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Current status, distribution, life cycle and ecology of *Rhithrogena germanica* EATON, 1885 in Switzerland: preliminary results (Ephemeroptera, Heptageniidae)

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ABSTRACT

Rh. germanica is a European species that, due to human impacts, has progressively disappeared from its original territories and is now considered rare. In Switzerland *Rh. germanica* has disappeared from the Aare, Broye and Kleine Emme rivers and is actually found in a limited reach of the River Rhine and some of its tributaries (Limmat, Sihl, Thur and Töss rivers). *Rh. germanica* is a univoltine species, hatching probably in summer. The emergence occurs from February to the beginning of April. It takes place on the water surface. Laboratory observations have shown that the subimaginal stage lasts four days. *Rh. germanica* occurs on different substrate types, ranging from stones and cobbles to pebbles and gravel. The larvae are more abundant in zones of erosion with coarse and porous sediments than in depositional zones with fine sediments and silts. They are most abundant in riffles with water velocities from 20 to 150 cm/sec. The species tolerates moderately organic-polluted waters.

The particular strategy concerning growth and emergence of *Rh. germanica* is also discussed.

Introduction

The species *Rhithrogena germanica* (syn. *Rh. haarupi* Esben-Petersen, 1909 and *Rh. ussingi* Esben-Petersen, 1910) was described by Eaton (1885) on a single male imago collected on the River Rhine near Laufenburg (Switzerland). Since then the species has been reported by Neeracher (1908, 1910) from the same river in Basel and about 90 km upstream in Englisau (Switzerland) as well as in Istein (Germany), where this species was quite abundant. *Rh. germanica* was recorded at the same time in Denmark (Esben-Petersen, 1909, 1910). Later on *Rh. germanica* was collected in Great Britain (Mosely, 1932), France (Despax, 1949), Czechoslovakia (Landa, 1959) and Poland (Sowa, 1962). It has been shown that all other sightings, especially from the Balkan area, refered probably to another species, *Rh. sowai* (Puthz, 1972).

Rh. germanica is regarded as a central European species (Sowa, 1975a), reaching its northern boundaries in Scotland and Denmark and its southern ones along the northern slopes of the Pyrenees and the Alps (Thomas et al., 1987). The species is almost exclusively found in medium to large rivers in lowlands below 1000 m a.s.l. and is therefore considered to be a characteristic element of the hyporhithral and epipotamal river reaches.

Due to human impacts this species has progressively disappeared from its original area: In 1971 when Sowa had to designate a neotype, he chose a specimen from the Raba River in Poland "...puisqu'une rencontre de *Rh. germainca* Eaton dans le Rhin serait peu probable si nous tenons compte de sa grande pollution..." (Sowa, 1971 p. 486). The present distribution of this species is as follows:

- Great Britain: considered rare (Elliott et al., 1988).
- Czechoslovakia: relic habitats and scarce occurrence (Landa and Soldán, 1985).
- Poland: no recent observations, but seems restricted to some large rivers of the Carpathian foothills (Sowa, 1975a).
- Denmark: found in only one location and considered to be almost extinct (Jensen and Jensen, 1980).
- France: probably disappeared from the Rhone River. Few populations in the Garonne River, upstream of Toulouse (Thomas et al., 1987).
- Germany: considered by Puthz (1984) as threatened to extinction. Already extinct in Baden-Württemberg (Malzacher, 1981); possibly one remaining population in South Germany (Malzacher, comm. pers.)

In Switzerland apart from Eaton's and Neeracher's data the following reports stem from the first half of this century: Aare River near Belp, 2. IV. 1929 (Naturhistorisches Museum Bern, A.G.B. Thomas vid.), Broye River near Payerne, 13. II. 1946, Aare River in Bern, 21. II. 1947, Kleine Emme River in Wolhusen, 25. IV. 1947, Sihl River in Sihlbrugg, 24. III. 1948 (Musée de Zoologie, Lausanne, coll. J. Aubert).

Rh. germanica has now disappeared from the Aare, Broye and Kleine Emme rivers (Sartori, 1987). Nevertheless Zurwerra and Tomka (1984) presented evidence that the species was present in the Thur River near its mouth on the Rhine. Moreover a recent survey of the Rhine proved that *Rh. germanica* was still present between the Thur and Aare mouths (Schröder and Rey, 1991). Recent field research in the canton of Zurich found additional populations of *Rh. germanica* in river reaches previously not known to be colonized by this species (Lubini, 1989, 1993, 1994). The results of some of these observations are presented.

