

EPHEMEROPTERA IN SWITZERLAND

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ABSTRACT

The Swiss mayfly fauna, to date 85 species, has been documented for the first time (Sartori and Landolt, 1999). Most of the 10,700 records were collected during the last twenty years. Over 1800 locations were investigated in streams, rivers, ponds and lakes situated on the northern and southern slopes of the Alps, in prealpine regions, on the Swiss Plateau and the Jura Mountains. Faunal distributions are attributed to geographical factors such as latitude, East-West extension and altitude, geological properties, physical characteristics such as current velocity and stream order.

INTRODUCTION

A distributional atlas, indicating the spatio-temporal spread of populations within a certain area, necessitates a solid systematic base. The work on Ephemeroptera in Swiss Fauna (Studemann et al., 1992) covers this need.

We have established that for some years now an important number of Ephemeroptera populations have been declining and some are even on the point of extinction. It is therefore urgent, to have a document that gives an objective appreciation of the current situation and that also serves as a measure for any future analysis of the evolution and distribution of these insects.

BACKGROUND

1. Geography of Switzerland

Switzerland lies in the heart of Europe and is influenced by all the major climatic regions of the continent —Atlantic, Mediterranean, Continental and Boreal. Its relief was moulded by alpine orogenesis and glaciations. A tough a small country (41,293 km²) these elements have resulted in an extraordinarily rich diversity in fauna and flora.

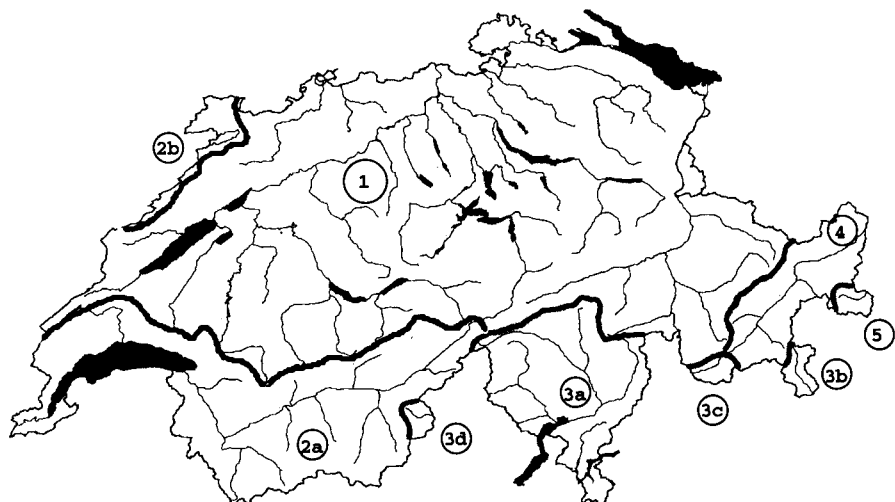


Fig. 1. The five catchment areas of Switzerland. 1 Rhine; 2 Rhone (2a) and Doubs (2b); 3 Tichino (3a), Posciavino (3b) and Mera (3c); 4 Inn and 5 Rombach.

Switzerland is traditionally divided into four major geographical regions: the Jura (a low limestone mountain range up to 1500 m a.s.l.), the Swiss Plateau (from Tertiary and Quaternary deposits), the Pre-alps (formed by the folding of secondary sedimentary rocks) and the Central Alps (from crystalline rocks reaching over 4000 m a.s.l.) and the Southern Alps (with crystalline rocks forming the foothills of the great Italian plains). The lowest point in Switzerland lies on the shores of Lake Maggiore (190 m a.s.l.), the highest is the Dufour peak (Monte Rosa Massive) at 4634 m a.s.l..

2. Hydrology

Switzerland is often described as the water tower of Europe, for the great rivers, Rhine and Rhone, have their sources there. Glaciers cover 4 % of the country and there are 2000 lakes and approx. 50,000 km of running waters (Anonymus, 1992).

The waters are divided into five catchment areas of varied size and importance (Fig. 1). The Rhine catchment (1) covers more than 50% of the total area of Switzerland; the Rhone (with the Doubs) about 20% (2); the Po (Ticino, Posciavino, Mera, Diviera) about 5% (3); the Danube (Inn) approx. 3.5% (4); and the Etsch (Rombach) less than 1% (5). Table 1 presents the ten longest Swiss rivers with their annual mean water discharge.

3. Database

The distribution atlas for the 85 species, currently or formerly found in Switzerland is based on 1814 investigated locations, 10,610 data sets and 87,020 identified individuals (13,175 imagos or subimagos and 73,845 larvae). In general, the area was well covered, although with a few exceptions such as the Upper Rhine, the Aargauer Mittelland and some valleys in Upper Wallis. Figure 2 illustrates the distribution of *Baetis rhodani* and Figure 3 that of *Ecdyonurus helveticus*.

The species analysis in Sartori and Landolt (1999) describes seven themes for every species:

Table 1. The ten longest Swiss rivers, their catchment area and annual mean water discharge measured at the confluence with other rivers or at the Swiss border, respectively

River	Length (km)	Catchment area (km ²)	Water discharge (m ³ /sec)
Rhine	375	35925	1040
Aare	295	11750	306
Rhone	264	10299	338
Reuss	158	3382	141
Limmat	140	2176	99
Sarine	128	1269	42
Thur	125	1696	45
Inn	104	1945	59
Ticino	91	1515	71
Broye	86	392	8

altitudinal distribution (steps of 200 m which we considered sufficiently precise), flight periods (in months), typology (stream order, see Table 2), life cycle (according to Clifford, 1982), ecology, distribution (including details about presence in other European countries, Table 3) and rarity status.

We determined stream order, using the maps with the scale of 1: 200,000 in the Swiss Hydrological Atlas. We assumed that the smallest watercourses automatically belonged to class 1 or 2. Consequently any eventual codification errors are the same for all locations. Only those locations with larvae were considered. Table 2 sums up the six selected typology classes.

This zonation seems to correspond well to the circumstances in Switzerland. No separate category was created for source zones (crenal). The Ephemeroptera colonising the springs as well as their outflows do not differ from those situated downstream (epirhithral), although this is not the case for other aquatic insects (Zollhöfer, 1997).

