Ann. Zool. Fennici 50: 176–188 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 28 June 2013

Life cycle and secondary production of mayflies and stoneflies in a karstic spring in the West Carpathians

Kvetoslava Bottová* & Tomáš Derka

*Department of Ecology, Faculty of Natural Sciences, Comenius University, Mlynská Dolina, SK-842 15 Bratislava, Slovakia (*e-mail: bottova@fns.uniba.sk)*

Received 30 Nov. 2012, final version received 4 Feb. 2013, accepted 14 Feb. 2013

Bottová, K. & Derka, T. 2013: Life cycle and secondary production of mayflies and stoneflies in a karstic spring in the West Carpathians. — *Ann. Zool. Fennici* 50: 176–188.

This study focused on life strategies of Ephemeroptera and Plecoptera species found in a karstic spring stream at the Malé Karpaty Mts. (West Carpathians, Slovakia), which is characterized by low thermal fluctuations throughout the year (6–10 °C). We examined the life cycle and secondary production of three mayfly species (*Baetis alpinus*, *Baetis rhodani* and *Rhithrogena semicolorata*) and three stonefly species (*Protonemura nitida*, *Protonemura hrabei* and *Nemurella pictetii*). We found an unusually slow univoltine cycle for *P. nitida* and an asynchronous life cycle for *B. alpinus*, with first-stage nymphs occurring almost all year round. Uncommonly low abundances of *B. rhodani* were found, which indicates that the population lives at its ecological limit. Moreover, for the first time we acquired and analysed the data on secondary production of *P. nitida*, which reached the highest values (3335 mg DW m^{-2} y^{-1}) among all investigated species. In summary, the total annual secondary production of the mayfly community (889 mg DW m^{-2} y^{-1}) was seven times lower than the annual secondary production of the stonefly community (6233 mg DW m^{-2} y^{-1}).

Introduction

Life history data provide combined environmental and genetic information about aquatic insect populations (Butler 1984). While some species have fixed voltinism, others are known to have flexible life history patterns under different water temperature and food levels (Sweeney 1984). Knowledge of life cycles of aquatic species is of fundamental importance for all aspects of stream conservation (Rustigian *et al*. 2003).

In several continental aquatic ecosystems, benthic macroinvertebrates constitute the main community component responsible for secondary production (Robertson 1995, Grubaugh *et al*. 1997), assuring high values of biomass and representing the main pathway of energy transfer from lower to higher trophic level. Since benthic invertebrates play a central role in the flow of energy and matter through many benthic freshwater food webs (Wallace & Webster 1996), measures of secondary production of stream communities are very appropriate to characterize ecosystems (Waters 1977, Benke 1984, 1993). The magnitude of secondary production of an aquatic invertebrate population is influenced by its life history parameters, especially voltinism (Waters 1979, Benke *et al*. 1984, Huryn & Wallace 2000) and environmental factors, such as water temperature and water chemistry

(Sweeney & Vannote 1986, Huryn *et al*. 1995, Robinson & Minshall 1998, Kozáčeková *et al*. 2009). The estimation of secondary production is accomplished by the analysis of various patterns of the life history of the species (Waters 1979, Benke 1984), and life history patterns may change with environmental conditions. In particular, hydrological and thermal variability are two of the most important factors affecting life history, especially growth rates and seasonal timing of stream invertebrate life-cycle attributes (Sweeney 1984, Hauer & Benke 1987).

Water temperature is one of the parameters in stream ecology that determines the overall heat of aquatic ecosystems (Coutant 1999). It influences the growth rate of aquatic organisms (Jensen 1990, Elliott & Hurley 1997) as well as their distribution (Ebersole *et al*. 2003). Seasonal and daily variations of water temperatures are important determinants for the distribution of aquatic species (Vannote *et al*. 1980). Adaptation of benthic macroinvertebrates to water temperature changes is especially apparent in Plecoptera and Ephemeroptera. Plecoptera are mostly cool-water species, while Ephemeroptera are common in tropical waters. Both orders have developed different strategies to adapt to their environment (Haidekker & Hering 2008). For example, successful egg development often demands lower temperatures in cold-adapted species like many Plecoptera (Pritchard *et al*. 1996). Consequently, these species often have a summer diapause to avoid high temperatures. On the other hand, warm-adapted species, like many Ephemeroptera, develop faster at higher temperatures and sometimes have winter quiescence (Brittain 1990, Pritchard *et al*. 1996). Some mayfly species live in cold environments with a diapause or quiescence in summer. As compared with Plecoptera, less information on the development of Ephemeroptera under different thermal regimes is available (Haidekker & Hering 2008). In our previous studies of a constant-temperature spring we found unusual asynchronous and plastic life cycles of representatives of Amphipoda (*Gammarus fossarum*), Plecoptera (*Protonemura intricata*, *Leuctra prima*) and Ephemeroptera (*Baetis alpinus*) (Kozáčeková *et al*. 2009, Beracko *et al*. 2012, Bottová *et al*. 2013). Furthermore, the annual secondary productions of a stonefly community and a *Gammarus fossarum* population were higher than previously noted in other types of streams (Beracko *et al*. 2012, Bottová *et al*. 2013).

The aim of the present study was to investigate the effect of low temperature with minimal fluctuations throughout the year on the life cycle, growth and secondary production of three mayfly and three stonefly species.

Material and methods

The studied locality is a karstic spring of the Stupava stream in the Malé Karpaty Mts. (West Carpathians) (GPS coordinates: 48°15´32.59´´N, 17°07´6.75´´E). The sampling site is located about 10 m below the spring in a mature beech forest, at an altitude 328 m a.s.l. (Fig. 1). The substrate was composed mainly of moss (90%) and stones (10%). Water depth in the channel was 0.3 m, and the channel was 2.5 m wide. Temperature differences were minimal throughout the year (Fig. 2). The mean annual temperature was 8.7 °C, minimal recorded temperature was 6 °C and maximal temperature was 10.5 °C. The studied spring is a source of drinking water.

Quantitative samples of macrozoobenthos were collected monthly, from October 2009 to September 2010, using a Hess sampler (area 0.03 m^2, mesh size 0.3 mm). Three samples were taken from moss, giving a total area of 0.09 m^2, and four samples were taken from mesolithal, giving a total area of 0.12 m^2. Collected material was preserved in 4% formaldehyde. In the laboratory, mayfly and stonefly nymphs were separated from detritus and other taxa, sorted, identified to species, and counted under a binocular microscope. The presence of mature nymphs (those showing black wind pads) in samples was used as an indicator of flight period. Water temperature was recorded hourly with the aid of a submerged data logger (VEMCO Minilog TR) placed in the studied stream. Temperature data were averaged for each day to produce mean daily temperatures (Fig. 2). Size-frequency histograms representing life cycles were constructed in Microsoft Excel. Once a month, the total body length without cerci of each nymph was measured to the nearest 0.1 mm with the