Materials and methods

In the lower reaches of the Thur and Sihl quantitative collections of larvae were made with a Surber sampler three to five times a year between 1990 and 1992 (Lubini, 1993, 1994). To estimate the distribution of the species, additional collections (qualitative samples) were made in the upper reach of the Thur, in the Sihl, Töss and Limmat rivers. The specimens were preserved in a 70% alcohol solution for later identification. The current velocities were measured with a propeller

anemometer MiniAir 2. To compare the different sites with different depths the measurements were made 3 cm below the surface.

To establish the life cycle, each individual was measured. Total length, from the front of the head to the end of the abdomen, as well as head width, were recorded using a micrometer eyepiece, and then categorised in 1 mm size groups. The geometric mean of the body lengths at the ±95% confidence interval was calculated (Humpesch, 1979) for each sample.

The specific growth rate G (expressed in mm % day^{-1}) was determined by fitting the exponential function (Humpesch, 1979, 1981) to the samples.

$$L_t = L_0 e^{kt}$$

Where L_t is the mean length (in mm) after an interval of time t (in days) and L_0 is the mean initial length (mm); k is the instantaneous growth rate and $G = 100\,k$.

Results

Distribution in Switzerland

Due to human impacts such as dams and chemical pollution, *Rhithrogena germanica* has now disappeared from the Aare, Broye and Kleine Emme rivers. The remaining populations are now concentrated in the Rhine and some of its tributaries in the north-eastern part of Switzerland (Fig. 1). Two such tributaries were previously not known to possess populations of this species i.e. the Töss River in the reach Kyburg (upstream of the city of Winterthur) to its mouth in the Rhine River and the

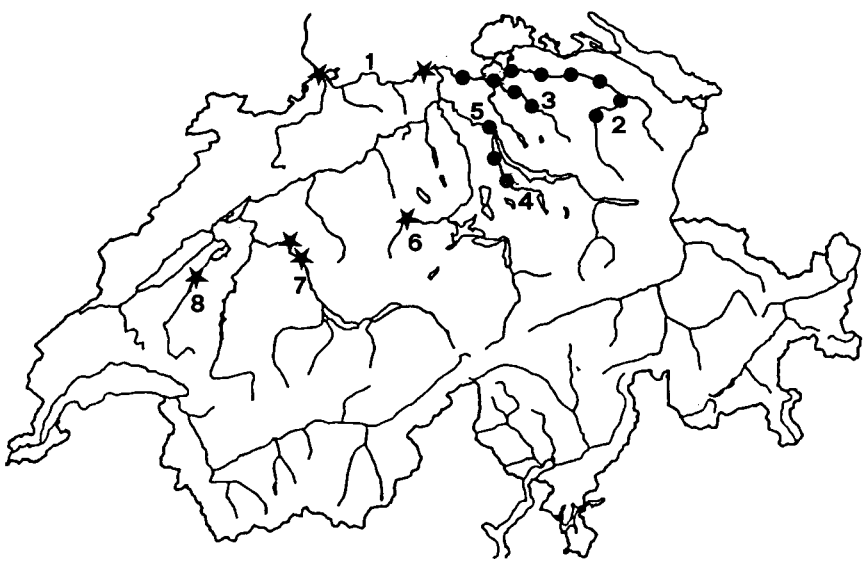

Figure 1. Former (*) and actual (•) distribution of *Rhithrogena germanica* EATON in Swiss rivers. 1 = Rhine; 2 = Thur; 3 = Töss; 4 = Sihl; 5 = Limmat; 6 = Kleine Emme; 7 = Aare; 8 = Broye

Limmat River at Zurich. The populations extend up to 620 m a.s.l., about 7 km upstream of Sihlbrugg in the Sihl River. In contrast to those of the rivers Thur and Töss, the populations of the Sihl and Limmat are isolated from the Rhine. this is due to the changed ecological conditions like lower current velocities resulting from the training of the Limmat River downstream of Zurich.