The "ecology" section has a number of details on each species observed; in particular phenology, altitudinal limits, preferred habitat, and, if known, any special ecological requirements.

The "distribution" section gives information on the known distribution of each species in Switzerland, and in a few cases elsewhere. Table 3 gives bibliographic references consulted to establish the presence or absence of a species in other European countries. A map of all sites of capture completes the details about the Swiss distribution.

With regards to status, the following classification was used:

if a species is present in less than 10 localities it is considered as "very rare", between 11 and 25 as "rare", between 26 and 50 as "uncommon", between 51 and 100 as "common" and beyond 100 as "widespread" (Table 4). It should be noted that these categories do not necessarily relate to the dangers threatening the species (Sartori et al., 1994). A species regarded as "uncommon" may be in greater danger of extinction than one regarded as "rare" (see also Discussion).

RESULTS AND DISCUSSION

1. Catchment Area

Table 5 illustrates the special status of the Rhine within Switzerland. All Swiss species of mayfly are found in its catchment area. This species diversity is not surprising as the Rhine is the largest catchment area in Switzerland and all hydrological, geomorphological and altitudinal units are covered.

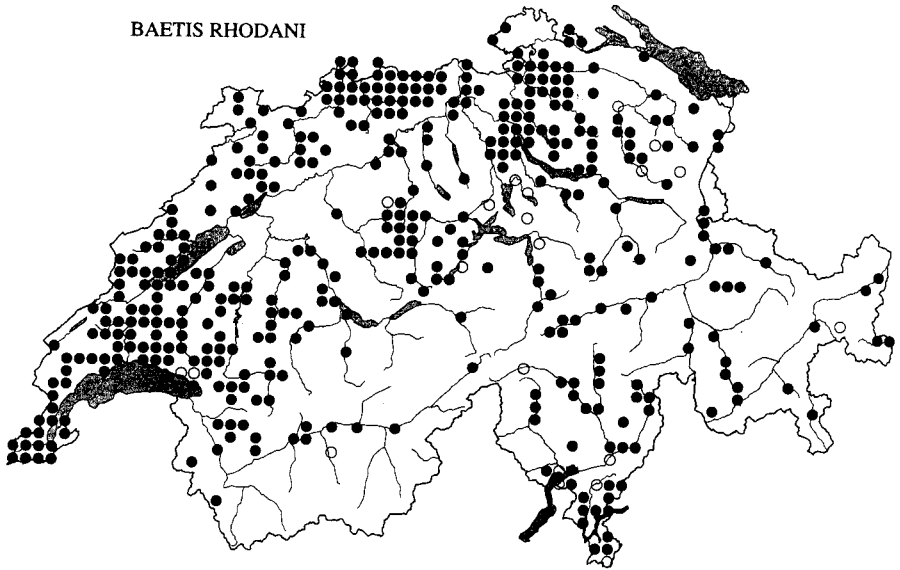


Fig. 2. Geographical distribution of *Baetis rhodani*. Territory covered for the atlas based on a grid of 5x5 km. O - stations with no data after 1970; ● - stations with data before and after 1970.

A second characteristic is that the smaller the catchment area, the fewer the number of species. There is a logarithmic relationship between the size of the catchment area (x) and the number of mayfly species (y): $y = 17.6 \ln x - 98.3$; $r^2 = 0.94$; $p < 0.001$).

Ten species, typical of higher regions, are found in all catchment areas. This is not surprising as all the river systems have an alpine origin. The matrix of similarity of the different regions, calculated according to Jaccard's index by dividing the number of species common and exclusive to each by the number of the species common to two regions shows that the greatest affinity exists between the Rhone and the Rhine (0.71), the Inn and the Etsch (0.68), and the Rhone and the Ticino (0.50).

2. Altitudinal Distribution

Species diversity in Switzerland is inversely proportional to the altitude i.e. with increasing altitude the number of species decreases (Fig. 4). Reasons for this are to be found in the brevity of the ice free period, the limited food supply and the extreme physiographical conditions at higher altitudes. The hill region (200-800 m) is the richest with an average of 61 species, then the mountain region (800-1400 m) with 44, the subalpine (1400-2000 m) with 19, and finally the alpine region with only 6. These numbers do not take into consideration any human influence and confirm what is often found in European specialist literature that the mayfly is greatest at lower and middle altitudes. This characteristic is diametrically opposed to that of the Plecoptera which prefer much higher situations (Brittain, 1983).

The altitudinal range of the individual species is interesting. Twenty-eight species are only found within the hill region, two species only in the mountain region and none are restricted solely to the sub-alpine or alpine regions.

A single species (*Baetis alpinus*) inhabits all altitudes. This pioneer species is adapted to a wide range of environmental conditions and, quickly becomes dominant when there is little competition.

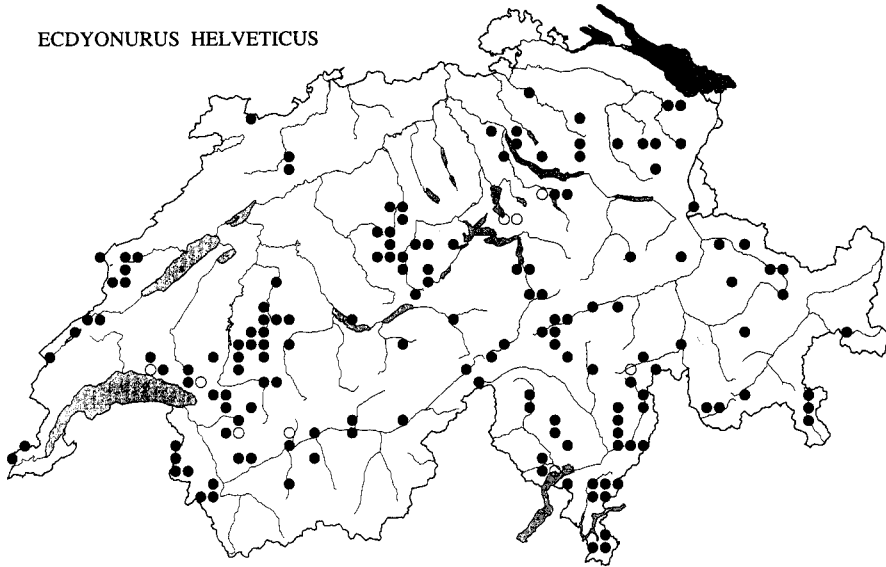


Fig. 3. Geographical distribution of *Ecdyonurus helveticus*. The same specifications as in Fig. 2.

