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Distribution, diversity, life cycle and growth of a mayfly community in a prealpine stream system (Insecta, Ephemeroptera)

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Abstract

Within the framework of a study on the ecology of Dippers in a prealpine stream system, the macroinvertebrate communities were also investigated, especially Ephemeroptera. Ten stations were sampled qualitatively, of which two (Saane and Turbach streams) were investigated quantitatively for 16 months (April 1983–July 1984). Fifteen mayfly species were found. The faunistic affinities among the 10 streams investigated reflect the main abiotic characteristics. There was no significant difference in species richness, diversity and evenness for Saane and Turbach streams. Life cycles of nine species were studied in these two watercourses. Those of *Rhithrogena degrangei*, *Rh. hybrida*, *Rh. savoiensis* and *Ecdyonurus helveticus* are described for the first time. *Baetis alpinus* is the only species to exhibit a bivoltine cycle, whereas all others have a univoltine summer or winter cycle. Specific growth rates were measured for most species. The summer generation of *B. alpinus* presents the highest growth rate (4.51% dry weight d^{-1}), whereas the lowest values were recorded for *Rh. degrangei* (0.76% dry weight d^{-1}). The importance of abiotic variables, especially water temperature, is also discussed.

Introduction

Ephemeroptera larvae form a major prey base for Dippers (*Cinclus cinclus*) during the breeding season. In the first few days of their life, nestlings are often fed mainly with soft-skinned mayfly larvae or nymphs. They can make up to 93% of the prey items brought to the nest (Jost, 1975; Ormerod, 1991). During a study on the ecology of Dippers in a prealpine stream system (Breitenmoser-Würsten, 1994a) we were therefore interested in food availability, especially in relation to the life cycles (size, growth and emergence period) of the ephemeropteran species. The material collected was also analyzed for community structure. Although recent studies have focused on the life histories of some alpine mayflies (e.g. Hefti & Tomka, 1990), we still lack basic information on the ecology of most species. However, rhithral biodiversity is probably much more endangered by human impact than actually recognized (Zwick, 1992). This knowledge is therefore important to understand the specific requirements of these mayflies. In the study, only mayflies were determined to species level. We therefore chose this taxonomic group and tried to link its structure to abiotic factors. Two stations on the main river and on one of its larger tributaries were analyzed quantitatively over a 16 months period. In addition, eight more stations at higher altitudes were sampled for species richness and pairwise comparison of faunistic affinities.

Material and methods

Investigated area

The prealpine stream system of the Saane river (canton of Berne, Switzerland) belongs to the drainage basin of the Rhine. The study area, the Saanenland, is situated on the northwestern edge of the Bernese Alps (Fig. 1). The catchment area is about 250 km^2 and contains

100 km of streams. The river sites investigated range in altitude from 1030 m to 1670 m above sea level (Table 1). The geological underground is calcareous (Badoux & Lombard, 1962). The flow of the rivers investigated is typical for a pluvio-nival regime. There are two hydropower reservoirs in the southern part of the study area (Fig. 1): 'Lac du Sénin' and 'Arnensee'. The water of the 'Arnensee' is flowing underground to the south and is therefore removed from the system of the Saane river. A wastewater treatment station has been working here since 1983. As there is no industry in the area the water is clean or slightly polluted by farming (Perret, 1977; Lang *et al.*, 1989). The climate is Atlantic with high variation in precipitation and temperature from year to year. The long-term average precipitation (1901–1960) is 1249 mm. The mean annual air temperature was 5.6 °C in 1983 and 5.5 °C in 1984. A detailed description of the study area is found in Breitenmoser-Würsten (1994b).

Abiotic factors

Physical-chemical data are given in Table 1. Water temperatures were measured monthly at the same time of the day with a thermometer (Jumotherm TDAW-30) from April 1983 to June 1985 and by a thermograph (YSI model 54) continuously from December 1984 until December 1985. Compared with the Turbach, the temperature of the Saane was higher in winter, but lower in summer (Fig. 2). This was due to a power station, and to two small glaciers in the south of the study area. The regular release of water in winter by the power station leads to higher temperatures in the Saane river. In summer, the melting ice and snow keep the river cool. The annual amplitude is correspondingly lower (Table 1). Conductivity was measured monthly at six stations. The six sites form three groups (in order of decreasing mean conductivity values): SA and LB with highly varying values (high values in winter with low water level and low values in spring/early summer with high water level due to melting snow and rain), TU and CH with lower values and lower variation, and SG and TS, where the influence of the reservoirs can be seen (Table 1, for site abbreviations see Fig. 1; Breitenmoser-Würsten, 1994b). Total hardness was determined with a Aquamerk quick test. The values correlate well with electrical conductivity (Table 1).

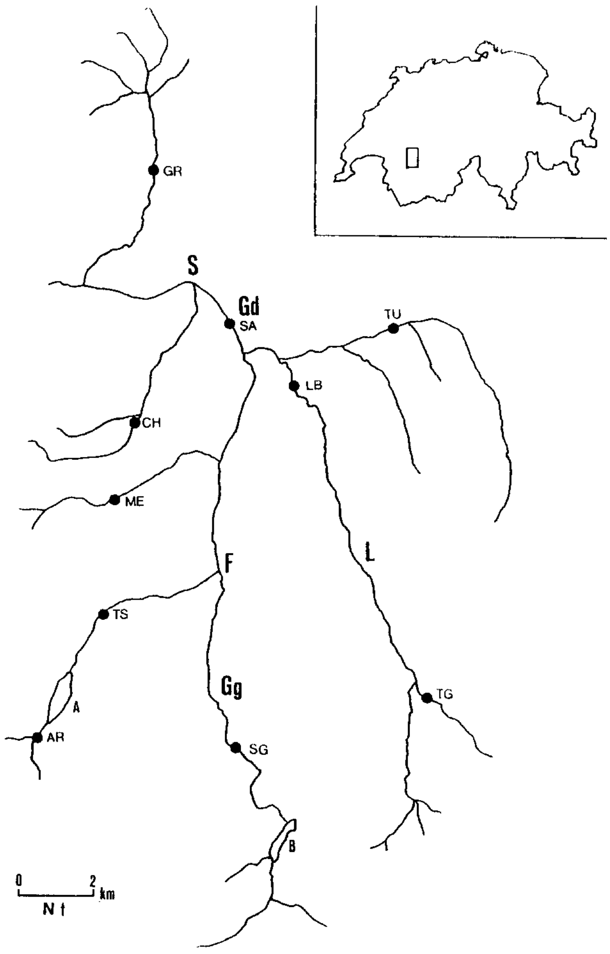

Fig. 1. Study area with locations of the sampling sites. A: Arnensee, B: lac de Sénin, AR: Arnen; CH: Chalberhöni; GR: Grischbach; LB: Louibach; ME: Meielsgrund; SA: Saane/Gstaad; SG: Saane/Gsteig; TG: Tungelbach; TS: Tschärzis; TU: Turbach, villages S: Saanen; Gd: Gstaad; L: Lauenen; F: Feutersoey; Gg: Gsteig.

Sampling methods

The benthic fauna of the rivers Saane and Turbach was sampled quantitatively during a 16-month period (April 1983–July 1984) with a modified Surber sampler (mesh size: 250 μm; net surface 1.35 m^2; size of the vertical frame: 40 cm). Six random samples were taken each month. In February 1984 the Turbach was completely frozen and no samples were taken. In both rivers the degree of precision (Elliott, 1983) over the 16-month period was on average 15.4% ± 7.4% for SA and 14.6% ± 4.4% for TU. The material was preserved in 70% alcohol for later identification and measurement of body size. For dry mass determination at generic level, some of the samples were dried

Table 1. List of physical and geochemical factors and the benthic sampling program for the 10 stations investigated. Abbreviation of the stations as in Fig. 1

	Station									
	SA	LB	GR	SG	TU	ME	CH	TS	TG	AR
	Altitude (m):-									
	1030	1090	1160	1210	1290	1320	1340	1405	1440	1670
Slope (%)	1.3	2.2	9.6	16.3	8.1	12.4	10.0	7.7	31.1	20.3
Thermal amplitude (°C)										
1983	7.7	8.8			12.9		10.8	7.6		
1984	8.9	9.0			10.9		9.3	9.1		
1985	10.2	11.3			15.4		8.2	10.0		
Electrical conductivity (μS/cm)										
x	398	398		199	312		317	260		
s	134	136		36	79		68	49		
n	26	26		22	26		26	26		
Total hardness (mval/l)										
x	5.9	5.6		2.9	4.4		4.5	3.8		
s	2.1	2.1		0.5	1.1		1.0	0.7		
n	20	20		19	20		20	20		
Benthos: monthly samples										
1983/84	+				+					
summer 1988	+	+	+	+	+	+	+	+	+	+

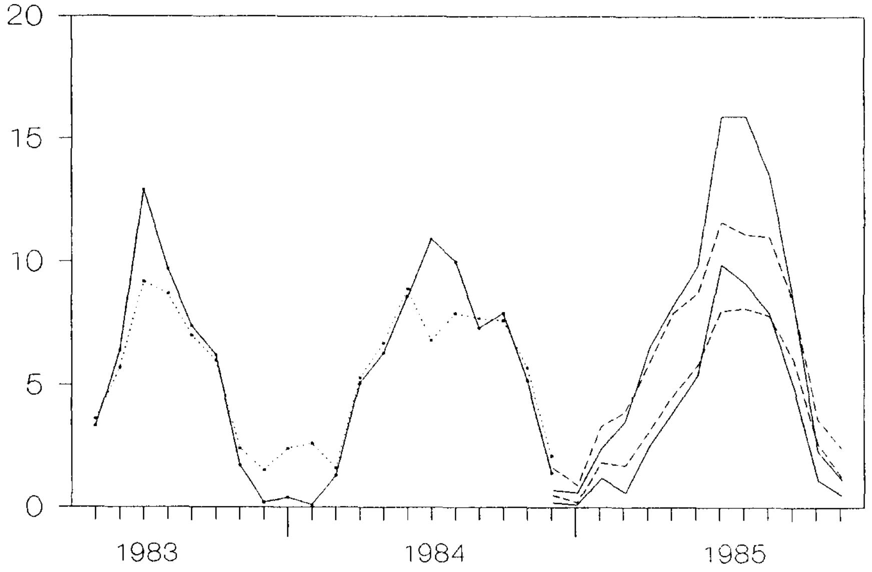

Fig. 2. Water temperatures from April 1983 until November 1985. From April 1983 until December 1984 the temperature was measured monthly by a digital thermometer and from December 1984 until December 1985 constantly by a thermograph. During this period a mean minimum (lower curve) and maximum value (upper curve) were calculated for each month. Solid line: Turbach (TU); dotted line: Saane (SA).

at 105 °C until the weight was stable, usually within 36 h. A total of ten stations on eight different rivers was sampled at the end of June/early July in 1988. Four samples were taken at each station.

