aug–26 Sep	1– 41	7.9	7.0– 8.8	324	2.97 ± 0.29	0.55
1966–67	1W	2 Sep –20 Apr	1–230	5.3	0.8– 8.8	162	1.19 ± 0.09	0.81
	(a)	2 Sep –13 Nov	1– 72	7.5	5.4– 8.8	79	2.10 ± 0.54	0.44
	(b)	13 Nov–20 Apr	72–230	4.2	0.8– 6.6	98	0.82 ± 0.14	0.60
1967	2W	29 Jan –24 Jun	1–146	5.1	2.6– 8.4	156	1.46 ± 0.13	0.76
1967	1S	20 Apr –31 Jul	1–102	7.1	5.4– 9.4	422	1.89 ± 0.10	0.76
1967	2S	23 May–16 Aug	1– 85	7.8	6.2– 9.5	463	2.33 ± 0.09	0.86
1967	3S	24 Jun –29 Sep	1– 97	8.5	6.9–10.1	523	1.87 ± 0.09	0.74
1967–68	1W	29 Sep –26 Mar	1–179	4.6	1.6– 8.8	313	1.56 ± 0.06	0.89
1968	2W	23 Feb –15 May	1– 82	5.0	2.4– 6.6	123	1.68 ± 0.18	0.73
Baetis lutheri								
1965–66	1W	20 Dec –12 May	1–133	4.7	2.0–13.1	136	1.10 ± 0.09	0.79
1966	2W	18 Jan –17 Jun	1–150	6.7	2.0–19.5	151	1.57 ± 0.15	0.74
1966	1S	20 Apr –15 Jul	1– 86	12.8	6.4–19.5	161	2.10 ± 0.30	0.53
1966	2S	17 Jun –24 Aug	1– 68	14.7	10.1–19.5	100	2.25 ± 0.22	0.81
1966	3S	15 Jul –24 Sep	1– 71	14.0	10.1–19.5	187	2.71 ± 0.18	0.83
1966–67	1W	24 Aug –24 May	1–273	6.9	1.6–16.1	339	0.96 ± 0.01	0.99
1966–67	2W	18 Nov –23 Jun	1–217	5.6	1.6–18.2	240	0.97 ± 0.06	0.80
1967	3W	28 Jan –13 Jul	1–166	7.5	2.0–19.2	334	1.23 ± 0.08	0.72
1967	S	13 Jul – 6 Sep	1– 55	18.0	13.8–21.0	151	3.33 ± 0.39	0.65
1967–68	1W	6 Sep –18 Apr	1–225	6.5	1.2–18.4	256	1.15 ± 0.03	0.94
1967–68	2W	14 Dec –16 May	1–154	4.4	1.2–11.6	101	1.15 ± 0.12	0.78

was then expressed as specific growth rate (% day^{-1}). Values for cohort growth rates are given in Tables 2 and 3, and these show that the growth rate varied with the mean temperature. The relationship between specific growth rate and mean water temperature was defined by eqn 3 (see also Fig. 6). Values of the constants, with 95% confidence limits, were $a = 0.30 \pm 0.84$ and $b = 0.25 \pm 0.13$ for *B. alpinus*, $a = 0.18 \pm 0.40$, $b = 0.16 \pm 0.04$ for *B. lutheri*, $a = 0.35 \pm 0.32$ and $b = 0.14 \pm 0.04$ for *B. rhodani*. The F-values from the variance ratio were significant ($P < 0.05$) for the three regression lines. The r^2 values indicated that the percentage of the variability in growth rate accounted for by variations in mean water temperature was 63% for *B. alpinus*, 91% for *B. lutheri* and 82% for *B. rhodani*. Therefore mean temperature was clearly the major factor affecting the growth rates in the field.

The regression lines describing the relationship between growth in individual larvae (G) and mean water temperature in the laboratory (see Fig. 2) have been added to Fig. 6 (broken line) so that some comparisons can be made between growth rates of cohorts in the field and larvae in the laboratory. Although the regression line for the combined *Baetis* spp. in the laboratory was slightly lower than that for *B. alpinus* in the field (Fig. 6a), the two regression equations were not significantly different ($P > 0.05$). There were significant differences ($P < 0.05$) between the field and laboratory regression lines for *B. lutheri* and *B. rhodani* (Fig. 6b, c). In both species the growth rates were similar in the field and the laboratory at low temperatures, but were always higher in the laboratory at higher temperatures.