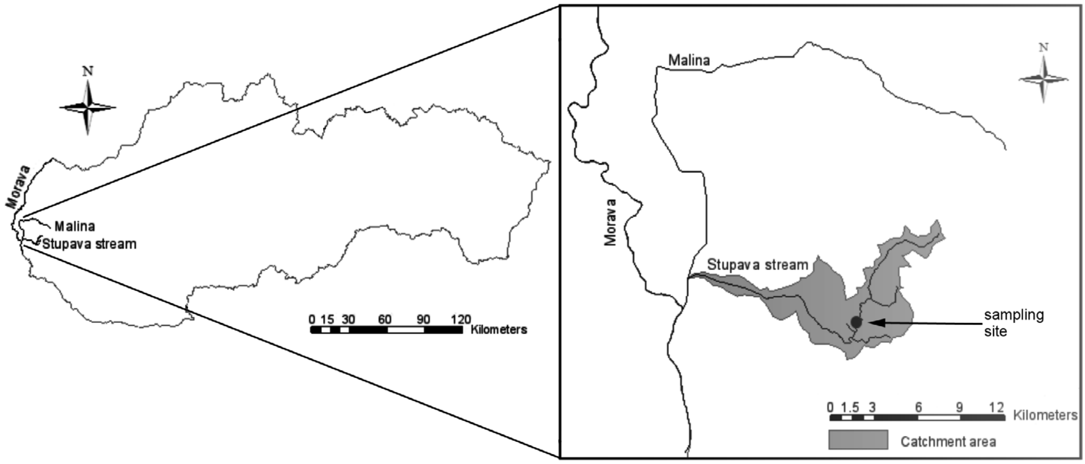

Fig. 1. Location of the sampling site.

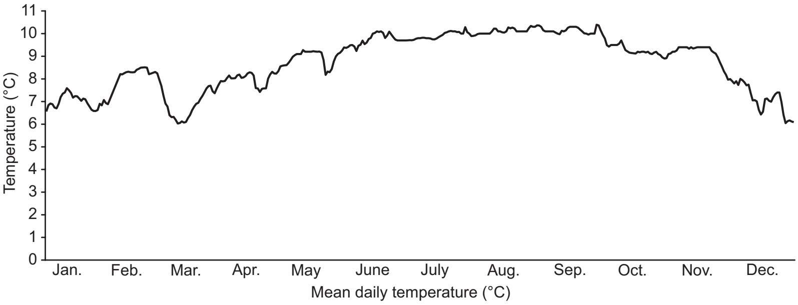

Fig. 2. Mean daily temperatures during the sampling period.

aid of a micrometer fixed to the binocular microscope. To avoid measurement errors produced by the curvature of the body, nymphs were placed between two slides before measuring them. Larvae were sorted into size classes with an interval of 0.5 mm. Biomass was calculated from predetermined length–mass relationships for each species according to Burgherr and Meyer (1997) and expressed as dry weight (mg DW m^{-2}).

Secondary production was evaluated using the size-frequency method (Benke 1979, Benke & Huryn 2006). We applied a correction for the cohort production interval (CPI, mean development time from hatching to final size; Benke 1979) for each species. Growth was calculated each month as the weighted mean of the nymphal total length, and the mean total length was weighted by the number of individuals in each size class.

Results

Altogether, five species of Ephemeroptera and seven species of Plecoptera were recorded. Life cycles were described and secondary productions were estimated for three mayfly species: *Baetis alpinus*, *Baetis rhodani* and *Rhithrogena semicolorata*. The last-mentioned species avoided moss and was only found in mesolithal. The most abundant stonefly species were *Protonemura nitida*, *Protonemura hrabei* and *Nemurella pictetii*, and also their life cycles and secondary productions were described. *Protonemura nitida* was found in mesolithal as well as in the moss, thus we compared its abundance, secondary production and life cycle in both substrates. Only few nymphs of *Baetis muticus*, *Ephemerella mucronata*, *Leuctra prima*, *Leuctra pseudosignifera*, *Nemoura sciurus* and *Isoperla oxylepis* were found, hence autecological characteristics

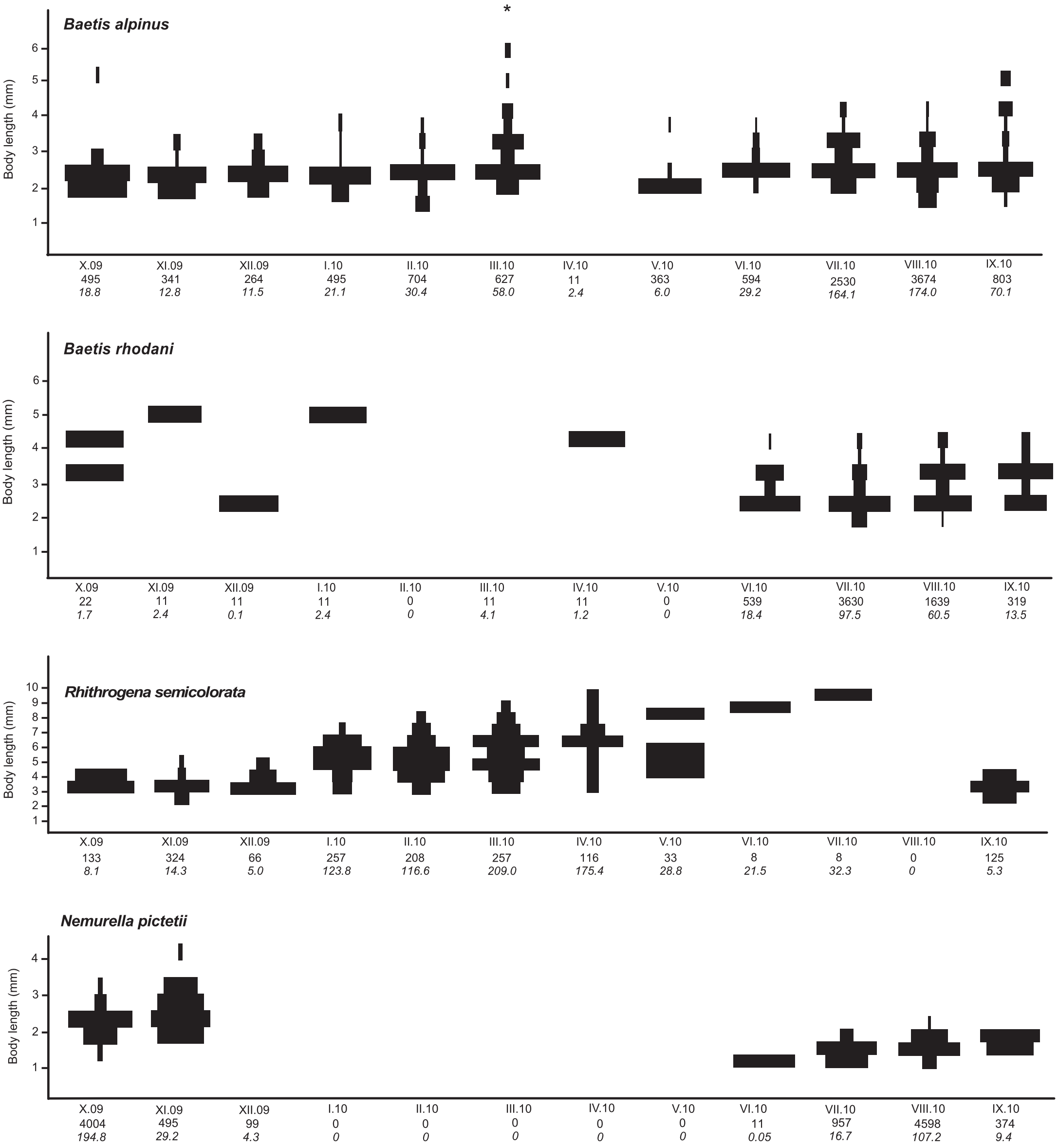

Fig. 3 (continued on the next page). Size-frequency distribution of nymph of *Baetis alpinus*, *Baetis rhodani*, *Rhithrogena semicolorata*, *Protonemura nitida*, *Protonemura hrabei* and *Nemurella pictetii* at the study site. Asterisks indicate the presence of mature nymphs. Numbers below the dates represent density (indiv. m^{-2}) of nymphs for each month and their biomass (mg DW m^{-2}; in italic).

of these species could not be studied. Of all investigated species, the highest density (13 585 indiv. m^{-2}) and biomass (3199 mg DW m^{-2}) were measured for *P. nitida* in the moss substrate.

