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Production of Several Species of Mayfly Larvae

With 8 Figures and 14 Tables

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1. Introduction

In studying production conditions in running waters also numerous populations of some mayfly species were followed, which made direct calculations of production possible. In the present paper results obtained for 10 mayfly species are summarized.

Up to the present there have been few realistic data concerning the production of mayfly larvae. More frequently the whole secondary production has been evaluated and/or separately the production of herbivores and carnivores, less frequently the production of mayflies as a whole. The reasons can be seen in methodological difficulties, i.e. in time-consuming requirements of production research and, particularly, in methodological confusion. Using different methods that have been suggested for the evaluation of zoobenthos production it is possible to arrive at rather different results (cf., Zelinka & Marvan 1976). The research into the production of water organisms is becoming more and more important not only in species utilized directly as the food of man and domestic animals, but in evaluating the whole food chains. Also in judging the endangering of water as environment (pollution, reduction of discharge rates, canalization, and others) production problems acquire more and more importance.

2. Methodological notes

The basis for the calculation of mayfly larvae production were quantitative samples collected in monthly intervals. The material was weighet "alive" (= wet weight) after drying, then measured and from the length-weight relations of the individual species known beforehand the mass was rechecked. The proper production calculations were carried out according to the increments of the individual size cohorts (maximum difference of 2 mm). A detailed description of the method can be found in papers by Zelinka (1973), Zelinka & Marvan (1976). For the individual species also dry weight or ashfree dry weight were established, the relations being evident from Table 1. Though there are not many data in this respect, in the conversions the ratio water: ashfree (organic) dry weight: mineral substances = 78:17.8:4.2 can be used. Further conversions are possible to caloric values whose survey is given in Table 2. On the average, for mayfly larvae the following values can be taken into consideration: 1 g wet weight = 1.124 kcal, 1 g dry weight = 5.482 kcal, 1 g ashfree (organic) dry weight = 6.486 kcal.

Table 1. Relations between wet weight, dry weight and ashfree dry weight in mayfly larvae

Taxon (1 g wet weight)	dry weight		ash-free dry weight		ash	Reference
	g	water %	g	%	%	
Baetis sp. div.	0.205	79.5	0.172	17.2	3.3	ZELINKA
Baetis rhodani	0.199	80.1	—	—	—	ZELINKA
Callibaetis sp.	0.240	76.0	—	—	—	DRIVER et al. 1974
Ecdyonurus venosus	0.228	77.2	—	—	—	ZELINKA
Ephemeroptera sp. div.	0.195 bis 0.245	80.5—75.5	—	—	—	ZELINKA 1977
∅	0.220	78.0	0.178	17.8	4.2	ZELINKA 1977
Rhithrogena semicolorata	0.245	75.6	0.189	18.9	5.4	ZELINKA
Stenonema pulchellum	0.200	80.0	—	—	—	TRAMA 1972

Table 2. Relations between mass and caloric value

Taxon	1 g wet weight = kcal	1 g dry weight = kcal	1 g ash-free dry weight = kcal	Reference
Baëtidae	1.124	—	6.409	CUMMINS & WUYCHECK 1971
Baetis sp.	—	—	6.409	TRAMA 1957
Caenidae	—	—	7.058	CUMMINS & WUYCHECK 1971
Baetis rhodani	—	6.04	—	CASPERS 1975a, b
Caenis robusta	—	5.33—5.34	—	SHERSTYUK 1973
Callibaetis sp.	—	6.090	—	DRIVER et al. 1974
Cloeon dipterum	—	5.25—5.81	—	SHERSTYUK & ZIMBALEVSKAJA 1973
Cloeon sp.	0.878—1.370	—	—	TRAMA 1957
Epeorus pleuralis	—	—	6.205	TRAMA 1957
Ephemeroptera sp. div.	—	5.469	6.553	CUMMINS & WUYCHECK 1971
Ephemeridae	—	4.885	—	CUMMINS & WUYCHECK 1971
Heptageniidae	—	5.586	6.216	CUMMINS & WUYCHECK 1971
Isonychia bicolor	—	5.155	—	SWEENEY 1978
Rhithrogena semicolorata	—	4.96	—	CASPERS 1975a, c
Stenonema pulchellum	—	5.295—5.975	—	TRAMA 1972
Ephemeroptera subim. + im.	—	5.392	—	BÖTTGER 1975
Leptophlebia marginata	—	5.65	—	CASPERS 1975a

In comparing our results with literary data one must take into consideration possible errors resulting from different methods in calculating the zoobenthos production. Each of the hitherto methods is loadet with a certain error. As follows from different comparative studies, the more basic intake data are used in the calculations, the more accurate the result (see ZELINKA & MARVAN 1976, WATERS & CRAWFORD 1973, FAGER 1969, ZWICK 1975, BENKE & WAIDE 1977, MENZIE 1980). On the other hand, such working methods are more time-consuming, requiring more frequent sampling, measuring individual pieces, plotting a reliable curve of length-weight relations and/or checking by direct weighing of samples and a number of calculation operations, even if they may be simple. That is why we think that the results obtained by our method approach the reality and data from literature are taken critically.

Another possible source of differences in comparing the results is the irregular population of the bottom of running waters by larvae of mayflies. The density of population by individual species is controlled mainly by the stream speed, this fact is also expressing considerably the bottom character (stones to muddy sediments), very rich in larvae of particularly small types being stands of macrovegetation. All these facts must be taken into consideration when taking the sample, the data then concerning either a certain partial habitat or a calculation must be carried out to obtain an average m^2 of the stream according to the relative representation of the individual partial habitats. Certain increase in the density of the number of benthic animals of running waters occurs in the drop of the discharge rate at the time when, at the same time, the submerged area of the bottom is reduced. This concerns mainly streams with relatively broad riverbed in relation to discharge rates and with a very slow gradient of the banks. The influence of this factor is sometimes considerable and the increase in the number of individuals on the area where the sample was taken does not mean an overall increase in the abundance in the stream. Also this factor must be observed in production research (see ZELINKA 1969). If not stated otherwise, our data concern this average or corrected m^2 for every stream.

3. Results

3.1. *Baetis rhodani* (PICTET, 1843—1845)

Larvae of this species are very frequent in mountain or sub-mountain trout to grayling streams, from the production point of view important not only in the ČSSR, but in Central Europe in general. Usually 2 generations develop in a year. In cold mountain brooks it often happens that not all larvae of the second generation emerge. They mature then very early in spring. Imagines emerge from the end of March to the beginning of October, at the end of June and at the beginning of July emergence very weak (also according to the annual development of temperatures). This results in the mingling of generations, so that in the samples larvae of considerably different sizes are found and under natural conditions it is not always possible to reliably follow separately the growth of the first and of the second generations. Even more complicated in that respect are the conditions in streams below deep reservoirs, where water temperature varies very little. The emergence of subimagines under such conditions was observed even at the beginning of December. In production calculations the growth of larvae was therefore followed irrespective of which generation they belonged to.

Detailed follow-up was carried in trout streams of the Beskydy Mountains and in the Bítýška, a trout stream of the Bohemian-Moravian Highland. The former are minimally influenced by human activity (detailed characteristics of living conditions in ZELINKA 1969, HELAN et al.

