Introduction

The importance of water temperature has long been recognized, and has been identified as responsible for the distribution and richness of species along altitudinal and latitudinal gradients (Quinn and Hickey 1990; Reyjol et al. 2001). Generally, water temperature is a key factor influencing the embryonic development, larval growth, emergence, metabolism and survival of many taxa (Sweeney and Vannote 1978; Watanabe et al. 1999; Haidekker and Hering 2008). Photoperiod has also an important influence on life cycles of aquatic insects. It is a factor influencing larval diapause, the amount of time necessary to complete larval development and emergence of adults. It is important for synchronizing life histories in a habitat (Sweeney 1984). Factors contributing to high levels of production appear to be closely related to mode of feeding and life-history attributes of communities in temperate stream. Highly productive communities tend to occur in warm to cool temperate streams and tend to be dominated by filter-feeding bivalves, black flies or caddisflies (Huryn and Wallace 2000).

The studies on macroinvertebrate productivity is an important step in understanding running water ecosystems. Species of the order Plecoptera constitute one of the main components, both in biomass and ecological roles, of the benthic macroinvertebrate community in the streams and rivers (Hynes 1970; Stewart and



Stark 1993). They are a group playing a very important role in most cool, natural, and clean streams with high dissolved oxygen content (Hynes 1961; Wigglesworth 1972). Life cycles of Plecoptera species last from less than a year to several years, with variations mainly depending on species and water temperature (Brittain 1973; Brittain and Lillehammer 1987; Williams et al. 1995).

In Central Europe, and particularly in Slovakia, life cycles and secondary production of some Plecoptera species have been studied in detail (Krno 1982; Krno 1984; Krno 1996; Krno 1997; Krno 1998; Derka et al. 2004; Kozáčeková et al. 2009). Krno (1997) summarized the production of the West Carpathian stonefly nymphs at species and taxocoenoses levels.

According to Graf et al. (2009) *Isoperla sudetica* (Kolenati, 1859), *Leuctra armata* Kempny, 1899 and *Leuctra prima* Kempny, 1899 could be univoltine, as it is the more general pattern in these genera. Nevertheless, studies on these species are needed, because cases of semivoltinism are known both in *Isoperla* and *Leuctra*, sometimes for particular populations of the species. Thus, growth rate and life cycle duration depend fundamentally of the environmental temperature (Brinck 1949; Hynes 1970) and the food quantity and quality (Lillehammer 1975; Anderson and Cummins 1979; Baekken 1981). According to Zwick (1991), *L. prima* has a univoltine life cycle, with adults emerging at the end of winter. Data on secondary production for *L. armata* and *I. sudetica* are reported by Krno and Šporka (2003), who also report an univoltine life cycle for both species.

Many studies have addressed the importance of food resources to stream consumers by examining their gut contents (e.g. Lamberti and Moore 1984). Nevertheless, feeding analyses need to be



Fig. 1. Map of the study area, showing its location in Slovakia, and the position of the sampling site (*).

combined with production estimates in order to understand the ecosystem significance of the study population (Benke and Wallace 1980; Wallace et al. 1987; Whiles et al. 1999). Although Graf et al. (2009) noted that L. armata and L. prima can belong to the Feeding Functional Group (FFG) gatherer-collector and, in a low concern, shredder and grazer, this was a generalization for Leuctra species, and, as far as we know, no specific studies on these species exist. The same is true for I. sudetica, noted to be mainly a predator (as the great majority of Isoperla species) by Graf et al. (2009). Nevertheless, the food habits of Isoperla are highly diverse, ranging from predatory to detritivory-herbivory or omnivory, and some studies confirm that the feeding habits of an unstudied species cannot be inferred from studies of congeners (Stewart and Stark 2002; López-Rodríguez et al. 2009). Moreover, the diet of a species can change in relation to body size, and dietary shifts should be considered, whenever possible, when describing a species feeding habits (López-Rodríguez et al. 2009).

The aim of this study is describe life cycles, nymphal feeding and secondary production of stonefly species and simultaneously to increase the knowledge of some aspects of the nymphal biology of these species in a stream with constant temperature throughout the year.

