GROWTH OF RHEOPHILIC MAYFLY LARVAE (EPHEMEROPTERA)

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Individual growth of mayfly larvae was investigated. The parameters for relationships between larval growth rates and body weight for sixteen species of three families of rheophilic mayfly larvae did not differ either at specific or generic levels within a family or family levels. Growth rates of mayfly larvae obtained by cage rearing were compared with the values estimated for field populations using size-frequency histograms.

INTRODUCTION

One method of estimating production in aquatic fauna populations is based upon the determination of the growth rate of the individuals which constitute the populations. The reliability of estimated production parameters depends on accurate determinations of individual growth rates. Initial data on mayfly larval growth may be obtained by different methods: rearing of larvae in cages in laboratory (HUMPESCH, 1979; GOLUBKOV, 1979) or in a stream (GREY, 1981; BENKE & JACOBI, 1986; TIUNOVA, 1988) or by studying population size-frequency histograms (WATERS & CRAWFORD, 1973; BENGTSSON, 1981; WELTON *et al.*, 1982). I consider that the most appropriate estimations on larval growth can be obtained from the *in situ* rearing method. Using this method, we can consider almost all the conditions characteristic of the natural environment of mayfly populations: daily fluctuations in temperature, water flow and oxygen content and feeding pattern of mayflies. The method based on the determination of growth rates of animals *in situ* has recently become very popular in the Russia (ALIMOV, 1981; GOLUBKOV & PAVLOV, 1986; BALUSHKINA, 1987; KOCHARINA,1989). I prefer this method as being more accurate.

On the other hand, the reliable results are obtained by studying population size-frequency histograms, when each size-class can be separated at any time. The separation of cohorts by histograms of size-frequency of the populations of mayfly larvae is difficult. This is for several reasons: first, the low number of larvae in many species of mayfly; secondly, the different mortality rates for individuals of different ages. Therefore, this paper is devoted to a study of the growth of rheophilic mayfly larvae and some quantitative parameters of this growth.

STUDY SITE AND ORGANISMS

The experiments were carried out at the Hydrobiological Field Station of our institute, located in the forest reserve «Kedrovaya Pad», situated along the west coast of Amur Bay, 30 km to the west of Vladivostok. The material was collected near the field station from the River Kedrovaya, a typical mountain stream in the Russian Far East.

The mean monthly water temperatures in the river for the research period from September 1985 to August 1986 varied as follows:

Month	IX	X	XI	XII	I	II
t°C	11.8	9.4	4.1	0.6	0.2	0.2
Month	III	IV	V	VI	VII	VIII
t°C	0.4	2.5	6.4	7.7	9.6	13.8

During the research period from 2 July to 12 September 1988, the mean river temperature was 12.9 °C with a range of 7.3 to 15.2 °C. Daily fluctuations of water temperature were less than 5 °C in summer and 2-3 °C in spring and fall. The oxygen concentration in the stream was about at the saturation level throughout the year. The total water hardness in the middle reach of the stream was about 0.32 mg-eqv/litre. The content of Ca^+-ions was 0.12 mg-eqv/litre.

The growth of mayfly larvae was next studied: for *Drunella aculea* and *Cincticostella levanidovae* from 8 October 1985 to 30 May 1986, for *Cincticostella tshernovae* from 16 September 1985 to 30 May 1986, for *Cinygmula grandifolia* from 25 November 1985 to 14 April 1986, for *Epeorus gornostajevi* and *Baetis pseudothermicus* from 10 October 1985 to 27 July 1986, for *Drunella solida*, *D. triacantha* and *D. cryptomeria* from 25 February to 8 August 1986, for *Cinygmula latifrons* and *C. cava* from 8 March to 29 April 1986, for *Baetis fuscatus* from 9 July to 24 September 1985, for *Ecdyonurus scalaris* from 13 August to 12 September 1985, for *Serratella setigera* and *Ephemerella kozhovi* from 2 July to 4 August 1988, for *Acentrella sibirica* from 8 June to 4 August 1988.