Table 3. Chief production data of larvae of the species *Baetis rhodani* in the streams of the Beskydy Mountains (average values from 3 stations for 1 year of investigation)

Month	$n \cdot m^{-2}$	$mg \cdot m^{-2}$	Mean weight of one individual (mg)	Mean daily production ($mg \cdot m^{-2}$)	Production ($mg \cdot m^{-2}$)
J	112	144	1.29	1.8	57
F	—	—	—	3.8	106
M	153	159	1.04	9.2	284
A	198	534	2.69	20.6	619
M	294	1514	5.15	28.3	878
J	357	500	1.40	21.6	648
J	289	681	2.36	17.9	554
A	224	308	1.38	13.5	419
S	272	602	2.21	12.1	364
O	244	200	0.82	6.4	198
N	177	151	0.85	2.7	81
D	—	—	—	1.5	46
annual $\bar{x}$ whole stream	232	479	2.06	11.7	S = 4254
annual $\bar{x}$ riffle	290	599	2.06	14.6	S = 5317

Table 4. Chief production data of larvae of the species *Baetis rhodani* in the Bítýška (average values for 2 years of investigation)

Month	$n \cdot m^{-2}$	$mg \cdot m^{-2}$	Mean weight of one individual (mg)	Mean daily production ($mg \cdot m^{-2}$)	Production ($mg \cdot m^{-2}$)
J.	385	601	1.56	19.7	613
F	489	1370	2.80	39.2	1099
M	442	1184	2.68	14.1	439
A	665	3149	4.74	68.7	2063
M	249	599	2.41	16.4	510
J	769	974	1.27	7.8	234
J	990	303	0.31	23.8	739
A	1853	1440	0.78	36.9	1146
S	423	772	1.82	31.0	932
O	789	1184	1.50	29.8	924
N	678	1245	1.84	31.3	940
D	555	936	1.68	24.7	767
annual $\bar{x}$ whole stream	689	1146	1.66	28.6	S = 10406
annual $\bar{x}$ riffle	766	1273	1.66	31.4	S = 11559

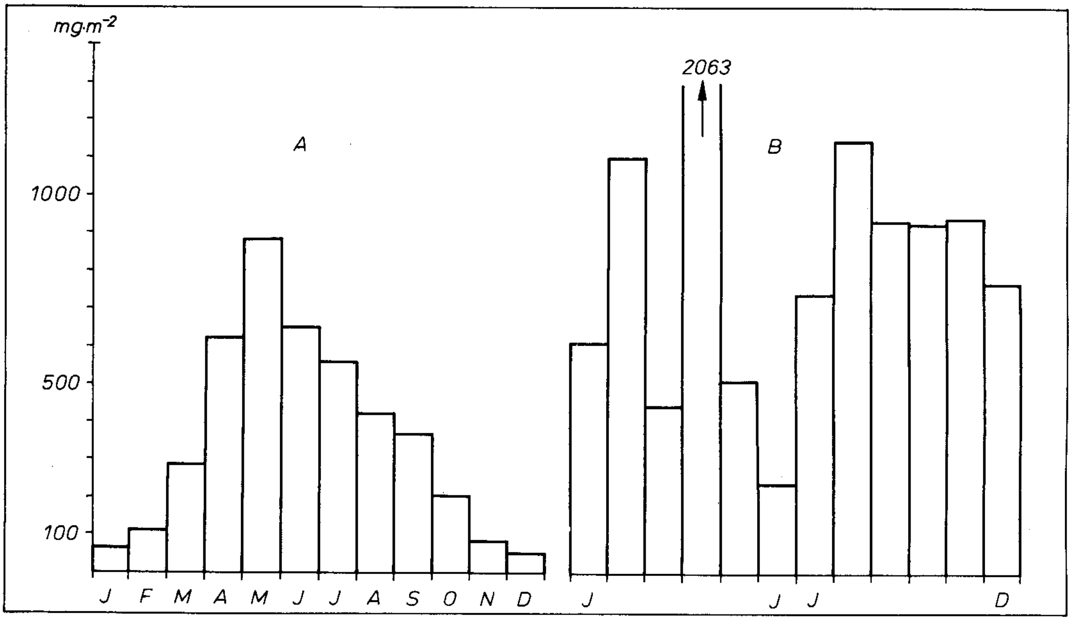

Fig. 1. *Baetis rhodani*; graph of the annual production;
A — Beskydy, B — Bítýška

1973), the latter is a stream polluted in the upper part but with a great self-purification ability, so that in the lower part conditions were reconstituted for the life of the trout, but with remaining increased primary production (see ZELINKA et al. 1977).

Table 3 gives the main production data for the species *Baetis rhodani* from the Beskydy streams, Table 4 for the same species from the trout stretch of the stream Bítýška. From the tables and graphs (Fig. 1) interesting results follow. In the trout streams of the Beskydy Mountains the production curve has clearly one peak. The quick growth of larvae begins at the end of March, in April subimagines emerge, in May production and emergence culminate. In June small larvae of the next generation appear, in isolated cases, however, subimagines of the first generation emerge. The growth of larvae of the following generation continues relatively very quickly and part of them emerge mostly towards the end of September. The average size of subimagines is, however, by one-fifth smaller than in the first generation. The major part of the larvae of the new generation matures only in the spring of the following year. The ratio between the number of second generation larvae in the year and between the number of hibernating larvae depends on thermal conditions of this or that particular year and also on the station. Differences found in the course of three years of study at 5 stations of these streams (elevation range between 450 and 620 m) were, however, not great. Maximum water temperature measured at the lowest-situated station in the course of the whole period of investigation did not reach 16 °C. The average temperature of all measurements was below 6 °C.

In the case of the stream Bítýška the production curve has two peaks. A relatively quick growth of larvae appears as early as in February, subimagines emerge at the end of March and in April practically all of the first generation emerge. In the summer months larvae of the second generation grew quickly and emerged gradually, subimagines (again smaller by one-fifth) emerged as early as at the end of August, but chiefly in October, when new small larvae appeared. Maximum water temperature measured at that station was 18.5 °C, mean temperature was 6.7 °C.

Another conspicuous difference between the studied trout streams of the two regions is the abundance of larvae of this species and thus also different biomass and production. In the stream Bítýška the mean annual abundance was by 197%, biomass by 139%, and production by 145% higher. The reason can be seen mainly in a higher biomass of algal periphyta by more than 200%; the total primary production — i.e. the food basis — was also considerably higher (see ZELINKA et al. 1977). The average size of larvae was clearly smaller at higher abundance: 1.66 mg as against 2.06 mg, i.e. drop in the average weight of the individual by 24%. The numbers of predating caddis-fly larvae and fish were roughly the same in both cases.

The production of larvae of the species *B. rhodani* is considerably decreased by organic water pollution, as could be proved in the stream Bítýška. Unless other life functions important for this species are changed (temperature, stream speed, bottom character), then in the worse part of β-mesosaprobity the production drops by 60%, in α-mesosaprobity on the average by 80%, in polysaprobity the species does not live.

Differences in the individual years are due to mainly the development of weather and discharge rates and also due to the development of predatory larvae. During our investigation in the streams of the Beskydy Mountains (3 years) and in the stream Bítýška (2 years) differences of $\pm 10\%$ were found, which is relatively small. The species *B. rhodani* copes very well with adverse life conditions. The fact that emergence and thus also laying eggs is extended to several months excludes the possiblity of decimating the species at a station, as, say, a result of bad weather or due to spate discharges. Small larvae of the first instars can be found in greater or smaller numbers practically throughout the year. Thus those of the summer egg laying are found not only in the autumn, but also in the winter and the first spring months. That means that there is a differently long diapause in part of the eggs or that the smallest larvae (many of them creeping into the intersticial particularly in winter) have a period of stopped growth. Under natural conditions this could not be found in detail. Very different growth rates of *B. rhodani* larvae are witnessed by the data by HUMPESCH (1979) who found the length of development to be 2.5—8 months.

Larvae of *B. rhodani* live in the stream parts of brooks. Where the stream speed drops permanently below 10 cm · s^{-1} they are practically lacking. In trout streams this means practically in the water near the banks. This area of "non-streaming" water took up 20% in the Beskydy streams and 10% in the Bítýška of total surface area. The figures and tables are converted for an average metre of the stream. Even thus the annual production of 4.254 and 10.406 g · m^{-2}, respectively, can be considered relatively high and the species in this type of stream is important as far as production is concerned and stable. Similar results were arrived at in the species *Baetis vagans* by WATERS (1966) who followed its production in the riffle streams of Minnesota. The mean annual biomass of 1.30 g · m^{-2} and production of 12.60 g · m^{-2} corresponds almost exactly to the conditions in the current of the Bítýška (see Table 4). The production of the species *B. rhodani*, which in stony streams reaches 10 g · m^{-2} · $year^{-1}$, can be denoted as maximum. Only in the running cold streams with stands of higher water vegetation the production can be still higher.