Therefore, although mean temperature was the major factor affecting growth rates, its

TABLE 3. Growth of cohorts of *Baetis rhodani* in the field, showing the period over which larvae were caught and measured; water temperature (T, °C mean with range) and mean specific growth rate (G, % length day^{-1} ± 95% CL). n is the number of larvae which were measured; r^2 is the coefficient of determination for regressions of ln length against time. All regressions were highly significant ($P < 0.01$). W = winter, S = summer cohort

Cohort		Period	Days	Mean T	Range of T	n	Mean G	r^2
Baetis rhodani								
1965–66	1W	20 Dec–12 May	1–143	4.3	2.0–13.1	231	0.79 ± 0.09	0.55
1965–66	2W	20 Dec–17 Jun	1–179	6.3	2.0–19.5	304	0.95 ± 0.08	0.63
	(a)	20 Dec–25 Mar	1– 95	3.0	2.0– 5.6	216	0.79 ± 0.13	0.39
	(b)	25 Mar–17 Jun	95–179	7.1	4.6–19.5	191	1.36 ± 0.19	0.51
1966	3W	25 Mar–15 Jul	1–112	10.8	4.6–19.5	106	1.14 ± 0.17	0.63
	(a)	25 Mar–17 Jun	1– 84	7.1	4.6–19.5	105	1.10 ± 0.17	0.61
	(b)	17 Jun–15 Jul	84–112	15.2	10.1–19.5	25	2.97 ± 1.34	0.48
1966	S	17 Jun–24 Sep	1– 99	14.3	10.1–19.5	63	2.33 ± 0.29	0.81
1966–67	1W	24 Aug–25 Apr	1–244	6.7	1.6–16.1	762	1.04 ± 0.05	0.71
	(a)	24 Aug–18 Nov	1– 86	12.2	6.2–16.1	615	1.39 ± 0.14	0.38
	(b)	18 Nov–28 Jan	86–157	3.1	1.6– 8.6	170	0.65 ± 0.17	0.26
	(c)	28 Jan –25 Apr	157–244	3.8	2.0– 7.2	108	1.09 ± 0.20	0.54
1966–67	2W	18 Nov–24 May	1–187	4.6	1.6–10.4	468	1.04 ± 0.06	0.68
	(a)	18 Nov–28 Mar	1–130	3.4	1.6– 8.6	390	0.93 ± 0.11	0.48
	(b)	28 Mar–24 May	130–187	6.8	2.0–10.4	123	1.82 ± 0.30	0.54
1967	3W	28 Jan –23 Jun	1–146	6.3	2.0–18.2	297	1.05 ± 0.09	0.62
	(a)	28 Jan –28 Mar	1– 59	2.8	2.0– 4.7	122	0.98 ± 0.33	0.22
	(b)	28 Mar–23 Jun	59–146	8.4	2.0–18.2	211	1.29 ± 0.18	0.50
1967	S	13 Jul – 6 Sep	1– 55	18.0	13.8–21.0	97	3.01 ± 0.25	0.85
1967–68	1W	6 Sep –18 Apr	1–225	6.5	1.2–18.4	518	0.82 ± 0.07	0.66
1967–68	2W	3 Nov–16 May	1–195	4.4	1.2–10.0	300	0.81 ± 0.05	0.64
	(a)	3 Nov–26 Mar	1–144	2.7	1.2–10.0	266	0.74 ± 0.06	0.53
	(b)	26 Mar–16 May	144–195	7.9	3.0–11.6	78	1.82 ± 0.41	0.54

effect was not the same in the field and the laboratory for at least two of the three *Baetis* spp. The possible reasons for this discrepancy will be discussed later.

Discussion

Landa (1968) classified the life cycles of Central European Ephemeroptera into groups and types according to the number of generations per year, and also divided each life cycle into periods of slow and fast growth. Several workers have used a similar approach, and have recognized slow-growing winter generations and fast-growing summer generations (see references cited in the introduction). Few workers have attempted to separate cohorts, but these must be recognized if growth rates and production rates are to be estimated accurately. Svensson (1977) found four cohorts of *Ephemera danica* in one year but each cohort took two or three years to complete the life cycle. Brittain (1976) probably had only one cohort in his study of *Leptophlebia vespertina*. No other workers have separated cohorts and the present study is the first to do so for *Baetis* spp.

