

## Effects of habitat on development, fecundity, and susceptibility to parasites in *Parameletus chelifera* and *Parameletus minor* (Ephemeroptera)

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Life history parameters of two mayflies were studied for 4 years in two habitats in northern Sweden: a river margin and a seasonal stream. Water temperature before river peak flood was higher and the C/N ratio of the dominating food fraction was lower in the seasonal stream than at the river margin. Over the entire season, the growth rate of *Parameletus chelifera* nymphs was higher in the seasonal stream than at the river margin, whereas that of *Parameletus minor* nymphs was similar in both habitats in 2 out of 4 years. Because of desiccation, emergence success of *P. chelifera* in the seasonal stream was low in some years while almost no specimens emerged successfully from the river. Emergence success was always high in *P. minor*, and in some years emergence was further advanced in the seasonal stream than at the river margin. Subimagos of both species were larger in the seasonal stream than at the river margin. Males of both species were larger than females in the seasonal stream, as were males of *P. minor* at the river margin. The fecundity of *P. chelifera* females was higher in the seasonal stream than at the river margin, while no difference could be found in *P. minor* between the two habitats. Only *P. chelifera* specimens were infested by mermithid nematodes; in some years as many as 21% of the female subimagos were infested. Such females were unable to reproduce.

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Les paramètres du cycle biologique ont fait l'objet d'une étude chez deux espèces d'Ephéméroptères durant 4 ans, en deux habitats du nord de la Suède, la bordure d'une rivière et un ruisseau saisonnier. La température de l'eau avant la crue principale de la rivière était plus élevée et le rapport C/N de la fraction nutritive dominante était plus faible dans le ruisseau saisonnier qu'en bordure de la rivière. Dans l'ensemble, les larves de *Parameletus chelifera* avaient un taux de croissance plus rapide dans le ruisseau saisonnier que dans la rivière, alors que les larves de *Parameletus minor* ont eu le même taux de croissance dans les deux habitats au cours de 2 années sur les 4. À cause de la dessiccation, le succès à l'émergence de *P. chelifera* s'est avéré plus faible durant certaines années dans le ruisseau saisonnier, mais peu de spécimens ont réussi à émerger dans la rivière. Le succès à l'émergence de *P. minor* était toujours élevé et, certaines années, l'émergence dans le ruisseau saisonnier précédait l'émergence dans la rivière. La taille des subimagos des deux espèces était plus grande dans le ruisseau que dans la rivière. Les mâles des deux espèces du ruisseau saisonnier, de même que les mâles de *P. minor* de la rivière, étaient plus gros que les femelles. Les femelles de *P. chelifera* avaient une fécondité plus élevée dans le ruisseau que dans la rivière, alors que la fécondité de *P. minor* était la même dans les deux habitats. Seuls les *P. chelifera* étaient parasités par des nématodes mermithidés; certaines années, jusqu'à 21% des subimagos femelles étaient infestés. Ces femelles étaient incapables de se reproduire.

[Traduit par la revue]

### Introduction

Temperature and food quality and (or) quantity are crucial to the growth of many aquatic invertebrates (e.g., Otto 1974; Lillehammer 1975; Brittain 1976a, 1978, 1983; Ward and Cummins 1979; Cianciara 1980; Sweeney and Vannote 1981; Ward and Stanford 1982; Sweeney 1984; Hawkins 1986). It has been suggested that an "optimum" thermal regime exists in which larval growth, adult size, and fecundity are maximized (Precht et al. 1973; Vannote and Sweeney 1980). High quality food often contains a high content of accessible nitrogen which is associated with high microbial activity (Iversen 1974; Bärlocher 1985). Aquatic invertebrates often choose food that is heavily colonized by microorganisms (Anderson and Cummins 1979). Although quality and (or) quantity of food can affect growth rate, the effects of food and temperature are often difficult to separate (Anderson and Cummins 1979; Cummins and Klug 1979; Sweeney 1984).

Seasonally recurrent habitat shifts have been shown in several aquatic invertebrates (e.g., Moon 1935; Lillehammer 1965; Boag and Bentz 1980; Olsson 1983). Causes proposed for such habitat shifts are a search for (i) optimal growth conditions (Bishop and Hynes 1969; Olsson and Söderström 1978), (ii) optimal pupation or emergence sites (Hultin et al. 1969; Otto 1971), and (iii) habitats with less predation pressure (Söderström and Nilsson 1987). These life history parameters

may be seen as factors that influence the individual's selection of an environment in which both fecundity and survival conditions maximize long-term reproductive output (Sibly and Calow 1986).

The two closely related mayflies *Parameletus chelifera* Bengtsson and *Parameletus minor* (Bengtsson) show a northern distribution in Fennoscandia and the European part of the U.S.S.R. (Söderström and Nilsson 1986). *Parameletus chelifera* has also been recorded from North America (Edmunds et al. 1976). Both species have univoltine life cycles. In a north Swedish boreal river, eggs are laid in late June to early July. Most likely, eggs pass through a dormant stage for a period of 6–10 months. Tiny nymphs of both species appear near mid-stream in winter (Söderström 1988). In spring most *P. chelifera* specimens migrate to a seasonal stream, while the *P. minor* specimens enter the seasonal stream and the river margin in about equal numbers (Söderström 1988). Nymphs of both species use seasonally flooded areas along river margins and seasonal streams for growth and emergence (Olsson and Söderström 1978; Söderström 1987, 1988). The habitats used by *P. chelifera* and *P. minor* nymphs seem to differ both in thermal regimes and in food quality and quantity (Olsson and Söderström 1978; Söderström 1988).

The aim of the present study was to investigate whether thermal regime and food quality and (or) quantity have any impact

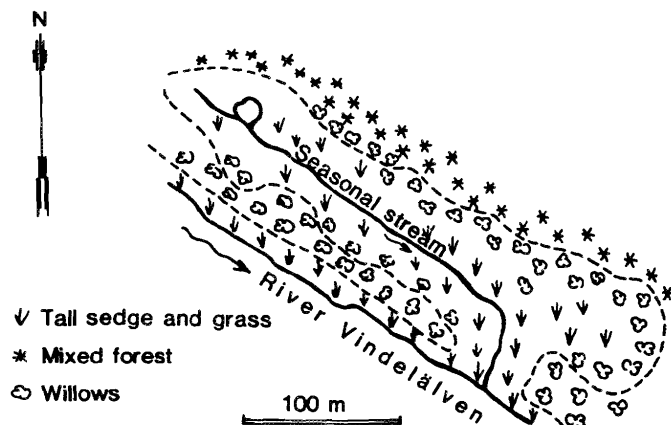


FIG. 1. Map of the seasonal stream and the river margin (modified from Söderström and Nilsson 1987). The solid line marks the seasonal stream and the river margin in early May, and the broken line shows the approximate extension of the river during spring flood.

on growth, emergence, adult size, and fecundity of *P. chelifera* and *P. minor* at a river margin and in a seasonal stream.