3. Phenology

The flight periods of adults in Switzerland are mainly during spring or summer (Fig. 5). A single species (*Baetis rhodani*) has been observed throughout the whole year. Two other species limit their flight phase mostly to the end of the winter and the beginning of spring: *Rhithrogena germanica* and *Rh. gratianopolitana*. These two species can emerge already in February. The former is not found after April, whereas the latter may still be flying at the beginning of May depending on the altitude. At least a dozen species are found mostly in summer and autumn. This group includes as well as lowland species like *Caenis pusilla*, *Ecdyonurus insignis*, *Baetis liebenauae*, species from higher situations such as *Rhithrogena loyolaea*, *Rh. nivata* and *Ecdyonurus parahelveticus*.

The flight times of mayflies also differ clearly from those of stoneflies which have their greatest emergence activity in early spring or autumn. The considerable duration of the flight period of some species has two main reasons. One is the presence of several generations in a year (polyvoltinism), a second is the time-lag because of the altitude. Figure 6 illustrates this with the example of *Baetis alpinus*. Development in lower regions shows two emergence peaks, one in spring, the other in autumn, typical for a bivoltine species. The higher the altitude, the later the peaks appear in the year. At about 1400 m development is reduced to a single emergence period in summer that takes place later at higher altitudes; over 2000 m (September/October).

4. Development Cycles

a) **Voltinism.** The species found in Switzerland are mainly univoltine. *Ephemera* species are all partivoltine, probably semivoltine with a generation every two years. High altitude populations of the Heptageniidae (e.g. *Rhithrogena loyolaea*, *Rh. nivata*, *Ecdyonurus alpinus*) may also belong to this group, exact autoecological data on the species in extreme habitats is lacking.

Table 2. Typology of rare Swiss mayfly species

Category	Stream order	Description	Number of stations	% of stations	Zonation
A	1-2	chiefly large and small streams	688	43%	epirhithral
B	3-4	small and medium rivers	545	34%	metarhithral
C	5-6	large rivers at foothills	175	11%	hyporhithral
D	7-8	large rivers in lowlands	63	4%	epipotamal
E		canals, drainage channels	19	1%	
F		lakes, ponds	116	7%	

The majority of the Baetidae and Caenidae are bivoltine (two generations a year), but for the Baetidae at least, this is not valid at higher altitudes where they are univoltine (e.g. *Baetis alpinus*, Fig. 6).

b) Embryonic development. One can separate the Swiss species into two large groups; one that presents a continuous embryonic development and one with an obligatory embryonic diapause. This interruption in the development very often allows the species to survive in unfavourable conditions (too high or too low temperatures). The conditions needed to restart the development are complex (see Ruffieux, 1997 for a view).

In contrast to voltinism there is no strategy common to one genus or family, as both types of development are found within the same genus (e.g. *Baetis*, *Rhithrogena*, *Ecdyonurus*).

5. Typology

Mayfly distribution in various habitats has been analysed. It is striking that most of the species are present in the three subunits of the rhithral: 63 in the epirhithral, 67 in the metarhithral, and 57 in the hyporhithral. The other three habitats are clearly poorer in species: 38 in the epipotamal, 30 in stagnant waters and 27 in canals. The drop in the diversity is caused by the loss of suitable habitats.

The majority of species have more or less clear habitat affinities. The following 13 species were found in all the habitats, were widespread in Switzerland and had a broad ecological valency: *Baetis alpinus*, *B. lutheri*, *B. rhodani*, *B. vernus*, *Cloeon dipterum*, *Centroptilum luteolum*, *Ecdyonurus venosus*, *Heptagenia sulphurea*, *Serratella ignita*, *Caenis luctuosa*, *C. macrura*, *Paraleptophlebia submarginata* and *Ephemera danica*.

Few species colonised only one type of habitat and also no species limited their presence to the hyporhithral or the artificial waterways. The following list indicates the species exclusive to the different habitats.

In the epirhithral *Ecdyonurus parahelvicus*, *E. zelleri* and *Rhithrogena colmarsensis* were present; in the epipotamal *Heptagenia coeruleans*, *H. longicauda* and *Ephoron virgo*; in lentic waters *Caenis lactea*, *Leptophlebia marginata*, *L. vespertina*, *Choroterpes picteti* and *Ephemera glaucops*.

Table 3. References consulted for the faunal analyses of European mayfly species

Austria	Bauernfeind, 1990 a, b, c; Moog, 1995; Weichselbaumer, 1997
Belgium	Müller-Liebenau, 1980; Mol, 1987
Bulgarien	Russev, 1993
Czech Republic	Landa and Soldán, 1985
Denmark	Jensen, 1974; Engblom, 1996
Finland	Saaristo and Savolainen, 1980; Engblom, 1996
France	Jacquemin and Coppa, 1996; Thomas and Masselot, 1996
Germany	Schönemund, 1930; Zimmermann, 1986
Great Britain	Elliot <i>et al.</i> , 1988
Greece	Puthz, 1978
Hungary	Ujhelyi, 1966
Ireland	Puthz, 1978
Italy	Gaino <i>et al.</i> , 1982; Belfiore, 1983 a, b, 1994; Belfiore and D'Antonio, 1991; Buffagni, 1992
Netherland	Mol, 1983, 1985 a, b, c
North Africa	Kraïem, 1986; Boumaiza and Thomas, 1986, 1995; Gagneur and Thomas, 1988
Norway	Engblom, 1996
Poland	Sowa, 1962, 1975 a, b, 1992
Portugal	Alba-Tercedor, 1981
Roumania	Bogoescu, 1958
Slovakia	Landa and Soldán, 1985
Slovenia	Zabric and Sartori, 1997
Spain	Alba-Tercedor, 1981
Sweden	Engblom, 1996
ex-Yugoslavia	Ikonomov, 1960

If species restricted to one type of habitat (Fig. 7) the number of occasional and accidental species is always greater. Habitats with the most restricted fauna are the epi- and metarhithral as well as lentic habitats (in $\geq 40\%$ of the sites in a habitat). The hyporhithral (80%) and the epipotamal (85%) have many occasional and accidental species. This can be explained by the downstream position of the habitats, thus receiving an important part of the fauna established upstream that drifts down. Artificial waterways appear of little interest to mayflies. A single species (*Caenis robusta*) is occasionally found in this type of habitat; any others are there by accident.