Analysis of data

Diversity

The structure of the mayfly community was calculated for the 10 stations sampled qualitatively during the period June/July 1988. To compare the diversity of pairs of sites, we used the Sörensen coefficient (Cs), defined as

$$C_S = 2y/(a+b), \qquad (1)$$

where y = number of species found in both sites and a = number of species in site A, and b = number of species in site B. It ranges from 0 (no affinity) to 1 (absolute identity). This index is the least unsatisfactory when qualitative samples are involved (Magurran, 1988). On the basis of the similarity matrix obtained, a cluster analysis was performed using the average linkage method (Sokal & Michener, 1958).

The distribution of the species at the two stations sampled quantitatively was also calculated using the mean number of specimens per m^2 in the 16 samples for SA and 15 for TU. Two non-parametric indices were used to test heterogeneity.

The Simpson index (S) defined as

$$S = \sum (p_i)^2, \qquad (2)$$

where p_i is the proportional abundance of the ith species. It also ranges from 0 to 1 and gives the probability that two individuals drawn at random from a population belong to the same species (Ludwig & Reynolds, 1988).

The Shannon-Wiener index (H) defined as (Krebs, 1989)

$$H = -\sum p_i \log_2 p_i, \qquad (3)$$

where $H = 0$ if there is only one species in the sample and is maximum when all species are represented by the same number of individuals (even distribution of abundance; Green, 1979; Ludwig & Reynolds, 1988).

On the basis of these results, an evenness index was calculated:

$$E = (1/S) - 1/2^H - 1, \qquad (4)$$

where S = Simpson index and H = Shannon-Wiener index. This evenness index (modified Hill's ratio) approaches 0 when a single species becomes more and more abundant in a community (Alatalo, 1981).

To analyse the structure of the community at the two stations, we fitted a truncated lognormal distribution to the species abundance data and calculated an expected distribution as outlined in Pielou (1975). We used the program LOGNORM described in Krebs (1989). The goodness of fit was determined by a χ^2-test. The lognormal distribution is described as

$$S(R) = S_0 e^{-a^2 R^2}, \qquad (5)$$

where $S(R)$ = the number of species in the Rth octave from the mode, S_0 = the number of species in the largest class, and $a = 1/\sqrt{2}\sigma^2$, is a measure of the spread of the lognormal distribution.

Life cycles and growth

For the establishment of the life cycles, each individual was measured. Total length, from the front of the head to the tip of the abdomen was recorded with a micrometer eyepiece to the nearest 0.125 mm, and then reported in 0.5 mm size groups. In each sample, the geometric mean of the body length (±95% confidence interval) was calculated (Humpesch, 1979a). Then the respective mean biomasses were established using the length-weight power equation by Smock (1980):

$$W = aL^b, \qquad (6)$$

where W is the dry weight expressed in mg and L the body length in mm. The constants a and b were determined for *Baetis* and *Rhithrogena* as:

- *Baetis:* $a = 0.0100$, $b = 2.5504$, $r = 0.97$;
- *Rhithrogena:* $a = 0.0138$, $b = 2.5603$, $r = 0.98$.

The specific growth rate (G, expressed in % mm or mg d^{-1}) was calculated by fitting the exponential function (Humpesch, 1979a, 1981; Lavandier, 1981; Hawkins, 1986):

$$L_t = L_0 e^{kt} \textit{ or } W_t = W_0 e^{kt}, \qquad (7)$$

where L_t and W_t are the mean length and mean dry weight, respectively, after an interval t (in days) and L_0 and W_0 are the mean initial length and dry weight; k is the instantaneous growth rate and G = 100k.

Table 2. Mayfly composition at the 10 stations investigated in 1988. 0: absent; *: <5 individuals/m^2; **: 5–50 individuals/m^2; ***: >50 individuals/m^2. Abbreviation of the stations as in Fig. 1

Stations	SA	LB	GR	SG	TU	ME	CH	TS	TG	AR
BAETIDAE										
Baetis alpinus (Pictet)	***	***	***	***	***	***	***	***	***	***
Baetis melanonyx (Pictet)	***	*	**	0	***	0	0	**	0	0
Baetis muticus (L.)	**	0	0	0	0	0	0	0	0	0
Baetis rhodani (Pictet)	**	*	*	0	**	0	0	*	0	0
HEPTAGENIIDAE										
Epeorus alpicola (Eaton)	*	*	**	0	*	0	*	*	*	*
Ecdyonurus helveticus Eaton	**	0	0	0	***	0	0	**	0	0
Ecdyonurus parahelveticus Hefti & al.	0	0	0	*	0	*	*	0	*	*
Rhithrogena alpestris Eaton	***	***	*	**	**	*	*	*	*	0
Rhithrogena degrangei Sowa	***	***	0	0	*	0	0	0	*	0
Rhithrogena dorieri Sowa	0	0	0	0	0	0	*	0	0	0
Rhithrogena hybrida Eaton	***	*	***	0	***	0	***	*	0	0
Rhithrogena iridina (Kol.)	0	0	*	0	***	*	**	**	0	0
Rhithrogena savoiensis Alba & Sowa	***	0	0	0	*	0	0	0	0	0
Rhithrogena semicolorata (Curt.)	***	*	0	0	0	0	0	0	0	0
LEPTOPHLEBIIDAE										
Habroleptoides auberti (Biancheri)	0	0	0	0	*	0	0	0	0	0
Total: 15	11	8	7	3	11	4	7	8	5	3

Table 3. Matrix of the faunistic affinities recorded among the 10 stations investigated in summer 1988, using the Sörensen coefficient. Abbreviation of the stations as in Fig. 1

	LB	GR	TS	SG	TU	CH	ME	TG	AR
SA	0.84	0.67	0.74	0.29	0.82	0.44	0.27	0.50	0.29
LB		0.80	0.75	0.36	0.74	0.53	0.33	0.62	0.36
GR			0.93	0.40	0.78	0.71	0.55	0.50	0.60
TS				0.36	0.84	0.67	0.50	0.46	0.36
SG					0.29	0.40	0.86	0.75	0.67
TU						0.56	0.40	0.50	0.29
CH							0.55	0.67	0.60
ME								0.67	0.57
TG									0.75

Results

Distribution

Fifteen mayfly species were identified (Table 2). Among them, only *Baetis alpinus*, a widespread and abundant species with a wide ecological valence, was found in all stations.

B. muticus, *B. rhodani* and *Rhithrogena semicolorata* are typical of lowland areas and reach their upper altitudinal limits here (*ca* 1000 m, 1400 m and 1100 m, respectively).

B. melanonyx, *Ecdyonurus parahelveticus*, *Rh. degrangei* and *Rh. hybrida* are characteristic of calcareous prealpine and alpine watercourses. Other typ-

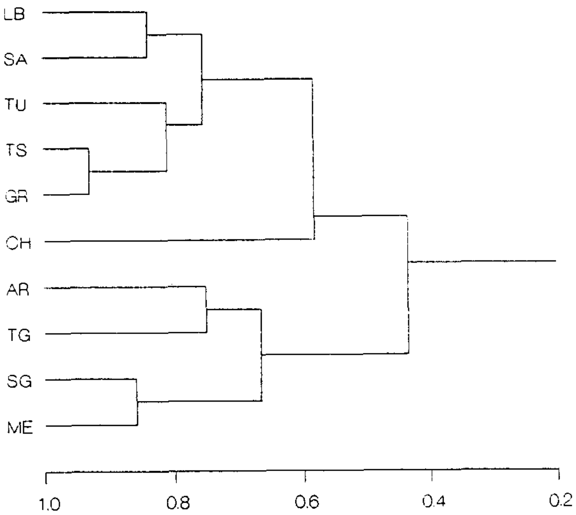

Fig. 3. Dendrogramm showing the faunistic affinities among the 10 stations sampled in summer 1988. Abbreviations of the sampling sites as in Fig. 1.

Table 4. Diversity measures for the two stations sampled quantitatively from April 1983 until July 1984.