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METHODS

The growth of the larvae was observed using the specially designed cages submerged in the localities of the natural habitats. The cage was a thin-walled polyvinilchloride cylinder, 30 mm in diameter and 20-25 mm deep. The cylinder had a fine mesh net at the bottom-No 25 threads per/cm. Each cage was fastened to a string 2-3 m long, anchored to the bottom by means of small stones and fitted tightly. A set of the cages was placed along the stream, at the downstream and of a small riffle (at 20-25 cm depth).
The mayfly larvae were weighed (wet weight) and their body length and head capsule width measured: for this purpose the larvae were put into cages in a low volume of water with pieces of ice. This rules out the possibility of temperature stress and the insects settle down quickly. The larvae, before being measured, should be dried on damp filter paper- if the larvae are large, thin strings of filter paper should be passed under the wing pads to eliminate the water. After measurements the larvae were replaced in a cage that was put into a container with at least 10 liters of water. Essential temperature and aeration were maintained. After the processing of 5-10 cages they were replaced in the river. At intervals (from 5-d to 25 days) the cages were temporarily removed from the stream to remeasure the mayflies.
The larvae fed on detritus particles and algae growing on the net covering the opening of the cages. Various small invertebrates were added to the cages with large specimens of the family Ephemerellidae which feed partially as predators.
Total length was measured from the anterior edge of the head to the edge of the abdominal tergitum 10 when this was in the normal resting position. Measurements were made under a binocular microscope at magnifications of x16 and x32. Torsal balances WT-20, WT-50, WT-250 with accuracies of 0.01 and 0.1 mg were used in the experiment.
To estimate growth rates of *Acentrella sibirica* and *Drunella cryptomeria* the seasonal differences in size-frequency distribution were analysed. Histograms were constructed for these species from measurement of larvae from monthly quantitative benthos samples. Quantitative samplings were made from July to August, 1988 for *Acentrella sibirica* and from May to August, 1980 for *Drunella cryptomeria*. Immediately after collection, the samples were fixed with 4%-formaldehyde. Using the equation of relationship between larval body weight (W, mg) and head capsule width (d, mm) for *Acentrella sibirica*: $W = 2.167\ d^{3.457}$ and for *Drunella cryptomeria:* $W = 1.370\ d^{3.671}$ (TIUNOVA, 1993) characteristics of weight growth were obtained.
Absolute (dW/dt) growth rates and specific (C^{w}) were estimated for larvae using the following equation (WINBERG, 1968):

$$dW/dt = C_w\ W',\ C_w = (\ln W_2 - \ln W_1) / (t_2 - t_1),\quad (1)$$

where: W_1 is body weight after the moult and W_2 is body weight after the next moult, (t_2-t_1) was the duration of the interval of the moult (TIUNOVA, 1987).
Mean exponential weight of a larva was found using the equation:

$$W' = (W_2 - W_1) / (\ln W_2 - \ln W_1)\quad (2)$$

Emperic data were processed using the equation (WINBERG, 1966):

$$dW/dt = N.W^{m},\quad (3)$$

where: dW/dt, absolute growth rate (mg day^{-1}), W, body weight (mg) and N and m, coefficients.
The growth rate obtained under different temperatures was converted to that of 11.5 °C using temperature corrections (q), that were calculated according to equation (WINBERG, 1968):

$$q = Q_{10}^{(T_2 - T_1)/10},$$

where: T_2 is the average water temperature in the River Kedrovaya during the period of intensive growth (11.5 °C); T_1 is average temperature at the experiment; Q is Vant-Hoffs coefficient. For the mayfly larvae species studied the following coefficients were used Q_{10}: *Cinygmula grandifolia* 1.40, *Drunella aculea* 1.85, *D. cryptomeria* 2.29, *D. triacantha* 2.11, *Cincticostella levanidovae* 2.41 (GOLUBKOV & TIUNOVA, 1988), for other species 2.25 (WINBERG, 1983).

The allometric growth equation was used to describe the relationship between body weight and length (SIMPSON *et al.*, 1960; WINBERG, 1971):

$$W = a\ L^{b},\quad (4)$$

where: W is body wet weight (mg), L is body length (mm) and a and b are coefficients.
Parameters of equations of degree function were obtained using the method of least squares and their confidence intervals using the method proposed by UMNOV (1976).