Study area

28

The study was carried out in Prosiek stream located in Chočské Vrchy Mts. (West Carpathians) in Northern Slovakia (GPS coordinates: N 49°09′43.49″, E 19°29′ 32.2″, altitude: 705 m a.s.l.) (Fig. 1). The sampling site is located in canyon about 100 m below spring. The spring temperature is almost constant throughout the whole year, 8 °C May–August, 7 °C September–April. The substrate, formed by limestone, is reflected in high water pH values. Chemical parameters were measured once on 25th October 2007: pH7.98, PO₄^{3–} = 0.03 mg l⁻¹, NO^{3–} = 4.5 mg l⁻¹, SO₄^{2–} = 15.5 mg l⁻¹. The riparian vegetation consists mainly of the spruces. Water depth in the channel was 0.25 m, water width in the channel was 3.7 m and bankfull width in the channel was 6 m.

Methods

Quantitative samples of macroinvertebrates (two samples from mesolithal and two from macrolithal, representing a total area of 0.4 m^2) were collected monthly, from January to December 2005, using a Kubíček's benthic sampler (area 0.1 m^2 , mesh size 0.5 mm). Supplementary semi-quantitative samples of nymphs were taken monthly from mesolithal (1 min) and macrolithal (1 min) with a kick net, mesh size 0.5 mm. Collected material was preserved in

4% formalin. Stoneflies nymphs were separated from detritus and other taxa in the laboratory. Nymphs were identified with Raušer (1980), Lillehammer (1988), Zwick (2004) and Krno (2011). Adults were captured, and preserved in 70% alcohol, for reconfirming the nymph identification. Water temperature was measured every sampling time with a hand-held thermometer.

Both, quantitative and semi-quantitative samples were used to study life cycles. Total body length without cerci of each nymph per month was measured to the nearest 0.1 mm with the aid of a micrometer fixed to the binocular microscope. Larvae were sorted into size classes with an interval of 0.5 mm.

Estimation of nymph body mass was made according to Burgherr and Meyer (1997) using the equation:

$$\ln DM = \ln a + b \ln L$$

where DM = individual dry mass; L = total body length; a = constant; b = slope of the regression.

Leuctra	spp. :	$\ln a = -6.12;$	b = 2.66
Isoperla	spp. :	$\ln a = -5.46;$	<i>b</i> = 2.8

The individual growth rate was estimated by using an exponential relationship between the log-transformed values of the mean individual dry mass for each date over time: $gw = (\ln M_{i+1} - \ln M_i)/t$, where M_i – mean individual mass at time *i*, M_{i+1} – mean individual mass at time i + 1, t - the time interval in days (Waters 1977). The sum of day-light hours per period between two samplings was considered as the photoperiod length. Regression between monthly individual growth rate and photoperiod length was calculated using STATGRAPHICS software (STATPOINT 2006). Secondary production was evaluated from quantitative samples using the size-frequency method (Benke 1979; Benke and Huryn 2006). The production of *L. armata* was estimated from: $P = \text{mean } B \times P/B$, where P/B ratio = 5.3 (Krno 1997), P – secondary production and B - biomass. The monthly productions were estimated according to Beracko (2007) using the equation: $P_i = \sum_{j=1}^{j=1} (P_j \times N_{ij}/N_j)$, where P_i - production of the population in the *i*th month, P_i - production in the jth size class (this production is known from the size-frequency method), N_{ij} - number of individuals in the *j*th size class and in the *i*th month, N_i – total number of individuals in the *j*th size class. To calculate total annual secondary production of the stonefly community, we included annual production of P. intricata which was 909 mg DW m^{-2} with an annual *P*/*B* ratio of 4.4 (Kozáčeková et al. 2009).

Gut contents were analysed following the methodology of Bello and Cabrera (1999), which was used in other studies of stoneflies nymphal feeding (e.g. Derka et al. 2004; Tierno de Figueroa et al.