		SA	TU
Number of species	N	11	11
Simpson Index	S	0.302 ± 0.116	0.325 ± 0.157
Shannon-Wiener Index	H	2.081 ± 0.378	1.999 ± 0.517
Evenness Index	E	0.775 ± 0.138	0.751 ± 0.119
Number of months	n	16	15

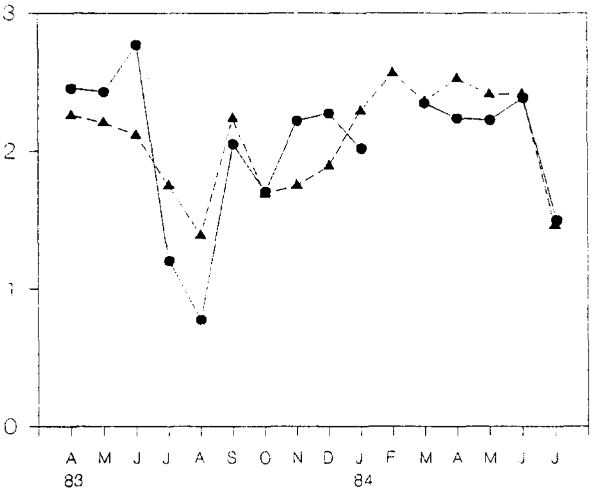

Fig. 4. Seasonal variation in diversity (Shannon-Wiener Index H) of the two stations Saane (SA) and Turbach (TU) during 16 months (April 1983–July 1984). Solid line: TU; dotted line: SA.

ical alticolous species are *Epeorus alpicola* and *Rh. alpestris*, which are also found on acid rocks.

Rh. dorieri is a rare species only reported from a few prealpine streams in Switzerland (Sartori, 1988). Its ecological requirements are still insufficiently known.

Diversity

The correlation matrix calculated from equation (1) that indicates the pairwise faunistic affinities of the 10 stations is given in Table 3. The highest index is between GR and TS ($C_s = 0.93$) whereas the lowest ($C_s = 0.29$) is within four pairwise comparisons, three of them involving station AR. The cluster analysis performed on the matrix is shown in a dendrogram (Fig. 3).

There is a negative correlation between the number of species found and the slope at the station sampled ($y = 9.44 - 0.23x$, $r = 0.69$, $n = 10$, $p = 0.027$), but not so between the number of species and the altitude of the station ($p > 0.05$). However, if we exclude station SG, that is special because of its position close to a hydropower station (Breitenmoser-Würsten, 1994a), also this relationship becomes significant ($y = 20.12 - 0.01x$, $r = 0.69$, $n = 9$, $p = 0.038$).

The diversity indices (S and H) as well as the evenness index (E) calculated from equations (2), (3) and (4) are presented in Table 4. Stations SA and TU do not differ significantly in these measures of heterogenity (Mann-Whitney U-test: $p > 0.1$). The diversity shows a seasonal pattern in both rivers (Shannon-Wiener Index, Fig. 4). Maximum values occur from late winter to early summer and there is a drop in July and August. In these summer months two species were dominant, representing 55–72% of all individuals in SA (*B. alpinus* in July and *B. melanonyx* in August) and 65–85% in TU (*B. melanonyx*), respectively. As a consequence of a large flood in September 1983 (Breitenmoser-Würsten, 1994b), densities fell and diversity rose.

We were able to fit a lognormal distribution to the species abundance data in every month for both stations (all $p > 0.05$) with the exception of July 1983 in SA ($\chi^2 = 10.47$, $0.01 < p < 0.025$).

Life cycles

Baetis alpinus was the most abundant species in the two localities. It exhibited a clearly bivoltine cycle

(MBws *sensu* Clifford, 1982), with an overwintering generation that emerges in spring/early summer, and a summer generation that grows rapidly to emerge in late summer–early autumn (Fig. 5). The main difference between the two populations is a less extended flight period in TU compared to SA. In both sites, there was overlap between the two generations, in September (TU) or October (SA), suggesting that only part of the winter generation is involved in the production of the summer one. The eggs laid by females in July, for instance, begin to hatch in September or October. An embryonic diapause was not detected.

Compared to the previous species, *B. melanonyx* exhibits a completely different life cycle, since its whole development takes place in summer. This species has a univoltine summer cycle (Us *sensu* Clifford, 1982), with larval recruitment beginning in late May and June, followed by rapid growth for 3–5 months (Fig. 6). Eggs of *B. melanonyx* seem to exhibit a long embryonic diapause of about 7–8 months. Contrary to what was found in *B. alpinus*, emergence appears to take place earlier in TU than in SA.

Rhithrogena alpestris presents also a Us life cycle (Fig. 7). Emergence occurs in July in both localities and is also probably followed by an egg diapause. In SA, young larvae were sampled in February whereas in TU they already appeared in December, suggesting an earlier recruitment at higher altitudes.

Rh. savoiensis exhibits a rapid Us life cycle (Fig. 8) since the first larvae were found in June and emergence occurred in August in SA. This species had the shortest development period of all univoltine species in the area investigated.

Rh. hybrida is a univoltine spring/early summer species (Uw *sensu* Clifford, 1982), emerging in May and June (Fig. 9). Recruitment seems to begin in August without egg diapause. At station TU, where this species was more abundant than in SA, there was only one month (July 1983 & 1984) where *Rh. hybrida* was missing in samples (with the exception of February 1984 when sampling was impossible). Moreover, the structure of the population suggests a synchronous development in a single cohort, as for *Rh. alpestris*.

As for *Rh. hybrida*, the life cycle of *Rh. degrangei* was previously unknown. The graph from the SA population shows a similar development pattern for these two species, with the same emergence period in May-June, and recruitment beginning in August followed by a even growth during autumn (Fig. 10).

Clearly a univoltine species, *Rh. semicolorata* presents some similarity in its life cycle with that of *B. alpinus*, i.e. a long emergence period of 5 months (June–October) with an overlap of both generations in Septembe–October (Fig. 11). This species is present all year long in the larval stage. With the exception of a more synchronous emergence period (July–August), *Rh. iridina* exhibits a rather similar life cycle (Fig. 12). There is no embryonic diapause, as young larvae are already present in September.

The development of *Ecdyonurus helveticus* was unknown until now. Figure 13 shows that development of this species is complicated and difficult to interpret. Larvae are found throughout the year. Emergence occurred from April to August, but contrary to the other species studied, several cohorts were found at the same time at a given place. This is shown by the different sizes present each month. At least four cohorts can be identified. There is no evidence for a one year development, but the continuous recruitment found in TU over 10 months (August until almost May) suggests delayed hatching.

Growth

Table 5 summarizes growth rates of the investigated species. No growth rate was calculated for *E. helveticus*, because it was impossible to distinguish cohorts at both study sites. The same problem arose with *B. alpinus* in the Turbach, where we assume that at least 4 cohorts occurred between January and July 1984. Due to missing values for the young larval stages, growth rates were also not calculated for *Rh. savoiensis*.

The highest growth rates, both in length and in weight, were recorded for the two *Baetis* species. The summer generation of *B. alpinus* had an extremely high growth rate, but *B. melanonyx*, which develops exclusively in late spring-summer, also exhibited a remarkable increase in length and weight. For the latter species, there was a significant difference between growth rates in the two localities SA and TU (Mann-Whitney *U*-test: $p<0.05$).

The growth rate of *Rh. alpestris*, also a summer species, showed highest values in spring and summer just before the emergence. Winter values were considerably lower. There was no difference between SA and TU (*U*-test: $p>0.1$). *Rh. alpestris* is the only species where higher values for G_L and G_W were recorded in TU than in SA, but only in spring and summer (April to July). *Rh. hybrida* had a constant growth rate during its whole cycle. Larvae grew faster in SA than in TU during the whole development (*U*-test: $p<0.05$). With *Rh. degrangei* highest growth rate

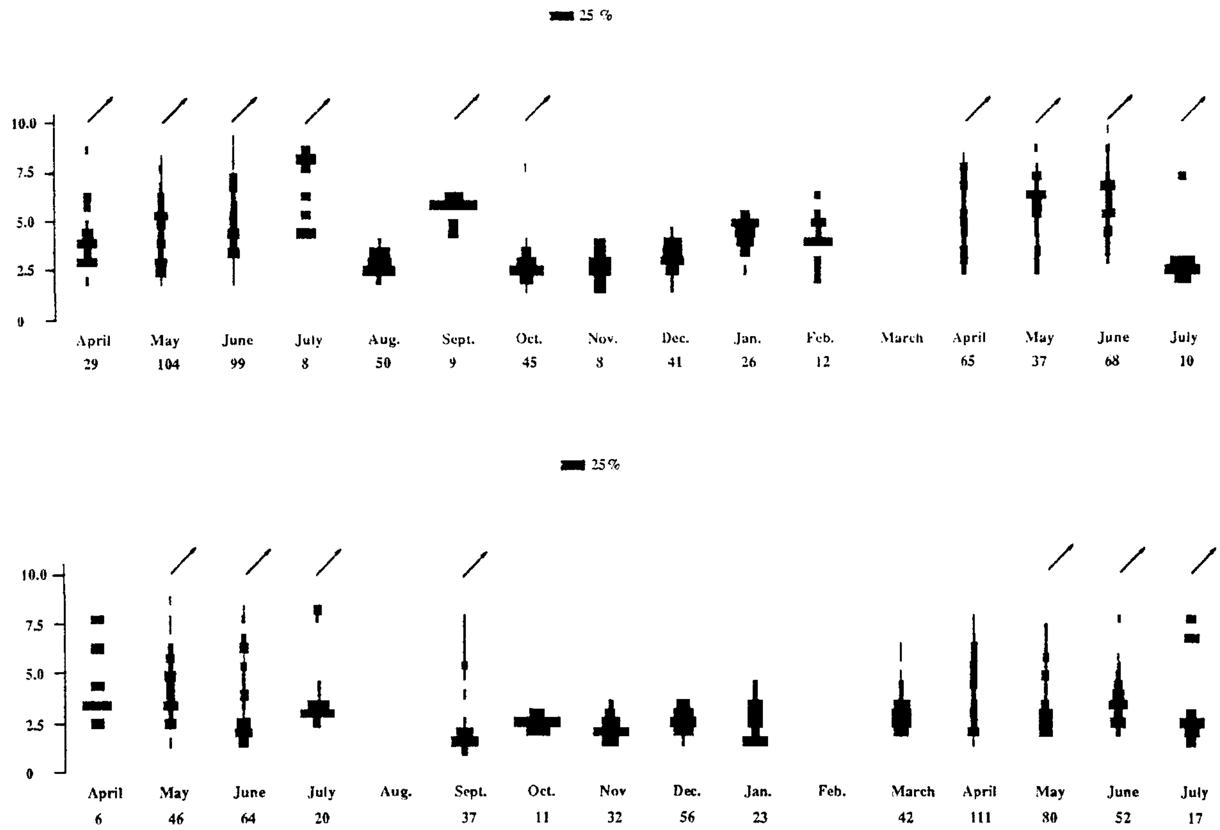

Fig. 5. Life cycle of *Baetis alpinus* in SA above (N=611) and in TU below (N=597). Each bar indicates the relative value (in %) for each 0.5 mm size groups/month. Arrows: emergence period. Numbers on the abcissa: absolute number of specimens measured.

values were recorded in SA just after eggs hatching (August–December). The growth slowed down during the winter months (December–March) and then increased until emergence in May or June. In contrast, *Rh. semicolorata* and *Rh. iridina* exhibited a rather low growth rate during the first months after hatching (September–March), but then it increased about three times before emergence.