RESULTS AND DISCUSSION

The biology of the species

The biology of the species under study, in particular their biomass, population density and life cycles were described in detail elsewhere (TIUNOVA, 1993). All species in the study are characterized by one year life cycles. Species under consideration can be classified into two major categories, univoltine and multivoltine with some subtypes by the classification system of CLIFFORD (1982). *Drunella aculea, D. solida, Cincticostella levanidovae, C. tshernovae, Cinygmula grandifolia* have a univoltine winter cycle, the populations overwinter in the nymphal stage. As a rule, the development of the larvae of these species continues throughout most of the year (Sept.-June) having insignificant growth delay or a decrease in growth rate (*C. grandifolia*) in winter. *Drunella triacantha, D. cryptomeria, Ephemerella kozhovi, Cinygmula cava* and *C. latifrons* have a univoltine winter cycle also. But they were hatched in autumn and remain in such stage up to the beginning of spring. These species begin to grow under 2-4 °C temperature conditions and their life cycles complete in a 120-140 day period. *Baetis fuscatus, Ecdyonurus scalaris* and *Serratella setigera* have a univoltine summer cycle. These species hatch and begin to develop and grow rapidly in summer when the optimal temperature for their growth (10-15°C) sets in. *Acentrella sibirica, Baetis pseudothermicus* and *Epeorus gornostajevi* were classified as species with a multivoltine type of life cycle. *B. pseudothermicus* and *E. gornostajevi* populations exhibit a seasonal bivoltine cycle with an overwintering generation in the nymphal stage and one summer generation. *A. sibirica* is a bivoltine summer species, with two summer generations.

Relationship between larval body weight and body length

The parameters were calculated for length-weight relationship equation for 16 species of mayfly larvae (Table 1). The data obtained show that the length-weight relationship equations for *Drunella solida, D. aculea, D. triacantha, D. cryptomeria, Cincticostella levanidovae, C. tshernovae, Serratella setigera* and *Ephemerella kozhovi* are very similar, their parameters do not differ significantly. These results allow us to calculate the parameters of the general equation for all species studied of the family Ephemerellidae (r = 0.98, n = 243):

$$W = (0.033 \pm 0.002)\ L^{(2.877 \pm 0.032)} \quad (5)$$

A comparison of the equation parameters for *Cinygmula grandifolia, C. cava, C. latifrons, Epeorus gornostajevi* and *Ecdyonurus scalaris* also did not reveal any significant differences. It allowed us to derive a general equation for all species studied in the mayfly Heptageniidae (r = 99, n = 158):

$$W = (0.036 \pm 0.002)\ L^{(2.728 \pm 0.028)} \quad (6)$$

It is worth noting an equation, deduced for *Baetis fuscatus* and *B. pseudothermicus* (r = 99, n = 58):

$$W = (0.027 \pm 0.001)\ L^{(2.652 \pm 0.039)} \quad (7)$$

The data obtained for *Acentrella sibirica* lie out side the confidence interval derived for the equation. Probably, it is necessary to obtain some additional data on the larvae of other species of the genus *Acentrella*. When comparing Equation (5) or (6) with Equation (7) we find a significant difference between their parameters, their curves do not overlap throughout the body weight range investigated (Fig. 1).

Thus, the power coefficient values for Equation (5-7) turn out to be less than 3 and varied within a range between 2.652 to 2.877. It suggest that a negative allometric growth predominates among the animals investigated. Since the

Table 1. Coefficients of the equation of the weight (W, mg) - length (L, mm) relationship for mayfly larvae: $W = a \cdot L^b$. ± represent variation of parameters.

Species	Lenght range, mm	n	a	b	r
Drunella solida	1.9 -12.6	34	0.031 ± 0.005	2.914 ± 0.058	0.99
Drunella sculea	1.0 -15.4	37	0.032 ± 0.003	2.952 ±0.029	0.99
Drunella criptomeria	1.7 - 9.5	30	0.026 ± 0.002	3.028 ± 0.036	0.99
Drunella triacanta	1.5 -12.5	35	0.040 ± 0.002	2.699 ± 0.026	0.93
Cincticostella levanidovae	1.3 - 11.3	32	0.038 ± 0.006	2.747 ± 0.050	0.99
Cincticostella tshernovae	1.8 -11.3	25	0.037 ± 0.003	2.857 ± 0.046	0.99
Ephemerella kozhovi	1.7 - 7.0	26	0.034 ± 0.002	2.754 ± 0.036	0.99
Serratella setigera	1.5 - 5.4	24	0.036 ± 0.003	2.806 ± 0.051	0.99
Cinygmula grandifolia	0.8 - 14.6	40	0.032 ± 0.003	2.820 ± 0.020	0.99
Cinygmula latifrons	1.6 - 8.3	25	0.025 ± 0.002	2.808 ± 0.052	0.99
Cinygmula cava	2.3 - 8.6	25	0.023 ± 0.002	2.908 ± 0.061	0.99
Ecdyonurus scalaris	1.8 - 6.5	25	0.036 ± 0.003	2.785 ± 0.074	0.99
Epeorus gornostajevi	0.7 - 13.8	43	0.048 ± 0.005	2.635 ± 0.025	0.99
Acentrella sibirica	1.2 - 4.4	27	0.043 ± 0.002	2.478 ± 0.044	0.99
Baetis fuscatus	1.0 - 9.4	32	0.028 ± 0.003	2.660 ± 0.030	0.99
Baetis pseudothermicus	2.4 - 7.5	26	0.027 ± 0.003	2.635 ± 0.068	0.99