The calculation is made easy by the conversion using the so-called P/B coefficients, i.e. the relations between biomass and production. For the species *B. rhodani* relatively constant relations were found between the mean annual biomass (samples taken every month) and production. In the Beskydy streams this relation varied from 1:8.02 to 8.93 (7 cases from 4 stations calculated), in the stream Bítýška it was 1:9.08. For the species *B. vagans* WATERS (1966) gives the ratio 1:9.69. In our opinion, particularly in cases when abundance is not sufficient for direct calculation of production, it is possible to use for the production of the species *B. rhodani* the coefficient 8.5 for cold streams (2 incomplete generations) and 9.0 for streams with somewhat higher temperatures (2 generations).

For finding out the biomass it is possible to use direct weighing of samples or calculations according to the curve of length-weight relations (Fig. 2). In that case, however, it is necessary to measure every individual. Several times

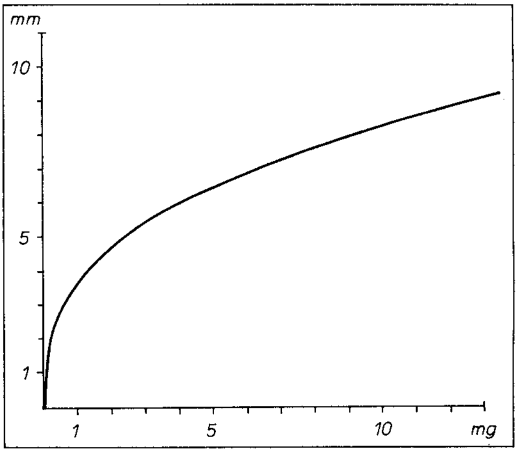

Fig. 2. The curve of lenght-weight relations of larvae of the species *Baetis rhodani*

the two methods were used and the curve can considered to be very realistic. Larvae were measured both alive and after fixing with 4% formaldehyde. In length only small differences were found in both directions, on the average differences between unfixed and fixed larvae were negligible.

ILLIES sums up the results of production studies of mayfly emergence in two streams near Lunz in a publication of 1980. In the stream Teichbach also the species *B. rhodani* was relatively abundant, its mean annual emergence reaching 209 mg · m^{-2} of dry weight, which, calculated to wet weight (80% water) means 1,045 mg · m^{-2}. Emerging subimagines are only a part of the total production of the species which in our calculations is so to speak the weight of the last larval stages — nymphae, closely before their emergence, reduced by the weight of larval skins. In the stream Bítýška the weight of these last stages was more than 1,100 mg · m^{-2} · $year^{-1}$ (average for the two years investigation), at a relatively high mean abundance of 689 pcs · m^{-2}. In the stream Breitenbach the weight of emerging mayflies of *B. rhodani* was three times as high (ILLIES 1975) and such abundance has not been come across under the conditions of this country. SPEIR & ANDERSON (1974) followed the relation of emergence to production in several species of Simuliidae. They state that production is about 4.8 times as high emergence. When comparing the emergence in the stream Teichbach (ILLIES 1980) and that in the stream Bítýška (where there are more or less concordant values of emergence), for *B. rhodani* this ratio is higher (emergence: production = 1:10).

Despite their small size the larvae and particularly the emerging subimagines of the *B. rhodani* are a comparatively high food component of the fishes of trout and grayling stretches of the streams. Large amounts of emerging individuals in certain hours of the day and a relatively long stay of the subimagines on the surface attract the attention of the trout and grayling. Finds of hundreds of individuals in one fish alimentary canal are by no means rare. A research into more than 1,000 alimentary canals of trout and into 500 of grayling has shown that larvae and particularly subimagines of *B. rhodani* constituted almost 15% of the biomass of food of the trout and 20% of that of the grayling in the annual average. In following the food of *Cottus* in the Beskydy streams it was found that larvae of *B. rhodani* were the second most frequently represented food component after Chironomidae (ORSÁG & ZELINKA 1974).

3.2. *Baetis lutheri* MÜLLER-LIEBENAU, 1967

The species populates sub-mountain streams, the most frequent occurrence being found in the lower parts of the graying stretches and in the upper parts of the barbel zones. Larvae live mostly in riffles under stones, frequently also in higher water plants. According to data from literature and also our information the species has one generation a year.

A relatively rich population was followed in the barbel zone of the Jihlava River, where there were rich stands of *Ranunculus fluitans* (see ZELINKA 1980, HELAN 1978). Larvae occurred everywhere in running water, mostly, however, in the stands of the riffles, least in pools. In the calculated ratio of the surfaces of the individual habitats the average annual abundance for the whole stream was 326 pcs $\cdot$ m^{-2} (see also Table 5).

At the station under investigation many small larvae appeared at the beginning of March in the first stages of development. Together with them also bigger larvae (about 7 mm) were found which survived the winter season. Larvae grew very quickly and in April subi-

Table 5. Chief production data of larvae of the species *Baetis lutheri* in the Jihlava River (average values for the whole stretch of the stream for 1 year of investigation)

Month	n $\cdot$ m^{-2}	mg $\cdot$ m^{-2}	Mean weight of one individual (mg)	Mean daily production (mg $\cdot$ m^{-2})	Production (mg $\cdot$ m^{-2})
J	162	120	0.74	4.1	127
F	—	—	—	3.2	89
M	808	827	1.02	19.0	589
A	730	1832	2.51	27.3	818
M	262	636	2.43	18.7	579
J	128	55	0.43	10.4	313
J	120	93	0.77	2.8	87
A	194	146	0.75	3.4	105
S	177	135	0.76	4.2	126
O	247	122	0.50	4.2	131
N	323	243	0.75	6.8	203
D	430	263	0.61	7.9	245
annual $\bar{x}$ whole stream	326	407	1.25	9.3	S = 3412
annual $\bar{x}$ riffle	507	619	1.22	14.2	S = 5188
annual $\bar{x}$ pool	61	101	1.65	2.3	S = 847

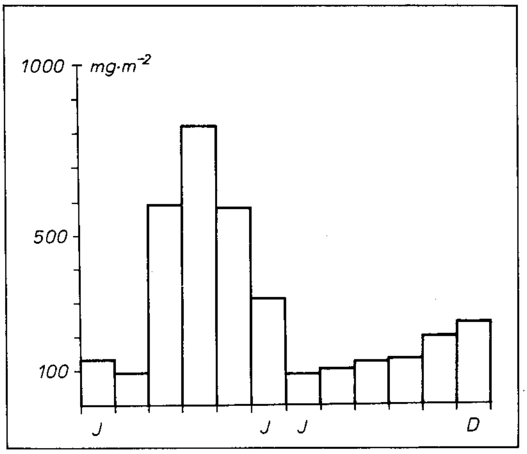

Fig. 3. *Baetis lutheri*; graph of the annual production; Jihlava River

magines emerged in masse, the same as in May (Fig. 3). As early as in April further small larvae (up to 2 mm) appeared, but they were not found by the middle of May. June was characterized by the hatching of a minor amount of larvae of the new generation, which continued with a gradual, but comparatively slow growth of larvae. It is interesting to note that up to the end of January we did not find larvae longer than 7 mm, but gradually small larvae of first stages appeared. From July onwards we did no longer find any imagines in spite of the fact that larger larvae kept disappearing from the population and already in September we found 2 nymphae of 6.1 mm. Large larvae seem to perish in autumn and in winter or individually emerging subimagines perish as well and the hatching of small larvae goes on gradually. Winter and above all the spring spates are critical periods for mayfly larvae. This fact was also reflected in our case, but the period before spring brought a new occurrence of small larvae hatched from hibernating eggs or surviving in the intersticial.

