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Springtime migration and growth of Parameletus chelifer (Ephemeroptera) in a temporary stream in northern Sweden

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The upstream migration of the nymphs of the mayfly *Parameletus chelifer* Bgtss., in a temporary stream, tributary to the river Vindelälven in northern Sweden, was investigated in May 1977. The tributary drains an alluvial meadow which has usually dried out by the middle of July. The upstream movement of nymphs lasted for about nine days, during which period hundreds of thousands of *P. chelifer* moved from the main river up into the small stream. The nymphs on the alluvial meadow grew significantly faster than did those in the river, probably because of a higher water temperature and a more plentiful supply of food in the temporary stream. Before the stream dried up completely the nymphs had emerged. Newly hatched nymphs were found in the main river in February. Thus, it seems as if *P. chelifer* has a colonization cycle which includes an upstream movement of nymphs and a subsequent 'downstream' return flight of adults.

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Миграция нимф *Parameletus chelifer* Bgtss.вверх по течению временного притока реки в Винделелвен (сев. Швеция) исследована в мае 1977 г. Приток дренирует аллювиальный луг, который обычно пересыхает к середине июля. Движение нимф ыыерх по течению продолжается примерно 9 дней, в течение этого периода сотни тысач *P. chelifer* мигрируют из основного русла вверх в маленький приток. Нимфы растут на лугу значительно быстрее, чем в реке, вероятно вследствие более высокой температуры воды и более обильной пищи во временном потоке. Развитие нимф заканчивается до полного пересыхания речки. Вновь отродившиеся нимфы найдены в русле реки в феврале. Таким образом, можно полагать, что *P. chelifer* имеют колонизационный цикл, включающий миграцию нимф вверх по течению и последующий обратный лет имаго " вниз по течению".

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Introduction

A basic concept in the ecology of running waters is the 'colonization cycle' (Müller 1954a), which involves a downstream drift of the larvae of amphibiotic insects (Waters 1972) and a compensatory upstream flight of the adults (Roos 1957, Elliott 1969). The compensation of the drift of amphibiotic insects may also be partially achieved by an upstream migration of the larvae (Bishop and Hynes 1969, Hultin et al. 1969, Elliott 1971). Larval drift and adult upstream flight are important in the recolonization of areas from which the fauna has been eliminated (Müller 1954b, Waters 1964, Otto and Svensson 1976), or as a means of annual transport between the overwintering sites and those at which continued growth occurs (Müller et al 1976).

During the break up of the ice in May 1976 upstream migration of nymphs of *Parameletus chelifer* Bgtss. was observed in a minor tributary of the river Vindelälven in northern Sweden. The tributary carries the meltwater and later the floodwater from an alluvial meadow and flows for only 2–3 months during the spring and early summer.

These observations stimulated the present investigation of a presumed 'colonization cycle', which involves the upstream migration of nymphs to alluvial meadows, the subsequent flight of adults back 'downstream' and egg-laying, hatching and overwintering in the main river courses.

The aims of the present investigation were: (1) to estimate the number of *P. chelifer* nymphs migrating upstream in a temporary stream, and (2) to compare the growth rate of the nymphs which remained in the main river with that of the nymphs which migrated upstream to the alluvial meadow.

Study area

The river Vindelälven rises on the eastern side of the Scandean mountain chain in northern Sweden, close to the Norwegian border. It joins the river Umeälven 42 km from the Gulf of Bothnia. The Vindelälven has not yet been exploited for hydro-electric power and the seasonal fluctuations in water flow are therefore very large. The mean maximum flow during the period 1971–1977 was 1022 $m^3 s^{-1}$ and the mean minimum flow 31 $m^3 s^{-1}$ (data from the Swedish Meteorological and Hydrological Institute). The duration of the ice-cover over the investigated part of the river is from the middle of November to the first or second week of May. This part of the river is located in the boreal coniferous zone and is classified by Brinck (1949) as a northern river.