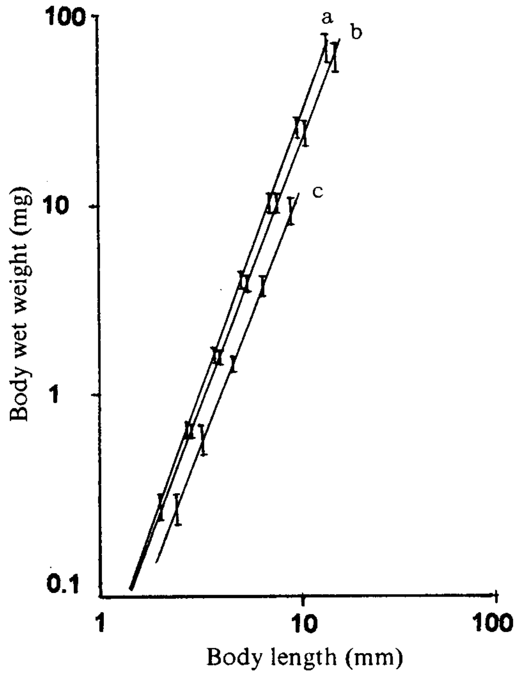

Fig. 1. A relationship between body wet weight (W, mg) and body length (L, mm) of larvae. a) an average relationship curve, calculated from equation (5); b) from equation (6); c) from equation (7). Vertical lines indicate confidence intervals at the 95% significance level. Both variates plotted logarithmically.

larval body shape of the families Ephemerellidae and Heptageniidae changes with their growth and becomes flatter and wider. The most distinct negative allometric growth was observed in Baetidae (b = 2.652), it is connected with an appreciable body extension during the growth process.

Larval Growth

GOLUBKOV (1979, 1988) clearly demonstrated that the mayfly larvae grow in accordance with the so-called low of parabolic growth suggested elsewhere by WINBERG (1966). Growth is proportional to the body weight and their relationship is expressed by a power function equation. Using our results on the growth rates over the period of observations, we obtained the equations for dW/dt as a function of W for 16 species mayfly larvae belonging to three families (Table 2). However, it turned out that the slope of growth rate on body weight did not differ significantly either on specific or generic levels within a family or between different families. Using growth rate estimates, the mayfly species studied were divided into three groups. Within these groups, *Acentrella sibirica, Baetis pseudothermicus, Ecdyonurus scalaris, Cinygmula latifrons* and

Table 2. Coefficients in equations of the relationship of absolute growth rate (dW/dt, mg day^{-1}) and body wet weight (W, mg) of mayfly larvae: $dW/dt = N W^m$ (corrected to 11.5°C). ±represent variation of parameters.