In literature we did not find any data concerning such a rich population as the species *B. lutheri.* The production established, which in this stretch of the stream is 3,412 mg $\cdot$ m^{-2} $\cdot$ year^{-1}, must be considered high. The P/B coefficient was 8.38. We should like to draw attention to considerable differences in the density of population of the individual habitats at the station under investigation and to the differences in annual production resulting from them:

plants in riffles	8,045 mg $\cdot$ m^{-2}
stones in riffles	4,786 mg $\cdot$ m^{-2}
plants in pools	2,556 mg $\cdot$ m^{-2}
stones in pools	377 mg $\cdot$ m^{-2}
grasses near the bank	0

In production studies it is therefore necessary to follow all partial habitats formed at the station.

3.3. *Baetis buceratus* EATON, **1870**

Larvae of this species are typical of warmer barbel streams, their occurrence is, however, stated to be relatively rare. At the above station of the Jihlava River they were the most frequent of all mayfly species, their average annual abundance for the whole stream being 423 pcs $\cdot$ m^{-2}. They form 2 generations per year, the emergence of both generations is considerably extendet, so that different size groups of larvae of the two generations overlap. Thus it is not possible to follow the growth of the individual generations separately under natural conditions.

In quantitative samples larvae of 2—3 mm prevailed in March, only some of them being larger than 5 mm. The growth was quick, so that in April sizes of 4—6 mm prevailed, some being over 7 mm. In May the size limit shifted again, many larvae being more than 8 mm long and subimagines emerged. During all these months also larvae of the size below 3 mm were found. In June the last subimagines of the first generation emerged and many small larvae of the second generation appeared. They grew very rapidly and as early as in the middle of June the first individual emerged and the emergence of the second generation culminated at the end of August and ended in September. The emerging nymphae of the second generation were smaller, 6.0—7.9 mm, as against 6.8 to 8.5 mm in the first generation. In September there appear small larvae of the hibernating generation which grow relatively slowly (a thermophile species as compared with the spring species *B. lutheri*) and in further months up to March new small larvae keep appearing.

Table 6. Chief production data of larvae of the species *Baetis buceratus* in the Jihlava River (average values for the whole stretch of the stream for 1 year of investigation)

Month	$n \cdot m^{-2}$	$mg \cdot m^{-2}$	Mean weight of one individual (mg)	Mean daily production ($mg \cdot m^{-2}$)	Production ($mg \cdot m^{-2}$)
J	115	101	0.88	7.1	219
F	—	—	—	8.0	225
M	585	163	0.29	15.6	483
A	496	877	1.77	33.9	1017
M	911	1989	2.18	40.3	1249
J	530	465	0.88	32.2	967
J	96	189	1.97	22.9	709
A	311	1020	3.28	19.0	590
S	247	371	1.50	10.3	310
O	232	156	0.67	6.6	205
N	537	327	0.61	11.4	343
D	589	540	0.91	10.8	335
annual $\bar{x}$ whole stream	423	563	1.33	18.2	S = 6652
annual $\bar{x}$ riffle	602	793	1.32	25.7	S = 9373
annual $\bar{x}$ pool	161	225	1.39	7.3	S = 2659

On the other hand, larvae reaching the lengths over 6 mm gradually left the population.

The total annual production of larvae of the species *B. buceratus* at the station under investigation was determined to be 6,652 $mg \cdot m^{-2}$, calculated for the whole stream. The chief production period is relatively long, as intensive growths of larvae of the two generations overlap (Table 6, Fig. 4). Like in the preceding species, there were great differences in the populations of the individual habitats which, calculated for production, appeared to be as follows:

plants in riffles	34,547 $mg \cdot m^{-2} \cdot year^{-1}$
stones in riffles	3,522 $mg \cdot m^{-2} \cdot year^{-1}$
plants in pools	8,333 $mg \cdot m^{-2} \cdot year^{-1}$
stones in pools	638 $mg \cdot m^{-2} \cdot year^{-1}$
grasses near the bank	1,927 $mg \cdot m^{-2} \cdot year^{-1}$

Larvae are thus the most frequent on plants in riffles, but they are not lacking even in the nearly stagnant water near the banks. Compared with the data about the frequency of occurrence of this species in other streams, its production in the barbel stretch of the Jihlava River can be considered very high. The P/B coefficient was higher than that in species with one generation per year, being 11.82.

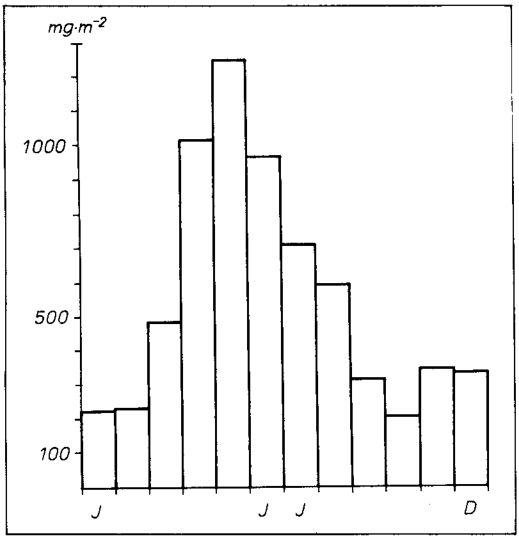

Fig. 4. *Baetis buc eratus*: graph of the annual production; Jihlava River

3.4. *Rhithrogena semicolorata* (CURTIS, 1834)

This species is very frequent in trout streams, in production it is often principal among mayfly larvae. It forms one generation in the year, larvae living only in running water among and under stones. The production of this species was followed in the Beskydy trout streams and in the trout stretch of the Bítýška (as for stations see the species *Baetis rhodani*). The results of investigation at all stations have shown that larvae grow relatively well even in the cold season (see Tables 7, 8, Fig. 5), with maximum production in early spring. In a comparatively warmer stream, the Bítýška, most of the larvae emerged in April, in June

Table 7. Chief production data of larvae of the species *Rhithrogena semicolorata* in the streams of the Beskydy Mountains (average values from 3 stations for 1 year of investigation)

Month	$n \cdot m^{-2}$	$mg \cdot m^{-2}$	Mean weight of one individual (mg)	Mean daily production ($mg \cdot m^{-2}$)	Production ($mg \cdot m^{-2}$)
J	138	481	3.48	10.5	327
F	—	—	—	24.2	677
M	225	673	2.99	47.3	1465
A	366	2415	6.60	90.9	2726
M	695	5920	8.52	98.5	3053
J	70	1004	14.34	16.9	507
J	13	181	13.92	6.6	204
A	2	49	24.50	1.0	32
S	18	27	1.50	5.1	154
O	167	243	1.46	10.3	318
N	154	297	1.93	9.4	282
D	—	—	—	7.5	237
annual $\bar{x}$					
whole stream	185	1129	6.10	27.3	S = 9982
annual $\bar{x}$ riffle	232	1411	6.09	34.2	S = 12478

Table 8. Chief production data of larvae of the species *Rhithrogena semicolorata* in the Bítýška (average values for 2 years of investigation)

Month	$n \cdot m^{-2}$	$mg \cdot m^{-2}$	Mean weight of one individual (mg)	Mean daily production ($mg \cdot m^{-2}$)	Production ($mg \cdot m^{-2}$)
J	574	1825	3.18	40.2	1245
F	495	1921	3.88	49.1	1376
M	452	2033	4.50	97.5	3023
A	708	7799	11.01	174.0	5220
M	517	4535	8.77	73.1	2267
J	35	378	10.80	20.6	618
J	3	21	7.00	2.4	73
A	111	92	0.83	2.1	64
S	123	227	1.84	8.1	244
O	534	1051	1.97	29.5	916
N	542	1781	3.28	49.0	1470
D	320	702	2.20	40.2	1251
annual $\bar{x}$					
whole stream	368	1864	5.06	48.7	S = 17767
annual $\bar{x}$ riffle	405	2051	5.06	53.5	S = 19544