This spread is a compromise determined by factors such as altitude, temperature, food supply and substrate.

6. Status of the Species

The status of the Swiss mayflies is shown in Table 4. About 40% (common and widespread) of the species are well represented in Switzerland. A further third (rare and uncommon) consists of species that are found at only a few sites and the remaining third of very rare species.

In his work on the concept of the rarity of living organisms Gaston (1994) suggests a simple definition for rarity "... I suggest that a useful cut-off point is the first quadrile of the frequency distribution of species abundances or range sizes (i.e. a cut-off of 25%)". If this rule is applied to Swiss mayflies and is used as a measure of frequency for the number of sites colonised by a species, then the pattern in Figure 8 is obtained. According to Gaston (1994) those species to the right of the quadrile should be considered as rare. The species considered by Gaston as rare correspond well to those estimated by us as very rare (25% to 28%), validating our category. Based on current knowledge, classification in the category of very rare species in Switzerland is presence in less than ten locations.

Table 4. Status of the species according to their present occurrence

Number of localities	Status	Number of species	Percentage
< 10	very rare	24	28%
11-25	rare	15	18%
26-50	uncommon	13	15%
51-100	common	14	16%
> 100	widespread	19	23%

7. The Future of Swiss Mayfly Fauna

The mayflies in Switzerland are relatively well known and are represented today by 85 species. A comparison of the diversity with that of other central and southern European countries shows that the size of the territory and the number of species corresponds well (see Sartori, this volume, p. 47). The rise in the number of species shows a positive correlation with the increase in the number of habitats. For the Nordic countries the relationship is clearly different (Engblom, 1996). Their northern latitude and the effects of the last glaciations are the main reason for this difference. In the case of the British Isles their insular nature has limited the number of species.

Certain species have been described for the first time from populations in Switzerland. These are *Baetis nubecularis* Eaton, 1898, *Habroleptoides auberti* (Biancheri, 1954), *Habroleptoides confusa* Sartori and Jacob, 1986, *Rhithrogena enedenensis* Metzler, Tomka and Zurwerra, 1985, *Rhithrogena germanica* Eaton, 1885, *Rhithrogena grischuna* Sartori and Oswald, 1988, *Rhithrogena nivata* (Eaton, 1871), *Ecdyonurus alpinus* Hefti, Tomka and Zurwerra, 1987, *Ecdyonurus helveticus* Eaton, 1883 and *Ecdyonurus parahelveticus* Hefti, Tomka and Zurwerra, 1986.

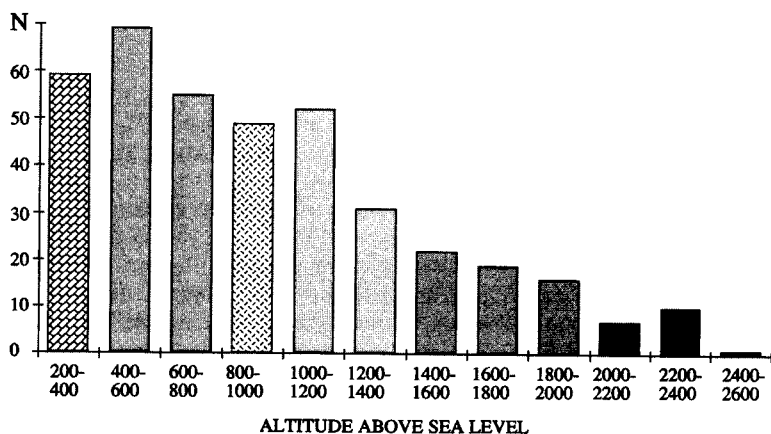


Fig. 4. Distribution of the species according to altitude. The categories correspond to the different altitudinal zones given in the text. N = number of species.

a) Physical changes threatening the mayfly fauna. The increase in erosion in the alpine region because of, among other things, changes in the precipitation (rain instead of snow) increases sediment loads. This change light conditions, hinder the respiration of macroinvertebrates, reduce substrate interstitial spaces and hampers embryonic and larval development of aquatic organisms, including mayflies. Moreover, organic pollution increases the danger of eutrophication of surface waters.

Human activities cause physical changes at various levels. In the mountainous regions the increase in hydroelectric power development is noticed, even when legal minimal flows are respected. The regulation of the flow produces a dramatic change in the natural composition of the fauna and flora.

Table 5. Distribution of species in the five Swiss catchment areas. Grey: species exclusive to Rhine; black: species found in all catchment areas.