Species	Weight range, mg	n	N	±	m	±	r
Acentrella sibirica	0.18-1.16	29	0.055	0.005	0.863	0.094	0.86
Baetis pseudothervicus	0.23-3.68	33	0.057	0.002	0.844	0.048	0.95
Baetis fuscatus	0.13-2.35	16	0.141	0.029	0.841	0.025	0.93
Ecdyonurus scalaris	0.24-3.92	24	0.067	0.004	0.847	0.072	0.93
Cinugmula cava	0.50-9.89	45	0.032	0.002	0.787	0.043	0.94
Cinygmula latifrons	0.42-5.90	33	0.045	0.003	0.884	0.068	0.92
Cinugmula grandifolia	0.28-42.6	16	0.031	0.003	0.757	0.034	0.98
Epeorus gornostajevi	2.30-50.5	21	0.047	0.008	0.694	0.069	0.92
Serratella sibirica	0.11-3.52	39	0.057	0.003	0.939	0.023	0.96
Ephemerella kozhovi	0.17-5.34	20	0.046	0.003	0.700	0.061	0.94
Cincticostella tshernovae	0.24-39.9	32	0.051	0.002	0.888	0.026	0.99
Cincticostella levanidovae	0.14-22.1	29	0.059	0.004	0.798	0.045	0.95
Drunella aculea	0.18-141	27	0.047	0.002	0.863	0.014	0.99
Drunella cryptomeria	0.14-18.9	24	0.041	0.002	0.925	0.025	0.94
Drunella triacantha	0.33-40.0	20	0.059	0.007	0.792	0.034	0.96
Drunella solida	0.85-26.0	21	0.079	0.007	0.680	0.020	0.95

Ephemerellidae species did not differ significantly. Accordingly, the general growth rate equation was developed for these species based on 356 measurements (converted to temperature: 11.5 °C):

$$dW/dt = (0.054 \pm 0.001)\ W^{(0.817 \pm 0.015)} \quad (8)$$

The correlation coefficient is equal to 0.95.
The growth rates for *Cinygmula cava, C. grandifolia* and *Epeorus gornostajevi* also showed no significant difference. Therefore, applying 82 growth rate measurements the general equation for dW/dt was also constructed as a function of W for these species:

$$dW/dt = (0.032 \pm 0.001)\ W^{(0.792 \pm 0.024)} \quad (9)$$

The correlation coefficient is equal to 0.96.

The values of parameter N for Equation (8) and (9) differ 1.7 times (Fig. 2: a, b) *Baetis fuscatus* shows the greatest difference in the growth rate. Its growth rate turned out to be 2.6 and 4.4 times of those for two other species observed, respectively (Fig. 2c).
The question about the accuracy of obtained data is of prime importance. Since the measuring and weighing were carried out with live larvae it was considered that this method can have a negative effect on the growth of the animals and obtained data did not reflect the real animal growth. In this connection I compared results obtained by two methods: rearing of larvae in cages as in the present study and studying population size-frequency histograms for *Acentrella sibirica* and *Drunella cryptomeria* larvae. The observations on the growth of *Acentrella sibirica* larvae were carried out in summer 1988. The animals were reared in cages and at that period samples for construction of size-frequency histograms were collected in the stream. As for *Drunella cryptomeria* larvae, growth data in cages and by studying histograms were obtained in different years. Materials for size-frequency histograms were collected in 1980 and the observations on the larval growth in cages were carried out in 1986. The analysis of size-frequency histograms of the population were carried out as follows. From Fig. 3, at least one distinct peak was recognized for each sampling data. I estimated the growth by tracing the peak from 30 July-19 August. It was difficult to separate cohorts since the present histograms consist of

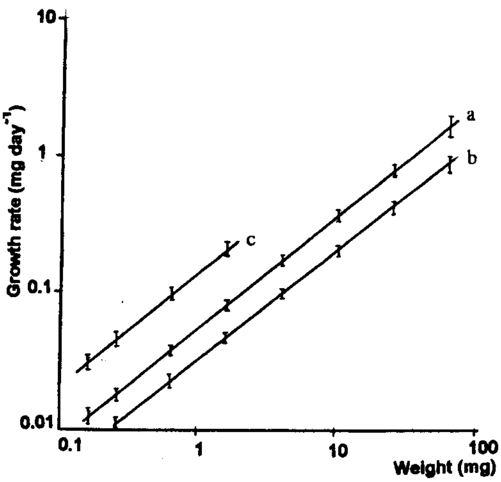

Fig. 2. A relationship between growth rate (dW/dt, mg day⁻¹) and body weight (W, mg) at 11.5°C of mayfly larvae on log/log scale. a) an average relationship curve, calculated from equation (8); b) from equation (9); c) *Baetis fuscatus*. Vertical lines indicate confidence intervals at the 95% significance level.