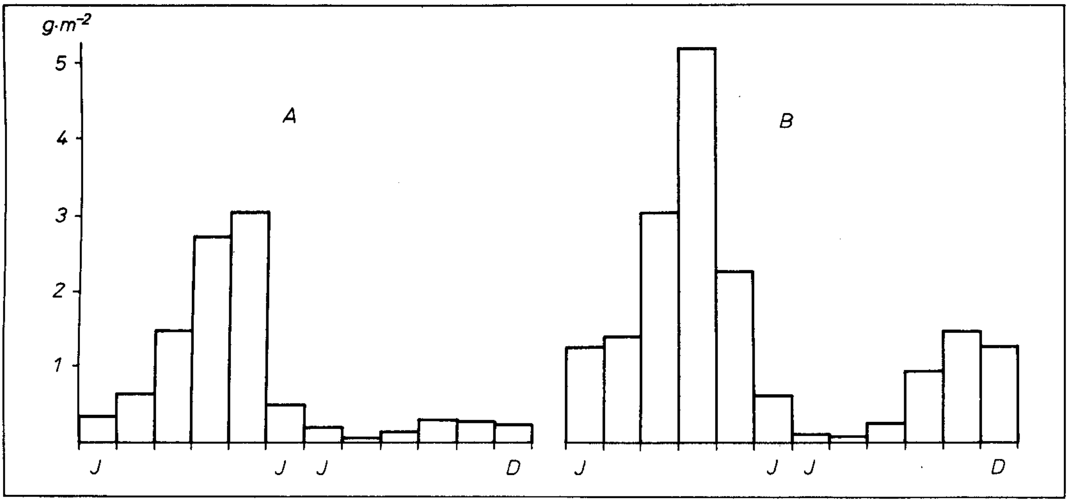

Fig. 5. *Rhithrogena semicolorata*; graph of the annual production; A — Beskydy, B — Bítýška

and July subimagines appeared in only isolated cases and were by 20% smaller than those of April. In the Beskydy streams all this development was shifted by one month. The first small larvae of the new generation started appearing in August (the Bítýška) or in September (the Beskydy streams).

Like in the species *Baetis rhodani* the production in the two stations was different. In the Bítýška the mean annual abundance was by 199% higher, biomass by 165% and production by 178%. From this it follows that the average weight of larvae at a nearly double abundance in the stream Bítýška was about 20% lower (Tables 7, 8). The reasons of all those differences are the same as in the species *B. rhodani*, i.e. mainly somewhat higher temperatures and a larger food basis in the Bítýška.

Annual production of this species in the streams of the Beskydy was determined to be 9,982 mg $\cdot m^{-2}$, in the Bítýška 17,767 mg $\cdot m^{-2}$, calculated for the whole stream. In the current the production was more than 10% higher (larvae are lacking in stagnant water near the banks). The P/B coefficient was much the same: at the stations of the Beskydy streams it varied from 8.75—9.05, in the Bítýška it was 9.53.

The production of the *R. semicolorata* was found by Brooker & Morris (1978) at two stations of the upper part of the River Wye in Wales. Their results were 1,016 at the first and 1,776 mg $\cdot m^{-2} \cdot year^{-1}$ at the second station (recalculated for wet weight), at P/B coefficient of 4.5. The annual mean abundance at the richer station was 110 pcs $\cdot m^{-2}$, biomass 420 mg $\cdot m^{-2}$. The frequency and mainly the biomass of larvae was substantially lower than at the stations of our investigation and, besides, the employed global method of production does not calculate with losses in the course of the growth of larvae and in the emergence of subimagines.

Taking into consideration various data about the abundance of larvae of *R. semicolorata* in different streams, the production of about 10 g $\cdot m^{-2} \cdot year^{-1}$ can be considered medium, that above 15 g high. It is interesting to note that this high production (compared with further mayfly species) is not adequately utilized by fish. Finds of about 100 larvae or subimagines in the alimentary canals of the trout were quite isolated, in the grayling these larvae were represented in the food in individual cases only (maximum 30 individuals). In our opinion this was mainly due to weak drifting of these larvae and to a relatively quick emergence of subimagines from the water.

3.5. *Ecdyonurus* EATON, 1868

At the stations studies always at least 3 species of this genus occurred together, mostly *E. torrentis* KIMMINS 1942, less *E. submontanus* LANDA 1970. The emergence is extendet to several months and small larvae cannot be distinguished reliably. That is why we calculated the production of the genus as a whole. The species followed have 1 generation per year: *E. torrentis* is a species of the late spring and of the early summer, whereas larvae of *E. submontanus* grow quickly in summer months and emerge at the end of summer. The abundance of larvae was practically the same both in running water and in stagnant water near

Table 9. Chief production data of larvae of the genus *Ecdyonurus* in the streams of the Beskydy Mountains (average values from 3 stations for 1 year of investigation)

Month	$n \cdot m^{-2}$	$mg \cdot m^{-2}$	Mean weight of one individual (mg)	Mean daily production ($mg \cdot m^{-2}$)	Production ($mg \cdot m^{-2}$)
J	104	1313	12.62	17.4	541
F	—	—	—	22.4	627
M	95	600	6.32	20.3	630
A	112	1145	10.22	23.6	708
M	111	1512	13.62	26.5	822
J	74	1244	16.81	27.5	825
J	53	1059	19.98	26.7	827
A	26	608	23.38	16.4	508
S	66	338	5.12	23.7	710
O	211	971	4.60	32.9	1019
N	147	1470	10.00	24.7	741
D	—	—	—	16.5	512
annual $\bar{x}$ whole stream	94	1026	10.91	23.2	S = 8470

Table 10. Chief production data of larvae of the genus *Ecdyonurus* in the Bítýška (average values for 2 years of investigation)

Month	$n \cdot m^{-2}$	$mg \cdot m^{-2}$	Mean weight of one individual (mg)	Mean daily production ($mg \cdot m^{-2}$)	Production ($mg \cdot m^{-2}$)
J	122	504	4.13	13.2	410
F	96	838	8.73	27.0	755
M	47	500	10.64	27.2	842
A	104	1251	12.03	42.5	1274
M	93	815	8.76	25.7	798
J	69	615	8.91	18.3	548
J	63	281	4.46	18.6	577
A	194	1452	7.48	16.8	522
S	94	467	4.97	20.0	601
O	152	840	5.53	24.2	749
N	74	575	7.77	25.5	767
D	107	1271	11.88	20.7	643
annual $\bar{x}$ whole stream	101	785	7.77	23.2	S = 8486

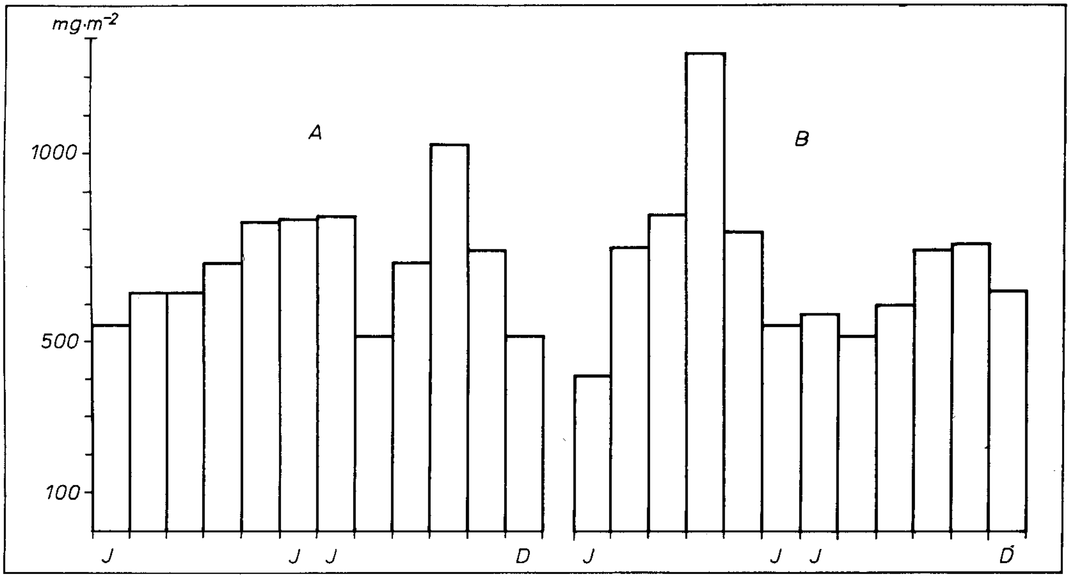

Fig. 6. *Ecdyonurus*; graph of the annual production; A — Beskydy, B — Bítýška

the banks. The growth was again followed at 3 stations of the Beskydy trout streams and in the trout stretch of the Bítýška, the calculations being carried out for the same stations (see *Baetis rhodani*).

