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Research Paper

Life History of a Population of *Protonemura intricata* (Ris, 1902) (Insecta, Plecoptera) in a Constant Temperature Stream in Central Europe

key words: stonefly, cohort splitting, secondary production, photoperiod, feeding.

Abstract

The nymphal biology (life cycle, secondary production and feeding) of a population of *Protonemura intricata* was studied in a calcareous stream with almost constant temperature (7–8 °C) through the year at Prosiek valley (Chočské Vrchy Mts., West Carpathians, Slovakia). The results were compared with those previously known for this species in other areas. According to our data, the species has a complicated life cycle consisting of two cohorts with different duration (probably a cohort splitting). This life cycle seems to be uncommon among the Plecoptera, which usually has simple univoltine or semivoltine life cycles, and could be probably attributed to the constant temperature regime similar to that of tropical environments. One factor, the photoperiod length, was positively correlated with monthly growth rates. The nymphal growth varied throughout the year, but the highest growth was in late spring and summer, and the lowest was in winter. The annual secondary production was very high (909.4 mg · m^{-2}) despite not being the most frequent taxon in the stream. The highest monthly production values were observed in the autumnal-winter period (November–December) due to massive hatching of nymphs. The lowest production values were observed in late summer and early autumn. Analyses of gut contents showed that this species behaves mainly as gatherer-collector, but also as shredder and, occasionally, as scraper. Changes in the gut content composition were detected in relation to the size. Comparing our results with those of the literature, it can be inferred that different populations of *P. intricata* can show notable differences in their life history when inhabiting places with different thermal conditions.

1. Introduction

One of the most important aspects for understanding freshwater ecosystems is the biology of the species that live in them. In this context, the study of the life history of single species is essential in order to achieve a full knowledge of the ecosystem itself and the relations within it. Many studies have tried to reach this goal through generalizations taken from the study of a reduced number of species, assuming that the rest of the members of their genus or family behave in the same manner. As pointed out by several authors (Zwick, 1981; Stewart and Stark, 1993), this is neither a good approximation nor an appropriate

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basis for ecological studies, and particular studies must be carried out in order to fulfill this lack of information. Furthermore, these studies must be developed in different habitats with particular characteristics, such as temporary streams, saline streams, streams with constant temperature, *etc.*, in order to characterize the key factors that influence the life history of the organisms in a given environment.

Species of the order Plecoptera constitute one of the main components, both in biomass and ecological roles, of the macroinvertebrate community in the running water ecosystems (HYNES, 1970; STEWART and STARK, 1993).

Protonemura intricata (RIS, 1902) is a species of Plecoptera that is widely distributed in Europe (ILLIES, 1978a; FOCHETTI and TIERNO DE FIGUEROA, 2004). It ranges in elevation between 140 and more than 2400 m a.s.l. It inhabits different kinds of running waters and, although its flight period is mainly spring-summer, its presence may sometimes extend to the beginning of autumn (*e.g.*, AUBERT, 1959; ILLIES, 1971; KIS, 1974; TIERNO DE FIGUEROA *et al.*, 2003). In Slovakia, previous studies have shown that this particular species flies and oviposits from May to July. It is also regarded as one eurytopic species that prefers brook-rivulets of submontane-colline areas (KRNO, 2004).

MARTEN and ZWICK (1989) studied the embryonic development of this species in Germany. They pointed out that the mean number of eggs by female was 627, and that, experimentally, a high number of eggs successfully hatched at temperatures ranging between 2 and 18 °C. They also recorded that the incubation period of this univoltine species normally consists of a first dormancy period [an obligatory summer diapause before the development starts, as previously pointed out by ZWICK (1981)] followed by other developmental period. According to them, the dormancy period depends on the oviposition date and the temperature, producing an approximately synchronic hatching during autumn. KRNO (1997) studied production dynamics of numerous stonefly species in Western Carpathian streams, pointing out for *P. intricata* a relatively low value of annual secondary production (24.6 mg · m^{-2}) in comparison with other Plecoptera species.

The aim of our study was to establish the life history of this species in a particular habitat with constant temperature through the year. Temperature is usually considered a major factor that regulates the life cycle and other biological parameters of stoneflies (HYNES, 1976; BRITTAIN, 1990), and of aquatic insects in general (VANNOTE and SWEENEY, 1980; BUTLER, 1984; SWEENEY, 1984; NEWBOLD *et al.*, 1994; HURYN, 1996; CAISSIE, 2006). Photoperiod has been identified as another regulatory factor in life cycles, acting as a signal for the beginning or ending of biological processes such as hatching, emergence, *etc.* (SWEENEY, 1984). In environments where temperature is constant through the year, photoperiod can be the main cue for seasonal changes that are critical to certain life history stages (SWEENEY, 1984). Our study sought to contribute to understanding the life history of a stonefly species when temperature changes <u>do not</u> control the sequence of events.