Catchment area	Rhine	Rhone	Ticino	Inn	Adige	Catchment area	Rhine	Rhone	Ticino	Inn	Adige
Siphonuridae						<i>Ecdyonurus alpinus</i>	+	+	+	+	+
<i>Siphonurus aestivalis</i>	+	+	-	-	-	<i>E. dispar</i>	+	+	-	-	-
<i>S. lacustris</i>	+	-	-	+	+	<i>E. helveticus</i>	+	+	+	+	+
Ameletidae						<i>E. insignis</i>	+	+	-	-	-
<i>Ameletus inopinatus</i>	+	-	-	-	-	<i>E. parahelveticus</i>	+	+	-	-	-
Baetidae						<i>E. picteti</i>	+	+	+	+	+
<i>Baetis alpinus</i>	+	+	+	+	+	<i>E. torrentis</i>	+	+	-	-	-
<i>B. buceratus</i>	+	-	+	-	-	<i>E. venosus</i>			+	+	-
<i>B. fuscatus</i>	+	+	-	-	-	<i>E. zelleri</i>	+	+	-	-	-
<i>B. liebenauae</i>	+	-	+	-	-	<i>Electrogena lateralis</i>	+	+	+	-	-
<i>B. lutheri</i>	+	+	-	-	-	<i>E. ujhelyii</i>	+	+	-	-	-
<i>B. melanonyx</i>	+	+	+	-	+	<i>Heptagenia coerulans</i>	+	-	-	-	-
<i>B. nubecularis</i>	+	-	-	-	-	<i>H. longicauda</i>	+	+	-	-	-
<i>B. rhodani</i>	+	+	+	+	+	<i>H. sulphurea</i>	+	+	-	-	-
<i>B. scambus</i>	+	+	-	-	-	Ephemerellidae					
<i>B. vardarensis</i>	+	-	-	-	-	<i>Serratella ignita</i>	+	+	+	-	-
<i>B. vernus</i>	+	+	+	+	-	<i>Ephemerella mucronata</i>	+	+	-	-	-
<i>Alainites muticus</i>	+	+	+	-	+	<i>E. notata</i>	+	-	-	-	-
<i>Nigrobaetis niger</i>	+	+	-	-	-	<i>Torleya major</i>	+	+	-	-	-
<i>Acentrella sinaica</i>	+	-	-	-	-	Caenidae					
<i>Centroptilum luteolum</i>	+	+	+	-	-	<i>Caenis beskidensis</i>	+	+	+	-	-
<i>Proclleon bifidum</i>	+	-	-	-	-	<i>C. horaria</i>	+	+	+	-	-
<i>P. pennulatum</i>	+	+	-	-	-	<i>C. lactea</i>	+	+	-	-	-
<i>Cloeon dipterum</i>	+	+	+	+	-	<i>C. luctuosa</i>	+	+	-	-	-
<i>C. simile</i>	+	+	-	-	-	<i>C. macrura</i>	+	+	-	-	-
Oligoneuriidae						<i>C. pusilla</i>	+	-	-	-	-
<i>Oligoneuriella rhenana</i>	+	-	-	-	-	<i>C. rivulorum</i>	+	+	-	-	-
Heptageniidae						<i>C. robusta</i>	+	+	-	-	-
<i>Epeorus alpicola</i>	+	+	+	+	+	Leptophlebiidae					
<i>E. sylvicola</i>	+	+	+	-	-	<i>Leptophlebia marginata</i>	+	-	-	-	-
<i>Rhithrogena allobrogica</i>	+	-	-	+	-	<i>L. vespertina</i>	+	-	-	-	-
<i>Rh. alpestris</i>	+	+	+	+	+	<i>Habroleptoides auberti</i>	+	+	-	-	-
<i>Rh. beskidensis</i>	+	+	-	-	-	<i>H. confusa</i>	+	+	+	-	-
<i>Rh. carpatoalpina</i>	+	+	+	-	-	<i>Habrophlebia lauta</i>	+	+	+	-	-
<i>Rh. colmarsensis</i>	+	-	-	-	-	<i>Paraleptophlebia cincta</i>	+	-	-	-	-
<i>Rh. degrangei</i>	+	+	+	+	+	<i>P. submarginata</i>	+	+	-	-	-
<i>Rh. dorierti</i>	+	-	-	-	-	<i>Choroterpes picteti</i>	+	+	+	-	-
<i>Rh. endenensis</i>	+	-	+	+	+	Ephemeridae					
<i>Rh. germanica</i>	+	-	-	-	-	<i>Ephemerella danica</i>	+	+	+	-	-
<i>Rh. gratianopolitana</i>	+	+	+	+	-	<i>E. glaucops</i>	+	+	-	-	-
<i>Rh. grischuna</i>	+	-	+	+	+	<i>E. lineata</i>	+	+	+	-	-
<i>Rh. hybrida</i>	+	+	+	-	-	<i>E. vulgata</i>	+	+	-	-	-
<i>Rh. iridina</i>	+	+	+	-	-	Potamanthidae					
<i>Rh. landai</i>	+	-	-	-	-	<i>Potamanthus luteus</i>	+	-	-	-	-
<i>Rh. loyolaea</i>	+	+	+	+	+	Polymitarcyidae					
<i>Rh. nivata</i>	+	+	+	+	+	<i>Ephoron virgo</i>	+	-	-	-	-
<i>Rh. pathzi</i>	+	-	-	-	-						
<i>Rh. puytoraci</i>	+	+	+	-	-						
<i>Rh. savoiensis</i>	+	+	-	-	-						
<i>Rh. semicolorata</i>	+	+	+	-	-						
						TOTAL	85	60	36	18	15

In the lowlands the water extraction (e.g. for irrigation) diminishes the volume of water and in summer leads to higher water temperatures that accelerate the growth of the population and may lead to the emergence of smaller individuals with reduced fertility, in some cases causing the disappearance of the population (Sweeney and Vannote, 1978). The damming of rivers, the reinforcement of the banks and the straightening of the rivers standardise the drainage and the sediment composition and leads, therefore, to a uniformity of habitat. Especially in the Swiss Plateau this has resulted in the disappearance of certain mayfly species.

The restoration of certain reaches is often the most promising method of creating new habitats. These "islands" encourage re-colonisation of other sectors.

b) Chemical changes threatening the mayfly fauna. Chemical changes can have important consequences for aquatic organisms. Even in low concentrations the combined effect of certain substances can insidiously cause sub-lethal effects, such as impaired respiration or a decrease in fertility. Increased concentration of nitrogen and phosphorus derivatives, mainly from farming, pesticides and heavy metals may endanger mayfly populations.

Pollution may be of short duration and damages only the individuals exposed. However, if the harmful substances are bound to the substratum they can remain there for a long time and endanger the organisms developing there. Floods can liberate these substances and their toxicity can endanger populations elsewhere. These dangers can appear in all habitats, although the greatest danger potential lies in the lower reaches of running waters and in lakes. An example is the eutrophication of the Lake of Geneva at the end of the 1950s. In this period *Choroterpes picteti*, *Ephemera glaucops* and *E. lineata* became extinct. In the last fifty years the lower reaches of the Rhine have shown an decrease in diversity with the disappearance of, among others, *Oligoneuriella rhenana*, *Heptagenia coeruleans*, *H. longicauda* and *Ephoron virgo*.