The abundance of larvae of the genus *Ecdyonurus* at the stations under investigation was practically the same (see Tables 9, 10). The influence of higher temperatures and a higher primary production of the Bítýška was thus not reflected in this case. The production was also practically the same, being 8,470 and 8,486 mg $\cdot$ m^{-2} $\cdot$ year^{-1}, respectively.

The production of this genus in the course of the year can be marked as relatively balanced; in following the individual species major variations would certainly be seen. Despite this, in both cases two clear peaks appeared: the spring (or summer) peak and the autumn peak (Fig. 6). Temperature differences between the two types of streams resulted in the fact that in the colder streams of the Beskydy subimagines of *E. torrentis* emerged mostly in June and July, those of *E. submontanus* in September. In the stream Bítýška the larvae of the former species grow very quickly in April, emerge mostly in May. In August rare emergences of subimagines of the species *E. dispar* and in September those of *E. submontanus* were registered. Larvae of *E. torrentis* grow relatively quickly in autumn, their growth continuing even during the winter. The P/B coefficient was 8.25 in the streams of the Beskydy (average) and 10.81 in the Bítýška. A greater difference might be due to a different percentual representation of the species.

A frequent occurrence of larvae of the genus *Ecdyonurus* is reported particularly from grayling streams where the population can be expected to be even twice as high. Analyses of many hundreds of alimentary canals of trout and grayling showed that the representation of the genus *Ecdyonurus* in their food is very small.

3.6. *Ephemerella ignita* (Poda, 1761)

Larvae of this typical summer species can be found in running waters of the most varied type. They are, however, most frequent in warm streams (lower grayling stretches and barbel zones), where they live under stones and, particularly, in water plants. They have 1 generation per year, small larvae hatch from eggs the winter diapause towards the end of May, they grow very quickly, emerging mainly in July, less in August. The last individual subimagines could be observed in September. This typical development was followed also in the barbel zone of the Jihlava River (Table 11, Fig. 7). The annual production for the whole stream was established to be 5,734 mg · m^{-2}, again with considerable differences at individual partial habitats:

stones in the current	1,068 mg · m^{-2}
plants in the current	23,826 mg · m^{-2}
stones in pools	407 mg · m^{-2}
plants in pools	6,638 mg · m^{-2}
grasses near the banks	693 mg · m^{-2}

The P/B coefficient was 11.01.
The production of the species *E. ignita* was followed by BROOKER & MORRIS (1978) in the upper quick part of the River Wye. At the richer station, with average annual abundance of larvae of 86 pcs · m^{-2} and average annual biomass of 480 mg · m^{-2} they determined the annual production to be 3,176 mg · m^{-2} (recalculated for wet weight) and the P/B coefficient 6.6. In view of the fact that they did not take into consideration the losses (which are smaller in this summer species when compared with species whose larvae hibernate), their results approach ours. WATERS & CRAWFORD (1973) compare some methods of production calculation in the species *E. subvaria*, according to the investigation of a very rich population in a small stream in Minnesota. The annual production varied about 30,000 mg · m^{-2}. Also in our streams the populations of this species are even considerably higher than at the station followed and the annual production of the species *E. ignita* can be expected to be over 10,000 mg · m^{-2}. Since this high production is reached in the course of 4 months, the species is an important food component of fish in the summer season.

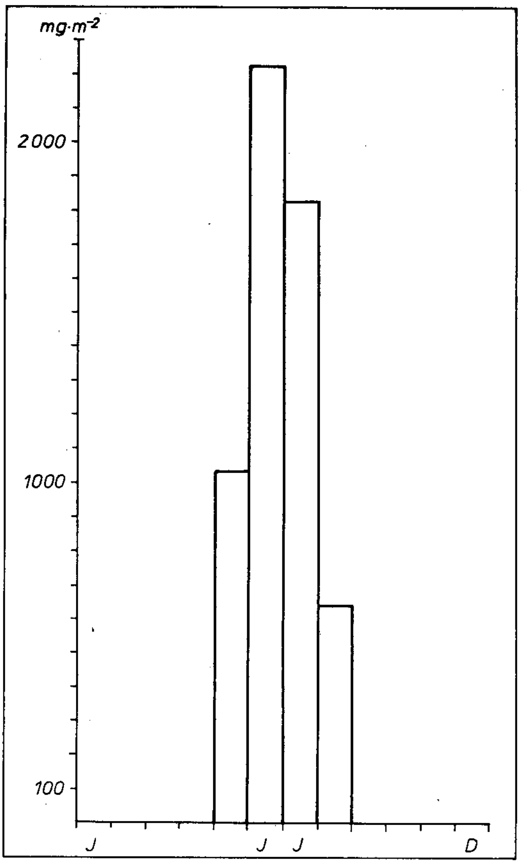

Fig. 7. *Ephemerella ignita*; graph of the annual production; Jihlava River

3.7. *Potamanthus luteus* (LINNÉ, 1767)

The species inhabits warm streams of the barbel character, it is usually the most frequent in the lower parts of barbel zones. It can withstand perhaps the greatest organic water pollution from all mayfly species. It populates regularly the whole bottoms of streams. Small larvae are, however, the most frequent in riffle stretches, big ones under stones of stretches with weaker current, and the highest percentage of big larvae was found in calm water near the banks. It forms one generation per year.
The production was followed in the upper part of the barbel zone of the Jihlava River (see *B. lutheri*), where the abundance of larvae was relatively low, in the annual average of 150 pcs · m^{-2} (Table 12). The hibernating larvae are very small, the growth being accelerated as late as at the end of April. The greatest increments were established in May, in June subimagines started emerging, and the emergence continued in July and in August. In July and in further months small larvae of the new population gradually appear, but their number grows mostly towards the end of autumn (Fig. 8). Like in a number of other

Table 11. Chief production data of larvae of the species *Ephemerella ignita* in the Jihlava River (average values for the whole stretch of the stream for 1 year of investigation)

Month	$n \cdot m^{-2}$	$mg \cdot m^{-2}$	Mean weight of one individual (mg)	Mean daily production ($mg \cdot m^{-2}$)	Production ($mg \cdot m^{-2}$)
J	0	0	—	0	0
F	0	0	—	0	0
M	0	0	—	0	0
A	0	0	—	0	0
M	—	—	—	33.2	1031
J	334	1756	5.26	74.2	2226
J	570	4239	7.44	58.9	1825
A	23	251	10.91	20.5	637
S	2	23	11.50	0.5	15
O	0	0	—	0	0
N	0	0	—	0	0
D	0	0	—	0	0
annual $\bar{x}$ whole stream	78	521	6.68	15.7	S = 5734
annual $\bar{x}$ riffle	104	689	6.63	20.8	S = 7586
annual $\bar{x}$ pool	43	303	7.04	9.1	S = 3336

Table 12. Chief production data of larvae of the species *Potamanthus* luteus in the Jihlava River (average values for the whole stretch of the stream for 1 year of investigation)

Month	$n \cdot m^{-2}$	$mg \cdot m^{-2}$	Mean weight of one invidivual (mg)	Mean daily production ($mg \cdot m^{-2}$)	Production ($mg \cdot m^{-2}$)
J	37	46	1.24	2.0	63
F	162	203	1.25	2.8	79
M	388	484	1.25	4.5	140
A	140	241	1.72	15.5	465
M	127	777	6.12	18.9	587
J	72	1210	16.80	14.2	427
J	62	689	11.11	8.9	276
A	54	117	2.17	5.5	169
S	70	82	1.17	1.6	48
O	92	110	1.19	3.5	109
N	313	340	1.10	10.4	314
D	283	362	1.28	5.7	176
annual $\bar{x}$ whole stream	150	388	2.59	7.8	S = 2853

species, one can observe a reduction in the number of chiefly big larvae throughout the winter which, however, are replaced by new small larvae with the onset of the spring.