### Study area

The area investigated (Fig. 1) is situated in a slow-flowing part of the River Vindelälven in the boreal coniferous zone near Sirapsbacken (64°22'N, 19°28'E) in northern Sweden. The Vindelälven has great seasonal fluctuations in water flow. The mean minimum and maximum flows in this area between 1971 and 1986 were 30 and 956 m<sup>3</sup> s<sup>-1</sup>, respectively (data from the Swedish Meteorological and Hydrological Institute). Normally the river is covered with ice from the middle of November to the first half of May. The spring flood usually has two main peaks, one at the end of May and another in the middle of June. The vertical difference in water level between the peak in the spring flood and the late winter minimum is normally about 4 m. The seasonal stream investigated is situated on an alluvial meadow. The stream, about 300 m long and 0.5–1 m wide, carries meltwater from late April to early May. When the river water level rises, the stream gradually becomes flooded, beginning at the lower part. In most years the river peak flood reaches the upper part of the seasonal stream, which then becomes the innermost part of an extensive river lagoon. The seasonal stream usually dries up in late June to mid-July.

The marginal vegetation in the river at the study area is dominated by *Carex acuta* L. The bottom of the seasonal stream is covered mainly by grasses (*Calamagrostis canescens* (Web.) Roth. and *Deschampsia caespitosa* (L.)), as is the surrounding alluvial meadow.

### Materials and methods

The water temperature at the river margin and in the seasonal stream was measured at irregular intervals between 5:00 to 7:00 p.m. during the experimental periods in the springs of 1981, 1982, 1984, and 1985. Data on daily water levels were obtained from a permanent meteorological station about 20 km downstream of the study area on the River Vindelälven. The date when river water flooded the upper part of the seasonal stream and the duration of the flood were recorded each year.

The amount and composition of organic material in the bottom sediment down to 2 cm below the substrate surface were measured in the seasonal stream (10 samples) and at the river margin (5 samples) on 13 June 1985. Each sample covered an area of 3.45 cm<sup>2</sup>. The samples were dried at 60°C to constant weight, and the weight was recorded. The samples were combusted at 600°C to obtain the amount of organic material. The amounts of carbon and nitrogen in the sediment were measured with an elemental analyzer (model 1106, Carlo Erba Strumentazione) from one sample per site taken on 13 June 1985.

Algal samples were taken at both sites on 13 June 1985. To estimate the algal composition on the bottom, algae were scraped from leaves, grass, and sedges. These samples were compared with the gut contents of *P. minor* and *P. chelifera* nymphs sampled in 1985. Ten individuals of equal size of each species were analyzed from the river margin (20 June) and the seasonal stream (13 June). A suspension of the gut contents was filtered through a 0.45-μm Millipore® filter. The filter was cleared in immersion oil and all particles identified. Number of algal cells and filaments, hyphae of Hyphomycetes, particles of decomposing sedge and grass (fine particulate organic matter (FPOM) from sedge and grass), and particles of unidentifiable decomposed fine particulate organic matter (unidentifiable FPOM) were counted. Algae from guts and bottom samples were specified and converted to volume by species-specific volume values given in Hustedt (1930a, 1930b, 1959), Huber-Pestalozzi (1955), Komarkova-Legnerova (1969), Ruzicka (1977), and Krammer and Lange-Bertalot (1986). The volume of Hyphomycetes, FPOM from sedge and grass, and unidentified FPOM were estimated by comparison with algal volumes. Thus the approximate compositions (percent counted by volume) of gut contents and available food were obtained.

Body length of nymphs of *P. chelifera* and *P. minor* was measured on specimens collected from the river margin and the seasonal stream at irregular intervals in 1981, 1982, 1984, and 1985. The nymphs were preserved in 70% ethanol and the length from the front of the head capsule to the end of the abdomen was measured to the nearest 0.1 mm. As the body length for nymphs of both species in samples taken before emergence did not differ between the sexes (*t*-test,  $P > 0.05$  for both species), nymphs of both sexes were pooled. In our material the relationship between body length and time was best described by a linear regression, less so by a geometric relationship. Growth rate (millimetres per day  $\pm$  95% CL) of *P. minor* and *P. chelifera* nymphs was estimated from the regression coefficient ( $b$ ) in  $L = a + bt$  for the linear relationship between body length ( $L$ , mm) and time ( $t$ , days) before and during the time the seasonal stream was flooded by river peak flood. Growth rate was estimated in the same way for both species during the whole nymphal period studied each year. Because *P. minor* as well as *P. chelifera* started to emerge roughly at the end of the peak flood, no "after peak" calculation was made. Comparisons of regression coefficients ( $b$ ) were made according to Bailey (1981).

Subimagos of *P. chelifera* and *P. minor* were collected in 1981, 1982, and 1984 in emergence traps (bottom area 0.25 m<sup>2</sup>) with a 1-mm mesh size. In 1981 and 1982 three traps were placed along the river margin and the seasonal stream, respectively. In 1984 six traps were operated at each site during the emergence period. The traps were emptied every 2nd day between 5:00 and 7:00 p.m. The subimagos were preserved in 70% ethanol and their length from the front of the head capsule to the end of the abdomen was measured to the nearest 0.1 mm.

In both species number of eggs of subimagos from both sites were counted in 1981 and 1984. In 1984 and 1985 eggs were also counted from mature nymphs of *P. chelifera*. To prevent the eggs from being damaged, subimagos and nymphs were put in Bouin's solution 12 h before counting. Mature nymphs from the river and the seasonal stream from 1977, 1979, 1981, 1982, 1984, 1985, and 1986 were also analyzed for infestation by a nematode belonging to the family Mermithidae.