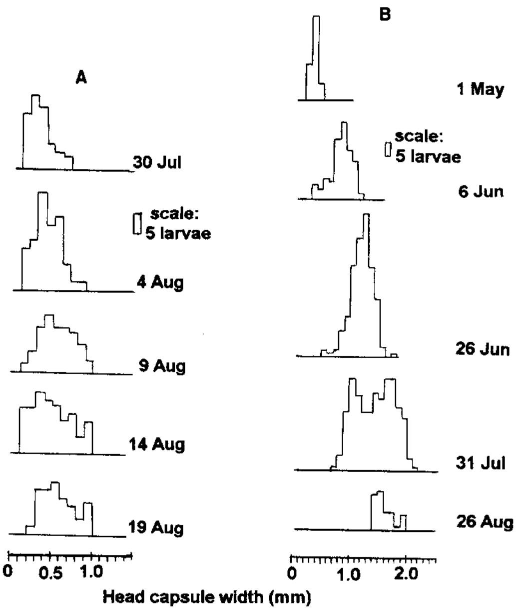

Fig. 3. Changes in the size-frequency distribution of *Acentrella sibirica* (A) and *Drunella cryptomeria* (B) in the River Kedrovaya.

only six to nine bars. Similarly from Fig. 4, one or two distinct peaks were recognized and traced to estimate larval growth (Table 3). With these data, relationships between absolute growth rate and body weight were calculated and can be expressed by the following equations:

for *A. sibirica*

$$dW/dt = (0.072 \pm 0.036)\ W^{(0.823 \pm 0.112)} \quad (10)$$

for *D. cryptomeria*

$$dW/dt = (0.068 \pm 0.027)\ W^{(0.755 \pm 0.087)} \quad (11)$$

The correlation coefficients in Equation (10) and (11) are rather high and equal 0.97 and 0.98 respectively. When comparing the relationship parameters for *Acentrella sibirica* and *Drunella cryptomeria*, that were calculated from data obtained by the different methods, one can confirm that they do not differ much. The confidence intervals overlapped in all the body weight range (Figs 4, 5). In addition the equation of relationship between absolute growth rate and body weight for *Baetis rhodani* was calculated using WELTON *et al.* (1982) data. In this paper the authors used probability paper methods to trace the change in average larval body length for each cohort from July, 1977 to February, 1978 and separated seven cohorts. Based on this material I calculate the equation of relationship to be between dW/dt and W for *Baetis rhodani* (corrected to 11.5°C) (Fig. 6):

$$dW/dt = (0.061 \pm 0.017)\ W^{(0.760 \pm 0.142)} \quad (12)$$

The correlation coefficient is equal to 0.82. It should be noted that water temperatures in summer of an experimental recirculating stream and the River Kedrovaya were compared: so, the average monthly water temperature in the experimental stream changed from 14°C in July to 9.2°C in February with maximum of 17.1°C and minimum of 8.1°C in these months. Then the comparison of the relationship between dW/dt and W parameter means in Equation (12) with parameters of Equation calculated for other species was carried out. The comparison did not show any significant difference in growth rate of *Baetis rhodani* and *Acentrella sibirica, Baetis pseudothermicus, Ecdyonurus scalaris, Cinugmula latifrons* and Ephemerellidae species that were united into one group before. Thus, it was shown that mayfly larvae growth rate data obtained in cages may be used for species with indistinguishable cohorts when estimates of growth rates are not available. Besides, the equation for *Baetis rhodani* that

Table 3. Absolute growth rate (dW/dt, mg day^{-1}) calculated from the peak values in the size-frequency histograms of the head capsule widths.

Data	Width* mm	Weight mg	Interval days	Mean weight mg	dW/dt	Tempe-rature °C	dW/dt**
			Drunella cryptomeria				
01-May	0.35	0.058	-	-	-	-	-
06-Jun	0.85	1.236	36	0,647	0.033	8.5	0.042
26-Jun	1.25	4.687	20	2.961	0.173	10.8	0.183
31-Jul	1.75	14.998	35	9,843	0.295	12.3	0.276
31-Jul	0.55	0.274	-	-	-	-	-
26-Aug	1.55	9.859	26	5.067	0.369	13.5	0.312
			Acentrella sibirica				
30-Jul	0.35	0.057	-	-	-	-	-
04-Aug	0.40	0.091	5	0.073	0.007	12.7	0.006
04-Aug	0.65	0.489	-	-	-	12.7	-
09-Aug	0.55	0.274	6	0.198	0.023	14.0	0.019
09-Aug	0.75	0.802	-	0.632	0.052	14.0	0.042
14-Aug	0.45	0.137	6	-	-	-	-
14-Aug	0.85	1,236	-	1.005	0.072	14.0	0.059
19-Aug	0.65	0.489	6	0.277	0.059	14.0	0.048
19-Aug	1.00	-	-	-	-	-	-