The annual production at the station under investigation was established to be 2,853 mg $\cdot m^{-2}$, which is 7.35 times more the average annual biomass. The differences at the individual habitats can be seen from the following:

stones in the current	2,580 mg $\cdot m^{-2} \cdot year^{-1}$
plants in the current	1,455 mg $\cdot m^{-2} \cdot year^{-1}$
stones in pools	3,712 mg $\cdot m^{-2} \cdot year^{-1}$
plants in pools	1,587 mg $\cdot m^{-2} \cdot year^{-1}$
grasses near the bank	8,225 mg $\cdot m^{-2} \cdot year^{-1}$

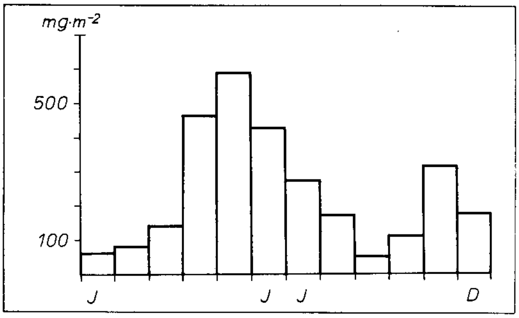

Fig. 8. *Potamanthus luteus*; graph of the annual production; Jihlava River

ZAHRÁDKA (1978, 1979) followed the production of this species in the lower part of the barbel zone of the Jihlava River, where living conditions for larvae of *P. luteus* were more favourable. With the average annual biomass of the population being 642 mg · m^{-2} he gives the production as 10,320 mg · m^{-2} · $year^{-1}$. The high P/B coefficient of 16.07 was partly affected by difficult possibilities of sample taking under persisting high discharge rates in the winter, when a relatively low number of larvae were obtained. Under favourable conditions the actual annual production of this species can be expected to be about 10,000 mg · m^{-2} and the average P/B coefficient about 11.

3.8. Some further species

The production was also established in some further mayfly larvae, but their populations were relatively poor, so that the results of production calculations may be loaded with greater error. Therefore only the chief information is given here.

Cloeon dipterum (LINNÉ, 1761):

A species typical of stagnant waters, but not lacking in overgrown waters flowing at a sluggish pace in plants near the banks of running waters. The population with the average annual amount of 113 pcs · m^{-2} and biomass of 418 mg · m^{-2} was followed in the barbel zone of the Jihlava River where the larvae lived near the banks in stands of *Baldingera arundinacea*. The annual production in these stands was established to be 4,678 mg · m^{-2}, the P/B coefficient 11.19. As, however, the area of grasses near the banks takes up only 5% of the water surface of the whole stream, the production of larvae of this species is of little significance for the type of stream investigated.

Baetis fuscatus (LINNÉ, 1761):

The population of average annual abundance of 126 pcs · m^{-2} and biomass of 143 mg · m^{-2} was again followed in the barbel zone of the Jihlava River. Larvae were most frequent in the plants in riffles. Two generations developed per year. The mean production for the whole stream was 1,601 mg · m^{-2} · $year^{-1}$, the P/B coefficient 11.19.

Caenis macrura STEPHENS, 1933:

In the barbel zone of the Jihlava River these larvae were found throughout the year. Larvae of two generations overlapped greatly as for the size. The production was highest in the warm season of the year, in winter it dropped considerably, but was not stopped altogether. With mean annual abundance of 102 pcs · m^{-2} and biomass of 91 mg · m^{-2} the annual production was determined to be 1,181 mg · m^{-2} on the average for the whole stream stretch and the P/B coefficient 12.98. In comparison with the species *C. horaria*, as stated by MASON (1977) from stagnant waters it is 5 × less.

4. Discussion

Mayfly larvae are an important component of the secondary production of the benthos of running waters, we carried out the calculation of the production of larvae of several most frequent species of our streams. We are aware of the error with which these calculations are loaded, starting with quantitative sampling over the determination of the mass and finishing with the calculation proper of the production. Having, however, the results of a large number of investigations of sufficiently rich sets in populations available, the obtained results are realistic. This is also witnessed by the comparison of our results with most of the literary data (Tables 13, 14).

Table 13. Annual production of some species of mayfly larvae in the running waters

Taxon Reference	Biomass wet weight $\bar{x}$ ($g \cdot m^{-2}$)	Production wet weight ($g \cdot m^{-2}$)	Coeff. P/B	% Total Ephemeroptera production	Notes Type
Baetis buceratus ZELINKA 1980	0.563	6.652	11.82	26.6	Barbel stream Jihlava epipotamon
Baetis fuscatus ZELINKA 1980	0.143	1.601	11.19	6.4	dtto
Baetis lutheri ZELINKA 1980	0.407	3.412	8.38	13.6	dtto
Baetis rhodani ZELINKA 1973	0.663	5.317	8.02	19.6	Mountains trout brooks epirhithron
Baetis rhodani ZELINKA et al. 1977	1.146	10.406	9.08	21.3	Highlands trout brook epirhithron
Baetis vagans WATERS 1966	1.300	12.600	9.69	—	torrential stream — Minnesota
Cloeon dipterum ZELINKA 1980	0.418	4.678	11.19	—	Barbel stream Jihlava grasser near the bank
Caenis macrura ZELINKA 1980	0.091	1.181	12.98	4.7	Barbel stream Jihlava epipotamon
Ecdyonurus sp. div. HELAN et al. 1973	1.027	8.470	8.25	31.2	Mountains trout brooks epirhithron
Ecdyonurus sp. div. ZELINKA et al. 1977	0.785	8.486	10.81	17.4	Highlands trout brook epirhithron
Ecdyonurus venosus ZELINKA 1980	0.305	2.907	—	11.6	Barbel stream Jihlava epipotamon
Ephemerella ignita BROOKER & MORRIS 1978	0.480	3.176	6.6	—	Trout brook
Ephemerella ignita ZELINKA 1980	0.521	5.734	11.01	23.0	Barbel stream Jihlava epipotamon
Ephemerella subvaria WATERS & CRAWFORD 1973	—	26.40 — 33.30	—	—	Calculation by ALLEN and by HYNES
Ephoron virgo ZAHRÁDKA 1978, 1979	—	25.920	17.45	48.6	Barbel stream Jihlava metapotamon
Potamanthus luteus OBRDLÍK et al. 1979	0.085	0.928	10.90	12.2	Barbel stream Oslava thermal pollution
Potamanthus luteus ZAHRÁDKA 1978, 1979	0.642	10.320	16.07	19.3	Barbel stream Jihlava metapotamon
Potamanthus luteus ZELINKA 1980	0.388	2.853	7.53	11.4	Barbel stream Jihlava epipotamon
Rhithrogena semicolorata ZELINKA 1973	1.412	12.478	8.84	45.9	Mountains trout brooks epirhithron
Rhithrogena semicolorata ZELINKA et al. 1977	1.864	17.767	9.53	36.4	Highlands trout brook epirhithron
Rhitrogena semicolorata BROOKER & MORRIS 1978	0.420	1.776	4.5	—	Trout brook