### Results

#### Environmental conditions

During all 4 years the maximum water level reached similar values but the time and duration of complete flooding of the seasonal stream by the river differed (Fig. 2). In 1984 and 1985 the seasonal stream was completely flooded for 16 and 19 days, respectively, while in 1981 and 1982 the flood lasted for only 9 and 8 days, respectively. Before the spring peak flood the afternoon water temperature was higher in the seasonal stream than in the river. During and after the peak flood the

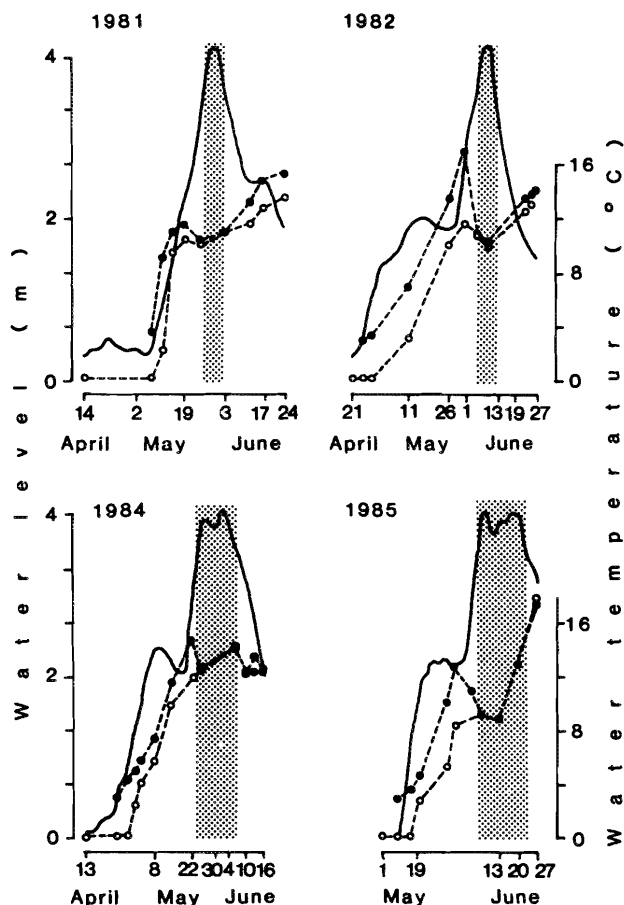


FIG. 2. Water level (solid line) in relation to a fixed point in the main river and water temperature in the seasonal stream (broken line, solid circles) and at the river margin (broken line, open circles) during 4 different years. Shaded areas denote the period when the river flooded the upper part of the seasonal stream.

temperature was almost the same at both sites except after the flood in 1981 (Fig. 2).

#### Food and feeding

The amount of organic material in the sediment from the river margin ( $\bar{x} = 4.26$  mg dry wt,  $SD = 0.88$ ) and the seasonal stream ( $\bar{x} = 4.04$ ,  $SD = 0.95$ ) did not differ (Mann-Whitney  $U$ -test,  $P > 0.05$ ). However, there were qualitative differences in the composition of the sediments. At the river margin the dominating fraction was unidentifiable FPOM while FPOM from sedge and grass was sparse. In the seasonal stream FPOM from sedge and grass dominated over unidentifiable FPOM. The C/N ratio was lower in the sediment from the seasonal stream (12.8) than in the sediment from the river margin (20.9).

Nymphs of *P. minor* consumed significantly more unidentifiable FPOM at the river margin than those in the seasonal stream (Mann-Whitney  $U$ -test,  $P < 0.01$ , Table 1). Further, *P. minor* nymphs in the seasonal stream consumed more FPOM from sedge and grass than did those at the river margin (Mann-Whitney  $U$ -test,  $P < 0.05$ ). There was no other significant difference by volume of the different food particles consumed by each species either within or between habitats. The only significant difference between species within a habitat was found at the river margin where nymphs of *P. chelifera* consumed more FPOM from sedge and grass than did nymphs

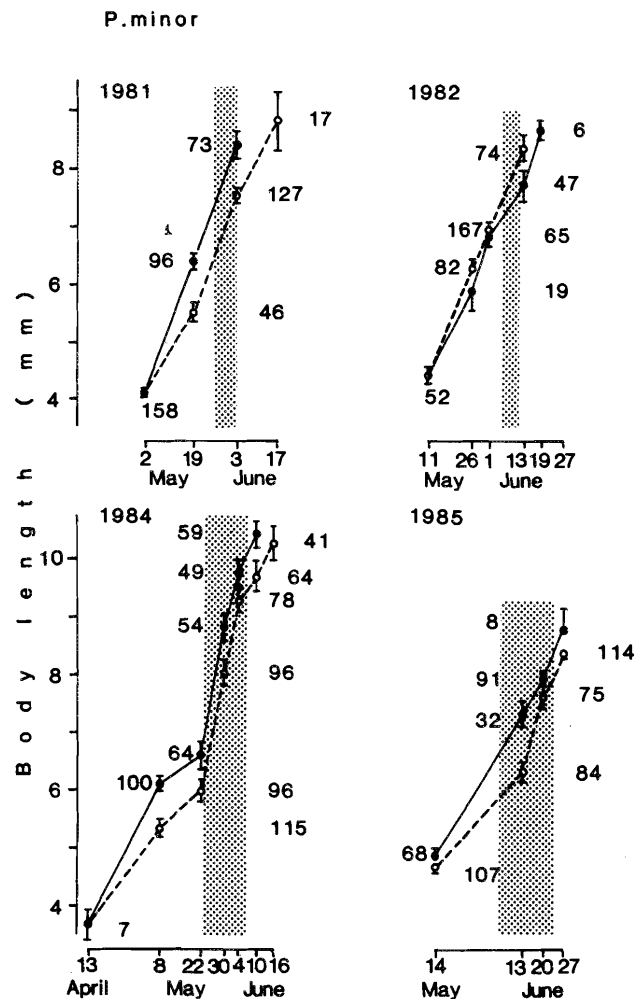


FIG. 3. Size of *Parametetus minor* nymphs in the seasonal stream (solid line) and at the river margin (broken line) during 4 years. Size is expressed in terms of mean body length (with a 95% confidence limit of the mean). Shaded areas denote the period when the river flooded the upper part of the seasonal stream. Number of nymphs per sampling occasion is given for each point.

of *P. minor* (Mann-Whitney  $U$ -test,  $P < 0.01$ ). Diatoms constituted at most 5.7% of the volume ingested by *P. minor* nymphs in the seasonal stream and 2% for *P. chelifera* nymphs at the river margin. Hyphomycetes made up a very small proportion of the food ingested by both species (Table 1). Thus, nymphs of *P. minor* and *P. chelifera* can be classified as fine particulate detritivores. Nöst (1985) also found that nymphs of *P. chelifera* are fine particulate detritivores.