Life cycle

The life cycle of *Rh. germanica* during the investigated period is shown in Fig. 2. Five species of *Rhithrogena* were found in the Thur (Lubini, 1994), one of them, *Rh. semicolorata* (Curtis) being very closely related to *Rh. germanica*. There are no characteristic features available to allow distinction of young larvae between the two species. The larvae with a body length < 5 mm were thus assigned to both species.

Young larvae of *Rh. germanica* probably appear in the samples already in summer, although there are still taxonomic difficulties to separate them from those of *Rh. semicolorata*. The emergence occurs from February to the beginning of April. This species exhibits a single generation per year, spending the winter period in the larval stage (univoltine winter species –Uw– according to Clifford, 1982). No young larvae of *Rh. germanica* could be found until July. The specific growth rates has been calculated for the periods from October 1990 to February 1991 and from October 1991 to February 1992. Growth rate values (G) were exactly the same for both periods i.e. $0.66 \pm 0.12\%$ mm day^{-1}. Thus no seasonal growth differences during the investigated periods were found.

Emergence generally takes place between 12.00 and 13.30 hrs. Once when the air temperature was very low, subimagos were found between 15.00 and 16.00 hrs in the afternoon. The nymphs drift on the water surface when moulting. The whole procedure lasts approximately 30 seconds. The freshly emerged subimagines fly to

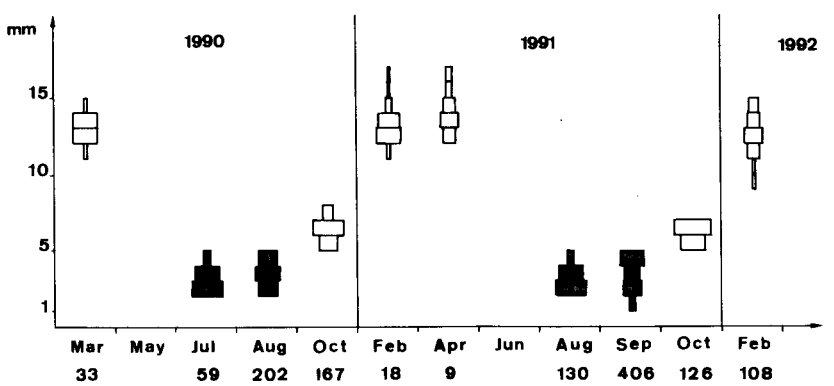

Figure 2. Life cycle of *Rhithrogena germanica* in the Thur River, based on samples from March 1990 until February 1992. White bars: larvae of *Rh. germanica*, shaded bars: larvae belonging to *Rh. germanica* and/or to *Rh. semicolorata*. Each bar indicates the relative value (in %) for each 1 mm size group per month. Numbers on the abcissa: absolute number of specimens measured