Nymphs of *Baetis alpinus* were present in the stream during the whole sampling period. This species showed an asynchronous bivoltine life cycle, with nymphs of early instars present during each month and mature nymphs captured in March (Fig. 3). The first cohort occurred probably from May to October, and the second emerged possibly in October and disappeared in April. However, due to high asynchrony, the separation of cohorts is unclear. Growth was

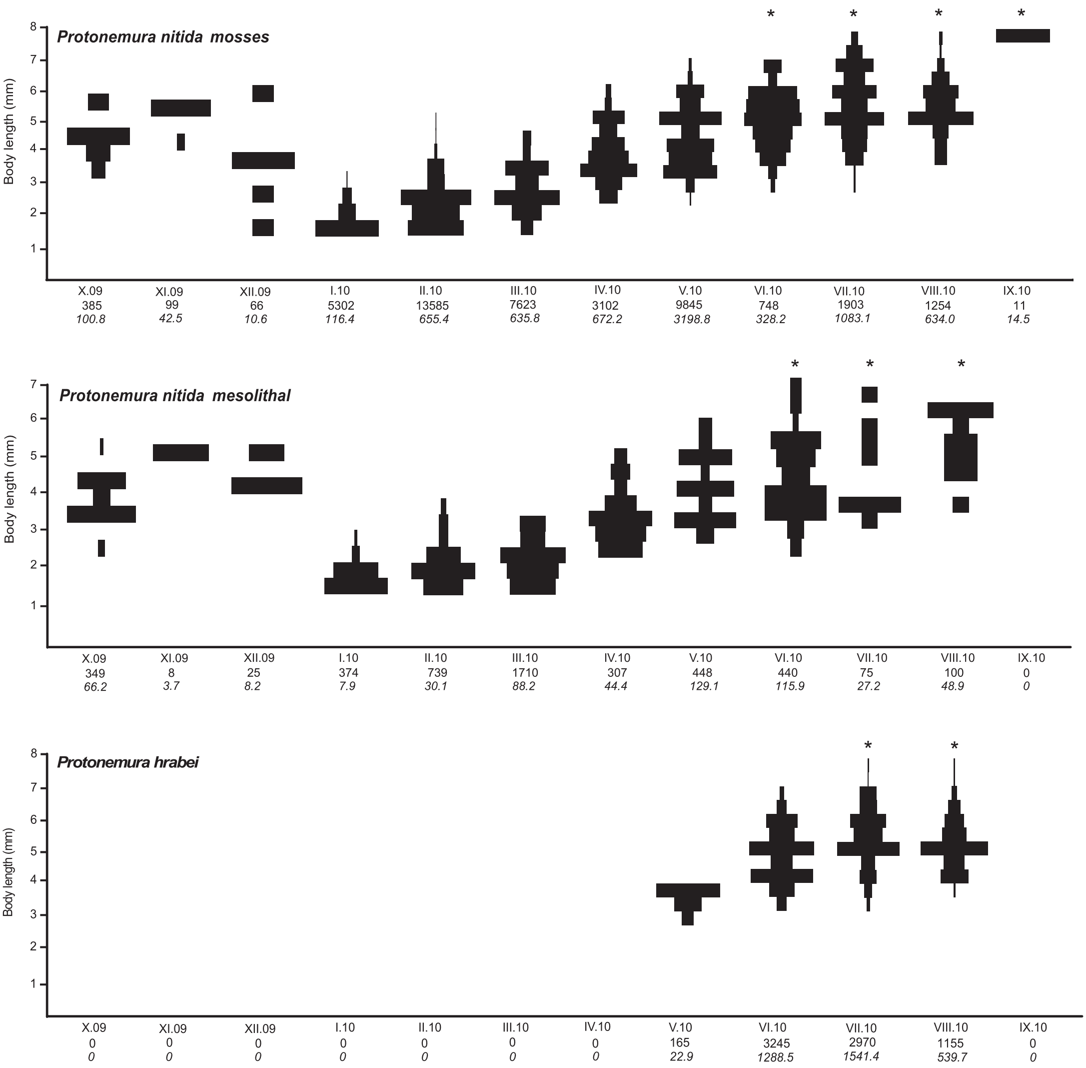

Fig. 3. Continued.

relatively constant, with a slight increase during March, coinciding with the emergence of adults (Fig. 4). Values of density and biomass culminated in July and August, when massive hatching occurred (Fig. 3). The annual secondary production and the annual production/biomass ratio (*P*/*B*) of *B. alpinus* in the study area were 332 mg DW m^{-2} y^{-1} and 7.8, respectively (Table 1).

Baetis rhodani showed a univoltine life cycle with hatching of nymphs from June to September. From October to May, there was a sudden drop in biomass and density values, suggesting suboptimal ecological conditions, which have caused high mortality and/or the emigration of young nymphs (Fig. 3). Only a few ansynchronous nymphs were found during this time. Growth was regular from June to September (Fig. 4). The annual secondary production and the annual *P*/*B* ratio were 141 mg DW m^{-2} y^{-1} and 8.2, respectively (Table 1).

Rhithrogena semicolorata appeared to have a univoltine life cycle. Nymphs were collected during the entire sampling period, with a maximum number of individuals in November, and very few individuals in the last months of nymphal development. Mature nymphs were not collected but the presence of large nymphs suggested that the flight period is in spring and