2. Methods

The study was carried out in Prosiek stream located in Chočské Vrchy Mts. (West Carpathians), next to Prosiek village, in Liptov region in Northern Slovakia (GPS coordinates: N 49°09′43.49″, E 19°29′32.2″, altitude: 705 m a.s.l.). The sampling site is located about 100 m below spring. The spring temperature is almost constant through the whole year, 8 °C May–August, 7 °C September–April. The geological substrate, formed by limestone, is reflected in high water pH values. Chemical parameters were measured once on 25th October 2007: pH = 7.98, PO_4^{3-} = 0.03 mg · l^{-1}, NO_3^- = 4.5 mg · l^{-1}, SO_4^{2-} = 15.5 mg · l^{-1}. The values measured meet Slovak norms for high quality drinking water.

Quantitative samples (2 samples from mesolithal and 2 from macrolithal, representing a total area of 0.4 m^2) of macrozoobenthos were collected monthly, from February to December 2005, using a Kubíček's benthic sampler (area 0.1 m^2, mesh size 0.5 mm). In January 2005, due to technical problems, only a semiquantitative sampling was carried out. Semiquantitative samples of nymphs were taken from

mesolithal (1 minute) and macrolithal (1 minute) with a kick net, mesh size 0.5 mm. Collected material was preserved in 4% formalin. *P. intricata* nymphs were separated from detritus and other taxa in the laboratory. Adults were captured, and preserved in 70% alcohol, for reconfirming the nymph identification. Water temperature was measured every sampling date with a hand-held thermometer.

Both quantitative and semiquantitative samples were used to study life cycle. Pronotum width and total length of 30 nymphs per month, when possible, were measured with the aid of a micrometer fixed to the binocular of a microscope. As these two measures were highly correlated (Spearman R = 0.97, $P < 0.05$), we used total length in order to represent the life cycle graphically. For statistical analysis, STATISTICA software (STATSOFT, 2005) was employed. FiSAT II software (GAYANILO *et al.*, 2002) was employed for generating the life cycle graph.

Secondary production was evaluated using the size-frequency method (BENKE, 1979; BENKE and HURYN, 2006). Estimation of nymph biomass was made according to BURGHERR and MEYER (1997) using the equation:

M (mass) = a L (length)^b
where (for *Protonemura* spp.):
$a = 0.00622$
$b = 2.51$

Secondary production values for January were estimated as arithmetic average of values calculated for previous and following month. The monthly individual growth rate was expressed as the difference between weighed arithmetical means of individual body lengths for two adjacent monthly samplings. The photoperiod length was calculated as sum of day-light hours per period between two samplings. Regression between monthly individual growth rate and photoperiod length, and monthly production and photoperiod length was calculated using STATGRAPHICS software (STATPOINT, 2006).

The analysis of gut contents was made following the methodology of BELLO and CABRERA (1999), which was used in other studies of Plecoptera nymphal feeding (*e.g.*, DERKA *et al.*, 2004; TIERNO DE FIGUEROA *et al.*, 2006; FENOGLIO *et al.*, 2007). For this, each specimen was introduced in a vial with Hertwigs´ liquid and heated in an oven at 65 °C for 48–72 hours. 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 size (measured as pronotum width) were analysed with a Gamma correlation test.

3. Results

A total of 1513 nymphs were collected in the sampling area through the whole studied period. Individuals were present in the stream all the months. The highest number of individuals was collected in November and December.