The relationship between the mean specific growth rates G (for length or weight) and the mean water temperature T_W can be described by the nonlinear regression equation

$$G = ae_w^{bT}. \qquad (8)$$

Values for the constants a and b for growth in length were $a = 0.181$ and $b = 0.385$ for SA, and $a = 0.535$ and $b = 0.185$ for TU (Fig. 14). For growth in weight the corresponding values were $a = 0.063$ and $b = 0.401$ for SA, and $a = 0.205$ and $b = 0.188$ for TU, respectively. In SA 86% and in TU 97% of the variability of G was accounted for by variation in mean water temperature.

Discussion

Distribution and diversity

The mayfly community of the Saanenland is typical of the mountainous prealpine region. Two families dominate, Baetidae and Heptageniidae, to which most of the cold stenothermous species such as *B. melanonyx*, *Rh. alpestris* or *E. alpicola* belong. Contrary to the Plecoptera, ephemeropteran communities reach their highest species richness in foothill watercourses. In prealpine streams, this richness is naturally reduced. The faunistic composition of mayfly communities in the Saanenland is similar to the one studied by Hefti & Tomka (1991) in another area of the Prealps (Singine River), as well as being comparable to data from other mountainous European regions such as the Carpathi-

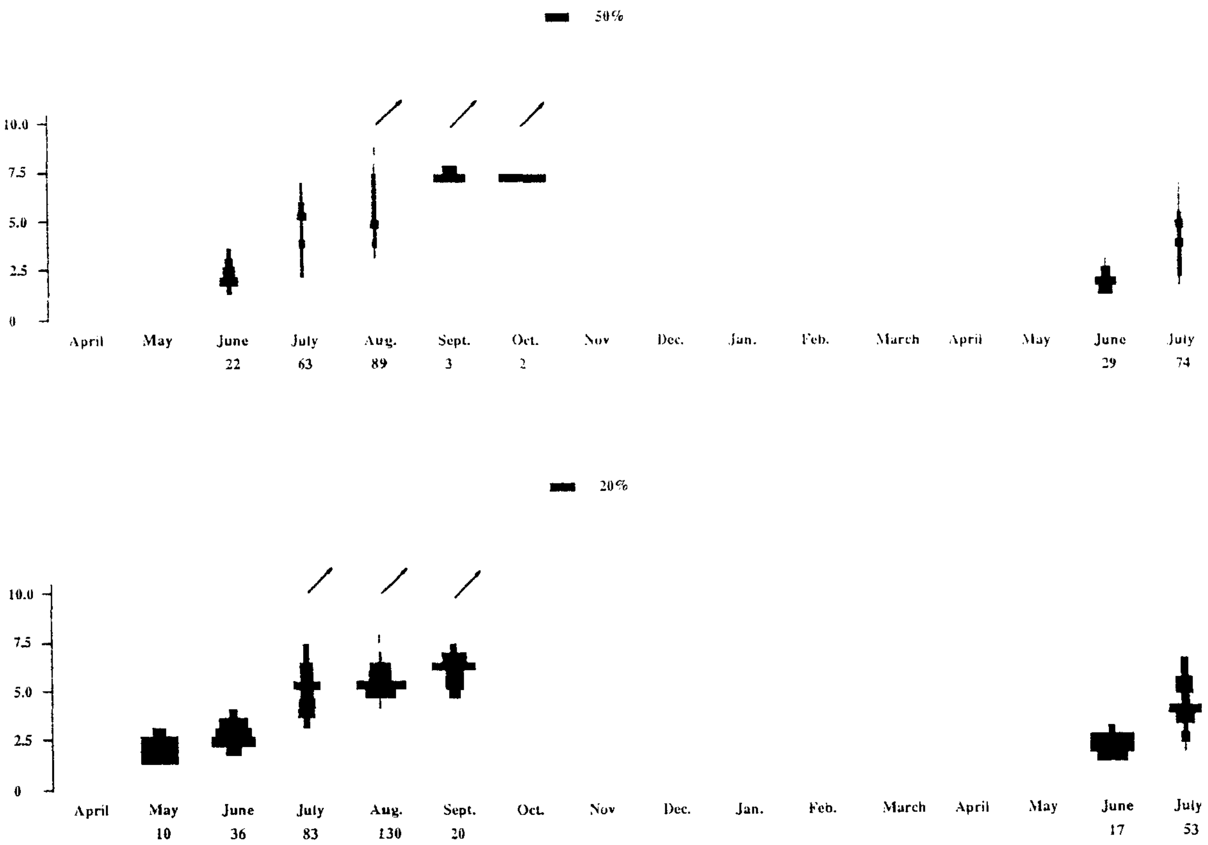

Fig. 6. Life cycle of *Baetis melanonyx* in SA above (*N*=282) and in TU below (*N*=349). For explanation see Fig. 5.

ans (Sowa, 1975a), the Pyrenees (Vinçon & Thomas, 1987) and the German Alps (Braukmann, 1987).

The faunistic affinities among the 10 streams investigated reflect the main abiotic characteristics presented in Table 1, especially the slope. The first five localities (slope <10%) are grouped together as well as the last four (slope >15%); in between lies CH with a mean slope value of 10% (Fig. 3). Stations SA and LB exhibit the lowest values for altitude or slope as well as the highest variation in conductivity and total hardness and are grouped together. TS, GR, as well as TU present medium values for most of the parameters, whereas SG and ME are characterized by higher slopes; TG and AR possess the highest values for altitude and slope and form one cluster. *B. rhodani* was only found in stations with a slope <10% (compare Table 2 and Fig. 3), suggesting that this factor is more important than altitude for this species.

There is a gradient in species richness with regard to topography. The highest localities (AR, TG) characterized by high slopes and probably low values in conductivity are also those with few species (3–5), whereas localities at lower altitude (SA, LB) are richer (8–11 species). This is in accordance with the concept that headwaters or first order streams possess low diversity (Vannote *et al.*, 1980). Such streams are characterized by pioneer species such as *B. alpinus* and *E. alpicola*.

The two streams sampled quantitatively (SA and TU) show some dissimilarity (Fig. 3). This can be explained by the fact that although they possess the same number of species, some important changes occur between them such as species replacement (*Rh. semicolorata* in SA vs *Rh. iridina* in TU). There was no significant difference in diversity or evenness, suggesting that the structures of the benthic communities at the two stations were comparable. This is also confirmed by the fact that species abundance in both streams followed a lognormal distribution.

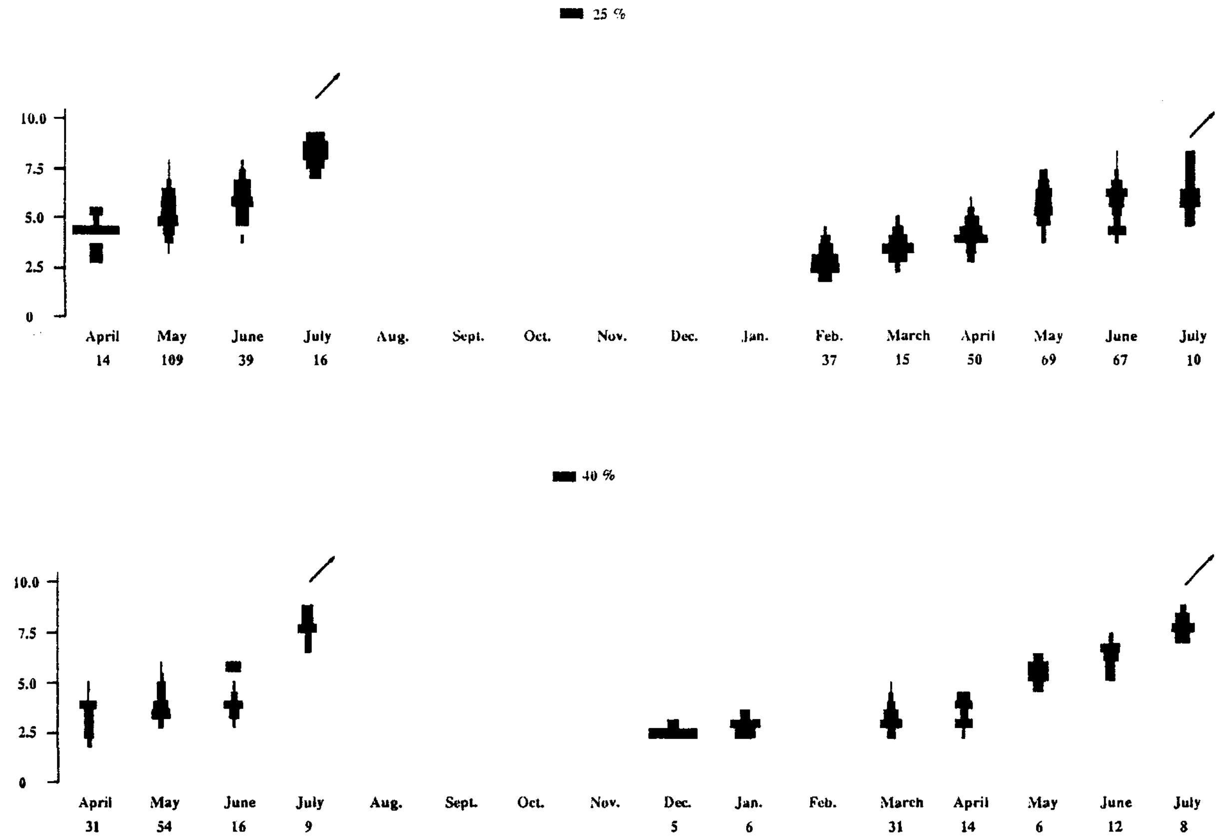

Fig. 7. Life cycle of *Rhithrogena alpestris* in SA above (*N*=426) and in TU below (*N*=192). For explanation see Fig. 5.