Most chemical changes, are however reversible. The macroinvertebrates and especially the mayflies show a remarkable capacity to re-colonise. A good example is the current situation of *Rhythrogena germanica*. In the 1970s it was thought to be extinct, but today as a result of a clear improvement in its original habitats, it is present in several locations.

The re-establishment of a varied fauna in the Rhine after the Schweizerhalle (Sandoz) accident, near Basel, demonstrates how important affluents are as reservoirs for the re-colonisation of the original habitats (Schröder and Rey, 1991). In lakes recovery is much more difficult and is linked to the presence of nearby faunal reservoirs which often do not exist.

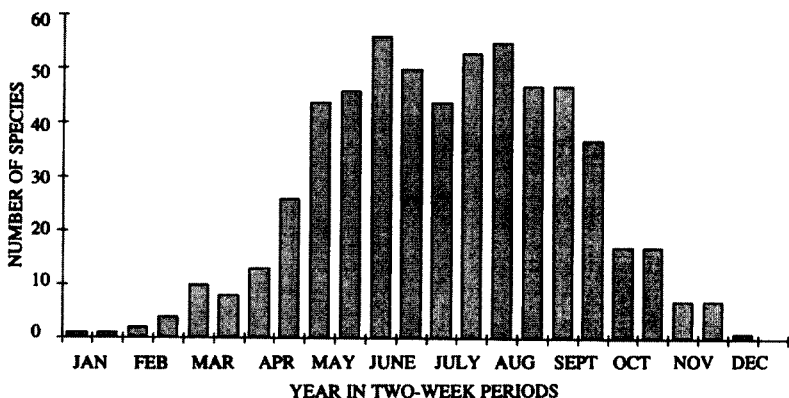


Fig. 5. Flight periods of mayfly species in Switzerland at all altitudes.

c) **Typology of Rare Species.** The rarity of a species is not only linked to its status in Switzerland, certain other factors must be taken into consideration. The whole distributional area plays a role; it can be vast and cover the greater part of Europe, or be small and limited to a certain region. The habitat requirements can be narrow or broad. Finally the size of the population in the benthic community can be dominant or rare (Rabinowitz, 1981). If one uses this classification system (Table 6), all species fit into one of eight categories. It is interesting that of the 24 species regarded as rare in Switzerland, the majority (75%) occur over a wide distributional area. These species are found in most regions of Europe. One would have expected first to find endemic and alpine species. According to the definition of Gaston (1994), the majority of alpine species do not comply with the criteria necessary to be regarded as rare. The majority of the above species with a wide distributional area inhabit either still waters or the epipotamal. Our conclusions concerning rare Swiss Ephemeroptera may also be valid for other countries. It is therefore desirable that comparable data on a European level be made available.

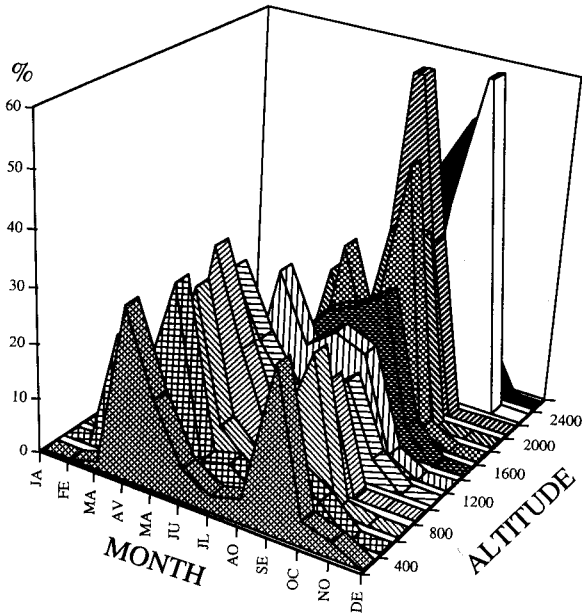


Fig. 6. Emergence of *Baetis alpinus* throughout a year, in relation to altitude. The scale used is the percentage of the numbers of specimens caught per 200 m section.

CONCLUSION

The present state of Ephemeroptera populations in Switzerland is still far from optimal. However, the current change of attitude towards our waters encourages hope for the future. The regeneration of several waterways, above all in German Switzerland, and the use of new technologies in water management point to a change of mentality and an increased sensitivity to the problems linked to the preservation of habitats. The greater the variety that a river offers within its course, the richer the flora and fauna.

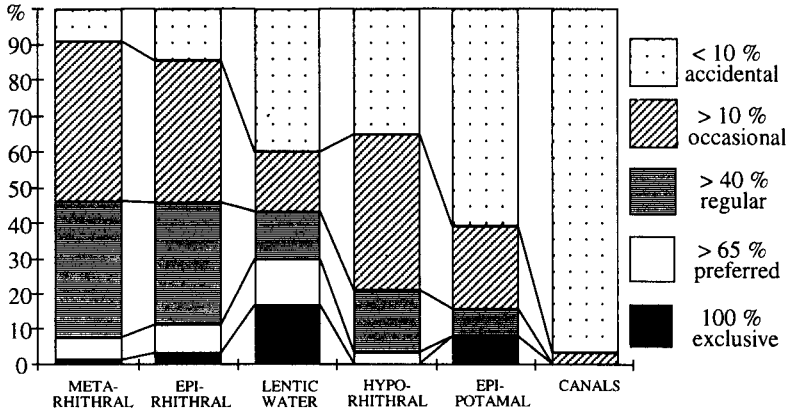


Fig. 7. Distribution by habitat of species (% of the species in the habitats).

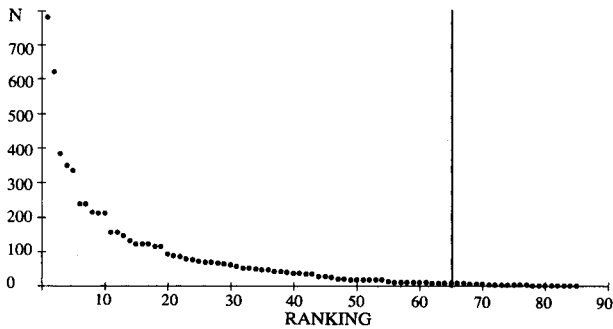


Fig. 8. Occurrence of the species according to the number of sites where they were found. The vertical line marks the limit of the 25% quadrile which delimits those species classified as rare.