#### Nymphal growth

Nymphs of *P. minor* showed an almost linear increase in body length from the beginning of spring until they emerged (Fig. 3). This increase was retarded only before the spring flood in 1984 at both sites and in 1985 at the river margin. In 1981, 1984, and 1985 the nymphs were significantly longer in the seasonal stream than at the river margin on all sampling dates ( $t$ -tests,  $P < 0.05$ ). Increase in body length of nymphs of *P. chelifera* was lower before than during the peak flood in both habitats in all years (Fig. 4). Nymphs inhabiting the seasonal stream were significantly larger on every sampling occasion ( $t$ -tests,  $P < 0.001$  in all years).

In addition to the increase in body length, the patterns of

TABLE 1. Composition (percent by volume) of algae on bottom substrate and in the guts (including Hyphomycetes and fine particulate organic matter (FPOM)) of *Parametetus minor* and *Parametetus chelififer* at the river margin and in the seasonal stream

	River margin						Seasonal stream					
	Bottom			<i>P. minor</i>			<i>P. chelififer</i>			Bottom		
	algae (%)	% of algae	% of total	% of algae	% of total	% of algae	% of algae	% of total	% of algae	% of algae (%)	% of total	% of total
Diatoms												
<i>Achnanthes</i> spp.	2.64	0.14	0.003	0.02	0.001	0.001	0.02	0.001	0.02	0.19	0.001	—
<i>Anomoeoneis</i> sp.	0.45	0.06	0.001	—	—	—	—	—	—	0.10	—	—
<i>Ceratonneis</i> sp.	0.83	0.36	0.008	—	—	—	—	—	—	—	—	—
<i>Cyclotella</i> sp.	0.09	0.12	0.003	0.11	0.002	0.002	0.08	0.005	0.08	—	0.005	—
<i>Cymbella</i> sp.	—	—	—	0.65	0.014	0.014	—	—	—	0.86	—	0.006
<i>Diatoma</i> sp.	0.16	—	—	—	—	—	—	—	—	—	—	—
<i>Eunotia</i> spp.	2.86	4.38	0.102	7.39	0.154	0.154	41.06	2.362	41.93	41.06	2.362	0.096
<i>Fragilaria</i> spp.	3.31	0.29	0.007	—	—	—	1.55	—	—	1.55	—	—
<i>Frustulia</i> sp.	3.17	2.07	0.048	—	—	—	4.97	—	—	4.97	—	—
<i>Gomphonema</i> spp.	1.16	1.08	0.025	0.78	0.016	0.016	—	0.005	0.09	—	0.005	—
<i>Hantzschia</i> sp.	—	0.03	0.001	—	—	—	—	—	—	—	—	—
<i>Melosira</i> spp.	0.18	7.20	0.167	5.84	0.122	0.122	—	0.014	0.25	—	0.014	0.009
<i>Navicula</i> sp.	—	0.17	0.004	—	—	—	—	0.004	0.07	—	0.004	—
<i>Nitzschia</i> spp.	0.20	—	—	—	—	—	—	—	—	—	—	—
<i>Pinnularia</i> spp.	72.72	28.16	0.654	42.83	0.891	0.891	50.57	2.955	52.47	50.57	2.955	0.419
<i>Stauroneis</i> sp.	—	—	—	—	—	—	—	0.004	0.07	—	0.004	—
<i>Synedra</i> spp.	3.35	1.42	0.033	—	—	—	—	0.003	0.06	—	0.003	—
<i>Tabellaria</i> spp.	8.89	52.07	1.210	41.35	0.861	0.861	0.69	0.104	1.84	—	0.104	0.005
Unidentifiable	—	0.68	0.016	1.03	0.021	0.021	—	0.051	0.91	—	0.051	0.005
Chlorophyta filament	—	0.73	0.017	—	—	—	—	0.115	2.04	—	0.115	—
Pyrrophyta	—	—	—	—	—	—	—	0.009	0.17	—	0.009	—
Euglenophyta	—	1.04	0.024	—	—	—	—	—	—	—	—	—
Hyphomycetes	—	—	0.112	—	0.005	0.005	—	0.153	—	—	0.153	0.004
FPOM from sedge and grass	—	—	9.478	—	40.066	40.066	—	59.514	—	—	59.514	63.828
FPOM unidentifiable	—	—	88.088	—	57.848	57.848	—	34.470	—	—	34.470	35.629
Total volume (mm <sup>3</sup> )	0.544 × 10 <sup>-3</sup>	1.250 × 10 <sup>-3</sup>	53.810 × 10 <sup>-3</sup>	0.924 × 10 <sup>-3</sup>	44.426 × 10 <sup>-3</sup>	44.426 × 10 <sup>-3</sup>	0.348 × 10 <sup>-3</sup>	53.600 × 10 <sup>-3</sup>	3.018 × 10 <sup>-3</sup>	0.348 × 10 <sup>-3</sup>	53.600 × 10 <sup>-3</sup>	52.484 × 10 <sup>-3</sup>