3.1. Life Cycle

In the study area, *P. intricata* showed an unusual and complicate life cycle, consisting of two cohorts (probably a cohort splitting) (Fig. 1). One cohort (cohort 1) extending from final summer-beginning of autumn to July–August, with the adult emergence occurring in later spring to summer (with mature nymphs from May to August) and the other cohort (cohort 2) beginning in summer and finishing in February–March. This last one probably presented a winter emergence (mature nymphs mainly in January and February). The presence of mature nymphs in these months, together with adults collected in October, seems to show the existence of an extended flight period for this species. The adults collected in October proceeded from the first generation, because the adult longevity of *Protonemura* species
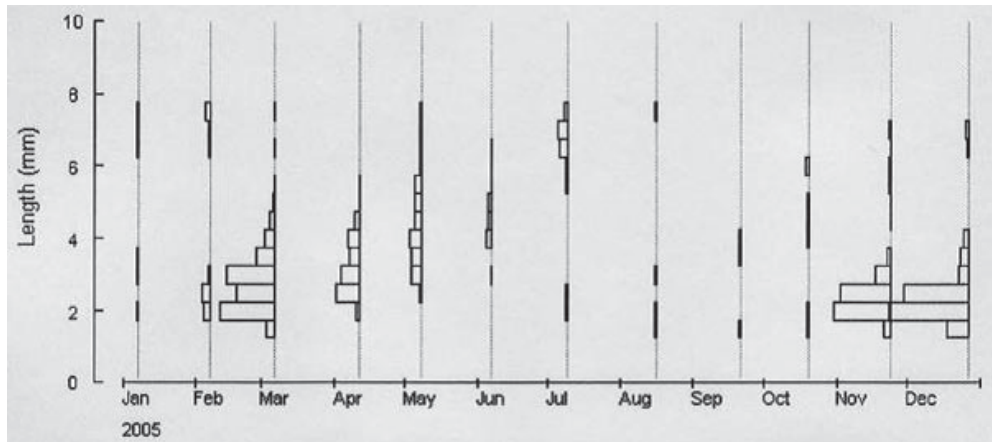
Figure 1.   Size-frequency distribution (total length) of *P. intricata* nymphs. Box width is proportional to the total number of nymphs.

can be long (up to two months according to KHOO, 1964). The second nymphal cohort was shorter (approximately nine months) than the first one (with a length of approximately eleven months). It was a remarkable fact that the first cohort was notably more numerous than the second one, reaching approximately 20 times higher density values and 3 times higher biomass values (Table 1). Nymphal growth rate varied through the year, showing the highest values in late spring and summer, while the lowest values were observed in winter (Table 2). Monthly nymphal growth rate was positively correlated with photoperiod length ($R = 0.82$; $P < 0.05$).

3.2. Secondary Production

The annual production rate of *P. intricata* in the study area was 909.43 mg · m^{-2} (dry matter), with an annual production/biomass (P/B) of 4.44 (Table 1). Monthly production values ranged between -0.20 mg DW · m^{-2} in September and 249.34 mg DW · m^{-2} in December (Table 2). Minimal mass of an individual was 0.0062 mg and the maximal was 0.8222 mg. Mean biomass of an individual varied from 0.045 mg in December, when massive hatching took place, to 0.501 mg in July when emergence occurred (Table 3). Mean annual biomass was 205.02 mg · m^{-2}, cohort biomass values were 156.75 mg · m^{-2} for the cohort 1

Table 1.   Annual and cohort mean density and biomass, production, P/B ratio and CPI (cohort production interval) of *P. intricata* at the sampling site.

	annual	cohort 1	cohort 2
mean density (ind · m^{-2})	209.30	200.00	9.30
mean biomass (mg DW · m^{-2})	205.02	156.75	49.27
production (mg DW · m^{-2})	909.43	771.76	137.67
P/B ratio	4.44	4.95	2.79
CPI	–	11	9

Table 2.   Sum of monthly day-light length, production, growth and daily growth of *P. intricata* at the sampling site. Temperature nearly constant 7–8 °C.

period (month/day)	sum of monthly				
	day-light length (h)	production (mg DW · m^{-2})	growth (mm/month)	growth (mm/day)	monthly growth (%)
02/06–03/06	284.9	129.40	0.395	0.01317	5.66
03/06–04/11	369.3	109.45	0.457	0.01343	6.54
04/11–05/07	411.9	12.44	1.319	0.04709	18.89
05/07–06/06	474.4	34.16	0.158	0.00526	2.26
06/06–07/08	483.7	86.96	1.543	0.04976	22.10
07/08–08/15	487.2	14.81	1.423	0.04743	20.39
08/15–09/20	444.1	3.23	1.032	0.02949	14.78
09/20–10/19	376.2	−0.20	0.580	0.01934	8.31
10/19–11/23	332.9	121.34	0.052	0.00154	0.75
11/23–12/26	275.5	249.34	0.022	0.00067	0.32

and 49.27 mg · m^{-2} for the cohort 2 (Table 1). Mean monthly biomass ranged between 0.36 mg · m^{-2} in September and 44.45 mg · m^{-2} in December. Similarly, mean monthly density varied from 2.5 individuals · m^{-2} in September to 993 individuals · m^{-2} in December (Table 3).