In spite of this lack of information on cohorts, an attempt has been made to summarize information on growth rate in Ephemeroptera (Table 4). Growth in length was approximately exponential in the present study and that of Brittain (1976), and it was assumed to be exponential in the other studies. Teckelmann (1974) is the only worker to conclude that growth was linear and gives a rate of 1.8 mm per month for *Baetis* spp. from the end of June to the beginning of September in Trubach, Germany. The growth rates in Table 4 are all expressed as specific growth rates in length (G_L% day^{-1}) and some values had to be re-calculated from the published data. Most of the estimates were obtained from production studies

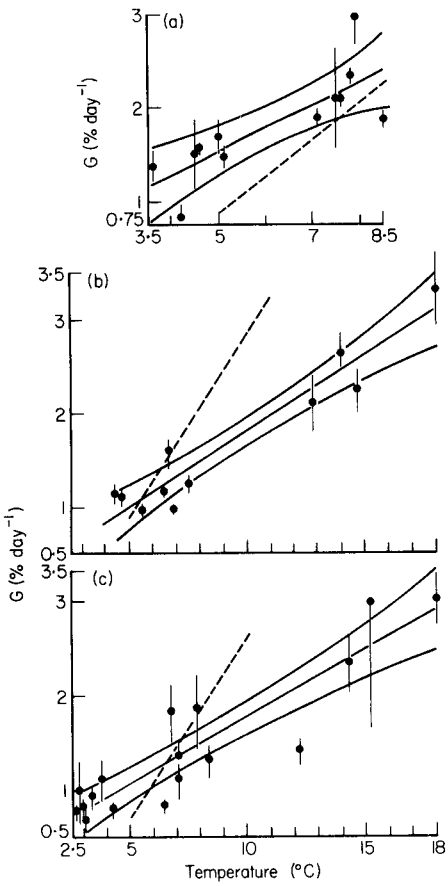

FIG. 6. Relationship between specific growth rate (% length $day^{-1} \pm 95\%$ CL) of cohorts in the field and mean water temperature (T°C) for (a) *Baetis alpinus*, (b) *B. lutheri*, (c) *B. rhodani*. 95% confidence limits are shown for the regression lines. The regression lines from the laboratory experiments (see Fig. 2) have been added for comparison (broken lines on figures).

in which growth rates were expressed in terms of weight (G_W% day^{-1}), not length. It was therefore necessary to know the relationship between weight (W) and length (L). This relationship is usually well described by the equation:

$$W = aL^b \tag{4}$$

Converting to common logarithms:

$$\log W = \log a + b \log L \tag{5}$$

where a and b are constants. Values of the weight exponent (b) were 2.80 for *Hexagenia limbata* (Hudson & Swanson, 1972) and 2.86 for *Ephemera danica* (Svensson, 1977). Values of 2.80 for *Ephemera strigata* and 2.20 for *Ephemerella subvaria* were estimated from the published data, and a general value of 2.98 for *Baetis* spp. was estimated from the data of Zelinka (1973). These weight exponents were then used to convert G_W into G_L from the relationship:

$$G_L = \frac{G_W}{b} \tag{6}$$

The values of G_L were expressed as ranges over summer and winter periods for *Baetis* spp., and as annual ranges for the other species. Growth values of the three *Baetis* spp. in the present study were generally higher than those for *Baetis* spp. elsewhere, especially in summer, but were comparable to the growth rates of all other species except *Ephemera danica*. The slow growth rates of *E. danica* (Table 4) are obviously related to its long life cycle of 2–3 years. *Ephemera strigata* had the highest growth rates with a value of *c.* 5.6% day^{-1}, but this high rate occurred only in the early part of the life cycle when the larvae were very small and temperatures were high. The highest rates of *c.* 3% day^{-1} in the present study usually occurred in the fast-growing summer cohorts of all three species.