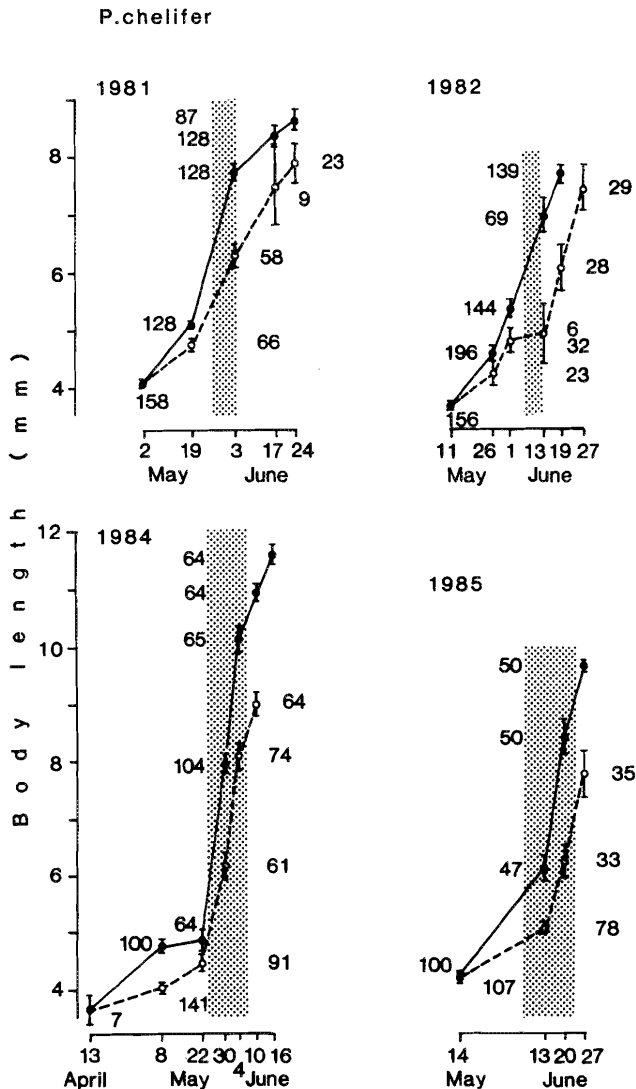


FIG. 4. Size of *Parameteletus chelifier* nymphs in the seasonal stream (solid line) and at the river margin (broken line) during 4 years. Size is expressed in terms of mean body length (with a 95% confidence limit of the mean). Shaded areas denote the period when the river flooded the upper part of the seasonal stream. Number of nymphs per sampling occasion is given for each point.

growth rate differed during the entire period studied each year, during the season within habitats, between habitats during the season, and between species.

#### Over the entire season

The growth rate of *P. minor* nymphs was equal in 2 out of 4 years in both the seasonal stream and the river margin, while nymphs of *P. chelifier* always had a significantly higher growth rate ( $P < 0.05$ ) in the seasonal stream (Fig. 5).

#### Over the course of the season

The growth rate of nymphs of *P. minor* was significantly higher during than before peak flood at the river margin ( $P < 0.05$ ) in 3 out of 4 years. In the seasonal stream no consistent pattern of growth rate was found in *P. minor* nymphs (Fig. 5). The growth rate of *P. chelifier* nymphs was always significantly higher during than before peak flood ( $P < 0.05$ ) in the seasonal stream and in 3 out of 4 years at the river margin ( $P < 0.05$ , Fig. 5).

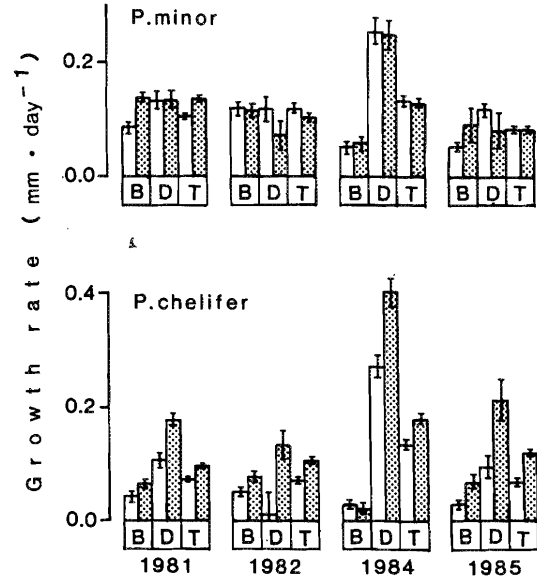


FIG. 5. Growth rate (with 95% confidence limits) of nymphs of *Parameteletus minor* and *P. chelifier* before (B) and during (D) peak flood and over the entire season studied each year (T) at the river margin (open bars) and in the seasonal stream (stippled bars) during 4 years.

#### Between habitats during season

Growth rate of nymphs of *P. minor* was significantly higher in 2 out of 4 years at the river margin ( $P < 0.05$ ) during peak flood and in 2 out of 4 years in the seasonal stream ( $P < 0.05$ ) before peak flood (Fig. 5). The growth rate of nymphs of *P. chelifier* was always significantly higher in the seasonal stream ( $P < 0.05$ ) during peak flood. The same difference was found before peak flood in 3 out of 4 years ( $P < 0.05$ , Fig. 5).

#### Between species

Before peak flood, growth rate of *P. minor* nymphs was always significantly higher than that of *P. chelifier* nymphs at the river margin ( $P < 0.05$ ) and in 3 out of 4 years in the seasonal stream as well ( $P < 0.05$ , Fig. 5). However, during peak flood in the seasonal stream, growth rate of *P. chelifier* nymphs always significantly exceeded that of *P. minor* nymphs ( $P < 0.05$ , Fig. 5). At the river margin during peak flood, no consistent pattern of growth rate could be found between the two species.

#### Emergence

In 1981 and 1982 the seasonal stream dried out completely on 25 and 26 June, respectively (see arrows in Fig. 6). This undoubtedly caused a decrease in emergence success of *P. chelifier* in both years and also in that of *P. minor*, to a certain degree, in 1982. Because of an earlier emergence in 1984, the desiccation of the seasonal stream (27 June) did not cause any decrease in emergence success for *P. chelifier*. In 1981 few subimagos of *P. chelifier* succeeded in emerging from the river.

In 1981 and 1984 the median emergence date of male and female subimagos of *P. minor* was significantly earlier from the seasonal stream than at the river margin (Mann-Whitney U-test,  $P < 0.01$ ). In *P. minor* the sex ratio at emergence was skewed significantly toward females ( $\chi^2$ -test,  $P < 0.01$  in all years) except at the river margin in 1981 where both sexes were equally common ( $\chi^2$ -test,  $P > 0.05$ ). Because of the desiccation of the seasonal stream, the sex ratio of *P. chelifier*