Production studies are relatively time consuming. They require careful sampling (see differences in the populations of different habitats at one station), quantitative sampling in at least one month's intervals for the period of one year. The collected material must be measured and weighet according to the individual species and also according to size groups, or the mass is determined from the length-weight relations (the most advantageous is mutual checking). Then only time consuming calculations of the production for the individual

Table 14. Overall annual production of mayfly larvae in the running waters

Type and locality Reference	Biomass $\bar{x}$ (g · m^{-2})		Production (g · m^{-2})		Coeff. P/B	% Total macrozoobenthos production	Notes
	dry weight	wet weight	dry weight	wet weight			
Welsh mountain stream, HYNES 1961	—	—	0.450	—	—	15.0	
Beskydy mountains trout brooks 1966, ZELINKA 1973	—	3.244	—	27.152	8.37	22.0	epirhithron
dtto, 3 year mean, HELAN et al. 1973	—	2.972	—	24.875	8.37	21.1	epirhithron
Yoshimo river, TSUDA et al. 1975	—	—	—	22.40	—	—	
Saale — Fischersdorf, FLÖSSNER 1976	0.50	—	2.0	—	4.00	2.5	March — September pollution
Saale — Maua FLÖSSNER 1976	0.11	—	0.5	—	4.55	0.8	March — September pollution
Trout brook Bítýška, ZELINKA et al. 1977		5.044	—	48.826	—	24.8	epirhithron
Spring rivulets, ZELINKA 1977	—	—	—	5.00	—	—	hypocrenon
Trout streams, ZELINKA 1977	—	—	—	28.00	—	—	epirhithron
Grayling streams, ZELINKA 1977	—	—	—	35.00	—	—	hyporhithron
Barbel zones — upper part, ZELINKA 1977	—	—	—	50.00	—	—	epipotamon
Barbel zones — lower part, ZELINKA 1977	—	—	—	57.00	—	—	epipotamon — metapotamon
Bream zones, ZELINKA 1977	—	—	—	20.00	—	—	metapotamon (less *Palingenia*)
Lowland warm brooks, ZELINKA 1977	—	—	—	10.00	—	—	roach zone
Barbel stream Jihlava, ZAHRÁDKA 1978, 1979	—	—	—	53.370	—	—	metapotamon
Barbel stream Oslava, OBRDLÍK et al. 1979	—	1.200	—	7.605	6.34	—	epipotamon thermal pollution
Barbel stream Jihlava, ZELINKA 1980	—	2.485	—	25.027	10.07	10.0	epipotamon

partial habitats become possible and then for the type or stretch of the stream under investigation. Every simplification increases the possibility of marking errors. Discussion to the employed methods of zoobenthos production calculations has been published (ZELINKA & MARVAN 1976, see also ZWICK 1975, BENKE & WAIDE 1977, MENZIE 1980, and others).

The work would be facilitated by production calculation on the basis of the determined biomass. In all cases these relations were followed and in our opinion this way is realistic. We found a relatively constant relation between the mean annual biomass and the annual production. The most important thing is to achieve a uniform determination of the mean annual biomass. We took samples every month, and if more samples were taken in a month, the monthly average was always taken for the calculation of the annual average. The range of P/B coefficients, as found by us, varied from 8.02—11.82 (or 12.98 for the species *Caenis macrura*) for all species followed by us in a large number of stations. The lowest indices are those of the species with one generation per year and the species from colder streams and those with a low feeding capacity (perhaps greater energetic losses). Higher indices were found in species with two generations and those from streams with higher feeding capacities. A high P/B coefficient was also found in the summer species *Ephemerella ignita*, where there are relatively low losses in comparison with a great loss of larvae in the winter. Within the limits of our P/B coefficients are also some data from literature (Tables 13, 14). Major differences are due to the fact that quantitative samples were not taken regularly throughout the year or that some less reliable global method was used for the production calculation.

In all cases followed hitherto one phenomen stands out clear, viz. that from the whole spectrum of mayfly species occurring at one station only a few species are production important. At the stations followed 20—30% of species constituted 75—90% of the total production.

With the exception of species with a winter egg diapause mayfly larvae grow at different growth rates throughout the year. As follows from the comparison of Figs. 1—8, there are, however, considerable differences in production in the course of the year. It is interesting to note that in the chief production species production peaks at a station differ in time, thus balancing to a certain extent the greatest food competition (ZELINKA 1980).

From hitherto investigations (see also Table 14) it follows that mayfly larvae in the natural unpolluted streams are an important production component of macrozoobenthos, 10 to 25% of the total production. Their production is rather different; the lowest was found in spring rivulets, where mayfly larvae are relatively rare, and further in streams where "catchers" prevail in the food chain. On the other hand, there is a high production in trout and grayling streams and in barbel streams with ample occurrence of the species *Potamanthus luteus*, *Ephoron virgo*, and/or *Oligoneuriella rhenana* (see ZELINKA 1977). The production is strongly reduced by the pollution of the streams (ZELINKA 1979). The investigation of mayfly production is at its beginning, and besides finding out real values the problems of methods employed must be solved hand in hand.

5. Summary

The paper brings detailed results of production studies of 7 taxa of mayfly larvae and preliminary results of another 3 taxa. It describes and discusses differences in production in the course of the year, at partial habitats, and in different streams. The possibilities of calculating production by means of P/B coefficients are described and substantiated.

The production of mayfly larvae in unpolluted streams can be marked as high, as it usually constitutes 10—25% of the overall annual macrozoobenthos production. The values established varied between 10—50 $g \cdot m^{-2} \times year^{-1}$ and more of wet weight. For the nutrition of some running water fishes mayflies (for the most part larvae and subimagines) are one of the most important food components.

Comparison tables of data on mayfly production in running waters are provided as well as conversion tables of different mass and caloric values.

Zusammenfassung

Die Arbeit enthält umfassende Resultate von Produktionsuntersuchungen an 7 Taxa von Larven von Eintagsfliegen und vorläufige Ergebnisse von 3 weiteren Taxa.

Es werden Unterschiede in der Produktion im Jahresverlauf, in einzelnen Lebensräumen und in verschiedenen Flüssen beschrieben und diskutiert. Die Möglichkeit, die Produktion durch Anwendung von P/B-Koeffizienten einzuschätzen, wird erläutert und bestätigt.

Die Produktion der Eintagsfliegen-Larven in unverschmutzten Flüssen kann als hoch bezeichnet werden, da sie im allgemeinen 10—25% der gesamten jährlichen Makrozoobenthos-Produktion ausmacht. Die ermittelten Werte für das Frischgewicht lagen zwischen 10 und 50 $g \cdot m^{-2} \cdot a^{-1}$ und darüber. Für die Ernährung einiger Fische in Fließgewässern sind Eintagsfliegen (zum größten Teil Larven und Subimagines) eine der wichtigsten Komponenten.

Es werden sowohl vergleichende Tabellen mit Produktionsdaten der Eintagsfliegen in Flüssen als auch Umrechnungstabellen für verschiedene Masse- und Kalorienwerte vorgelegt.

Резюме

В работе приведены многочисленные результаты исследований продукции с 7 таксонами личинок подёнок и предварительные результаты 3 дальнейших таксонов.

Описаны и обсуждены различия между таксонами в продукции в течение года, в отдельных средах оби-

тания и в различных реках. Обсуждена и подтверждена возможность оценить продукцию применением коэффициентов P/B. Продукцию личинок подёнок в незагрязненных реках можно считать высокой, потому что она в общем составляет 10—25% общей годовой продукции макрозообентоса. Найденные значения для сырого веса лежат в пределах 10—50 г $\times м^{-2} \cdot a^{-1}$ и выше. Для питания некоторых рыб в проточных водах подёнки (главным образом личинки и субимага) являются одной из самых важных компонентов.

В работе представлены сравнительные таблицы, содержащие данные продукции подёнок в реках, а также таблицы пересчета для различных величин массы и калорий.

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