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Table 6. Attempt at a typology of mayfly species in Switzerland with respect to rarity, modified according to Rabinowitz (1981).

Distribution	Habitat specificity	Size and dominance of population	Examples
wide	wide	large, often dominant	<i>common species</i>
wide	wide	small, seldom dominant	<i>Ephemera vulgata</i> <i>Ecdyonurus insignis</i>
wide	narrow	large, often dominant	<i>Siphonurus aestivalis</i> <i>Ephemera glaucops</i> <i>Ephemera lineata</i> <i>Leptophlebia marginata</i> <i>Choroterpes picteti</i> <i>Ephoron virgo</i>
wide	narrow	small, seldom dominant	<i>Ameletus inopinatus</i> <i>Nigrobaetis niger</i> <i>Acentrella sinaica</i> <i>Procoleon bifidum</i> <i>Baetis vardarensis</i> <i>Heptagenia longicauda</i> <i>Heptagenia coeruleans</i> <i>Leptophlebia vespertina</i> <i>Paraletophlebia cincta</i>
restricted	wide	large, often dominant	<i>Baetis libenauae</i>
restricted	wide	small, seldom dominant	<i>Rhithrogena puthzi</i>
restricted	narrow	large, often dominant	<i>Baetis nubecularis</i>
restricted	narrow	small, seldom dominant	<i>Rhithrogena allobroatica</i> <i>Rhithrogena colmarsensis</i> <i>Rhithrogena landai</i> <i>Ecdyonurus zelleri</i>

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REFERENCES

- Alba-Tercedor, J. 1981. Recopilacion de citas de efemerópteros en la Peninsula iberica e islas Baleares. Trab. Monogr. Dep. Zool. Univ. Granada (N.S.) 4 (2): 41-81.
- Anonymus, 1992. Atlas Hydrologique de la Suisse. Service hydrologique et geologique national, Berne.

- Bauernfeind, E. 1990a. Der derzeitige Stand der Eintagsfliegen-Faunistik in Österreich (Insecta, Ephemeroptera). Verh. Zool.-Bot. Ges. Österreich 127: 61-82.
- Bauernfeind, E. 1990b. Einige für Österreich neue oder wenig bekannte Eintagsfliegen (Insecta, Ephemeroptera). Linzer Biol. Beitr. 22: 341-347.
- Bauernfeind, E. 1990c. Eintagsfliegen. Nachweise aus Oberösterreich (Insecta, Ephemeroptera), die Sammlung Adlmannseder am O.Ö. Landesmuseum Linz. Linzer Biol. Beitr. 22: 349-356.
- Belfiore, C. 1983a. Efemeroterri. Guide per il ricinascimento delle specie animale delle acque interne italiane. AQ/1/2011-113.
- Belfiore, C. 1983b. Note su alcune specie del genere *Habroleptoides* Schönemund, con segnalazione per l'Italia di *H. auberti* Biancheri, 1954. Boll. Soc. ent. ital. 115(1-3): 5-6.
- Belfiore, C. 1994. Gli Efemeroterri dell'Appennino marchigiano (Insecta, Ephemeroptera). Biogeographica 17:173-181 (1993).
- Belfiore, C. and D'Antonio C. 1991. Faunistic, taxonomic and biogeographical studies of Ephemeroptera from Southern Italy. In: Alba-Tercedor, J. and Sanchez-Ortega, A. (Eds). Overview and strategies in Ephemeroptera and Plecoptera. Sandhill Crane, Gainsville: 253-262.
- Bogoescu, C. 1958. Ephemeroptera. Fauna Rep. Pop. Rom. VII (3):1-187.
- Bouzaïma, M. and A. G. B. Thomas. 1986. Répartition et ecologie des Ephemeropteres en Tunisie:lère partie (Insecta,Ephemeroptera). Arch. Inst. Pasteur Tunis 63 (4): 567-600.
- Bouzaïma, M. and A. G. B. Thomas. 1995. Distribution and ecological limits of Baetidae vs the other mayfly families in Tunisia: a first evaluation (Insecta, Ephemeroptera). Bull. Soc. Hist. Nat.Toulouse 131: 27-33.
- Brittain, J. E. 1983. The influence of temperature on nymphal growth rates in mountain stoneflies (Plecoptera). Ecology 64: 440-446.
- Buffagni, A. 1992. *Baetis liebenauae* Keffermüller, 1974 (Ephemeroptera, Baetidae) in Pianura Padana. Boll. Mus. reg. Sci. nat.Torino 10: 333-340.
- Clifford, H. C. 1982. Life cycle of mayflies, with special reference to voltinism. Quest. Ent. 18 (1-4): 15-90.
- Elliott, J. M., U. H. Humpesch and T. T. Macan. 1988. Larvae of the British Ephemeroptera: a key with ecological notes. Sci. Publs Freshw. Biol. Assoc. 49: 1-145.
- Engblom, E. 1996. Ephemeroptera, Mayflies. In: Nilsson, A. (ed.). Aquatic Insects of North Europe - A taxonomic handbook. Apollo Books, Stenstrup: 13-53.
- Gagneur, J. and A. G. B. Thomas. 1988. Contribution à la connaissance des Ephéméroptères d'Algérie. I. Répartition et écologie (lère partie) (Insecta, Ephemeroptera). Bull. Soc. Hist. Nat.Toulouse 124: 213-223.
- Gaino, E., C. Belfiore and S. Spano. 1982. Gli Efemeroterri delle Alpi Liguri. Lav. Soc. ital. Biogeogr. 9: 1-19.
- Gaston, K. J. 1994. Rarity. Population and community biology series 13. Chapman and Hall, London: 1-205.
- Ikonomov, P. 1960. Die Verbreitung der Ephemeroptera in Macedonien. Acta Mus. Mac. Sc. Nat. Skopje 7: 59-74.
- Jacquemin, G. and G. Coppa. 1996. Inventaire des Ephémères de Lorraine et de Champagne-Ardenne (N-E France): premiers résultats (Ephemeroptera). Mitt. schweiz. ent. Ges. 69: 141-155.
- Jensen, C. F. 1974. Dagsländor (Ephemeroptera) i Kältsjökkrädet. Norrb. Natur smäsk 1.
- Kraïem, M. 1986. Contribution a l'étude hydrobiologique de trois cours d'eau du nordouest de la Tunisie. Bull. mens. Soc. Lin. Lyon 55 (3): 96-104.
- Landa, V. and Soldan, T. 1985. Distributional patterns, chronology and origin of the czechoslovak fauna of mayflies (Ephemeroptera). Acta ent. bohemoslov. 82 (4): 241-268.
- Mol, A. W. M. 1983. *Caenis lactea* (Burm.) in the Netherlands. Ent. Bericht. (Deel) 43: 119-123.
- Mol, A. W. M. 1985a. Een overzicht van de Nederlandse haften (Ephemeroptera). 1. Siphonuridae, Baetidae en Heptageniidae. Ent. Ber. 45: 105-111.
- Mol, A. W. M. 1985b. Een overzicht van de Nederlandse haften (Ephemeroptera). 2. Overige families. Ent. Ber. 45: 128-135.
- Mol, A. W. M. 1985c. Enkele interessante en nieuwe Nederlandse haften (Insecta: Ephemeroptera) uit de province Limburg. Natuurhist. Maandblad 74: 5-8.
- Mol, A. W. M. 1987. *Caenis beskidensis* Sowa new to Belgium, with remarks on the Ephemeroptera of the river Meuse. Ent. Ber. (Amst.) 47 (4): 60-64.
- Moog, O. (ed.). 1995. Fauna Aquatica Austriaca. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Wien.
- Müller-Liebenau, I. 1980. Die Arten der Gattung *Baetis* Leach der belgischen Fauna aus der Sammlung im Museum des Institut royal des Sciences Naturelles de Belgique in Brüssel. Bull. Inst. r Sci. nat. Belg. 52 (3): 1-31.
- Puthz, V., 1978. Ephemeroptera in: J. Illies Ed. Limnofauna Europaea. G. Fischer Verlag, Stuttgart: 256-263.