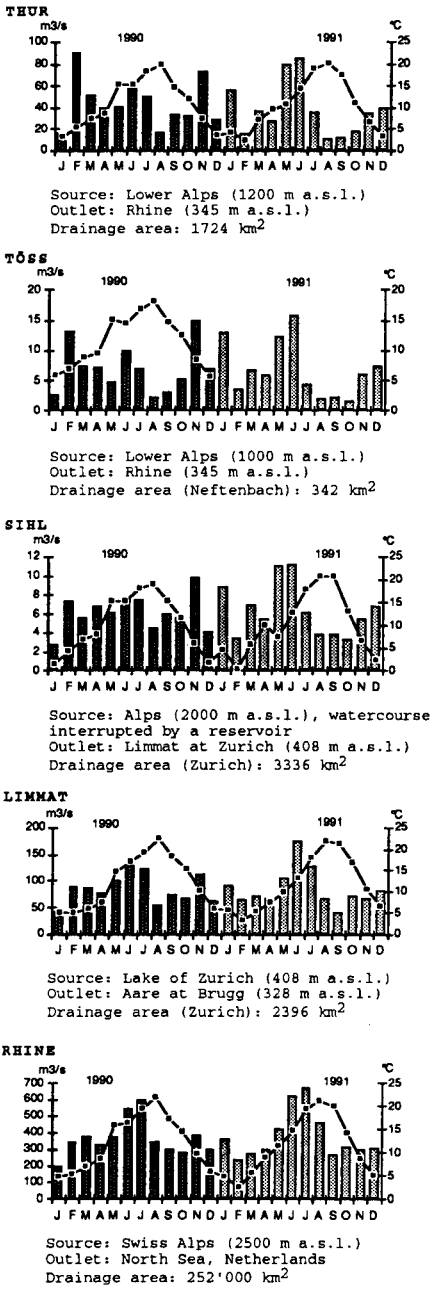

Figure 3. Hydrological characteristics of five rivers in Switzerland, where *Rh. germanica* is present. Bars represent the mean monthly discharge in 1990 and 1991, dotted lines the mean monthly water temperature in 1990 (all rivers) and 1991 (Thur and Rhine rivers). In 1991 water temperatures in the Limmat and the Sihl rivers has been measured only once a month, whereas no measurements were done in the River Töss

Table 1. Annual mean and maximum values of selected chemical parameters for the investigated rivers in 1990 (Public Works Departement of the Canton of Zurich; Landeshydrologie und -geologie, 1990)

	NO3–N		NO4–N		PO4		Ptot		DOC	
	mean	max	mean	max	mean	max	mean	max	mean	max
Rhine	1.4	2.2	–	–	0.03	0.05	0.1	0.52	1.9	3.1
Thur	2.6	5.3	–	–	0.1	0.19	0.34	0.98	2.8	5.1
Töss	5.9	9	0.2	1.22	0.04	0.17	0.09	0.23	3.5	6.7
Sihl	1.5	3	0.2	0.65	0.01	0.05	0.13	0.84	3.5	6.7
Limmat	0.6	1.4	0.05	0.8	0.01	0.08	0.06	0.21	1.0	5

the river bank immediately, where they rest on stones or grass for a short period of time before flying up to nearby trees. Rearings in the laboratory under natural conditions (temperature, daylight) show that the subimaginal stage lasts about four days.

Ecology

Habitat: Rh. germanica lives in the lower reaches of smaller (Töss, Sihl), medium (Thur, Limmat) and large rivers (Rhine). Such rivers originate in the Alps or Lower Alps and have nival to pluvial hydrologic regimes (Fig. 3). The populations in the Limmat are supposed to originate from its tributary the Sihl. The stream systems where *Rh. germanica* is most abundant belong to the hyporhithral or epipotamal river reaches. Table 1 shows the values of selected chemical parameters of the investigated rivers.

Substrate: Rh. germanica occurs on different substrate types, ranging from stones and cobbles to pebbles and gravel. The larvae are significantly more abundant

Table 2. Average (and maximum) larvae count per m^2 in the Sihl River near Zurich: A and B = rehabilitated reaches i.e. with pools and riffles. C = channelized reach

	A	A	B	B	C
	Riffle	Pool	Riffle	Pool	
Oct. 1991	56.7 (190)	0	153.0 (520)	21.7 (60)	9.2 (30)
Feb. 1992	45.0 (180)	6.7 (30)	21.7 (60)	18.3 (40)	7.5 (20)
Oct. 1992	68.3 (190)	0	58.3 (100)	15.0 (60)	11.7 (110)

Table 3. Average and maximum number of larvae of *Rh. germanica* in the lower reach of the Thur River in the canton of Zurich. N = number of samples

	average number of larvae m^{-2}	maximum number of larvae m^{-2}	N
1990: March	2.7	30	128
1990: July	5.6	40	105
1990: October	15.9	270	105
1991: February	5.0	20	36
1991: April	3.9	30	36
1991: October	35.0	170	36
1992: February	57.1	200	24

($p < 0.001$, Wilcoxon test) in zones of erosion (riffles) with coarse and porous sediments than in depositional zones (pools) with fine sediments and silts (Tab. 2). Populations have been observed in rivers with current velocities from 20 to 150 cm sec^{-1}. In reaches with low average current velocities ($< 20-30$ cm sec^{-1}) they occur only in riffle areas.

Abundance: Tables 2 and 3 show the recorded larvae from populations in the Sihl River and the Thur River respectively. Their abundance is greatest in autumn and declines during winter until the emergence period from February to April. The differences in abundance between the two rivers are the effects of the differing sediment compositions and hydrologic regimes: in the regulated Sihl River with regulated discharge the sediment is coarser and the river bed is much more stable than that of the Thur. The low density of larvae in the pools and the channelized reach of the Sihl (Tab. 2) are the result of the sealed bed almost without interstices. The variability between successive years reflects differences in environmental conditions like discharge (Lubini, 1994) and the patchy distribution of the species.