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Species	Mean D (ind m ⁻²)	Mean $B (mg DW m^{-2})$	$P(\text{mg}\text{DW}\text{m}^{-2})$	P/B
Isoperla sudetica	291	304	2190	7.2
Leuctra prima	292	197	1069	5.4
L. prima cohort 1	66	52	325	6.3
L. prima cohort 2	226	145	744	5.1
L. armata	28	26	136	5.3
Protonemura intricata	209	205	909	4.4
P. intricata cohort 1	200	157	772	4.95
P. intricata cohort 2	9	49	138	2.8
Total		732	4304	

2006; Fenoglio et al. 2007; Kozáčeková et al. 2009). For this, each specimen was introduced in a vial with Hertwig's liquid and heated in an oven at 65 °C for 48–72 h. After this, they were mounted on slides for study under the microscope. The percentage of the absolute gut content (at 40×), as the total area occupied by the content in the whole digestive tract, and the relative gut content (at 400×), as the area occupied for each component within the total gut content, were estimated using the microscope with an ocular micrometer. For the feeding study, mean, standard deviation and minimum and maximum were calculated. None of the data analyzed agreed with the normality assumption needed to use parametric statistics, so non-parametric analyses were chosen. The variations of the gut contents in relation to the body length were analyzed with a Gamma correlation test. Feeding niches overlap was calculated by the formula $O_{jk} = O_{kj} =$

$$p_{ij} \cdot p_{ik} / \sqrt{\left(\sum p_{ij}^2 \cdot \sum p_{ik}^2\right)}$$
 where p_{ij} and p_{ik} = proportion of i

food ingredients for the feeding composition in a species (j) and species (k). The value of the overlap index of feeding niche ranges of values from 0 to 1, where 0 is no overlap of two species and 1 mean absolute overlap of feeding niches (Pianka 1973).

Results

 $(\sum$

Table 1

Altogether 8160 individuals of 10 species of Plecoptera were recorded: *Isoperla sudetica, Leuctra prima, L. armata, L. albida* Kempny, 1899, *L. braueri* Kempny, 1898, *L. aurita* Navás, 1919, *Siphonoperla neglecta* (Rostock and Kolbe, 1888), *Brachyptera seticornis* (Klapálek, 1902), *Nemoura uncinata* Despax, 1934 and *Protonemura intricata* (Ris, 1902). The last-mentioned species was already processed by Kozáčeková et al. (2009). For *I. sudetica* and *L. prima* the life cycles were constructed, the values of *P/B* ratio and

gut contents were studied. For *L. armata* the values of secondary production, biomass and *P*/*B* ratio were calculated. In nymphs of *L. armata* gut contents were also analyzed. Only few nymphs of *L. albida, L. aurita, L. braueri, B. seticornis, S. neglecta* and *N. uncinata* were captured, thus autecological characteristics could not be studied for these species.

Life cycle and secondary production

I. sudetica showed an univoltine life cycle with nymphs occurring during all sample period. Adult emergence occurred from March to July (Fig. 2). Mean annual biomass was 304 mg DW m^{-2} and mean annual density was 291 ind m⁻². Secondary production was 2190 mg DW m⁻² with an annual production/biomass (*P*/*B*) of 7.2 (Table 1). The highest monthly production value was measured in April (366 mg DW m⁻²). The lowest monthly production values were measured from June to September (44–69 mg DW m⁻²) (Fig. 3).

L. prima showed a complicate life cycle consisting of two cohorts. Nymphs of the first cohort hatched from July to September and the adult emergence occurred from October to December/January. Nymphs of the second cohort hatched from October to December, grew up in the spring and the adult emergence occurred from April to June (Fig. 4). The development of the second cohort was longer (approximately 9 months) than the first one (with a length of approximately 6 months). The second cohort was more numerous than the first one, reaching approximately four times higher density values and three times higher biomass values. Mean annual biomass was 197 mg DW m⁻², cohort biomass values were 52 mg DW m⁻² for the first cohort and 145 mg DW m⁻² for the second one. Mean annual density was 292 ind m⁻², cohort density values were 66 ind m⁻² for the first cohort and 226 ind m⁻² for the second cohort. Monthly nymphal growth rate was positively



Fig. 2. Size-frequency distribution of *Isoperla sudetica* nymph at the study site. Asterisks indicate the presence of adults. Density (ind m⁻²) of nymphs for each month is shown below the date of the sampling.