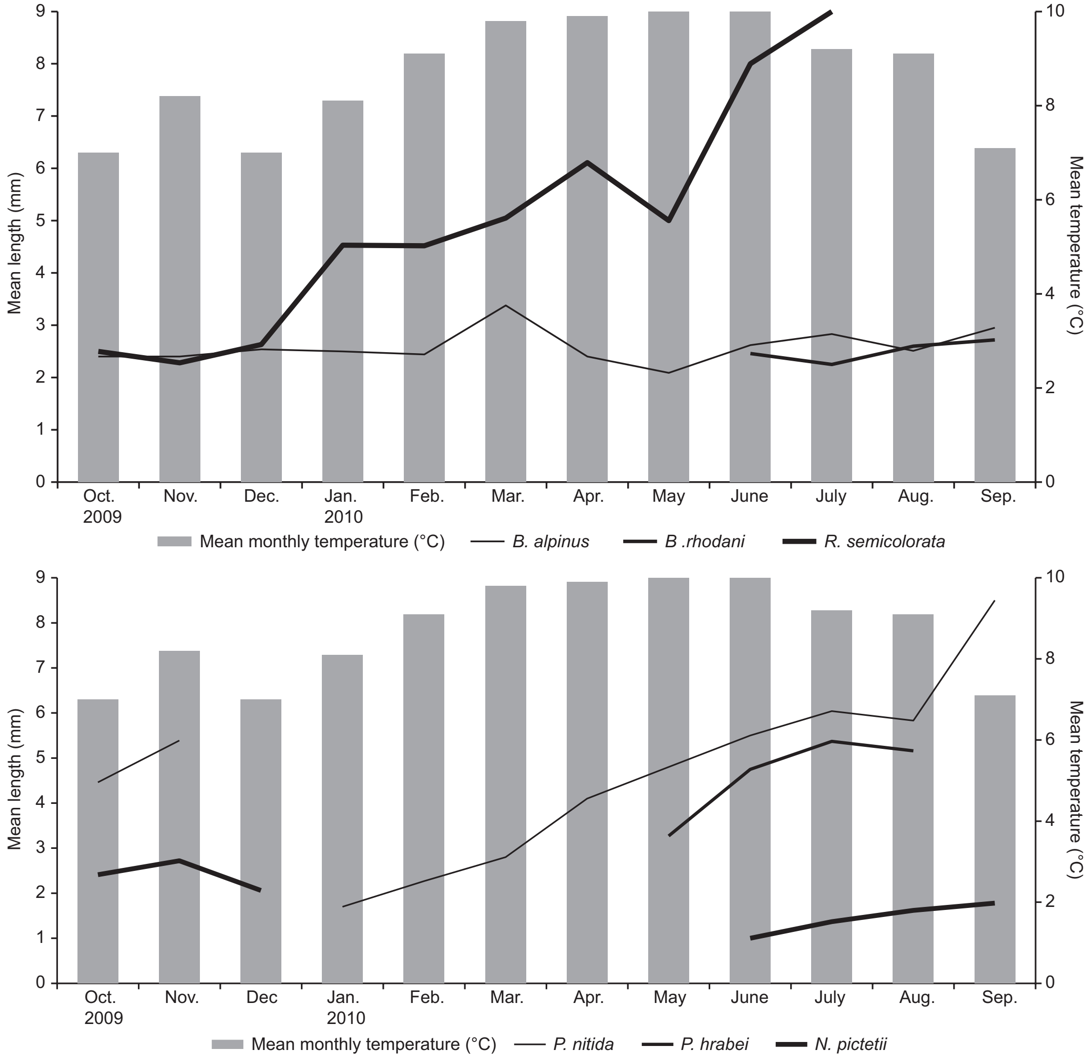

Fig. 4. Growth patterns of *Baetis alpinus*, *Baetis rhodani*, *Rhithrogena semicolorata*, *Protonemura nitida*, *Protonemura hrabei* and *Nemurella pictetii*, and mean monthly temperatures during the sampling period.

summer (Fig. 3). Growth was irregular throughout the larval development (Fig. 4). The annual secondary production and the annual *P*/*B* ratio were 415 mg DW m^{-2} y^{-1} and 7.4, respectively (Table 1).

Protonemura nitida in the moss substrate showed a slow univoltine life cycle with the presence of nymphs throughout the year. Mature nymphs occurred from June to September. The size of the nymphs varied videly, and an increase in mortality over time was reflected in lower numbers of individuals collected in the last months of the nymphal development period (Fig. 3). The highest density of individuals was recorded in February (13 585 indiv. m^{-2}) indicating massive hatching of nymphs, while the highest biomass was reached in May (3198.8 mg DW m^{-2}), coinciding probably with the beginning of the flight period. Growth was gradual, with an increase during summer, coinciding with emergence (Fig. 4). The annual secondary production and the annual *P*/*B* ratio were 3335 mg DW m^{-2} y^{-1} and 6.3, respectively (Table 1).

The the life cycle of *P. nitida* in the mesolithal substrate was identical to that in moss (*see* Fig. 3) but with noticeably lower values of density, biomass and annual secondary production which equalled 281 mg DW m^{-2} y^{-1}. The annual *P*/*B* ratio in this case was 6.4.

Nymphs of *Protonemura hrabei* showed a univoltine life cycle lasting four months. The first small nymphs were collected already in May. They grew rapidly, and mature nymphs were present in July and August, indicating a flight period occurring mainly in summer (Fig. 3). Growth was relatively constant, with a slight increase during the last months, coinciding with emergence (Fig. 4). The annual secondary production and the annual *P*/*B* ratio were was 2680 mg DW m^{-2} y^{-1} and 4.8, respectively (Table 1).

The nymphal development of *Nemurella pictetii* lasted for seven months. This species displayed a univoltine life cycle with the egg diapause during winter and spring (Fig. 3). Growth slowly increased in summer and autumn (Fig. 4). The highest density occurred in August (4598 indiv. m^{-2}), while the highest biomass was reached in October (194.8 mg DW m^{-2} y^{-1}) (Fig. 3). The annual secondary production and the annual *P*/*B* ratio were 218 mg DW m^{-2} y^{-1} and 5.0, respectively (Table 1).

The total annual secondary production of the stonefly community was seven times higher (6233 mg DW m^{-2} y^{-1}) as compared with that of the mayfly community (889 mg DW m^{-2} y^{-1}) (Table 1). The main producers were *P. nitida*, which contributed 53% to the total stonefly production, and *R. semicolorata*, which contributed 47% to the total mayfly production. The second most important producers were respectively *P. hrabei* (43%) and *B. alpinus* (37%).

Discussion

Low water-temperature variability in springs and low temperatures typical for cold springs, have been hypothesized to restrict the species composition and also to affect their life histories strategies and productivities (Williams & Hogg 1988, Wallace & Anderson 1996, Dobrin & Giberson 2003). A significantly larger proportion of species with asynchronous development was found in cold springs as compared with that in non-spring habitats. These observations suggest that thermal patterns do have an effect on species composition in cold springs, possibly by favouring taxa that already feature asynchronous development. Since species living in cold springs must be able to complete their development also at low summer temperatures, it is possible that high population asynchrony is simply a result of differences in life-history patterns allowing the species to colonize and survive in these habitats (Dobrin & Giberson 2003).

The life cycle of *Baetis alpinus* showed high plasticity, being bivoltine at lower altitudes and univoltine at higher altitudes (Landa 1968, 1969). These findings are in agreement with the study of Kukula (1997) who found that in two Polish streams *B. alpinus* had a winter–summer life cycle with two generations at low altitudes and one generation at higher altitudes. Studemann *et*

Table 1. Mean density (*D*), mean biomass (*B*), annual secondary production (*P*), annual and cohort *P*/*B* ratios, and cohort production interval (CPI) of mayflies and stoneflies species collected at the study site.