*Head capsule width at the peak of the histogram
**Corrected for the value at 11.5°C

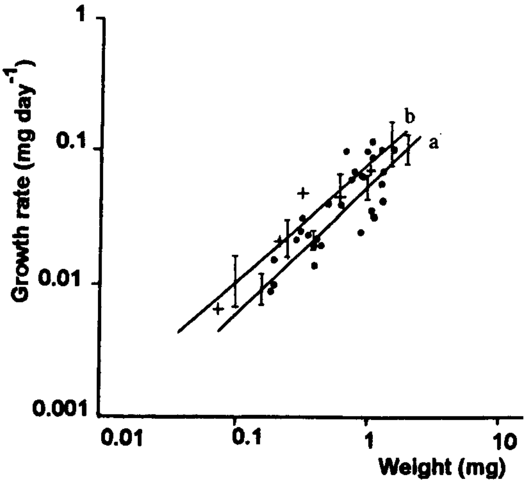

Fig. 4. A relationship between growth rate (dW/dt, mg day^{-1}) and body weight (W, mg) of larvae by data obtained a) in cages (y = -1.260 + 0.863x; r = 0.86), and b) in histogram (y = -1.143 + 0.823x; r = 0.97) in *Acentrella sibirica*. Both variates plotted logarithmically. Vertical lines indicate confidence intervals at the 95% significance level.

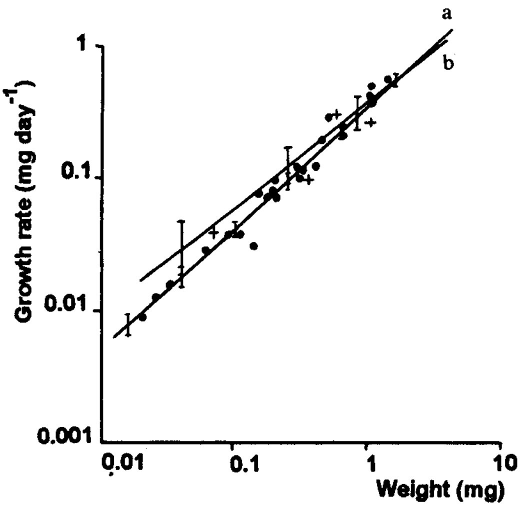

Fig. 5. A relationship between growth rate (dW/dt, mg day^{-1}) and body weight (W, mg) of larvae by data obtained a) in cages ($y = -1.387 + 0.925x$; $r = 0.94$), and b) in histogram ($y = -1.167 + 0.755x$; $r = 0.98$) in *Drunella cryptomeria*. Both variates plotted logarithically. Vertical lines indicate confidence intervals at the 95% significance level.

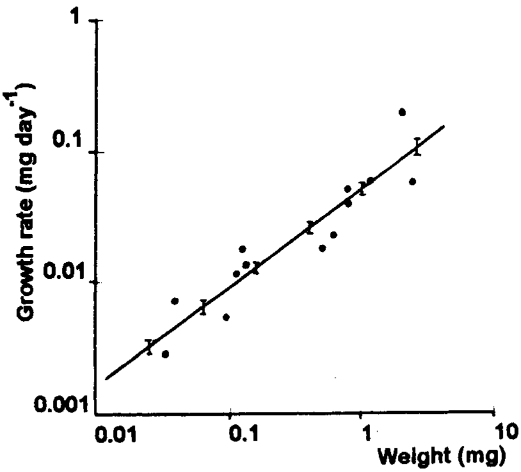

Fig. 6. A relationship between growth rate (dW/dt, mg day^{-1}) and body weight (W, mg) in *Baetis rhodani* by data WELTON *at el.* (1982) on log/log scale. Vertical lines indicate confidence intervals at the 95% significance level.

was obtained according to WELTON'S *et al.* (1982) data turned out to be close to and supplemented one of our group. In our view, the method of obtaining mayfly larvae growth data in cages is simple and effective.

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