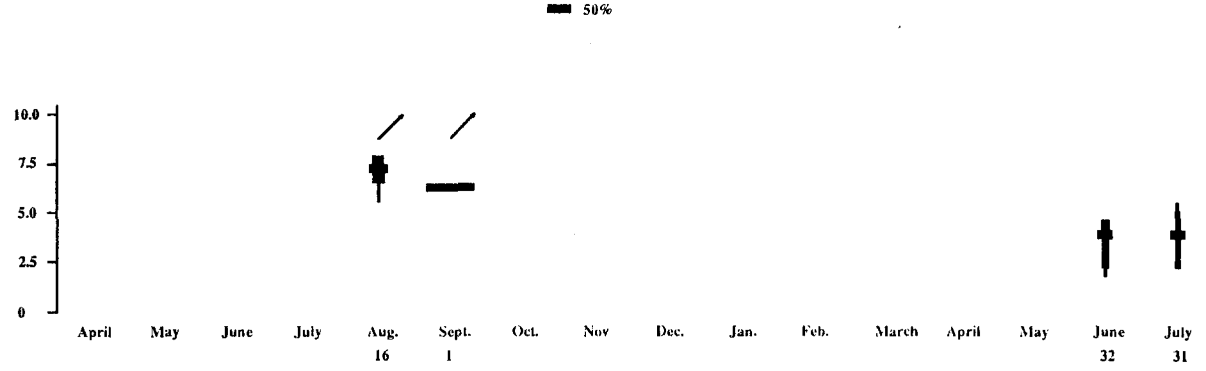

Fig. 8. Life cycle of *Rhithrogena savoiensis* in SA (*N*=80). For explanation see Fig. 5.

Life cycle and growth

Of the nine species studied for development, all were univoltine, except *B. alpinus* (Table 6). Its life cycle is well known and is one of the most plastic. Several studies have shown that this species may exhibit different strategies, depending on environmental conditions. The long recruitment of young larvae in TU could be due to the greater thermal fluctuations in this river. Temperature has been shown to be the major factor to explain differences in life cycle strategies in this species (Humpesch, 1979a). As already mentioned, the summer generation of *B. alpinus* exhibited the highest mean growth rates recorded during this

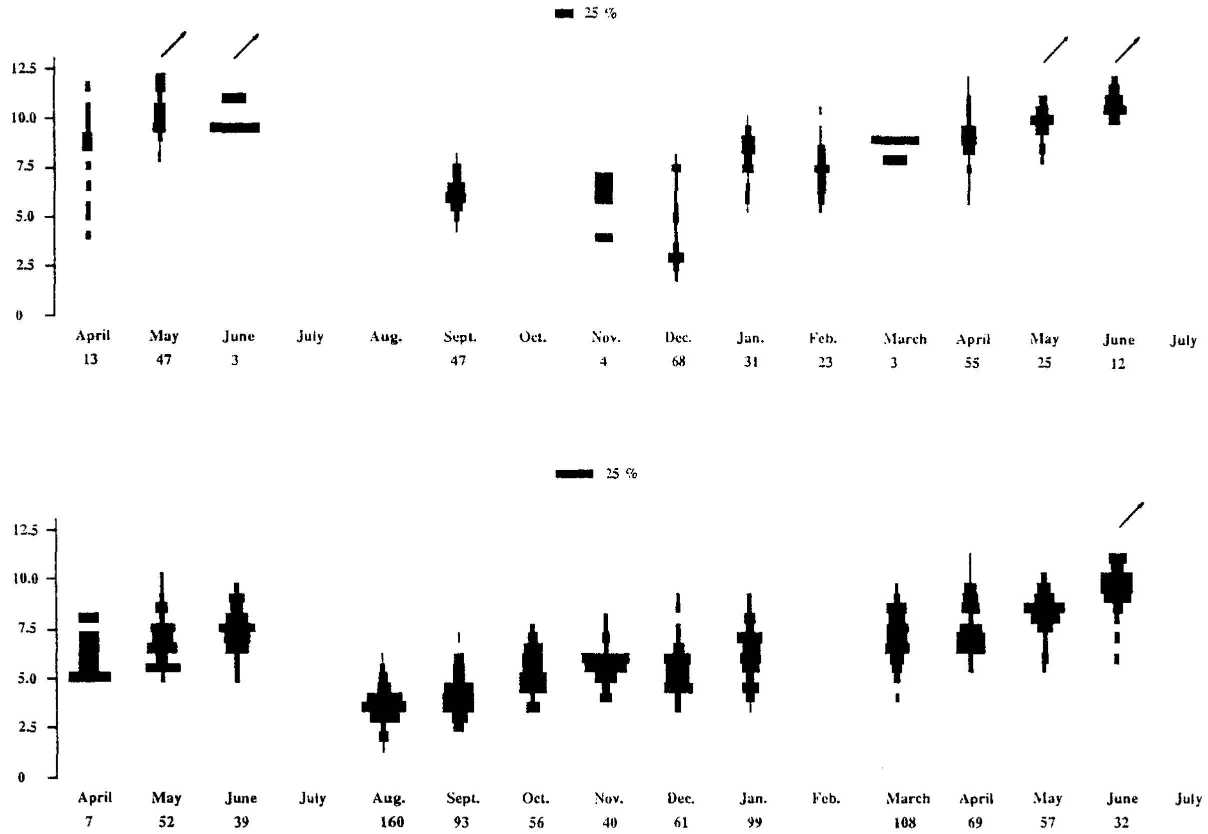

Fig. 9. Life cycle of ***Rhithrogena hybrida*** in SA above (*N*=331) and in TU below (*N*=873). For explanation see Fig. 5.

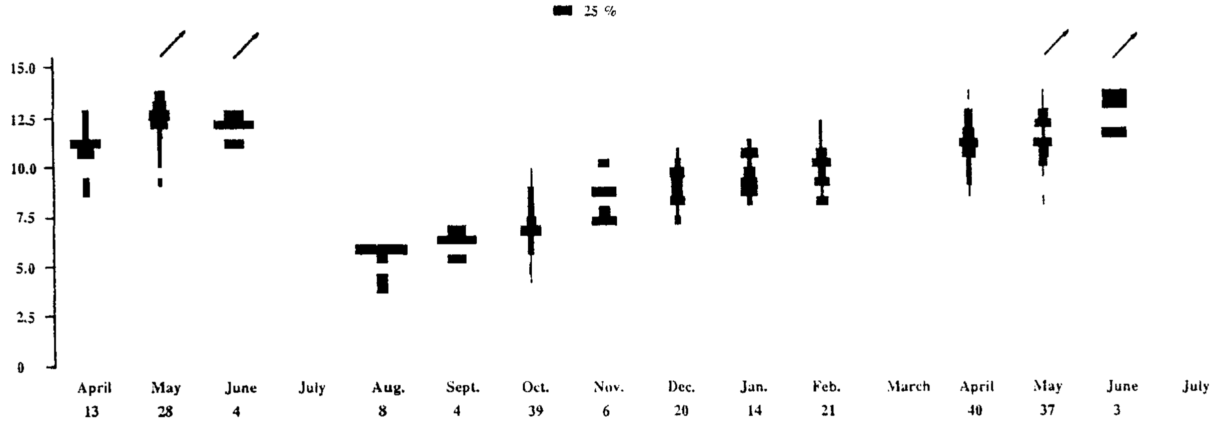

Fig. 10. Life cycle of ***Rhithrogena degrangei*** in SA (*N*=237). For explanation see Fig. 5.

study (1.79% d^{-1} in length and 4.51% d^{-1} in weight). The winter generation had values similar to univoltine winter species such as *Rh. degrangei* or *Rh. hybrida*. In SA, we can predict a winter generation development of 7 months, egg hatching in October or November producing mature nymphs in April or May respectively and those hatching in December producing mature nymphs in June–July. In TU, the development seems to be longer (about 2 months) since specimens hatching in September did not emerge before May.