This high secondary production was the consequence of the high density of individuals from the first cohort during November (565 individuals · m^{-2}), December (995 individuals · m^{-2}) and March (297.5 individuals · m^{-2}). Monthly production values were negatively correlated with photoperiod (R = –0.79; *P* < 0.05).

3.3. Feeding

The study of the gut contents of 222 nymphs (Table 4) showed that the main component was detritus, followed by diatoms and, in a lesser extent, other algae and fungi (both

Table 3.   Changes in density, biomass and mean biomass of individual of *P. intricata* at the sampling site.

sampling date (month/day)	density (ind · m^{-2})	biomass (mg · m^{-2})	mean biomass of individuals (mg)
02/06	77.5	11.75	0.152
03/06	300.0	22.12	0.074
04/11	180.0	14.02	0.078
05/07	40.0	8.08	0.202
06/06	50.0	10.10	0.202
07/08	50.0	25.07	0.501
08/15	5.0	2.21	0.442
09/20	2.5	0.36	0.144
10/19	10.0	0.75	0.075
11/23	595.0	32.38	0.054
12/26	993.0	44.45	0.045

Table 4.   Nymphal gut contents of *P. intricata* at the sampling site.

	N	Mean	S.D	Min.	Max.
% absolute	222	43.82	30.72	0.00	100.00
% detritus	176	77.58	19.97	14.00	100.00
% diatoms	176	8.98	15.83	0.00	80.00
% hyphae	176	3.86	6.91	0.00	50.00
% ascospores	176	0.52	2.29	0.00	25.00
% algae	176	4.39	10.63	0.00	60.00
% vegetal remains	176	2.01	5.25	0.00	50.00
% phyllidia	176	1.89	5.91	0.00	40.00
% animal remains	176	0.59	2.96	0.00	25.00
% non-identifiable matter	176	0.23	3.02	0.00	40.00

hyphae and ascospores). The remaining components were not abundant, although some of them could occasionally be a considerable percentage of the gut content. Some individuals contained animal remains, particularly cuticle fragments, claws and mandibles.

When we analyzed the variation of the gut content in relation to the pronotum width, we found a positive correlation between size and detritus (Gamma correlation = 0.13; $P < 0.05$), phyllidia (Gamma correlation = 0.27; $P < 0.05$) and animal remains (Gamma correlation = 0.45; $P < 0.05$). On the other side, a negative correlation between size and diatoms (Gamma correlation = -0.26; $P < 0.05$) was detected.

4. Discussion

4.1. Life Cycle

According to HYNES (1970) the studied population of *P. intricata* would present a "slow seasonal life cycle" for the first cohort (with nymphs growing almost all the year and with short diapause, if present), and "fast seasonal life cycle" for the second cohort (with nymphs growing only nine months and with a longer egg dormancy period). The existence of an egg dormancy period for this species has been demonstrated by ZWICK (1981) and MARTEN and ZWICK (1989), and these authors also pointed out that this period was variable. Thus, the whole incubation period can last almost three months (ZWICK, 1981).

The first cohort, the most numerous one, coincides approximately with the typical life cycle of *P. intricata* in other studied areas (*e.g.*, ZWICK, 1981), showing a mainly spring-summer emergence and a flight period that can extend until autumn (*e.g.*, ILLIES, 1971; KIS, 1974; KRNO, 2004). The presence of an extended flight period, lasting more than two seasons, is not unusual for other *Protonemura* species from Europe (*e.g.*, TIERNO DE FIGUEROA *et al.*, 2001).

It is usually accepted that *P. intricata* has a simple univoltine life cycle (ZWICK, 1981; MARTEN and ZWICK, 1989). For Plecoptera, the simple univoltine and the semivoltine life cycles are the most general patterns, with the bivoltinims and non-semivoltine cycles with cohort splitting being very uncommon (HYNES, 1976; BRITTAIN, 1990). The cohort splitting has been cited, for example, in some Perlidae, which are characterized by relatively long life cycles (varying from two to five years) (MOREIRA and PECKARSKY, 1994). In Europe, *Nemurella pictetii* KLAPÁLEK, 1900 is the only known species that has a highly variable life cycle, being semivoltine, univoltine or plurivoltine in different areas (LIESKE and ZWICK, 2007). A possible bivoltinism or cohort splitting has also been pointed out for some *Pro-*

tonemura species [*e.g.*, PRETTY *et al.* (2005) for *P. meyeri* (PICTET, 1842)] although more data are needed for confirmation. Our results clearly show the existence of two separate cohorts, indicating that this species has a complicated life cycle in the studied area. The peculiar life cycle exhibited by *P. intricata* in our study area could be related to the temperature uniformity through the year. Future researches in nearby areas, but with variable temperatures along the year, could confirm this hypothesis.

