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

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


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 (Protoneumura 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.
Life cycle and secondary production of mayflies and stoneflies


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).

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.

Material and methods

Quantitative samples of macrozoobenthos were collected monthly, from October 2009 to September 2010, using a Hess sampler (area 0.03 m², mesh size 0.3 mm). Three samples were taken from moss, giving a total area of 0.09 m², and four samples were taken from mesolithal, giving a total area of 0.12 m². 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
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 nym- phal 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 *Protone- mura 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. 1. Location of the sampling site.

Fig. 2. Mean daily temperatures during the sampling period.
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
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 asynsynchronous 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...
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 widely, 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 life cycle of *P. nitida* in the mesolithal substrate was identical to that in moss (see Fig. 3) but with noticeably lower values of den-
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.

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

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
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-Rodriguez 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, Cérégghino 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 Turieic 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Spring</th>
<th>Stream</th>
<th>River</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>P/B</td>
<td>Source</td>
</tr>
<tr>
<td>Baetis alpinus</td>
<td>332</td>
<td>7.8</td>
<td>this study</td>
</tr>
<tr>
<td></td>
<td>970.9</td>
<td>4.8</td>
<td>K. Bottová unpubl. data</td>
</tr>
<tr>
<td>Baetis rhodani</td>
<td>54.7</td>
<td>6.5</td>
<td>K. Bottová unpubl. data</td>
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<td></td>
<td>141</td>
<td>8.2</td>
<td>this study</td>
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<td></td>
<td>–</td>
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<td>–</td>
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<tr>
<td>Rhithrogena gr.</td>
<td>415</td>
<td>7.4</td>
<td>this study</td>
</tr>
<tr>
<td>semicolorata</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<td></td>
<td>–</td>
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<td>–</td>
</tr>
<tr>
<td>Nemurella pictetii</td>
<td>218</td>
<td>5.0</td>
<td>this study</td>
</tr>
<tr>
<td>Protonemura nitida</td>
<td>3660</td>
<td>4.8</td>
<td>this study</td>
</tr>
<tr>
<td>Protonemura hrabei</td>
<td>628</td>
<td>5.0</td>
<td>this study</td>
</tr>
<tr>
<td></td>
<td>1654.8</td>
<td>–</td>
<td>K. Bottová unpubl. data</td>
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</tbody>
</table>
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. Twelve-fold 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 pluvivoltine, 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 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. Iľja 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).

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