The small temporary stream investigated flows into the river Vindelälven at Sirapsbacken (64°22′N, 19°28′E), about 25 km upstream Vindeln. It has a total length of about 300 m and is 0.5–1 m broad. It drains an alluvial meadow (Fig. 1), which is partially flooded every year at the time of the spring flood. The spring flood in the river Vindelälven has two peaks; one at the end of May and one around midsummer. The first is

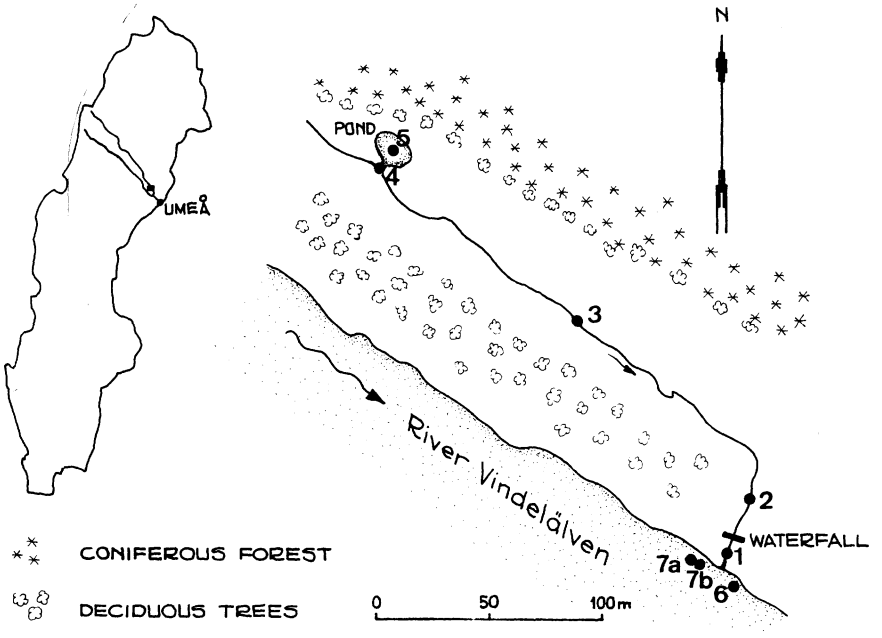

Fig. 1. Position of the sampling sites. No. 1–4 were in the temporary stream flowing from the alluvial meadow, no. 5 in the pond and no. 6–7b in the main river. Site 1 was a locality influenced by the prevailing river water-level. Sites 2 and 3 were subjected to current during the migration. Sites 4 and 5 lay in stagnant water. Sites 6, 7a and 7b lay in the *Carex* zone near the river margin.

caused by the snow-melt in the coniferous forest zone and the second by the snowmelt in the mountains. The meadow usually dries out about the middle of July. In some years heavy rainfalls in the autumn may fill up the drainage ditches on the meadow, but this water always freezes into the substrate during the winter.

Ten meters from the mouth of the stream there is a small waterfall (0.4 m high) and there is a shallow pond near its source. The vegetation near the banks of the river consists mainly of *Carex acuta* L. and on the lowerlying parts of the alluvial meadow of *Calamagrostis canescens* (Web.) Roth. and *Carex acuta.*

The positions of the sampling sites are shown in Fig. 1.

In 1977 the ice-cover broke up about 13 May. The water temperature of the shallow pond rose much faster than did that of the river water (Fig. 4), but fluctuated more widely in the pond, both during the day and from day to day. The greatest temperature differences between the pond water and the river water were recorded in May. After the river flooded over onto the meadow, 11–18 June, this difference decreased (cf. Fig. 4). At the time of the mayfly nymph migration, pH was about 6.8 and conductivity about 20 $\mu S_{20} \cdot cm^{-1}$, with no great difference between the river water and that in the temporary stream.

Methods

The study was carried out between 12 May and 6 July 1977. Catches of mayfly nymphs migrating upstream were made at 2-h intervals throughout the day and night at sites 1, 2 and 3 and in stagnant water at sites 4 and 5.