Discussion

In Switzerland the species is generally regarded as vulnerable (Sartori et al. in press). In their whole geographical range, *Rh. germanica* populations are considered threatened and only occur in small numbers. An increase in human impacts such as pollution and river training to the medium and lower courses of European rivers has led to the extinction of most populations since about 1950. Sowa's statement in 1971 on the high pollution level of the River Rhine is relevant of this situation.

Nevertheless our investigations have shown that populations are more numerous in Switzerland than a *priori* considerations lead us to believe. A possible explanation is the absence of previous methodical investigations in those rivers and reaches which contain populations of *Rh. germanica*. It could also be that the species migrated to these sites with improved environmental conditions, provided

that there were surviving populations. This is most likely the case in the River Rhine upstream of the mouth of the Aare River. If this hypothesis is correct, there should be populations in tributaries on either side of the River Rhine. This is, however, not the case for the right catchment side, although the water quality on both sides has improved recently (Schröder and Rey, 1991). Thus there must be additional factors which determine the distribution of the species.

The hypothesis of upstream migration from the River Rhine is not valid for the populations of the Limmat and the Sihl, since these are isolated from the Rhine. We assume therefore, that a surviving population was able to maintain the species in the upper reach of the Sihl. Recolonization with improved environmental conditions has also been observed for the German reach of the Rhine and other rivers in Gemany (Burmeister, 1989; Kureck, 1992; Marten, 1986).

Concerning its ecological requirements, our results show that *Rh. germanica* can endure low to moderate organic-pollution. The species colonizes different types of substrata. We assume that its occurrence is strongly dependent on the oxygen content of the water, because the larvae are most abundant in riffles where the water is saturated with oxygen. These results confirm the observations of other authors (Sowa, 1975a; Elliott et al., 1988). The limiting factors for its distribution seems to be the discharge regime and the current velocity.

In the investigated sites, the life cycle of *Rh. germanica* is similar to those of other populations in Poland (Sowa, 1975b) or in England (Wise, 1980). In all areas observed *Rh. germanica* is a clear univoltine species that emerges in late winter to early spring where environmental conditions are generally unfavourable to other heptageniid species. This strategy possibly allows this species to avoid stronger competition for food resources from others, as has been suggested for other sympatric *Rhithrogena* species (Breitenmoser-Würsten and Sartori, in press). We assume that the synchronization of emergences during the warmest period of the winter days around noon reduces mortality due to bad weather conditions (cold temperature, rain or even snow). It is well known that air temperature has a direct effect on the duration of the subimaginal stage (Sartori and Sartori-Fausel, 1991). As a consequence, the duration of the subimaginal stage is fairly long, reaching up to four days. This is the longest period recorded among the mayflies to date (Edmunds and McCafferty, 1988).

The growth rate observed during winter for *Rh. germanica* is significant, greater than that which has been observed for other *Rhithrogena* species during the same period (Hefti and Tomka, 1990; Breitenmoser-Würsten and Sartori, in press). These results are opposed to those obtained by Sowa (1975b) and Wise (1980) who observed rapid autumnal growth followed by slower winter growth. It was not expected to find identical specific growth rates for the two investigated periods. Analyses of daily mean water temperatures and discharges show that there were significant differences in both parameters between the two periods ($p < 0.001$, Wilcoxon test). Growth rate seems to be independant of environmental conditions. Such strategy is not common among the mayflies of temperate regions, and has been reported in Europe only for *Rh. hybrida* (Breitenmoser-Würsten and Sartori, in press). Further studies, including a comparison of growth characteristics in rivers with different thermal and discharge regimes (see Fig. 3) might supply important complementary results.

Rh. germanica exhibits a particular growth behaviour among mayflies of the temperate regions. There seems to be a balance between the advantage of growing fast during the winter when other species are dormant, and the disadvantage of emerging and molting during unfavourable weather conditions. This delicate balance could explain why *Rh. germanica* is among the first to disappear when natural and/or artificial changes occur influencing the growth period. Further studies are needed to determine the viability of populations which occur in changing environmental conditions.

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