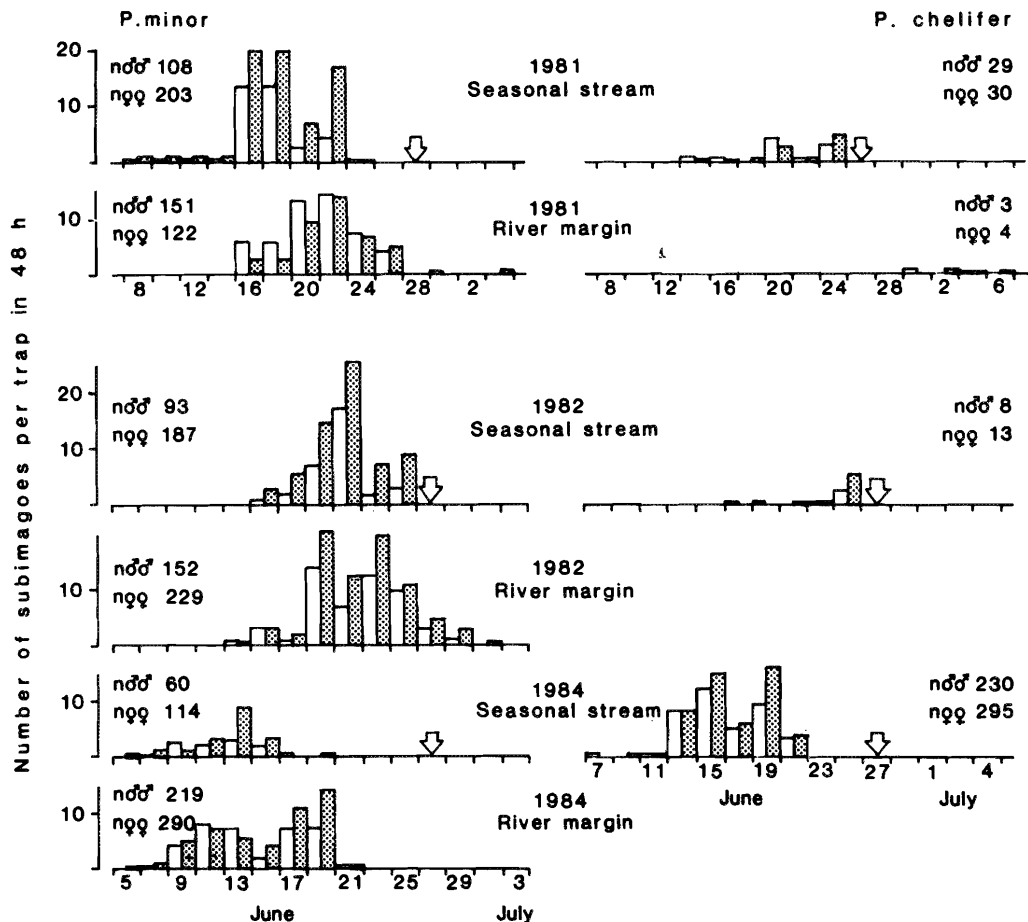


FIG. 6. Number of males (open bars) and females (stippled bars) of *Parametetus minor* and *P. chelifer* emerging per trap over 2 days in the seasonal stream and at the river margin during 1981, 1982, and 1984. Arrows denote dates when the seasonal stream dried out completely, and *n* denotes total number of males and females captured.

could only be tested in 1984. There the number of females emerging significantly exceeded that of males ( $\chi^2$ -test,  $P < 0.01$ ). The sex ratio (female:male) at emergence ranged from 1.25 to 1.94 in *P. minor* and was 1.23 in *P. chelifer*.

#### Adult size

In all years male subimagoes of *P. minor* were significantly larger (body length) than females in all habitats (Mann-Whitney *U*-test,  $P < 0.05$ , Table 2). Males from the seasonal stream were significantly larger than males from the river habitat in all years (Mann-Whitney *U*-test,  $P < 0.001$ ), and the same pattern was found for females in 1982 and 1984 (Mann-Whitney *U*-test,  $P < 0.001$ ) but not in 1981.

Male *P. chelifer* subimagoes in the seasonal stream were significantly larger (body length) than females in all years (Mann-Whitney *U*-test,  $P < 0.05$ ). No significant difference in body length was found between the sexes in *P. chelifer* specimens from the river in 1981 (Table 2). This result was probably due to small samples. In 1981 both male and female *P. chelifer* subimagoes from the seasonal stream were significantly larger than males and females from the river margin (Mann-Whitney *U*-test,  $P < 0.05$ ). However, in 1981 the emergence periods of males as well as females of *P. chelifer* were truncated because of desiccation of the seasonal stream.

#### Fecundity and parasite infestation

No difference in fecundity of *P. minor* subimagoes could be found between the two habitats in 1981 or 1984 (Mann-

Whitney *U*-test,  $P > 0.05$ , Table 3). Female *P. chelifer* subimagoes emerging from the seasonal stream produced a significantly greater number of eggs than subimagoes from the river margin in 1981 (Mann-Whitney *U*-test,  $P < 0.05$ ). This result could have been influenced by the early desiccation of the seasonal stream in 1981. In 1984 no significant difference in fecundity was found between last-instar *P. chelifer* nymphs and subimagoes from the seasonal stream (Mann-Whitney *U*-test,  $P > 0.05$ ). In 1985 the fecundity of last-instar nymphs of *P. chelifer* from the seasonal stream was significantly higher than that of nymphs captured at the river margin (Mann-Whitney *U*-test,  $P < 0.001$ , Table 3). Subimagoes of both *P. chelifer* and *P. minor* showed a positive correlation between body length and fecundity (Table 4).

The infestation of mermithid nematodes differed markedly between the two species (Table 5). Rate of infestation ranged from 3.5 to 21.3% in nymphs of *P. chelifer*, but no nymphs of *P. minor* were infested. Only one nematode was found in each infested female. The nematode was much longer than the host and occupied the entire abdomen. No difference in degree of infestation was found between the two habitats.

#### Discussion

##### Nymphal growth

Our results show that growth rates of nymphs are affected by habitat more in *P. chelifer* than in *P. minor*. Nymphs of *P. chelifer* always grew faster in the seasonal stream than at the

TABLE 2. Size (body length, in mm) of male and female subimagos of *Parameletus minor* and *Parameletus chelifier* at the river margin and in the seasonal stream in 1981, 1982, and 1984

	Male			Female		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n
<i>Parameletus minor</i>						
1981						
Seasonal stream	8.89	0.056	104	8.31	0.033	188
River margin	8.59	0.039	138	8.29	0.047	108
1982						
Seasonal stream	8.30	0.063	89	7.89	0.044	173
River margin	7.94	0.047	146	7.45	0.040	218
1984						
Seasonal stream	8.77	0.075	56	8.34	0.051	98
River margin	8.08	0.048	213	7.91	0.042	266
<i>Parameletus chelifier</i>						
1981						
Seasonal stream*	9.42	0.112	25	9.03	0.100	29
River margin	8.62	0.132	3	8.30	0.191	4
1982, seasonal stream*	9.56	0.228	8	8.44	0.188	11
1984, seasonal stream	9.97	0.043	229	9.73	0.040	281

\*Years in which desiccation of the seasonal stream affected emergence success.