- Rabinowitz, D. 1981. Seven forms of rarity. pp. 205-217. In: H. Synge (ed.). The biological aspects of plant conservation. Wiley and Sons, New York.
- Ruffieux, L. 1997. Réserves énergétiques et stratégies de reproduction chez les Ephéméroptères (Insecta, Ephemeroptera). PhD Thesis, Université de Lausanne: 1-168.
- Russev, P. 1993. Review of literature and established mayfly species (Ephemeroptera) from Bulgaria. *Lauterbornia* 14: 71-77.
- Saaristo, M. I. and E. Savolainen. 1980. The Finnish mayflies. *Notul. ent.* 60: 181-186.
- Sartori, M. and P. Landolt. 1999. Atlas de distribution des éphémères de Suisse (Insecta, Ephemeroptera). Centre Suisse de cartographie de la faune et Société entomologique suisse, Neuchâtel (eds.). *Fauna Helvetica* 2: 1-212.
- Sartori, M., P. Landolt and A. Zurwerra, A. 1994. Liste rouge des éphémères de Suisse (Ephemeroptera). In: Duelli, P. (Ed.). Liste rouge des espèces animales menacées de Suisse. Office fédéral de l'environnement, des forêts et du paysage: 72-74.
- Schönemund, E. 1930. Eintagsfliegen oder Ephemeroptera. *Dahl's Tierwelt Deutschlands* 19: 1-103.
- Schröder, P. and P. Rey. 1991. Fliessgewässernetz Rhein und Einzugsgebiet. IFAH-Scientific Publications, Konstanz: 1-303.
- Sowa, R. 1962. Material for the study of Ephemeroptera and Plecoptera in Poland. *Acta Hydrobiol.* 4: 205-224.
- Sowa, R. 1975a. Ecology and biogeography of mayflies of running waters in the Polish part of the Carpathians. 1: Distribution and quantitative analysis. *Acta Hydrobiol.* 17 (3): 223-297.
- Sowa, R. 1975b. Ecology and biogeography of mayflies of running waters in the Polish part of the Carpathians. 2: Life cycles. *Acta Hydrobiol.* 17 (4): 319-353.
- Sowa, R. 1992. Ephemeroptera. In: Glowacinski, Z. (Ed.), Red list of threatened animals in Poland, Polish Academy of Sciences, Krakow: 97-101
- Studemann, D., P. Landolt, M. Sartori, D. Hefti and I. Tomka. 1992. Ephemeroptera. *Insecta Helvetica, Fauna* 9: 1-174.
- Sweeney, B. W. and R. L. Vannote. 1978. Variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. *Science* 200: 444-446.
- Thomas, A. and G. Masselot. 1996. Les Ephémères de la France: inventaire des espèces signalées et des espèces potentielles (Ephemeroptera). *Bull. Soc. ent. France* 101: 467-488.
- Ujhelyi, S. 1966. The mayflies of Hungary, with the description of a new species, *Baetis pentaplebedes* sp. n. (Ephemeroptera). *Acta Zool. Acad. Sc. Hung.* 12: 203-210.
- Weichselbaumer, P. 1997. Die Eintagsfliegen Nordtirols (Insecta: Ephemeroptera). *Ber. Nat.-Med. Ver. Innsbruck* 84: 321-341.
- Zabric, D. and M. Sartori. 1997. First contribution to the mayfly fauna from Slovenia (Ephemeroptera). In: P. Landolt and M. Sartori (eds). Ephemeroptera and Plecoptera: Biology-Ecology-Systematics. MTL, Fribourg: 147-151.
- Zimmermann, W. 1986. Neue Funde bemerkenswerter Eintagsfliegen (Ephemeroptera) aus Thüringen. *Ent. Nachr.* 30 (2): 69-71.
- Zollhöfer, J. M. 1997. Quellen, die unbekannte Biotope erfassen, bewerten, schützen. Bristol-Stiftung, Zürich 6: 1-153.