In both localities *B. melanonyx* exhibited a univoltine summer cycle (Table 6). The only difference

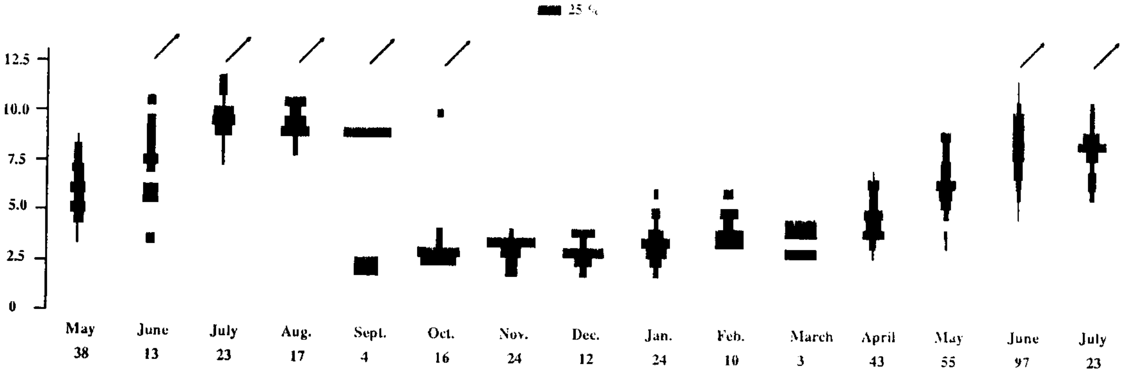

Fig. 11. Life cycle of *Rhithrogena semicolorata* in SA (N=402). For explanation see Fig. 5.

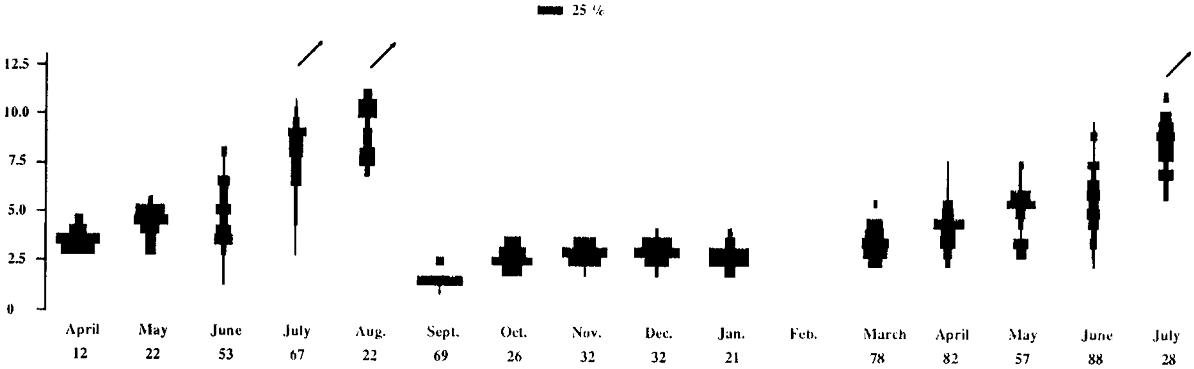

Fig. 12. Life cycle of *Rhithrogena iridina* in TU (N=689). For explanation see Fig. 5.

between the two populations was that, in 1983, young larvae appeared earlier in TU than in SA (May vs June) and that the emergence of the adults also took place one month earlier. As this species only develops when water temperatures are increasing, the higher summer temperature found in TU cannot explain why *B. melanonyx* begin to hatch earlier than in SA, since spring and autumn temperatures are similar in the two streams (Fig. 2). Low winter temperatures may affect the length of the embryonic diapause and hatching of the eggs, as suggested for other species (Bohle, 1969; Illies & Masteller, 1977; Humpesch, 1979a; Schmidt, 1984). The mean growth rate was significantly lower in TU than in SA. Other investigations are needed in order to understand which factors are involved. The synchronous appearance of young larvae in June 1984 at both places could indicate some annual fluctuations in egg hatching.

The development of *Rh. alpestris* in the Alps was unknown. Our results confirm those obtained from Carpathian populations (Landa, 1968). At our two stations, this species exhibits the same synchronous emergence period. The only difference was found in the hatching of eggs, which occurs two months earlier in TU than in SA (December vs February). One hypothesis would be that the eggs of this species, as those of *B. melanonyx*, require a low temperature period before hatching. Due to the lower winter temperatures in TU, this period could be shorter and therefore hatching could occur earlier. This is consistant with the fact that in some species, low or seasonally decreasing temperatures often terminate diapause (Snellen & Stewart, 1979). On the other hand, the development of larvae was slower in TU during the winter months, probably also because of the lower water temperature. The larvae, however, did catch up with those from the SA population in summer, when the water temperature in TU was considerably higher than in SA (Fig. 2). Despite this, we could detect no difference in the growth rate of the two populations. The fact that changes in temperature do not always affect a species' developmental time and growth rate to the same extent was also mentioned by Sweeney (1984).

Table 5. Values of the mean specific growth rate in length (G_L. % length d^{-1}) and in weight (G_W, % dry weight d^{-1}) of the larvae in both streams during different periods (n= number of data points used to calculate G; r^2= coefficient of determination describing fit of data)

Species	Stream	Period	Growth in length G_L (±95%CL)	r^2	Growth in weight G_W (±95%CL))	r^2	n
B. alpinus	Saane	August–October 83	1.79% (±0.10)	0.94	4.51% (±0.23)	0.94	3
		October 83–May 84	0.37% (±0.16)	0.82	0.96% (±0.35)	0.81	8
B. melanonyx	Saane	June–September 83	1.28% (±0.12)	0.98	3.32% (±0.32)	0.98	4
	Turbach	May–September 83	1.06% (±0.10)	0.96	2.69% (±0.23)	0.96	5
Rh. alpestris	Saane	April–July 83	0.81% (±0.29)	0.97	2.08% (±0.85)	0.97	4
		February–April 84	0.70% (±0.10)	0.97	1.74% (±0.41)	0.98	3
		April–July 84	0.50% (±0.15)	0.98	1.27% (±0.22)	0.98	4
		February–July 84	0.58% (±0.15)	0.97	1.46% (±0.26)	0.98	6
	Turbach	April–July 83	1.01% (±0.12)	0.91	2.59% (±0.31)	0.88	4
		December 83–April 84	0.29% (±0.11)	0.94	0.75% (±0.12)	0.94	4
		April–July 84	0.92% (±0.20)	0.90	2.35% (±0.26)	0.91	4
		December 83–July 84	0.56% (±0.20)	0.93	1.44% (±0.20)	0.93	7
Rh. degrangei	Saane	April–June 83	0.14% (±0.04)	0.90	0.37% (±0.05)	0.89	3
		August–December 83	0.44% (±0.08)	0.98	1.13% (±0.11)	0.99	5
		December 83–March 84	0.17% (±0.08)	0.97	0.44% (±0.11)	0.97	4
		March–June 84	0.23% (±0.08)	0.97	0.59% (±0.21)	0.96	4
		August 83–June 84	0.30% (±0.08)	0.97	0.76% (±0.21)	0.98	11
Rh. hybrida	Saane	April–June 83	0.46% (±0.15)	0.93	1.19% (±0.22)	0.94	3
		December 83–June 84	0.52% (±0.13)	0.98	1.35% (±0.31)	0.99	7
	Turbach	April–June 83	0.33% (±0.12)	0.91	0.85% (±0.28)	0.91	3
		August 83–June 84	0.34% (±0.05)	0.99	0.91% (±0.08)	0.99	11
Rh. iridina	Turbach	April–June 83	0.52% (±0.08)	0.93	1.35% (±0.21)	0.93	3
		June–August 83	0.98% (±0.08)	0.98	2.51% (±0.09)	0.98	3
		September 83–March 84	0.17% (±0.06)	0.98	0.45% (±0.14)	0.99	6
		March–June 84	0.54% (±0.05)	0.93	1.41% (±0.13)	0.92	4
		June–July 84	1.40% (±0.05)	1.00	3.55% (±0.12)	1.00	2
		September 83–July 84	0.54% (±0.05)	0.94	1.37% (±0.12)	0.94	10
Rh. semicolorata	Saane	September 83–March 84	0.24% (±0.18)	0.89	0.65% (±0.51)	0.88	7
		March–July 84	0.73% (±0.10)	0.97	1.84% (±0.12)	0.97	5
		September 83–July 84	0.43% (± 0.10)	0.95	1.56% (± 0.12)	0.95	11

The life cycle of *Rh. savoiensis* was characterized by a short summer period of larval development. To obtain sufficient data for growth rate analysis, we would need at least bimonthly samples.

The life cycle of *Rh. degrangei* was as expected, i.e. a univoltine species with a single winter generation (Table 6). The first young larvae are found already in August suggesting that there is no embryonic diapause. It was possible to divide the development in SA into three periods, with highest values of mean growth rates being obtained in autumn, just after hatching.

The development of *Rh. hybrida* was not precisely known, although some authors (Studemann *et al.*, 1992) have suggested a univoltine species with a single winter generation (Table 6). As already mentioned, the life cycle of *Rh. hybrida* does not differ from that of *Rh. degrangei*. Our a priori hypothesis suggested that there were some differences between these two sibling species. Although life cycle data do not support our hypothesis, growth rates provide some evidence for species differences. The mean growth rate of *Rh. hybrida* was constant during the whole cycle, which therefore cannot be divided into different periods as in *Rh. degrangei*. The two populations of *Rh. hybrida* also exhibited different mean growth rates (0.95% d^{-1} for TU vs 1.35% d^{-1} for SA, U-test: $p<0.05$). We

Table 6. Summary of life cycle and growth strategies among the investigated species. Life cycle abbreviations according to Clifford, 1982. References: (1) Brooker & Morris, 1978 (2) Degrange, 1957 (3) Humpesch, 1979b (4) Landa, 1968 (5) Lavandier, 1988 (6) Müller-Liebenau, 1966 (7) Riederer, 1981(8) Ritter, 1985 (9) Sartori, 1987 (10) Sowa, 1975b (11) Studemann, *et al.*, 1992 (12) Thibault, 1971(13) Weichselbaumer, 1984 (14) Wise, 1980.