There were only five to nine moults between larval stages III and VII in the present study and these values are very low compared with those obtained for other species of Ephemeroptera (e.g. Lubbock, 1863, 1866; Gros, 1923; Rawlinson, 1939; Schmidt, 1951; Fröhlich, 1969; Brittain, 1976). Therefore, there must be a large number of moults in the larval stages prior to stage III. There are usually seventeen to nineteen moults in a summer cohort and twenty-five to twenty-seven moults in a winter cohort of *B. rhodani* in a small stony stream in the English Lake District (J. M. Elliott, personal communication). The intervals between moults in the present study were similar to those recorded for other species of Ephemeroptera (e.g. Lubbock, 1863; Dürken, 1923; Lichtenberg, 1973), but Schmidt (1951) has shown that moulting frequency can vary in injured larvae.

Temperature has been shown to be a major regulatory factor in the growth of *B. alpinus*,

TABLE 4. Summary of information on growth rates in Ephemeroptera. For each species is given the location where the larvae occurred; the water temperature (range in °C); the duration of the life cycle (in months); the number of cohorts per year, and the range of the specific growth rates for body length (G_L % day^{-1}; see text pp. 475–476)

Species	Locality (country)	Water temperature	Duration of life cycle	Cohorts	G_L Summer	G_L Winter	Reference
Baetis alpinus Pictet	Seebach (Austria)	0.5–10.1	3–8	5	1.87–2.97	0.82–2.10	
B. lutheri Müller-Liebenau	Unterseebach (Austria)	1.2–21.0	2.5–9	4–5	2.10–3.33	0.96–1.57	
B. rhodani Pictet	Unterseebach (Austria)	1.2–21.0	2.5–8	4	2.33–3.01	0.65–2.97	
B. vagans McDunnough	Valley Creek (USA)	9.0–18.0	3–7	–	0.98–1.20	0.31–1.53	Waters (1966)
B. bicaudatus Dodds	Logan River (USA)						
	Site 1	4.8– 6.1	3–8	–	0.00–1.11	0.00–1.44	Pearson & Kramer (1972)
	Site 2	*c.* 3.0–*c.* 7.5		–	0.13–1.34	0.27–1.11	
	Site 3	*c.* 2.5–*c.* 10.0		–	0.25–1.85	0.07–1.01	
	Site 4	0.0–17.1		–	0.20–1.78	0.10–0.97	
Ephemera danica Müller	Stampen (Sweden)	0.8–14.6	24–36	4	0.00–0.70		Svensson (1977)
E. strigata Eaton	Niu-gawa (Japan)	*c.* 4.0–26.0	12	–	0.05–5.58		Gose (1970)
Hexagenia limbata (Serville)	Lewis and Clark Lake (USA)	? –26.7	12–24	–	0.03–2.73		Hudson & Swanson (1972)
Leptophlebia vespertina (L.)	Lyan Dinas (Wales)	*c.* 2.0–*c.* 24.0	12	1?	0.39–1.36		Brittain (1976)
Ephemerella subvaria McDunnough	Luxemburg Creek (USA)	–	12	–	0.39–2.7		Waters & Crawford (1973)

B. lutheri and *B. rhodani* in both the laboratory and the field. Brittain (1976) found a similar relationship for *Leptophlebia vespertina*, but Maxwell & Benson (1963) could not clearly demonstrate that temperature affected the growth of *Epeorus* sp. in the field.

In the present study, there was agreement between the growth rates of *B. alpinus* in the field and the laboratory. This was probably due to the similar temperature ranges, food and light conditions in both the field and the laboratory. The growth rates of *B. lutheri* and *B. rhodani* were slower in the field than in the laboratory at higher temperatures. This discrepancy may have been due to differences in temperature conditions, crowding and food. The growth rates in both the field and the laboratory were clearly related to mean temperature but whilst the temperature conditions in the laboratory were fairly constant, there were often large diel variations in temperature in the Unterseebach, and these may have affected growth in the field. In the laboratory, a single larva was kept in each cage and was provided with fresh food from the Seebach. Therefore the larvae in the laboratory could graze on this food without having to compete with other larvae, whilst possible competition between larvae in the field may have been partially responsible for the lower growth rates at higher temperatures. As the algal communities on the stones in Seebach and Unterseebach are not the same, especially in summer (Kann, 1978), there is the possibility that differences in the quality and quantity of food caused differences in growth rates, as has been shown for other freshwater invertebrates (e.g. Willoughby & Sutcliffe, 1976; Cianciara, 1979; Marcus, Sutcliffe & Willoughby, 1978). It is not known if some or all of these factors are important and it is possible that another factor may be responsible for the differences in growth rates. It can be concluded, however, that temperature is the major factor affecting growth rate and further work is necessary to separate the effects of other environmental variables.