TABLE 3. Size (mm) and fecundity (no. of eggs per female) of subimagos of *Parameletus minor* and *Parameletus chelifier* and last-instar nymphs of *P. chelifier* from the river margin and the seasonal stream in 1981, 1984, and 1985

	Body length (mm)		Fecundity		
	$\bar{x}$	SE	$\bar{x}$	SE	n
<i>Parameletus minor</i> subimagos					
1981					
Seasonal stream	8.40	0.10	268.0	13.7	30
River margin	8.20	0.09	266.2	11.8	35
1984					
Seasonal stream	8.37	0.05	294.0	7.9	49
River margin	8.23	0.09	302.1	11.2	60
<i>Parameletus chelifier</i> subimagos					
1981					
Seasonal stream*	9.35	0.11	329.1	14.2	13
River margin	8.20	0.23	160.7	13.3	3
1984					
Seasonal stream					
Overall	9.86	0.10	358.5	11.1	45
17–19 June	9.79	0.14	367.7	16.6	18
Nymphs					
16 June 1984, seasonal stream	10.41	0.08	355.5	11.2	12
1985					
Seasonal stream	8.71	0.12	368.5	14.4	21
River margin	9.18	0.15	220.6	15.8	12

\*Year in which desiccation of the seasonal stream may have affected emergence success and fecundity.

river margin over the season. The difference between the two species may indicate that nymphs of *P. minor* are more independent of temperature or that they have a lower "optimum" thermal regime than nymphs of *P. chelifier*. Growth rates of nymphs of other mayfly species are affected by water temperature (e.g., Brittain 1976a; Clifford et al. 1979; Sweeney 1978; Sweeney and Vannote 1981, 1984).

In spite of almost identical water temperatures in the two habitats during peak flood, nymphs of *P. chelifier* always grew faster during that period in the seasonal stream than at the river margin. The growth rate of *P. minor* was about the same in

TABLE 4. Parameters of regression equations ( $y = a + bx$ ) relating egg number ( $y$ ) to female body length ( $x$ ) in millimetres for *Parameletus minor* and *Parameletus chelifier* in 1984

	a	b	r <sup>2</sup>	P
<i>Parameletus minor</i>				
Seasonal stream	-357.1	77.8	0.29	<0.001
River margin	-564.7	105.3	0.76	<0.001
<i>Parameletus chelifier</i>				
Seasonal stream	-334.5	70.3	0.39	<0.001

TABLE 5. Numbers of male and female nymphs of *Parameletus minor* and *Parameletus chelifera* infested by nematodes of the family Mermithidae in the seasonal stream and in the river

	Seasonal stream				River margin			
	No. infested				No. infested			
	n	Male	Female	Total (%)	n	Male	Female	Total (%)
<i>Parameletus minor</i>								
1977	83	0	0	0	—	—	—	—
1979	92	0	0	0	118	0	0	0
1981	73	0	0	0	88	0	0	0
1982	112	0	0	0	78	0	0	0
1984	111	0	0	0	64	0	0	0
1985	149	0	0	0	114	0	0	0
1986	186	0	0	0	323	0	0	0
<i>Parameletus chelifera</i>								
1977	80	1	6	8.8	—	—	—	—
1979	160	3	31	21.3	38	0	6	15.8
1981	215	3	13	7.4	81	0	4	4.9
1982	165	0	18	10.9	57	0	2	3.5
1984	142	0	14	9.9	62	0	8	12.9
1985	378	2	38	10.6	84	2	14	19.0
1986	480	2	98	20.8	57	0	3	5.3

NOTE: n, no. of nymphs examined.

both habitats during peak flood. Thus, temperature is not the only factor that affects growth rate in *P. chelifera*.

Nymphs of *P. minor* and *P. chelifera* are most abundant in shallow water with dense emergent vegetation (Söderström 1988). As river water level rises in spring, new areas gradually become available. During the peak flood, larger shallow areas are made available around the seasonal stream than at the river margin. Although the sediment contains an equal amount of organic matter at both sites, the total amount available should be higher in and around the seasonal stream during peak flood. However, no difference in total volume, volume of FPOM from sedge and grass, or unidentified FPOM consumed per individual could be found in nymphs of *P. chelifera* or *P. minor* from the two habitats. This result indicates that food was not in short supply.

The qualitative differences between the organic material from the two habitats were not caused by different original composition of plant material as dead (not decomposed) grass and sedge did not differ with respect to C/N ratio (around 49 in both plant materials). The difference in C/N ratio in decomposed vascular hydrophytes may instead have been caused by different amounts of microorganisms in the material. It may be that *P. chelifera* can utilize microorganisms on decomposed grass more efficiently than *P. minor* (cf. Bärlocher 1985). Food quality is crucial for growth in several mayflies such as *Leptophlebia intermedia* (Travers) (Sweeney et al. 1986), *Cloeon triangulifer* McDunnough (Sweeney and Vannote 1984), *Cloeon dipterum* (L.) (Cianciara 1980), and *Baetis* spp. (Humpesch 1979).

#### Emergence, adult size, fecundity, and parasitism

In both species the emergence period was short, restricted to about 2 or 3 weeks in June and early July. The earlier emergence in the seasonal stream compared with the river margin of both species in 1981 and of *P. minor* in 1984 was probably the result of the relatively higher temperature. This has previously

been demonstrated for other mayfly species (e.g., Brittain 1976b, 1979; Sweeney 1978).

The greater length of males and females of *P. minor* and *P. chelifera* emerging from the seasonal stream compared with those from the river margin may be an effect of different temperature regimes and (or) food quality differences. Vannote and Sweeney (1980) showed that adult body size of several mayfly species largely depends on thermal conditions during nymphal growth. Anderson (1976, 1978) found that pupae of the caddisfly *Clistoronia magnifica* (Banks) grew larger on an alder leaf diet with enchytraeid worms than on a diet of pure alder leaves.