Species	Type of life cycle in our study	Life cycle in literature	References	Period of max. growth rate
B. alpinus	MBws	MBws (<1500 m)	2,4,10	Summer
		Uw (<2000 m)	3,8,9,13	
		2Y (>2000 m)	5	
B. melanonyx	Us	Us	6,10	Summer
Rh. alpestris	Us	Us	4	Summer
Rh. savoiensis	Us			Summer
Rh. degrangei	Uw	Uw?	11	Autumn
Rh. hybrida	Uw	Uw?	11	Constant
Rh. iridina	Uw	MBws	12	Spring
		Uw	10	
Rh. semicolorata	Uw	Uw	1,7,14	Spring

thus assume that the differences in growth observed may explain how two closely related species can live together in the SA locality. Larvae of different physiological stages have been found to possess different food requirements (Brittain, 1976; Anderson & Cummins, 1979). Although belonging to the group of herbivore animals feeding on algae (scrapers), *Rhithrogena* species probably exhibit the same pattern that North American heptageniid *Stenonema* for which important detrital feeding in early instars was found (Cummins, 1973). These age-specific variations for food resources, with a shift to more algal feeding in later instars, would thus avoid strong competition between these two species.

Rh. iridina had a univoltine cycle with a winter generation in the area investigated (Table 6). The emergence period was later than for *Rh. degrangei* and *Rh. hybrida*. It was possible also to separate the development of this species into three periods, as for *Rh. degrangei*, but contrary to the latter, maximum specific growth rate was observed prior to emergence, especially during the last month where G values were high (1.40% d^{-1} and 3.55% d^{-1} in length and weight, respectively).

Rh. semicolorata can be considered as the vicariant species of *Rh. iridina* in SA, and shows a comparable life cycle, with the exception of a longer emergence period. Only two distinct growth periods could be detected for *Rh. semicolorata*, a low autumn-winter growth rate and a high spring-summer one. Our values fit those obtained by Hefti & Tomka (1990). With respect to the mean annual growth rate, no significant differences were found between *Rh. semicolorata* and *Rh. iridina*.

Finally, even if the life cycle of *E. helveticus* has been studied, little can be said to categorize its development. This species seems to exhibit a univoltine life cycle in TU whereas in SA, the presence of mature larvae in April and August suggest a bivoltine cycle. This difference may also be explained by a shift in developmental times between the two populations, as already indicated for *E. venosus* (Imhof *et al.*, 1988). In order to solve these problems, a specific study is needed involving laboratory rearing to estimate the temperature relationships of the egg stage (Humpesch, 1982).

Finally, our results confirm that water temperature is a major factor affecting growth in Ephemeroptera larvae.

Conclusions

The mayfly community of the Saanenland presents a structure comparable to that from other prealpine areas. In the two localities sampled quantitatively over 16

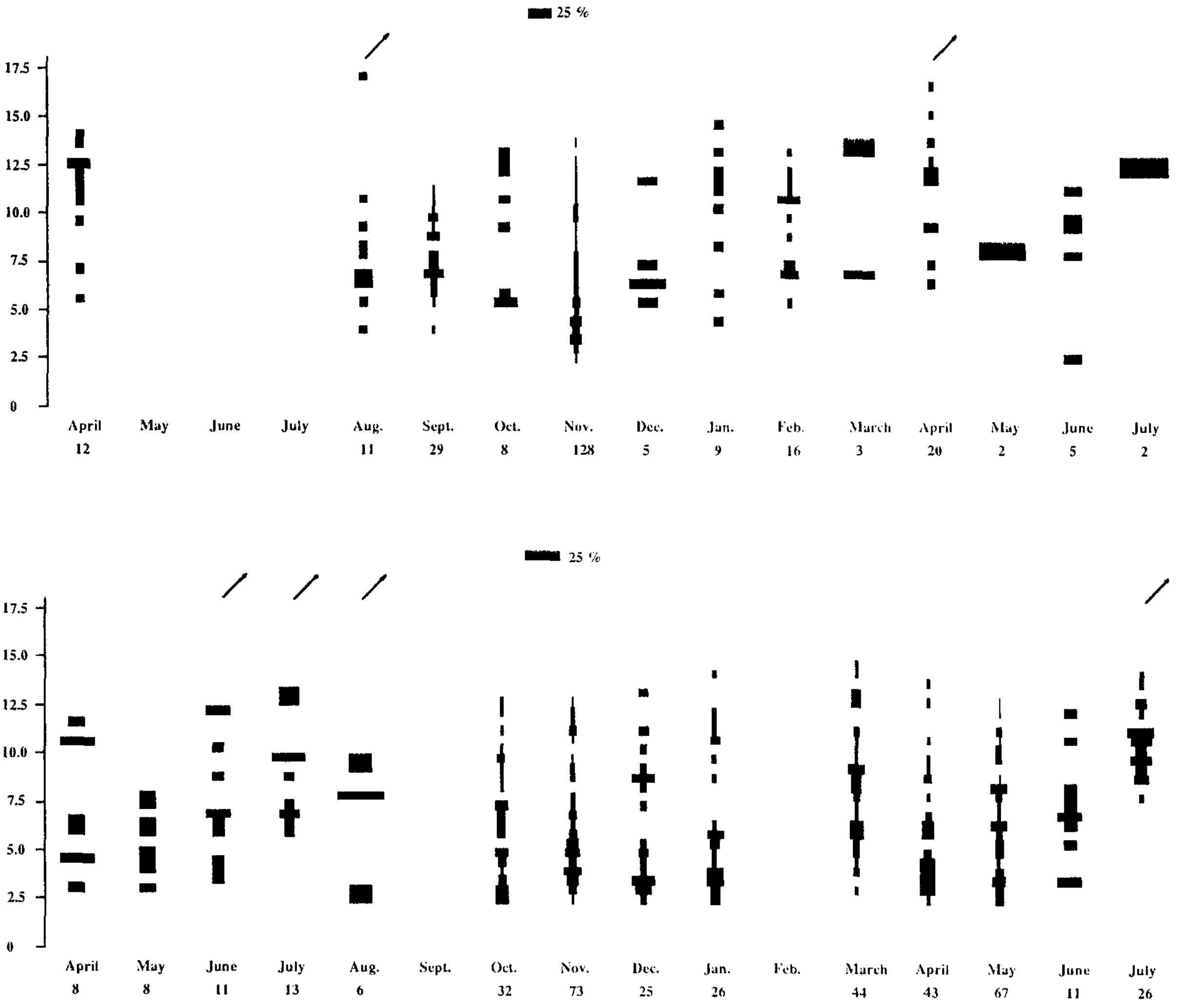

Fig. 13. Life cycle of *Ecdyonurus helveticus* in SA above (*N*=251) and in TU below (*N*=393). For explanation see Fig. 5.

months, we found no differences in diversity or evenness. The life cycles and growth rates of the populations studied may be divided into four main groups:

a. species that exhibit a bivoltine life cycle (type MBws) with a rather low winter generation growth rate and high summer generation growth rate: *B. alpinus*

b. species that have a univoltine summer cycle (type Us), with a growth rate increasing with time: *B. melanonyx*, *Rh. alpestris*, *Rh. savoiensis*

c. univoltine winter species (type Uw) that exhibit the lowest mean growth rate in the first instar larvae, it increases with time until emergence in summer: *Rh. iridina*, *Rh. semicolorata*

d. species with univoltine winter cycle (type Uw) that display the highest growth rate in the first instar larvae, decreasing during winter and increasing again before emergence in spring: *Rh. degrangei* (*Rh. hybrida*).

The growth in *Rh. hybrida* is constant throughout the year and independent of water temperatures. This strategy seems rare among mayflies and has only been reported in few species (e.g. Minshall, 1967; Waters & Crawford, 1973).

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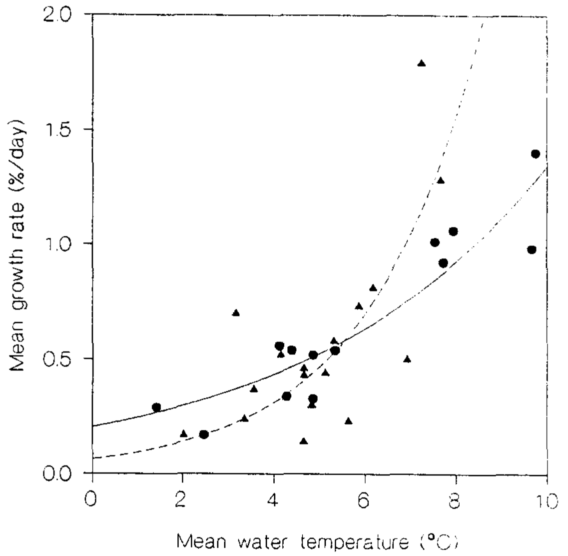

Fig. 14. Relationship between mean specific growth rate (G_L, % length d^{-1}) and mean water temperature (°C). Solid line and dots for TU, broken line and triangles for SA. For the regression equation see text.

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References

Alatalo, R. V., 1981. Problems in the measurement of evenness in ecology. Oikos 37: 199–204.

Anderson, N. H. & K. W. Cummins, 1979. Influences of diet on the life histories of aquatic insects. J. Fish. Res. Bd Can. 36: 335–342.

Badoux, A. & H. Lombard, 1952. Geologische Atlas der Schweiz. Notice explicative. Feuille Lenk, Bern.

Bohle, H. W., 1969. Untersuchungen über die Embryonalentwicklung und die embryonale Diapause bei *Baetis vernus* Curtis und *Baetis rhodani* (Pictet) (Baetidae, Ephemeroptera). Zool. Jb. Anat. 86: 493–575.

Braukmann, U., 1987. Zoozönologische und saprobiologische Beiträge zu einer allgemeinen regionalen Bachtypologie. Arch. Hydrobiol. Beiheft 26: 1–355.