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References

Bench V. (1972a) Le polyvoltinisme chez *Baetis rhodani* Pictet (Insecta, Ephemeroptera) dans un ruisseau a truites des Pyrénées-Atlantiques, le Lissurga. *Ann. Hydrobiol.* 3, 141–171.

Benech V. (1927b) Étude expérimentale de l'incubation des oeufs de *Baetis rhodani* Pictet. *Freshwat. Biol.* 2, 243–252.

Bohle H.W. (1969) Untersuchungen über die Embryonalentwicklung und die embryonale Diapause bei *Baetis vernus* Curtis und *Baetis rhodani* (Pictet) (Baetidae, Ephemeroptera). *Zool. Jb. Abt. Anat. u. Ontog.* 86, 493–557.

Bretschko G. (1965) Zur Larvalentwicklung von *Cloëon dipterum, Cloëon simile, Centroptilum luteolum* und *Baetis rhodani*. *Z. wiss. Zool.* 172, 17–36.

Brittain J.E. (1976) Experimental studies on nymphal growth in *Leptophlebia vespertina* (L.) (Ephemeroptera). *Freshwat. Biol.* 6, 445–449.

Brown D.S. (1961) The food of larvae of *Cloëon dipterum* L. and *Baetis rhodani* (Pictet) (Insecta, Ephemeroptera). *J. Anim. Ecol.* 30, 55–75.

Cianciara S. (1979) Studies on the biology and bioenergetics of *Cloëon dipterum* (L.). *Proc. 2nd Int. Conf. Ephemeroptera* (in press).

Dürken B. (1923) Die postembryonale Entwicklung der Tracheenkiemen und ihre Maskulatur bei *Ephemerella ignita*. *Zool. Jb. Abt. Anat. u. Ontog.* 44, 439–614.

Einsele W. (1956) Untersuchungen über die Atmungsphysiologie sich entwickelnder Salmonideneier; ihre Anwendung auf die Natur und auf die züchterische Technik. *Öst. Fisch.* 10, 2–18.

Elliott J.M. (1967) The life histories and drifting of the Plecoptera and Ephemeroptera in a Dartmoor stream. *J. Anim. Ecol.* 36, 343–362.

Elliott J.M. (1972) Effect of temperature on the time of hatching in *Baetis rhodani* (Ephemeroptera: Baetidae). *Oecologia (Berl.)*, 9, 47–51.

Fröhlich C.G. (1969) *Caenis cuniana* sp.n., a parthenogenetic mayfly. *Beitr. neotrop. Fauna*, 6, 103–108.

Gose K. (1970) Life history and production rates of *Ephemera strigata* (Ephemeroptera) *Jap. J. Limnol.* 31, 21–26.

Gros A. (1923) Études sur les premiers stades des Ephémères du Jura français. *Ann. Biol. lacustre*, 12, 49–74.

Hudson P.L. & Swanson G.A. (1972) Production and standing crop of *Hexagenia* (Ephemeroptera) in a large reservoir. *Studies in Nat. Sci., Nat. Sci. Res. Inst., Eastern N.M. Univ.* 1, 1–42.

Humpesch U. (1971) Zur Faktorenanalyse des Schlüpfrhythmus der Flugstadien von *Baetis alpinus* Pict. (Baetidae, Ephemeroptera). *Oecologia (Berl.)*, 7, 328–341.

Humpesch U. (1979) Autökologische Untersuchungen zum Entwicklungszyklus einiger mitteleuropäischer Ephemeropterenarten. *Proc. 2nd Int. Conf. Ephemeroptera* (in press).

Kann E. (1978) Systematik und Okologie der Algen österreichischer Bergbäche. *Arch. Hydrobiol.* 53, Suppl. 4, 405–643.

Landa V. (1968) Developmental cycles of Central European Ephemeroptera and their interrelations. *Acta ent. bohemoslav.* 65, 276–284.

Langford T.E. (1971) The distribution, abundance and life-histories of stoneflies (Plecoptera) and mayflies (Ephemeroptera) in a British river, warmed by cooling water from a power station. *Hydrobiologia,* 38, 339–377.