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Fig. 3. Monthly production of Isoperla sudetica divided into four size groups according to body length.

correlated with photoperiod length (R=0.72; P<0.05). Relationship between monthly individual growth rate and photoperiod length was expressed by a regression model where: growth rate = 0.00398 – 0.555 g/photoperiod length (Fig. 5). The annual secondary production of *L. prima* was 1069 mg DW m⁻² with an annual production/biomass (P/B) of 5.4. Secondary production of the first cohort was 325 mg DW m⁻² with cohort P/B of 6.3. Secondary production of the second cohort reaching 744 mg DW m⁻² constitutes to nearly two-thirds of the total production with cohort P/B of 5.1 (Table 1). Monthly production values ranged between 5 mg DW m⁻² and 350 mg DW m⁻² (Fig. 6).

Due to low abundance of *L. armata* we could not precisely determine its life cycle. Estimated annual secondary production was calculated at 136 mg DW m⁻² with an annual production/biomass (*P*/*B*) of 5.3. Estimated mean annual biomass was 26 mg DW m⁻² and mean annual density was 28 ind m⁻² (Table 1).

Total secondary production of the stonefly community was $4304 \text{ mg DW m}^{-2}$ and mean annual biomass was 732 mg DW m^{-2} (Table 1). The main producer was *I. sudetica* which contributed to 51% of total stonefly production. The second most important producer was *L. prima* (25%) followed by *P. intricata* (21%).

Feeding

30

The main gut component of *I. sudetica* was detritus, followed by animal remains consisting mainly from head capsules chironomid larvae, and mandibles and claws of stoneflies and mayflies.

Table 2
Nymphal gut contents of Isoperla sudetica at the study site

	Ν	Mean	SD	Min.	Max.
% absolute	205	44.37	35.57	0	100
% detritus	145	55.76	41.27	0	100
% diatoms	145	7.62	20.23	0	90
% plant remains	145	1.07	4.65	0	50
% fungi	145	0.28	3.32	0	40
% animal remains	145	33.9	41.62	0	100

Diatoms, plant remains and fungi were represented in a lesser content (Table 2). When we analyzed the variation of the gut content in relation to the total body length, we found a positive correlation between nymphal size and animal remains (Gamma correlation = 0.53; P < 0.05) and negative correlation between nymphal size and detritus (Gamma correlation = -0.48; P < 0.05), diatoms (Gamma correlation = -0.03; P < 0.05) and plant remains (Gamma correlation = -0.07; P < 0.05). Therefore, changes in feeding habits were detected in *I. sudetica* as it grew. During growth species passed from detritus feeder to animal feeder thus from gatherer-collector to predator.

The most important feeding components of *L. prima* were detritus and plant remains. We found other components in the gut, such as diatoms and animal remains, but they were ingested less frequently (Table 3). Correlation between nymphal size and the percentage of each component found in the gut revealed that *L. prima* did not experience changes in food intake pattern in relation



Fig. 4. Size-frequency distribution of *Leuctra prima* nymphs at the study site. Asterisks indicate the presence of adults. Density (ind m⁻²) of nymphs for each month is shown below the date of the sampling.

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Fig. 5. Regression analysis of growth rate and length of photoperiod of *Leuctra prima* nymphs.

Table 3

Nymphal gut contents of Leuctra prima at the study site.

	Ν	Mean	SD	Min.	Max.
% absolute	150	75.33	24.54	0	100
% detritus	140	95.71	9.4	30	100
% diatoms	140	0.07	0.85	0	10
% plant remains	140	4.0	9.14	0	70
% fungi	140	0.14	1.19	0	10
% animal remains	140	0.07	0.85	0	10

Table 4

Nymphal gut contents of Leuctra armata at the study site.

	Ν	Mean	SD	Min.	Max.
% absolute	54	74.81	23.69	0	100
% detritus	50	88.2	10.09	0	100
% diatoms	50	0.6	2.4	0	10
% plant remains	50	11.0	9.1	0	40
% animal remains	50	0.2	1.41	0	10

to size (Gamma correlation non significant in any case). This species can be considered a gatherer-collector.

The study of the gut contents of *L* armata showed that the main components were detritus and plant remains (Table 4). When we analyzed the variation of the gut content in relation to the total body length, we found a positive correlation between nymphal size and plant remains (Gamma correlation = 0.52; P<0.05) and negative correlation between



Fig. 7. Feeding niches overlap between species *Isoperla sudetica*, *Leuctra prima* and *Leuctra armata* at the study site.

nymphal size and detritus (Gamma correlation = -0.49; P < 0.05). This means that smaller nymphs feed mostly on detritus, while larger nymphs feed mainly on plant remains. During development the individuals passed from mainly gatherer-collector to shredder.