Species	Mean *D* (indiv. m^{-2})	Mean *B* (mg DW m^{-2})	*P* (mg DW m^{-2} y^{-1})	*P*/*B*		CPI (days)
				Annual	Cohort	
Mayflies						
Baetis alpinus	908	50	332	7.8	6.5	360
Baetis rhodani	517	17	141	8.2	6.8	300
Rhithrogena semicolorata	128	62	415	7.4		335
TOTAL	1553	129	889	–	–	–
Stoneflies						
Protonemura nitida	3660	624	3335	6.3	5.2	360
Protonemura hrabei	628	283	2680	4.8	4.0	155
Nemurella pictetii	878	30	218	5.0	4.2	215
TOTAL	5166	937	6233	–	–	–

al. (1992) reported a univoltine winter cycle for this species at an altitude below 1500 m a.s.l. and a bivoltine winter–summer cycle above 1500 m a.s.l. López-Rodríguez *et al*. (2008) suggested a bivoltine life cycle for *B. alpinus* in Sierra Nevada with mature nymphs appearing in February–May at lower altitudes, and a univoltine life cycle with mature nymphs in January–April at higher altitudes. In the Italian Alps, *B. alpinus* showed bivoltine and trivoltine life cycles depending on environmental conditions such as temperature or hydrological instability (Erba *et al*. 2003). Buffagni and Comin (2000) also found three cohorts in northern Italy. In the French Pyrenees, Céréghino and Lavandier (1998) discovered a bivoltine life cycle with long flight periods lasting from April to October. Populations of *B. alpinus* exhibited several life-cycle types, although they are generally bivoltine with a nymphal winter generation (Clifford 1982). We confirmed a bivoltine life cycle for *B. alpinus* but in our case it was highly asynchronous with nymphs of early instars present each month suggesting continuous growth throughout the year. Temperature has been shown to be the major factor in explaining differences in life cycle strategies in this species (Humpesch 1979). We found first-stage nymphs during almost the entire sampling period, indicating asynchronous hatching. In a recent study, we found a bivoltine life cycle with asynchronous hatching for *B. alpinus* in a constant-temperature spring at the Prosiek stream (K. Bottová unpubl. data). Williams and Hogg (1988) and Wallace and Anderson (1996) suggested that life cycles of at least some aquatic insects in springs should be less synchronous than life cycles of those inhabiting non-spring habitats, possibly due to the lack of temperature cues to synchronize development (Dobrin & Giberson 2003).

Flexibility of life cycle strategies enables *Baetis rhodani* to inhabit different watersheds and makes it a widely distributed species (Illies 1978). The highly plastic development models of *B. rhodani* range from a fairly synchronous univoltinism in cold-water habitats to a wide range of more or less synchronous, multivoltine cycles (Brittain 1991). One characteristic of *B. rhodani* is its ability to complete its life cycle in a wide range of temperatures (Fahy 1973). The life cycle of *B. rhodani* is frequently described as bivoltine with a slow-growing overwintering generation emerging in spring and a fast-growing summer generation emerging during late summer and autumn (e.g. Ghetti *et al*. 1979, Wise 1980). Interestingly, three generations of *B. rhodani* have been identified in northern Italy (Buffagni *et al*. 2002, Erba *et al*. 2003). Our investigation showed that *B. rhodani* is univoltine with increasing mortality during winter, spring and at the beginning of summer. We found similar patterns in this species' life strategies in a constant-temperature spring at the Prosiek stream (K. Bottová unpubl. data). Interestingly, annual secondary production measured at our study site was very low as compared with that reported in other studies (Larsen 1968, Zelinka 1973, 1977a, 1984, Deván & Krno 1996, Bottová *et al*. 2012) (Table 2). The low values of annual secondary production, uncommonly low mayfly abundances, and the occurrence of a few asynchronous nymphs throughout the majority of the year in cold springs could indicate that *B. rhodani* lives at its ecological limit, possibly due to suboptimal environmental conditions.

Rhithrogena semicolorata is a typical submontane species distributed mainly at altitudes of 300–650 m (Soldán *et al*. 1998). Its life cycle is univoltine with larval development mainly in spring and the emergence period in spring and summer (Krno 1982, Hefti & Tomka 1990, Buffagni *et al*. 2009). This life cycle pattern was confirmed in the present study. Secondary production measured in our study was several times lower than the values reported by Deván and Krno (1996) from the Turiec river and by Zelinka (1973, 1977a) from Beskydy streams. This difference could indicate suboptimal ecological conditions at our study site (Table 2).

Very little is known about the life cycle and secondary production of *Protonemura nitida*. According to Soldán *et al*. (1998), it is a rather submontane species occurring within a wide range of altitudinal zones (230–950 m). The nymphs prefer small streams largely overgrown by aquatic mosses, similar to our study site. The life cycle is univoltine with a flight period from July to November (Soldán *et al*. 1998). Krno (1996) showed it to have a fast summer life cycle with adult emergence in autumn. Interestingly, we found a slow univoltine life cycle and nymphs present during the whole year. One

Table 2. Comparison of annual secondary production (*P*) (mg DW m^{-2} y^{-1}) and annual *P*/*B* ratios of mayfly and stonefly species and communities from different water habitats. x = no published data.

Species	Spring			Stream			River		
	P	*P*/*B*	Suorce	*P*	*P*/*B*	Suorce	*P*	*P*/*B*	Suorce
Baetis alpinus	332	7.8	this study	10–500	4.0–6.7	Ritter (1985)	–	–	–
	970.9	4.8	K. Bottová unpubl. data	1036	7.6	Weichselbaumer (1984)	–	–	–
Baetis rhodani	54.7	6.5	K. Bottová unpubl. data	266	3.4	Bottová *et al.* (2012)	197	–	Larsen (1968)
	141	8.2	this study	835	4.4	Bottová *et al.* (2012)	1179.9	9	Deván & Krno (1996)
	–	–	–	1063	8	Zelinka (1973)	1120–1370	6.4–7.9	Neveu *et al.* (1979)
	–	–	–	2081	9.1	Zelinka (1977a)	–	–	–
	–	–	–	2454	8.0–8.9	Zelinka (1984)	–	–	–
Rhithrogena gr. *semicolorata*	415	7.4	this study	3045	8.8	Zelinka (1973)	590–680	4.8–5.6	Neveu *et al.* (1979)
	–	–	–	4335	9.5	Zelinka (1977a)	738	6.4	Russev & Doshkinova (1985)
	–	–	–	–	–	–	1482.1	8.8	Deván & Krno (1996)
Nemurella pictetii	218	5.0	this study	354.9	–	Krno (1998)	–	–	–
Protonemura nitida	3660	4.8	this study	x	x				
Protonemura hrabei	628	5.0	this study	x	x				
Ephemeroptera	889	–	this study	732	–	Krno *et al.* (2006)	6257	–	Zelinka (1980)
	1654.8	–	K. Bottová unpubl. data	1446	–	Bottová *et al.* (2012)	7000	–	Zelinka (1977b)
	–	–		3568	–	Bottová *et al.* (2012)	10 086	–	Deván & Krno (1996)
Plecoptera	6233	–	this study	340	–	Krno (2000)	1275	–	Krno (1996)
	4304	–	Bottová *et al.* (2012)	364–519	–	Krno (1997)	–	–	–
	–	–		914–1318	–	Krno (1997)	–	–	–

possible explanation for this difference is an almost constant temperature of the spring, providing no reliable seasonal cues that are critical to certain life-history stages (Sweeney 1984). Another possibility to consider is that nymphs of *P. nitida* were not able to complete their development under such low temperatures. According to Lindegaard and Thorup (1975), species with long-lasting life cycles quantitatively dominate the moss fauna of spring streams. The levels of secondary production measured in mosses and in mesolithal were clearly different, although annual *P*/*B* values were quite similar. Twelvefold higher secondary production in moss substrates was the result of high abundances of individuals here. Colonization of submerged mosses by enormous numbers of invertebrates is a well-known phenomenon (Hynes 1961, Lindegaard & Thorup 1975, Suren 1991, Tada & Satake 1994). To date, however, no data on *P. nitida* secondary production have been published.