The nymphs migrating upstream were caught in a steel-sided trap (mesh size 0.4 mm; see Fig. 2). In the stagnant water (sites 4 and 5) and in the main river (sites 6, 7a and 7b) we used a glass-sided trap of the type described by Werner (1968) but with nylon mesh (mesh size 0.5 mm) instead of glass at the end of the

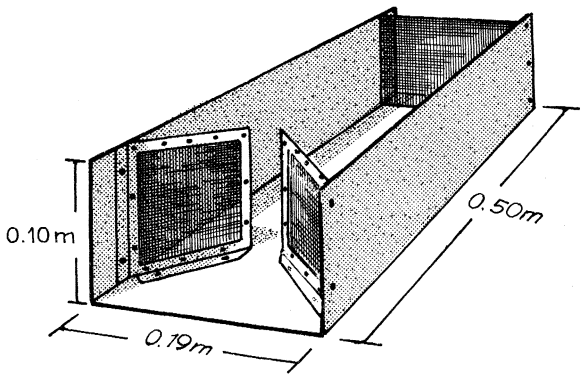

Fig. 2. Design of the steel-sided trap used to catch nymphs moving upstream in shallow, running waters. Mesh size 0.4 mm.

Tab. 1. Total numbers of mayfly nymphs caught during 24-h periods on the alluvial meadow (sites 1–5) and in the main river (sites 6–7b) at different dates in 1977. A steel-sided trap was used at sites 1–3 and a glass-sided trap at sites 4–7b. *Siphlonurus* spp. = *S. lacustris* Etn., *S. aestivalis* Etn., and *S. alternatus* Say.

Site no.	1			2			3		4		5		6	7a		7b
Dates	13–14 May	16–17 May	13–14 May	16–17 May	19–20 May	19–20 May	21–22 May	25–26 May	25–26 May	2–3 Jul	moving up-stream 19–20 May	moving down-stream 19–20 May	moving down-stream 21–22 May	moving up-stream 21–22 May
Parameletus chelifer	13797	44853	2705	24962	414	3137	653	1590	1009	412	819	13743	6691	964
Heptagenia fuscogrisea	119	1916	0	46	110	190	83	111	16	7	238	45052	11559	506
Siphlonurus spp.	2	502	0	20	21	38	8	35	2	541	105	8603	1645	144
Leptophlebia vespertina	1	28	0	0	12	10	0	74	16	0	26	104	1333	221
Leptophlebia marginata	0	16	0	0	0	2	0	5	1	0	8	11	15	4

trap. At sites 6 and 7b the trap opening pointed downstream, at site 7a upstream. Further samples, for growth and biomass studies, were taken with a polenet (mesh size 0.5 mm) from the river and in the pond on the alluvial meadow. All catches were preserved in 70% ethanol.

The head capsule width of each nymph was measured to the nearest 0.1 mm under a binocular microscope fitted with a micrometer. To obtain the dry weights, the preserved nymphs were dried at 60°C for 24 h and weighed on a precision balance (accurate to the nearest 0.1 mg).

The nomenclature follows 'Limnofauna Europaea' (Illies 1978). The *Parameletus* nymphs captured in this study agree with the description of *P. chelifer* given by Ulmer (1943).

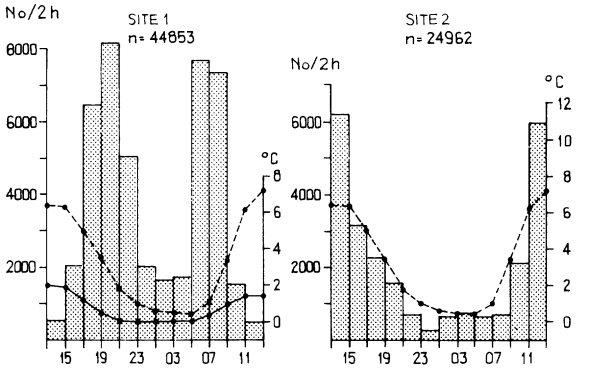

Fig. 3. The numbers of *Parameletus chelifer* nymphs caught at 2-h intervals throughout a 24-h period on 16–17 May in a steel-sided trap. The dashed curve represents the course of the water temperature in the stream flowing from the alluvial meadow and the solid curve the water temperature in the main river.

Results

On 12 May some pole-net samples were taken from the lower reaches of the stream, which had by this time thawed out, and a few *Parameletus chelifer* were caught. These nymphs had already entered the stream, although the main river was still frozen over. There were some pools of water on the ice surface near the river bank and some minor holes in the ice-cover existed through which the nymphs could move up and down. In the lower reaches of the temporary stream the *P. chelifer* nymphs had to pass under several snow bridges, about 5 m long, and climb up a small waterfall.