We found 99.7% overlap between feeding niches of *L. prima* and *L. armata* Overlap between *L. armata* and *I. sudetica* was 84.6% and between *L. prima* and *I. sudetica* was 84.9% (Fig. 7).

Discussion

Life cycle and production

All studied species have been classified as taxa with univoltine life cycle (Graf et al. 2009). The study of the life cycle of every single species is essential because both genera *Isoperla* and *Leuctra* include species with semivoltine life cycle, e.g. *Isoperla obscura* (Zetterstedt, 1840) or *Leuctra nigra* (Olivier, 1811) (Lillehammer 1988). Similar pattern was found for *Protonemoura intricata* which showed an unusual and complicate life cycle, consisting of two cohorts (Kozáčeková et al. 2009) even though it is usually accepted that *P. intricata* has a simple univoltine life cycle (Zwick 1981; Marten and Zwick 1989). This could be related to the temperature uniformity through the year. Williams and Hogg (1988) and Wallace and Anderson (1996) suggested that the life cycles of at least some aquatic insects in springs should be less synchronous than the life cycles of those in nearby non-spring habitats, owing to a lack of temperature cues to synchronize development (Dobrin and



Fig. 6. Monthly production of *Leuctra prima* divided into four size groups according to body length.

32

Giberson 2003). The large proportion of species with asynchronous development in the cold spring compared with non-spring habitats suggests that thermal patterns do have an effect on species composition in these habitats, possibly by favouring taxa that already possess asynchronous development. Since species that live in cold springs must also be able to complete their development at low summer temperatures, it is possible that the high population asynchrony is simply a result of the life-history patterns of the species which can colonize and survive in these habitats (Dobrin and Giberson 2003).

I. sudetica is a Central-European species (Fochetti and Tierno de Figueroa 2004). The species is cold stenothermophilous associated with various montane habitats (Krno 2000) and it inhabits epirhithral zone and, in a less concern, hypocrenal, metarhithral and eucrenal zones (Graf et al. 2009). It is a species with univoltine life cycle (Krno 1997; Krno and Šporka 2003; Graf et al. 2009) and spring–summer emergence (Krno 1982) coinciding with our findings. The secondary production of *I. sudetica* in West Carpathians measured by Krno (1997) was 357.6 mg DW m⁻², which represents only one-sixth of the secondary production observed at our study site. Annual *P*/*B* ratio measured by Krno (1997) was 7.1 and almost corresponded with our results. In the High Tatras the secondary production was only 121.5 mg DW m⁻² with an annual *P*/*B* ratio of 5.6 (Krno and Šporka 2003).

L. prima is a Central-European species reaching the south Pyrenees, Macedonia and Northern Italy (Fochetti and Tierno de Figueroa 2004). The species is eurythermophilous restricted to different types of lotic biotopes, traversing a large altitude gradient and it inhabits epirhithral zone and, in very less concern, the hypocrenal zone (Graf et al. 2009). L. prima has an univoltine life cycle with winter-spring flight period (Illies 1955; Aubert 1959; Krno 1982; Krno 1998; Zwick 1990; Vinçon and Ravizza 2001; Fochetti and Tierno de Figueroa 2008; Graf et al. 2009). This also applies to the life cycle of L. prima which had two cohorts at our study site. The constant temperature regime in many headwater streams and spring brooks does not reliably cue the seasonal changes that are critical to certain life-history stages (e.g. air temperatures suitable for adult flight, feeding, reproduction). One might expect that photoperiod would provide a more reliable and informative signal than temperature in this constant-temperature habitat (Sweeney 1984). Indeed, our results showed that this is only partially true because growth rates of L. prima were positively correlated with the length of the photoperiod. However, the life cycles were relatively asynchronous, with wide nymphal size ranges along the year which can be explained by the constant temperature. The same patterns were recorded for P. intricata (with two cohorts) at the same study site (Kozáčeková et al. 2009). Krno (1997) found this species in two sites at Myjava brook in West Carpathians. At the first one the secondary production was only 26 mg DW m^{-2} and 42 mg DW m^{-2} at the second site with quite high an annual *P*/*B* ratio 9.7 and 15. Even in these streams the values of the secondary production are considerably lower than at our site. CPI intervals were similar as the CPI of the first and second cohorts at our site. This means that the development of one cohort at our site is comparable with development of whole population at both sites studied by Krno (1997).