According to Soldán *et al*. (1998), *P. hrabei* is a typical autumn species with a wide altitudinal range of 250–1400 m. Its life cycle lasts from May to September (Krno 1982). The fast univoltine cycle of *P. hrabei* has also been reported in different types of streams by Krno (1982, 1996). Nymphs of *P. hrabei* mostly occur together with *P. nitida* (Soldán *et al*. 1998) as we also found in our study. Although nymphs of *P. hrabei* were present in the stream only for four months, its annual secondary production — for the first time presented here — was relatively high.

Nemurella pictetii is an extremely widespread species, abundant in a variety of habitats, from springs (Zwick 1977, Nesterovitch & Zwick 2003) to acid waters (Rupprecht & Frisch 1992, Krno 1998). Its life cycle is very flexible and varies from univoltine (e.g. Hynes 1976, Hildrew *et al*. 1980) and semivoltine (Brittain 1978) to plurivoltine, with three emergence periods every year (Zwick 1977, Wolf & Zwick 1989). Krno (1998) described a bivoltine life cycle in an acidified stream in the Malé Karpaty Mts. In the present study, we found different patterns: the nymphs were absent from January to May, and we did not found any mature nymphs or adults. Nesterovitch and Zwick (2003) suggested that the development and growth of *N. pictetii* terminates at temperatures below 6 °C. However, at our study site, temperature ranged between 7–9 °C during the period of no growth. It is obvious that *Nemurella* nymphs grew faster in warmer than in cooler streams (Nesterovitch & Zwick 2003). Previous records of secondary production of *N. pictetii* are limited. Krno (1998) found nearly two times higher secondary production in an acidified stream in the Malé Karpaty Mts. (Table 2).

High annual secondary production of the stonefly community at our study site was mainly related to the high abundances of two species: *P. nitida* and *P. hrabei*. This value is even higher than measured in the constant-temperature cold spring at the Prosiek stream (Bottová *et al*. 2013). Furthermore, in the other West Carpathians streams as well as in the Turiec river in Slovakia (Krno 1996, 1997, 2000), secondary production values for the stonefly community were markedly lower than presented in this study (Table 2). High stonefly secondary production values could be related to the type of substrate, since mosses provide a stable substrate commonly containing a high density of invertebrates (Lindegaard & Thorup 1975). Partially, this could be related to the almost stable thermal regime in the karstic spring, which could allow for high production values, irrespective of seasons. Huryn and Wallace (2000) suggested that low-production macroinvertebrate communities occur in cool-temperate streams. Our results show that it is not true for all groups, and that secondary production of stoneflies can be especially high. On the other hand, total annual secondary production of the mayfly community at our study site reached only 889 mg DW m^{-2} y^{-1} as compared with 1654.8 mg DW m^{-2} y^{-1} in the spring at the Prosiek stream (K. Bottová unpubl. data). Deván and Krno (1996) reported eleven times higher secondary production values in the Turiec river than presented here. Secondary production of the mayfly community in several other streams (Zelinka 1977b, 1980) was approximately seven times higher than in our study (Table 2). Low secondary production values of the mayfly community, which was measured in cold springs, could be related to the thermal ability of mayflies that are generally adapted to warmer conditions and develop faster at higher temperatures (Brittain 1990, Pritchard *et al*. 1996).

Conclusions

Our recent studies on Ephemeroptera and Plecoptera communities in springs with a stable thermal regime throughout the year support the hypothesis that cold springs have a large proportion of species with asynchronous life cycles (Williams & Hogg 1988, Wallace & Anderson 1996, Dobrin & Giberson 2003). Consequently, thermal patterns do have an effect on species development in these habitats because temperature does not synchronize development. In the present study, we identified an asynchronous life cycle for first-stage nymphs of *B. alpinus* during almost the whole year. Interestingly, we found an uncommonly slow univoltine life cycle for *P. nitida*. Moreover, we showed that *B. rhodani* had a low abundance in the spring streams, while *B. alpinus* was the most abundant mayfly species. We conclude that as compare with Ephemeroptera, Plecoptera are the more successful group in habitats with constant temperature. They reach high densities and high secondary production. High plasticity in the life history is one of the most important factors that preadapt species to life in cold springs.

Acknowledgments

The authors thank prof. Il'ja Krno for help with identification of the stoneflies and for his kindness and valuable comments. We also thank two anonymous reviewers for their useful and interesting comments that clearly improved the original manuscript. The study was supported by a Ph.D. scholarship of the Comenius University (project nos. UK/252/2009 and UK/185/2010), and by the Slovak Grant Agency VEGA, (project no. 11/077/00).

References

Benke, A. C. 1979: A modification of the Hynes method for estimating secondary production with particular significant for multivoltine population. — *Limnology and Oceanography* 24: 168–174.

Benke, A. C. 1984: Secondary production of aquatic invertebrates. — In: Resh, V. H. & Rosenberg, V. (eds.), *The Ecology of aquatic insects:* 289–322. Praeger Publishers, New York.

Benke, A. C. 1993: Concepts and patterns of invertebrate production in running waters. — *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte. Limnologie* 25: 15–38.

Benke, A. C. & Huryn, A. D. 2006: Secondary production of macroinvertebrates. — In: Hauer, F. R. & Lamberti, G. A. (eds.), *Methods in stream ecology*, 2nd ed.: 691–710. Academic Press, New York.

Benke, A. C., Van Arsdall, T. C. Jr., Gillespie, D. M. & Parrish, F. K. 1984: Invertebrate productivity in a subtropical blackwater river: The importance of habitat and life history. — *Ecological Monographs* 54: 25–63.

Beracko, P., Sýkorová, A. & Štangler, A. 2012: Life history, secondary production and population dynamics of *Gammarus fossarum* (Koch, 1836) in a constant temperature stream. — *Biologia* 67/1: 164–171.

Bottová, K., Derka, T. & Svitok, M. 2012: Life history and secondary production of mayflies (Ephemeroptera) indicate disturbance in two small Carpathian streams. — *International Review of Hydrobiology* 97: 100–116.

Bottová, K., Derka, T., Beracko, P. & Tierno de Figueroa, J. M. 2013: Life cycle, feeding and secondary production of Plecoptera community in a constant temperature stream in central Europe. — *Limnologica* 43: 27–33.

Brittain, J. E. 1978: Semivoltinism in mountain populations of *Nemurella pictetii* (Plecoptera). — *Oikos* 30: 1–6.