The total numbers of mayfly nymphs collected in the traps at the different sites are shown in Tab. 1. During the first 24-h catch, on 13–14 May, a total of 13797 *P. chelifer* were caught in the trap downstream from the waterfall (site 1) but only 2705 upstream from the waterfall (site 2). No other mayfly species was caught beyond the waterfall at this time. During the second 24-h catch, on 16–17 May, we caught 44853 *P. chelifer* at site 1 and 24962 at site 2. During this 24-h period the waterfall had virtually disappeared because of the rise in the river water-level, and other mayfly species, *Siphlonurus* spp. and *Heptagenia fuscogrisea* Retz., were now also caught at site 2. The biomasses (dry weight basis) of the *Parameletus* nymphs caught at site 1 during these two periods were 1.8 and 5.0 g, respectively. At the third 24-h catch, on 19–20 May, the water had risen to the level of site 2 and the flow velocity at mouth of the temporary stream was now very low. Few *P. chelifer* were captured at site 2 during this third 24-h period.

As the trap width was around 1/5 of the stream width, we estimated that a single trap caught 1/5 of the total number of nymphs migrating during a 24-h period. A very rough estimate for the whole migration period is thus about 900000 individuals, or about 0.7–0.8 kg (wet wt) of *P. chelifer* moved from the river into the small temporary stream.

During the migration the diel activity pattern of *P. chelifer* became modified from a crepuscular activity to a pure noon activity (Fig. 3). Our results furthermore indicate that a small number of nymphs moved during the night, in which way it differs from the purely diurnal activity pattern reported for *Leptophlebia cupida* Say. (Hayden and Clifford 1974).

The total catches at site 6 (19–20 May) and 7b (21–22 May) of nymphs of *P. chelifer* moving upstream in the main river were 819 and 964, respectively (Tab. 1). During the same two periods the catches at site 7a of nymphs moving downstream were 13743 and 6691, respectively.

The mean widths of the head capsules of the nymphs caught on the alluvial meadow were greater than the mean values of those caught in the river (Fig. 4). The differences are statistically significant (except for the period 13–17 May). Over a period of 6.5 wk the nymphs on the alluvial meadow increased in weight 17-fold and those in the river 12-fold.

In connection with the present study 27 perch *Perca fluviatilis* L. were caught at the mouth of a similar stream to obtain data about possible perch predation on *P. chelifer*. About 80% of the total number of food items found in their stomachs belonged to this mayfly species.

Discussion

The nymphs of many mayfly species are known to move shorewards at springtime when the water-level rises (Moon 1935, Verrier 1956). Our results show that *Parameletus chelifer* not only moves towards the river-banks but continues migrating up into small tributaries. This upstream movement into the temporary stream was not prevented by the presence of snow bridges or by minor waterfall near the stream mouth. This behaviour of *P. chelifer* corresponds well with that