Comparing the growth of both cohorts found in our study with the one cited for this species by MARTEN and ZWICK (1989), some differences were noted. Thus, these authors noted that growth was extremely slow in the first period of life cycle (up to April), then accelerated in spring, and coincided partially with the first cohort but not with the second.

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 likely true because growth rates of *P. intricata* were correlated with the length of the photoperiod.

4.2. Secondary Production

The high annual secondary production of *P. intricata* in the study locality is mainly related to the abundance of this species and the permanence of nymphs in the water through the whole year. Nevertheless, *P. intricata* is not the most common taxon in the study area. Ephemeroptera and Gammaridae species are much more numerous, indicating that total secondary production of the benthic macroinvertebrates must be very high. The negative correlation between monthly production and photoperiod length can be explained by the presence of first stages coinciding with months with the shortest day length.

Our results are approximately 37 times higher than those published by KRNO (1997) for *Protonemura intricata* (24.6 mg $\cdot$ m^{-2}) in another Slovak stream. When comparing our results with the data on secondary production of other *Protonemura* species from Slovakia [*e.g.*, *P. nitida* 11.2–13.2 mg $\cdot$ m^{-2} (KRNO, 2000); *P. montana* 17.8 mg $\cdot$ m^{-2}, *P. nimborum* 144.1 mg $\cdot$ m^{-2} (KRNO and ŠPORKA, 2003)], *P. intricata* shows higher values. In fact, this species is usually very common in the places where it is present; for instance ILLIES (1978b) noted that *P. intricata* in Breitenbach (Germany) is the most common stonefly and one of its most important secondary producers.

4.3. Feeding

According to our data, the species could be considered as mainly gatherer-collector (*sensu* CUMMINS and MERRIT, 1996). Nevertheless, a relatively high percentage of the detritus inside the guts was of vegetal origin (mean= 37.27%; *S.D.* = 39.26), making possible that they could come from vegetation shredded by them. This, together with the presence of phyllidia and other plant remains, showed that this species could also act as shredder. On the other hand, due to the relatively high presence of epilithic and epiphytic diatoms and fungi in some individuals, the species could occasionally behave as scraper. Feeding studies of other *Protonemura* species also showed very diverse results. For example *P. nitida* from Oberer Seebach (Austria) behaves mainly as scraper (STEINER, 1991). In contrast *P. meyeri* in Río Blanco (Southern Spain), and in an acidic stream in England, is mainly a collector-shredder (LÓPEZ-RODRÍGUEZ and TIERNO DE FIGUEROA, 2006; PRETTY *et al.*, 2005). Thus, we can see that a population of one species or different species belonging to the same genus could be

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catalogued into different functional feeding groups (*sensu* Cummins and Merrit, 1996). If so, and depending on the circumstances, characterization to a family level, as usually employed in ecological studies, may be an excessive simplification.

The presence of animal remains in the gut content of *P. intricata* is unusual for Nemouroidean nymphs. Although they have been found in the gut of other nymphs belonging to this superfamily [*e.g.*, in *Brachyptera risi* (Morton, 1896), Fenoglio *et al.*, (in press)], the presence of animal remains usually does not make a high percentage of the gut content and it is not clear if animals are actively or accidentally ingested (considering the relatively low size of the ingested organisms).

As pointed out for other Plecoptera species (Monakov, 2003), changes in feeding habits were detected in *P. intricata* as it grew. The bigger nymphs may act less as scrapers, ingest a lower quantity of diatoms, and also occupy a different mesohabitat. More studies are needed to confirm this but, if so, it would suggest the intraspecific competition may be decreased as size is gained in that species.

5. Conclusion

The present study in a particular habitat with constant temperature through the year lets us examine how a population of *P. intricata* behaves when it is likely that the photoperiod (but not temperature) is the main control on the sequence of events in the life cycle. Thus, we found a complicated life cycle, different from many other localities, that has two cohorts with different duration (probably a cohort splitting). The annual secondary production of this species was also considerably higher than that previously noted in other streams. This could reflect the absence of extreme temperature conditions, detected in other streams, where the same species was present. Finally, regarding feeding, a generalist condition was detected.

6. Acknowledgements

7. References

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