Male subimagos of both *P. minor* and *P. chelifera* had greater body lengths than the females. Sexual size dimorphism with larger males has recently been reported in the mayfly species *Epeorus longimanus* Eaton (Flecker et al., manuscript submitted for publication<sup>1</sup>). The opposite situation, with females exceeding males in body length and weight, was found in other studies (Brittain 1975; Clifford et al. 1979; Cianciara 1980). The sexual dimorphism in size observed in *P. minor* and *P. chelifera* may be explained by sexual selection, as in *E. longimanus* (Flecker et al., manuscript submitted for publication<sup>1</sup>). However, sexual selection in mayflies is not well known.

Although *P. minor* females in the seasonal stream were larger than those at the river margin in 1984, no difference in fecundity was observed. The high fecundity of *P. chelifera* nymphs from the seasonal stream compared with those from the river margin in 1985 cannot be explained by different body lengths as nymphs from the river margin were significantly longer. The different fecundity response of *P. chelifera* and

<sup>1</sup>Flecker, A. S., Allan, J. D., and McClintock, N. C. Swarming and sexual selection in a Rocky Mountain mayfly. Manuscript submitted for publication.



*P. minor* may result from different efficiency of food utilization. Although only a few *P. chelifera* specimens emerged from the seasonal stream in some years, their mean emergence success in this habitat was much higher than that in the river margin: many nymphs of *P. chelifera* were found at the river margin a few weeks before emergence, but few actually emerged. The low emergence success at the river margin indicates a high mortality, probably caused by fish predation (Söderström and Nilsson 1987).

Clifford and Boerger (1974) proposed that an indication of the favourability of the environment is given by the number of eggs required to produce an adult. The number of eggs produced in a given area should be compared with the number of males and females emerging from the same area 1 year later (in univoltine species). As emergence data usually cover only one season, the assumption that the total number of males and females of each species emerging per square metre approximates the total number that will emerge 1 year later is often applied (Clifford and Boerger 1974). In this study we can use a calculation based on this assumption as well as the real number of subimagos emerging the following year (Table 6). Further, the net reproductive rate (geometrical mean) was here calculated from the same data (Table 6). In our opinion these values give a better measurement of the favourability of the environment. *Parameletus minor* and *P. chelifera* require a low number of eggs to produce one adult compared with many other mayfly species (cf. Clifford and Boerger 1974; Brittain 1980). Nymphs of *P. minor* and *P. chelifera* probably have a short nymphal period of 2–6 months (Söderström 1988). A brief nymphal period may minimize predation (Clifford 1982). This could explain the low number of eggs required to produce an adult in *P. minor* and *P. chelifera*.

*Parameletus minor* had a higher net reproductive rate at the river margin than in the seasonal stream, indicating that the river margin is the more favourable habitat for *P. minor*. The opposite situation was apparent for *P. chelifera*. Thus, in spite of the desiccation, which was severe in 1982, *P. chelifera* seems to have a pronounced advantage by colonizing the seasonal stream.

Only nymphs of *P. chelifera* were infested by mermithid nematodes, and in some years over 20% were infested. All females infested had lost all of their eggs. In spite of being reproductively "dead" animals, they still survived, emerged, and probably also participated in mating. The mayflies must have suffered from infestation at an early stage, as small nymphs (<3 mm) captured in the river and reared in the laboratory were infested. Because of difficulties in rearing mermithids to the adult stage, we do not yet know their species. Representatives of the Mermithidae family are known to infest mayflies (Peters and Arvy 1979; Hominick and Welch 1980; Flecker and Allan 1983). The sterility of the female imagoes seemed to have been caused by depletion of nutrients (Needham et al. 1935; Hominick and Welch 1980; Flecker and Allan 1988). The different nematode susceptibility of *P. chelifera* and *P. minor* may result from differences in size (instar) and (or) microhabitat when preparasitic juveniles occur. Successful host penetration must occur within a few days and shows a decreasing probability with increasing host instar (Hominick and Welch 1980). Another possibility is that the early instars of *P. minor* and *P. chelifera* use different foods.

#### Concluding remarks

By utilizing the seasonal stream, specimens of *P. chelifera*

TABLE 6. Number of eggs required to produce one adult and net reproductive rate of *Parameletus minor* and *Parameletus chelifera*

	<i>Parameletus minor</i>						<i>Parameletus chelifera</i>			
	1981		1982		1984		1981		1982	
	Stream	River	Stream	River	Stream	River	Stream	River	Stream	River
Avg. no. of eggs per female (parasitized females excluded)	268	266			294	302	329	161		359
Total no. of females emerging/m <sup>2</sup> each year	271	163			76	193	40	5		197
% females infested by a nematode	0	0			0	0	11.9	7.5		15.2
Total no. of eggs/m <sup>2</sup> each year after compensation for parasite infestation (A)	72 628	43 358			22 344	58 286	11 594	745		59 973
Total no. of males and females emerging/m <sup>2</sup> each year (B)	415	364			116	339	79	9		350
No. of eggs required to produce one adult (A/B)*	175	119	187	85	193	172	147	83	297	>745
Net reproductive rate	0.94	1.40					0.49	<0		
1981–1982 ( $R_0 = B_{1982}/B_{1981}$ )										
1982–1983 and 1983–1984,										
geometric mean					0.55	0.82				3.00
( $R_0 = (B_{1984}/B_{1982})^{1/2}$ )										

\*For 1982, 1981 values of A were used in this calculation.

experience a higher growth rate, greater emergence success, higher fecundity, and probably also a larger subimago size. Assuming that the seasonal stream carries water until the emergence period has started, *P. chelifera* specimens will do better there than at the river margin. According to the net reproductive rate, *P. chelifera* seems to achieve an advantage when using the seasonal stream. A higher thermal regime as well as higher food quality seem important in explaining the positive effects on the life history parameters of *P. chelifera* there. Regardless of habitat, a certain number of *P. chelifera* specimens will be infested by nematodes, drastically reducing the reproductive success of those specimens.

Individuals of *P. minor* in the seasonal stream emerge earlier and acquire a larger subimago size. On the other hand, no difference was found in growth rate, emergence success, or fecundity between the two habitats. The net reproductive rate was higher at the river margin, indicating that this habitat may be more favourable to *P. minor* specimens. As *P. minor* seems to have a lower "optimum" temperature for growth, the environmental conditions in the river may be as favourable as in the seasonal stream.

Because both species occur in both habitats, the long-term reproductive output probably varies irregularly. Occasionally specimens of *P. minor* using the seasonal stream obtain a higher reproductive success than those in the river, and vice versa for specimens of *P. chelifera*.

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