Brittain, J. E. 1990: Life history strategies in Ephemeroptera and Plecoptera. — In: Campbell, I. C. (ed.), *Mayflies and stoneflies*: 1–12. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Brittain, J. E. 1991: Life history characteristics as a determinant of the response of mayflies and stoneflies to manmade environmental disturbance (Ephemeroptera and Plecoptera). — In: Alba-Tercedor, J. & Sandez-Ortega, A. (eds.), *Overview and strategies of Ephemeroptera and Plecoptera*: 539–545. Sandhill Crane Press, Gainesville, Florida.

Buffagni, A. & Comin, E. 2000: Secondary production of benthic communities at the habitat scale as a tool to assess ecological integrity in mountain streams. — *Hydrobiologia* 422/423: 183–195.

Buffagni, A., Erba, S. & Origgi, G. 2002: Efemerotteri. 2. Cicli biologici e sviluppo larvale. — In: *Atlante della biodiversità del Parco del Ticino*, vol. 2 Monografie: 60–73. Parco del Ticino, Corbetta.

Buffagni, A., Cazzola, M., López-Rodríguez, M. J., Alba-Tercedor, J. & Armanini, D. G. 2009: *Distribution and ecological preferences of European freshwater organisms*, volume 3: *Ephemeroptera*. — Pensoft Publisher, Sofia–Moskow.

Burgherr, P. & Meyer, E. I. 1997: Regression analysis of linear body dimensions *vs.* dry mass in stream macroinvertabrates. — *Archiv für Hydrobiologie* 139: 101–112.

Butler, M. G. 1984: Life histories of aquatic insects. — In: Resh, V. H. & Rosenberg, D. M. (eds.), *The ecology of aquatic insects*: 24–55. Praeger Publisher, New York.

Céréghino, R. & Lavandier, P. 1998: Infuence of hypolimnetic hydropeaking on the distribution and population dynamics of Ephemeroptera in a mountain stream. — *Freshwater Biology* 40: 385–399.

Clifford, H. F. 1982: Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. — *Quaestiones Entomologicae* 18: 15–90.

Coutant, C. C. 1999: *Perspective on temperature in the Pacific Northwest's fresh water.* — Environmental Sciences Division, Publication no. 4849, Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Deván, P. & Krno, I. 1996: Mayflies (Ephemeroptera). — In: Krno, I. (ed.), *Limnology of the Turiec river basin (West Carpathians, Slovakia)*: 8–41. Biologia, Bratislava.

Dobrin, D. & Giberson, D. J. 2003: Life history and production of mayflies, stoneflies, and caddisflies (Ephemeroptera, Plecoptera, and Trichoptera) in a spring-fed stream in Prince Edward Island, Canada: evidence for population asynchrony in spring habitats? — *Canadian Journal of Zoology* 81: 1083–1095.

Ebersole, J. L., Liss, W. J. & Frissell, C. A. 2003: Cold water patches in warm streams: physicochemical characteristics and the influence of shading. — *Journal of the American Water Resources Association* 39: 355–367.

Elliott, J. M. & Hurley, M. A. 1997: A functional model for maximum growth of Atlantic salmon parr, *Salmo salar*, from two populations in northwest England. — *Functional Ecology* 11: 592–603.

Erba, S., Melissano, L. & Buffagni, A. 2003: Life cycles of Baetidae (Insecta: Ephemeroptera) in a North Italian Prealpine stream. — In: Gaino, E. (ed.), *Research update on Ephemeroptera and Plecoptera*: 177–186. University of Perugia Press, Perugia, Italy.

Fahy, E. 1973: Observation on the growth of Ephemeroptera in fluctuating and constant temperature conditions. — *Proceedings of the Royal Irish Academy* 73: 133–149.

Ghetti, P. F., Bonazzi, G., Musi, G. & Ravanetti, U. 1979: Cicli vitali di Efemerotteri e Plecotteri in un torrente sperimentale. — *Acta Naturae* 149–157.

Grubaugh, J. W., Wallace, J. B. & Houston, E. S. 1997: Production of benthic macroinvertebrate communities along a southern Appalachian river continuum. — *Freshwater Biology* 37: 581–596.

Haidekker, A. & Hering, D. 2008: Relationship between benthic insects (Ephemeroptera, Plecoptera, Coleoptera, Trichoptera) and temperature in small and medium-sized streams in Germany: a multivariate study. — *Aquatic Ecology* 42: 463–481.

Hauer, F. R. & Benke, A. C. 1987: Influence of temperature and river hydrograph on blackfly growth rates in a subtropical blackwater river. — *Journal of the North American Benthological Society* 6: 251–261.

Hefti, D. & Tomka, I. 1990: Abundance, growth and production of three mayfly species (Ephemeroptera, Insecta) from the Swiss Prealps. — *Archiv für Hydrobiologie* 120: 211–228.

Hildrew, A. G., Townsend, C. R. & Henderson, J. 1980: Interactions between larval size, microdistribution and substrate in the stoneflies of an iron-rich stream. — *Oikos* 35: 387–396.

Humpesch, U. H. 1979: Life cycle and growth rates of *Baetis* spp. (Ephemeroptera, Baetidae) in the laboratory and in two stony streams in Austria. — *Freshwatater Biology* 9: 467–479.

Huryn, A. D., Benke, A. C. & Ward, G. M. 1995: Direct and indirect effects of geology on the distribution, biomass, and production of the freshwater snail *Elimia*. — *Journal of the North American Benthological Society* 14: 519–534.

Huryn, A. D. & Wallace, J. B. 2000: Life history and production of stream insects. — *Annual Review of Entomology* 45: 83–110.

Hynes, H. B. N. 1961: The invertebrate fauna of a Welsh mountain stream. — *Archiv für Hydrobiologie* 57: 344–388.

Hynes, H. B. N. 1976: Biology of Plecoptera. — *Annual Review of Entomology* 21: 135–153.

Illies, J. 1978: *Limnofauna Europaea*. — Gustav Fischer Verlag, Stuttgart, New York.

Jensen, A. J. 1990: Growth of young migratory brown trout *Salmo trutta* correlated with water temperature in Norwegian rivers. — *Journal of Animal Ecology* 59: 603–614.

Kozáčeková, Z., Tierno de Figueroa, J. M., López-Rodríguez, M. J., Beracko, P. & Derka, T. 2009: Life history of a population of *Protonemura intricata* (Ris, 1902) (Insecta, Plecoptera) in a constant temperature stream in Central Europe. — *International Review of Hydrobiology* 94: 57–66.

Krno, I. 1982: Macrozoobenthos structure and dynamics in the River Ľupčianka and its tributaries (Nízke Tatry Mts.). — *Biologické Práce SAV* 28: 1–126.

Krno, I. 1996: Limnology of the Turiec river basin (West Carpathians, Slovakia). — *Biologia* 51: 1–122.

Krno, I. 1997: Production and distribution of stoneflies (Plecoptera) of Slovakia. — In: Landolt, P. & Sartori, M. (eds.), *Ephemeroptera and Plecoptera: biology-ecology-systematic*: 199–204. MTL, Fribourg.

Krno, I. 1998: Influence of abiotic and biotic factors on the life cycles and production of stoneflies (Plecoptera) in an acidified spring area. — *Biologia* 53: 195–204.

Krno, I. 2000: Stoneflies (Plecoptera) in some volcanic mountain range of the West Carpathians (Slovakia) and the impact of human activities. — *Limnologica* 30: 341–350.