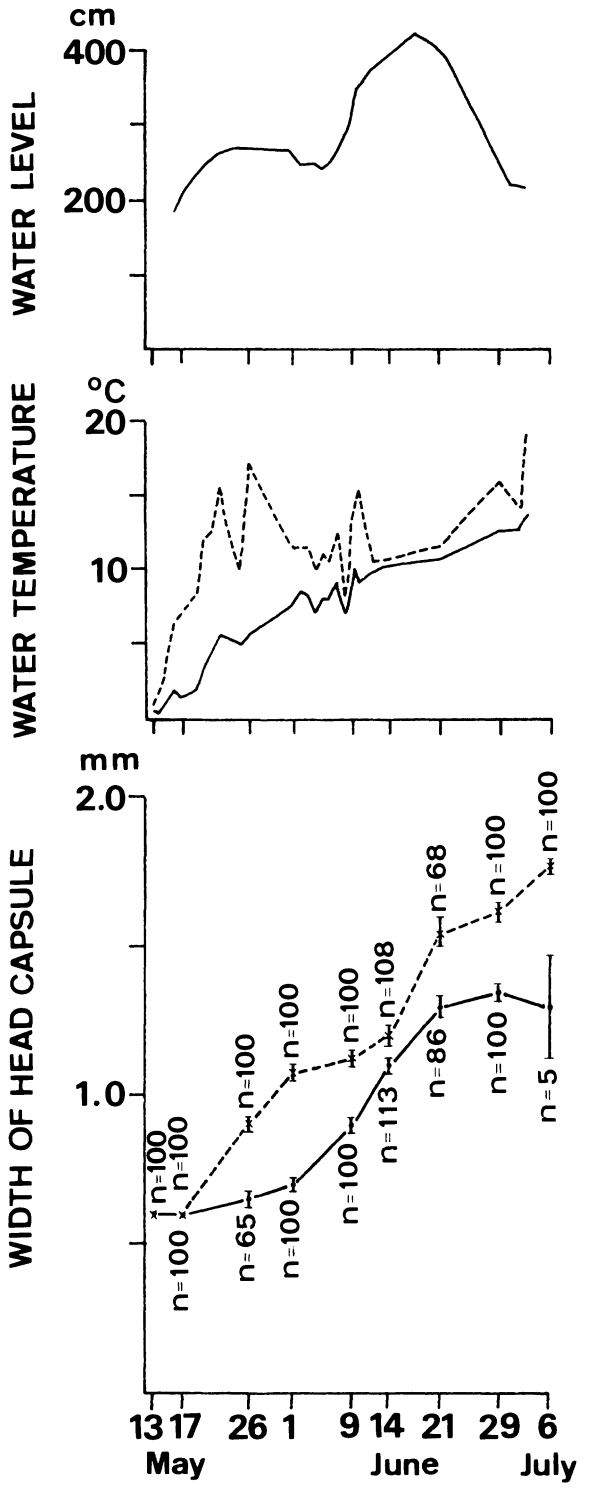

Fig. 4. The upper graph shows the water-level in relation to a fixed point in the main river, the middle graph the water temperature in the pond on the alluvial meadow (dashed) and in the main river (solid) and the lower graph the size of *Parameletus chelifer* nymphs in the alluvial meadow pond (dashed) and in the river (solid), on different dates between 13 May and 6 July. Size is expressed in terms of the mean widths of the head capsules (with a 95% confidence limit of the mean).

described for the North American species *Leptophlebia cupida* by Neave (1930) and Hayden and Clifford (1974).

The migration of the *P. chelifer* nymphs was restricted to a short period at and after the time of the break up of the ice-cover in the main river. Our observations indicate that the migration lasted for about nine days. During this period a transference of biomass occurred from the main river into its tributaries. Thus, beside an input of allochthonus material into the river there is also an output of organic material from the river.

According to Hayden and Clifford (1974) *L. cupida* nymphs followed the main river shore-line upstream until they came to the mouth of a tributary. In our investigation the catches of nymphs moving downstream in the main river were about ten times greater than those of nymphs moving upstream (Tab. 1). Although this result is derived from the end of the migration period it seems likely that the behaviour of *P. chelifer* in the main river differs from that of *L. cupida.*

The rapid nymphal growth which took place at the alluvial meadow sites (Fig. 4) was probably connected with the rapid rise in water temperature and the plentiful supply of organic detritus and algae. After a short period of rapid growth the nymphs started to emerge at the end of June and emergence was over before mid–July, when the alluvial meadow dried out. The adults then had to fly back to the main river for egg-laying. We found the first nymphs in the main river in February. In this way *P. chelifer* completes its life-cycle and colonization cycle whithin the cource of one year.

We suggest that the major advantages of this colonization of the alluvial meadows are the possibility for rapid growth afforded by higher temperature of the water there and an ample food supply. In addition, the nymphs leave the main river before the time of the spring flood and the increase in current strength; conditions to which the full-grown nymphs are poorly adapted. At the same time they are colonizing an unoccupied habitat free from predatory fish. At the time for emergence the nymphs in the pond are larger than those in the river. These larger nymphs probably give rise to larger adults which are capable of producing more eggs than smaller individuals.

Nevertheless there are also some disadvantages connected with this behaviour, e.g. the risk of desiccation. Furthermore, about 25 species of Dytiscidae are present in the alluvial meadow biotope, compared to only 7 species in the main river (Nilsson 1978). All these species are capable to prey on the mayfly nymphs, as does the wood sandpiper *Tringa glareola* L. which breeds on the alluvial meadow.

The colonization cycle of *P. chelifer* allows the species to utilize different biotopes for overwintering and growth which has been shown for Plecoptera nymphs (Müller et al. 1976). This is different from the customary type of colonization cycle because it involves an

upstream movement of nymphs and a subsequent 'downstream' return flight of adults.

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