Larsen R. (1968) The life cycle of Ephemeroptera in the lower part of Aurland river in Sogn and Fjordane, Western Norway. *Norsk. ent. Tidsskr.* 15/1, 49–59.

Lichtenberg R. (1973) Die Entwicklung einiger charakteristischer Benthosorganismen des 'Hallateiches' südlich von Wien. *Annln. naturh. Mus. Wien,* 77, 305–311.

Lubbock J. (1863) On the development of *Cloëon (Ephemera) dimidiatum.* Part I. *Trans. Linn. Soc. Lond.* 24, 61–78.

Lubbock J. (1866) On the development of *Cloëon (Ephemera) dimidiatum.* Part II. *Trans. Linn. Soc. Lond.* 25, 477–492.

Macan T.T. (1957) The life-histories and migrations of the Ephemeroptera in a stony stream. *Trans. Soc. Br. Ent.* 12, 129–156.

Marcus J.H., Sutcliffe D.W. & Willoughby L.G. (1978) Feeding and growth of *Asellus aquaticus* (Isopoda) on food items from the littoral of Windermere, including green leaves of *Elodea. Freshwat. Biol.* 8, 501–521.

Maxwell G.R. & Benson A. (1963) Wing pad and tergite growth of mayfly nymphs in winter. *Am. Midl. Nat.* 69, 224–230.

Pearson W.D. & Kramer R.H. (1972) Drift and production of two aquatic insects in a mountain stream. *Ecol. Monogr.* 24, 365–385.

Pleskot G. (1958) Die Periodizität einiger Ephemeropteren der Schwechat. *Wasser und Abwasser,* 1958, 1–32.

Pleskot G. (1961) Die Periodizität der Ephemeropteren–Fauna einiger österreichischer Fliessgewässer. *Verh. int. Verein. theor. angew. Limnol.* 14, 410–416.

Rawlinson R. (1939) Studies on the life-history and breeding of *Ecdyonurus venosus* (Ephem.). *Proc. zool. Soc. Lond.* 109, 377–450.

Schmidt H. (1951) Amputation und Regeneration von Schwanzfäden und Abdominalsegmenten bei Larven der Ephemeridenart *Cloëon dipterum* L. und ihr Einfluss auf die Häutungsintervalle. *Zool. Jb. Abt. Physiol.* 62, 395–428.

Strenger A. (1979) Die Ernährung der Ephemeridenlarven als funktionsmorphologisches Problem. *Proc. 2nd Int. Conf. Ephemeroptera* (in press).

Svensson B. (1977) Life cycle, energy fluctuations and sexual differentiation in *Ephemera danica* (Ephemeroptera), a stream-living mayfly. *Oikos,* 29, 78–86.

Teckelmann U. (1974) Temperaturwirkungen auf Wachstum und Stoffwechsel kaltstenothermer Fliesswassertiere. *Arch. Hydrobiol.* 74, 479–527.

Thibault M. (1971) Le développement des éphéméroptères d'un ruisseau à truites des Pyrénées-Atlantiques, le Lissuraga. *Annls. Limnol.* 7, 53–120.

Thorup J. (1963) Growth and life-cycle of invertebrates from Danish springs. *Hydrobiologia,* 22, 55–84.

Thorup J. (1973) Interpretation of growth-curves for animals from running waters' *Verh. int. Verein. theor. angew. Limnol.* 18, 1512–1520.

Ulfstrand S. (1968) Life cycles of benthic insects in Lapland streams (Ephemeroptera, Plecoptera, Trichoptera, Diptera, Simuliidae). *Oikos,* 19, 167–190.

Waters Th.F. (1966) Production rate, population density, and drift of a stream invertebrate. *Ecology,* 47, 595–604.

Waters Th.F. & Crawford G.W. (1973) Annual production of a stream mayfly population: comparison of methods. *Limnol. Oceanogr.* 18, 286–296.

Willoughby L.G. & Sutcliffe D.W. (1976) Experiments on feeding and growth of the amphipod *Gammarus pulex* (L.) related to its distribution in the River Duddon. *Freshwat. Biol.* 6, 577–586.

Zelinka M. (1973) Die Eintagsfliegen (Ephemeroptera) in Forellenbächen der Beskiden. II.–Produktion. *Hydrobiologia,* 42, 13–19.

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