L. armata is a Central-European species (Fochetti and Tierno de Figueroa 2004). The species inhabits eucrenal, hypocrenal and epirhithral zones (Graf et al. 2009). It is a typical spring species with slow life cycle (with nymphs growing almost all the year) (Krno 1982). Flight period extends from the end of spring to the beginning of autumn, but occurs mainly in summer (Illies 1955; Fochetti and Tierno de Figueroa 2008; Graf et al. 2009). Krno and Šporka (2003) noted for this species an univoltine life cycle in the High Tatras and in the catchment of Ľupčianka river (Krno 1997). Our estimated annual secondary production (136 mg DW m⁻²)

was two times higher than in High Tatras where the secondary production reached 69 mg DW m^{-2} and seven times higher than in catchment of Lupčianka river were it reached only 18 mg DW m⁻².

The high annual secondary production of the stonefly community (4304 $mg\,DW\,m^{-2})$ at the study site is mainly related to the abundance of three dominant species - I. sudetica, L. prima and P. intricata – and to their aquatic permanence through the whole year. The secondary production of the stonefly community in other West Carpathians streams was 340 mg DW m⁻² in Hučava brook (Krno 2000) what is approximately 13 times lower than our results. The secondary production of the stonefly community measured in Turiec river in Slovakia was 3.5 times lower than our results, reaching the value $1275 \text{ mg DW m}^{-2}$ (Krno 1996). Furthermore, secondary production measured at Lupčianka brook ranged from 914 mg DW m^{-2} to $1318 \text{ mg DW m}^{-2}$ (Krno 1997) and at Myjava brook in Slovakia ranged from 364 mg DW m^{-2} to $519\,mg$ DW m^{-2} (Krno 1997), both with markedly lower values than in our results. Compared with these results, the total secondary production of the stonefly community at our study site is very high. This could be related to the stable thermal regime which could allow a high production values, irrespective of seasons. However, our results did not correspond with Huryn and Wallace (2000), who suggested that the lowest production for macroinvertebrate communities is in cooltemperate streams. Our results showed that it is not true in Prosiek stream.

Feeding

In most studies, I. sudetica has been categorized as predator (Krno 1992; Krno and Šporka 2003; Graf et al. 2009). Nevertheless, we found that during growth species passed from mainly detritivorous to predator. In fact, the feeding habits of Isoperla are highly diverse, and range from predatory to partially detritivorous-herbivorous or omnivorous (Stewart and Stark 2002; López-Rodríguez et al. 2009). Moreover, the diet of a species can change in relation to body size, and dietary shifts should be considered, when describing a species feeding habits (López-Rodríguez et al. 2009). Our results show that L. prima and L. armata are mainly detritivorous as pointed out by Krno (1992) and Graf et al. (2009). Both species are classified as gatherer-collector and, in a low concern, shredder and grazer (Graf et al. 2009; Krno 2003). Nevertheless, we found that smaller nymphs of L. armata feed mostly detritus, while larger nymphs ingest plant remains as a major component. Thus, changes in diet composition over the life cycle are evident in this species. All the previous data indicate that studies on gut contents must be made at species/population scale and that the existence of ontogenetic shifts in diet should be considered studying the population during all its life cycle.

Conclusion

The present study shows patterns of a stonefly community not controlled by variable water temperature. We found that for *L. prima* and *P. intricata* photoperiod correlates with growth rates, but this is not true for *I. sudetica*. The observed asynchrony in growth could be related to the lack of temperature control. For the two former species, we found a complicated life cycle with two cohorts with different duration, different from those found in many other localities. The annual secondary production of the stonefly community was considerably higher than that previously noted in other streams from Slovakia. This could reflect the absence of temperature fluctuations, detected in other streams, where the same species were present. Regarding feeding, we found changes in the diet in relation to body size in some species. This is an important aspect that should be considered in ecological studies.

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