Breitenmoser-Würsten, Ch., 1994a. Zur Ökologie der an Fliessgewässer gebundenen Wasseramsel *Cinclus cinclus* im Saanenland. Teil I: Untersuchungen zur Fliessgewässerfauna im System der Saane. Teil II: Zur Nahrungökologie der Wasseramsel *Cinclus cinclus*. Teil III: Die Einnischung der beiden den gleichen Lebensraum bewohnenden Vogelarten Wasseramsel *Cinclus cinclus* und Bergstelze *Motacilla cinerea*. Diss. Univ. Bern.

Breitenmoser-Würsten, Ch., 1994b. Die Fliessgewässerfauna im System der Saane (Berner Oberland, Schweizer Nordalpen) als Grundlage der Nahrungsökologie der Wasseramsel (*Cinclus cinclus*). Mitt. Schweiz. Ent. Ges. 67: 77–135.

Brittain, J. E., 1976. Experimental studies on nymphal growth in *Leptophlebia vespertina* (L.) (Ephemeroptera). Freshwat. Biol. 6: 445–449.

Brooker, M. P. & D. L. Morris, 1978. Production of two species of Ephemeroptera (*Ephemerella ignita* Poda and *Rhithrogena semicolorata* (Curtis) in the upper reaches of the river Wye, Wales. Ver. Int. Ver. Limnol. 20: 2600–2604.

Clifford, H. F., 1982. Life cycles of mayflies (Ephemeroptera) with special reference to voltinism. Quaest. Ent. 18: 15–90.

Cummins, K. W., 1973. Trophic relations of aquatic insects. Ann. Rev. Ent. 18: 183–206.

Degrange, Ch., 1957. Description de l'adulte et de la nymphe de *Baetis dorieri* n.sp. (Ephemeroptera, Baetidae). Trav. Lab. Hydrobiol. Pisc. Uni. Grenoble 48-49: 17–31.

Elliott, J. M., 1983. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwat. Biol. Ass. Sci. Publ. 25: 159 pp.

Green, R. H., 1979. Sampling design and statistical methods for environmental biologists. John Wiley, New York, 257 pp.

Hawkins, C. P., 1986. Variation in individual growth rates and population densities of Ephemerellid mayflies. Ecology 67: 1384–1395.

Hefti, D. & I. Tomka, 1990. Abundance, growth and production of three mayfly species (Ephemeroptera, Insecta) from the Swiss Prealps. Arch. Hydrobiol. 120: 211–228.

Hefti, D. & I. Tomka, 1991. Mayfly communities in a prealpine stream system of Switzerland. Aquat. Sci. 53: 20–38.

Humpesch, U. H., 1979 a. Life cycle and growth rates of *Baetis* spp. (Ephemeroptera, Baetidae) in the laboratory and in two stony streams in Austria. Freshwat. Biol. 9: 467–479.

Humpesch, U. H., 1979 b. Autoökologische Untersuchungen zum Entwicklungszyklus von *Baetis alpinus* (Pict.). In: Pasternak, K. & R. Sowa (ed.), Proc. 2nd Intern. Conf. Ephemeroptera, Pol. Akad. Nauk: 159–173.

Humpesch, U. H., 1981. Effect of temperature on larval growth of *Ecdyonurus dispar* (Ephemeroptera, Heptageniidae) from two English lakes. Freshwat. Biol. 11: 441–457.

Humpesch, U. H., 1982. Effect of fluctuating temperature on the duration of embryonic development in two *Ecdyonurus* spp. and *Rhithrogena* cf. *hybrida* (Ephemeroptera) from Austrian streams. Oecologia 55: 285–288.

Illies, J. & E. C. Masteller, 1977. A possible explanation of emergence patterns of *Baetis vernus* on the Breitenbach. Int. Rev. ges. Hydrobiol. 62: 315–321.

Imhof, A., I. Tomka & G. Lampel, 1988. Autoökologische und enzymelektrophoretische Untersuchungen an zwei *Ecdyonurus venosus* Populationen (Ephemeroptera, Heptageniidae). Bull. Soc. Frib. Sc. Nat. 77: 55–129.

Jost, O., 1991. Zur Ökologie der Wasseramsel (*Cinclus cinclus*) mit besonderer Berücksichtigung ihrer Ernährung. Bonner Zool. Monogr. 6: 1–183.

Krebs, C. J., 1989. Ecological methodology. Harper and Row, New York, 654 pp.

Landa, V., 1968. Developmental cycles of central European Ephemeroptera and their interrelations. Acta ent. bohemoslov. 65: 276–284.

Lang, C., G. L'Eplattenier & O. Reymond, 1989. Water quality in rivers of western Switzerland: Application of an adaptable index based on benthic invertebrates. Aquat. Sci. 51: 224–234.

Lavandier, P., 1981. Cycle biologique, croissance et production de *Rhithrogena loyolaea* Navàs (Ephemeroptera) dans un torrent pyrénéen de haute montagne. Annls Limnol. 17: 163–179.

Lavandier, P., 1988. Semivoltinisme dans des populations de haute montagne de *Baetis alpinus* Pictet (Ephemeroptera). Bull. Soc. Hist. Nat. Toulouse 124: 61–64.

Ludwig, J. A. & J. F. Reynolds, 1988. Statistical Ecology. John Wiley, New York, 337 pp.

Magurran, A. E., 1988. Ecological diversity and its measurment. Croom Helm, London, 179 pp.

Minshall, J. N., 1967. Life history and ecology of *Epeorus pleuralis* (Banks) (Ephemeroptera: Heptageniidae). Am. Midl. Nat. 78: 369–388.

Müller-Liebenau, I., 1966. Beschreibung einer neuen deutschen Eintagsfliegen-Art. Gewäss. Abwäss. 43: 65–79.

Ormerod, S. J. & S. J. Tyler, 1991. Exploitation of prey by a river bird, the dipper *Cinclus cinclus* (L.), along acidic and circumneutral streams in upland Wales. Freshwat. Biol. 24: 105–116.

Perret, P., 1977. Etat des cours d'eau en Suisse en 1974/1975. Projet MAPOS. Office fédéral de la protection de l'environnement/EAWAG: 274 pp.

Pielou, E.C., 1975. Ecological diversity. John Wiley, New York.

Riederer, R., 1981. Die Eintags- und Steinfliegenfauna (Ephemeroptera und Plecoptera) im Mittellauf der Töss. Ph.D. Diss., ETH-Zurich, n° 6935, 169 pp.

Ritter, H., 1985. Die Ephemeropteren des Stocktalbaches (Kühtai, Tirol). Diss, Abt. Limnol. Innsbruck, 153 pp.

Sartori, M., 1987. Contribution à l'étude taxonomique et écofaunistique des Ephéméroptères de Suisse (Insecta, Ephemeroptera). Thèse Uni. Lausanne, 561 pp.

Sartori, M., 1988. Quelques compléments à la faune des Ephéméroptères de Suisse (Insecta, Ephemeroptera). Mitt. schweiz. ent. Ges. 61: 339–347.

Schmidt, H. H., 1984. Einfluss der Temperatur auf die Entwicklung von *Baetis vernus* Curtis. Arch. Hydrobiol. Suppl. 69: 364–410.

Smock, L. A., 1980. Relationships between body size and biomass of aquatic insects. Freshwat. Biol. 10: 375–383.

Snellen, R. K. & K. W. Stewart, 1979. The life cycle of *Perlesta placida* (Plecoptera: Perlidae) in an intermittent stream in northern Texas, USA. Ann. Ent. Soc. America 72: 659–666.

Sokal, R. R. & C. D. Michener, 1958. A statistical method for evaluating systematic relationships. Univ. Kansas Sc. Bull. 38: 1409–1438.

Sowa, R., 1975a. Ecology and biogeography of mayflies (Ephemeroptera) of running waters in the Polish part of the Carpathians. 1. Distribution and quantitative analysis. Acta Hydrobiol. 17: 223–297.

Sowa, R., 1975b. Ecology and biogeography of mayflies (Ephemeroptera) of running waters in the Polish part of the Carpathians. 2. Life cycles. Acta Hydrobiol. 17: 319–353.

Studemann, D., P. Landolt, M. Sartori, D. Hefti & I. Tomka, 1992. Ephemeroptera. Insecta Helvetica Fauna 9: 175 pp.

Sweeney, B. W., 1984. Factors influencing life-history patterns of aquatic insects. In: V.H. Resh & D.M. Rosenberg (eds), The ecology of aquatic insects: 56-100. Praeger Scientific, New York, 625 pp.

Thibault, M. 1971. Le développement des Ephéméroptères d'un ruisseau à truites des Pyrénées-Atlantiques, le Lissuraga. Annls Limnol. 7: 53- 120.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Can. J. Fish. Aq. Sci. 37: 130–137.

Vinçon, G. & A. G. B. Thomas, 1987. Etude hydrologique de la vallée d'Ossau (Pyrénées-Atlantiques). I. Répartition et écologie des Ephéméroptères. Annls Limnol. 23: 95–113.

Waters, T. F. & G. W. Crawford, 1973. Annual production of a stream mayfly population: a comparison of methods. Limnol. Oceanogr. 18: 286–296.

Weichselbaumer, P., 1984. Die Populationsdynamik von *Baetis alpinus* (Pictet) und anderer Baetidae (Ephemeroptera) in einem kleinen Mittelgebirgbach (Piburger Bach, Tirol). Diss. Abt. Limnol. Innsbruck, 171 pp.

Wise, E. J., 1980. Seasonal distribution and life histories of Ephemeroptera in a Northumbrian river. Freshwat. Biol. 10: 101–111.

Zwick, P., 1992. Stream habitat fragmentation - a threat to biodiversity. Biodiversity & Conservation 1: 80–97.