Krno, I., Šporka, F., Štefková, E., Tirjaková, E., Bitušík, P., Bulánková, E., Lukáš, J., Illéšová, D., Derka, T., Tomajka J. & Černý, J. 2006: Ecological study of a high-mountain stream ecosystem (Hincov potok, High Tatra Mountains, Slovakia). — *Acta Societatis Zoologicae Bohemicae* 69: 299–316.

Kukula, K. 1997: The life cycles of three species of Ephemeroptera in two streams in Poland. — *Hydrobiologia* 353: 193–198.

Landa, V. 1968: Developmental cycles of central European Ephemeroptera and their interrelations. — *Acta Entomologica Bohemoslav* 65: 276–284.

Landa, V. 1969: *Ephemeroptera. Fauna ČSSR*. — Academia, Praha.

Larsen, R. 1968: The life cycle of Ephemeroptera in the lower part of Aurland River in Sogn and Fjordane, western Norway. — *Norsk Entomologisk Tidsskriff* 15: 49–59.

Lindegaard, C. & Thorup, J. 1975: The invertebrate fauna of the moss carpet in the Danish spring Ravnkilde and its seasonal, vertical and horizontal distribution. — *Archiv für Hydrobiologie* 75: 109–139.

López-Rodríguez, M. J., Tierno de Figueroa, J. M. & Alba-Tercedor, J. 2008: Life history and larval feeding of some species of Ephemeroptera and Plecoptera (Insecta) in the Sierra Nevada (Southern Iberian Peninsula). — *Hydrobiologia* 610: 277–295.

Nesterovitch, A. & Zwick, P. 2003: The development of *Nemurella pictetii* Klapálek (Plecoptera: Nemouridae) in two springstreams in central Europe. — *Limnologica* 33: 231–243.

Neveu, A., Lapchin, L. & Vignes, J. C. 1979: Le macrobenthos de la basse Nivelle, petit fleuve côtier des Pyrénées-Altantique. — *Annales de Zoologie Ecologie Animale* 11: 85–111.

Pritchard, G., Harder, L. D. & Mutch, R. A. 1996: Development of aquatic insect eggs in relation to temperature and strategies for dealing with different thermal environments. — *Biological Journal of the Linnean Society* 58: 221–244.

Ritter, H. 1985: Die Ephemeropteren des Stocktalbaches (Kűhtai, Tirol). *Diss. Abt. Limnol. Univ. Innsbruck* 20: 1–153.

Robertson, A. L. 1995: Secondary production of a community of benthic Chydoridae (Cladocera: Crustacea) in a large river, U.K. — *Archiv für Hydrobiologie* 134: 425–440.

Robinson, C. T. & Minshall, G. W. 1998: Macroinvertebrate communities, secondary production, and life history patterns in two adjacent streams in Idaho, USA. — *Archiv für Hydrobiologie* 142: 257–281.

Rupprecht, R. & Frisch, S. 1992: The sensitivity of *Nemurella pictetii* (Insecta: Plecoptera) to acidity. — *Verhandlungen des Internationalen Verein Limnologie* 24: 2892–2894.

Russev, B. K. & Doshkinova, M. G. 1985: On the development and productivity of mayfly larvae (Ephemeroptera, Insecta) in a stretch of the Iskar River. — *Hydrobiology* 25: 3–16.

Rustigian, H. L., Santelmann, M. & Schumaker, N. H. 2003: Assessing the potential impacts of alternative landscape designs on amphibian population dynamics. — *Landscape Ecology* 18: 65–81.

Soldán, T., Zahrádková, S., Helešic, J., Dušek, L. & Landa, V. 1998: Distributional and quantitative patterns of Ephemeroptera and Plecoptera in the Czech Republic: A possibility of detection of long-term environmental changes of aquatic biotopes. — *Folia Facultatis Scientiarium Naturalium Universitatis Masarykianae Brunensis, Biologia* 98: 1–305.

Studemann, D., Landlot, P., Sartori, M., Hefti, D. & Tomka, I. 1992: *Inescta Helvetica fauna*. — Imprimerie mauron + Tinguely & Lachat Sa, Fribourg.

Suren, A. M. 1991: Bryophytes as invertebrate habitat in two New Zealand alpine streams. — *Freshwater Biology* 26: 399–418.

Sweeney, B. W. 1984: Factors influencing life history patterns of aquatic insects. — In: Resh, V. H. & Rosenbergm D. M. (eds.), *The ecology of aquatic insects*: 56–100. Praeger Publisher, New York.

Sweeney, B. W. & Vannote, R. L. 1986: Growth and production of a stream stonefly: influences of diet and temperature. — *Ecology* 67: 1396–1410.

Tada, M. & Satake, K. 1994: Epiphytic zoobenthos on bryophyte mats in a cool mountain stream, Toyamazawa. — *Japanese Journal of Limnology* 55: 159–164.

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R. & Cushing, C. E. 1980: The river continuum concept. — *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–137.

Wallace, J. B. & Anderson, N. H. 1996: Habitat, life history, and behavioral adaptations of aquatic insects. — In: Merritt, R. W. & Cummins, K. W. (eds.), *An introduction to the aquatic insects of North America*, 3 ed.: 41–73. Kendall/Hunt Publishing Co., Dubuque, Iowa.

Wallace, J. B. & Webster, J. R. 1996: The role of macroinvertebrates in stream ecosystem function. — *Annual Review of Entomology* 41: 115–139.

Waters, T. F. 1977: Secondary production in inland waters. — *Advances in Ecological Research* 10: 91–164.

Waters, T. F. 1979: Influences of benthos life history upon the estimation of secondary production. — *Journal of the Fisheries Research Board of Canada* 36: 1425–1430.

Weichselbaumer, P. 1984: Die Populationsdynamik von *Baetis alpinus* (Pictet) und anderer Baetidae (Ephemeroptera) in einem kleinen Mittelgebirgbach (Piburger Bach, Tirol). — *Dissertation Abstracts, Institute of Limnology, University of Innsbruck* 19: 1–171.

Williams, D. D. & Hogg, I. D. 1988: Ecology and production of invertebrates in a Canadian coldwater spring–springbrook system. — *Holarctic Ecology* 11: 41–54.

Wise, J. E. 1980: Seasonal distribution and life historiesof Ephemeroptera in a Northumbrian River. — *Freshwater Biology* 10: 101–111.

Wolf, B. & Zwick, R. 1989: Plurimodal emergence and plurivoltinism of central European populations of *Nemurella pictetii* (Plecoptera: Nemouridae). — *Oecologia* 79: 431–438.

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

Zelinka, M. 1977a: Production conditions of the polluted trout brook. — *Folia Facultatis Scientiarum Naturalium* 18: 7–105.

Zelinka, M. 1977b: The production of Ephemeroptera in running waters. — *Hydrobiologia* 56: 121–125.

Zelinka, M. 1980: Differences in the production of mayfly larvae in partial habitats of a barbel stream. — *Archiv für Hydrobiologie* 90: 284–297.

Zelinka, M. 1984: Production of several species of mayfly larvae. — *Limnologica* 15: 21–41.

Zwick, P. 1977: Plecopteren-Emergenz zweier Lunzer Bäche, 1972–1974. — *Archiv für Hydrobiologie* 80: 458–505.