Mayfly communities in a prealpine stream system of Switzerland

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ABSTRACT

The mayfly fauna of twelve localities belonging to a calcareous stream system of the Swiss Prealps was investigated during the last three years. The stream system was divided into three distinct topographical sections, each characterized by specific thermic and geomorphologic components. Thirty-five mayfly species, that belonged to different faunistic groups according to their respective longitudinal distribution, were found. A coefficient of interspecific association was determined for every pair of species. Non-parametric indices of diversity, as well as a parametric analysis, were calculated for the three stations investigated quantitatively. The faunistic classification of the twelve stations reflected the main topographical organization of the stream system.

Introduction

Neither organisms nor species exist by themselves in nature. They are always part of a larger entity known as a community, which can be defined generally as "any assemblage of populations of living organisms in a prescribed area or habitat" (Krebs, 1987). As all ecological constraints of an ecosystem act finally at species level, the changes in community structure can be used to investigate the effect of varying physico-chemical parameters on the local fauna. This topic is of fundamental interest to pure and applied ecology. In running water systems, the longitudinal zonation of species is a natural phenomenon. As a consequence, the taxonomic elements of aquatic communities change along the river course. Due to the complexity of the system, it becomes extremely difficult to isolate natural change from that brought about by human agency. It is, therefore, particularly useful to be able to provide a descriptive analysis of aquatic communities in an unperturbed drainage basin constituted of various, different ecological components.

In the present study, the concept of community was not applied to the whole biocoenosis but was restricted to the Ephemeroptera, a distinct order of benthic insects. This reduction allowed us to work at species level, which is the true ecological

unit. The aim of the study was to describe qualitatively the structure of mayfly communities living in a swiss prealpine calcareous stream and to investigate the interaction of the insect communities with abiotic parameters. A quantitative analysis was also performed, using three stations of different topographical section. Quantitative indices like the diversity, the equitability and rank-abundance diagrams, as well as the taxonomic composition were used to compare the different communities (May, 1973, 1975; Cody and Diamond, 1975; Pielou, 1969, 1975).

Methods

Presentation of the stream system

The river "Singine" (canton Fribourg, Switzerland) belongs to the drainage basin of the Rhine. The stream flows on the north-western side of the Swiss Prealps, ranging in altitude from 1400 to 490 m and with catchment area of 352 km^2.

Geologically, the stream system originates in a limestone formation with intercalations of marl (Imhof, 1965/1978). The system exhibits two hydrologic regimes (Aschwanden and Weingartner, 1985): its upper part is a nival transition regime with a maximum Pardé coefficient of 1.4 to 2.2 (April to June), and in its lower part the flow is typical for a nivo-pluvial regime with a maximum Pardé coefficient of 1.5 to 1.8 (April to June).

Topographically, the Singine system can be divided into three sections (Fig. 1): the lowest part of the system includes stations 1–4 and is called "Singine" (490–870 m); the medial section, called "Warm Singine", includes stations 5 to 7 (870–1040 m), station 7 being situated in a lake ("Lac Noir"). Station 8 is situated above the "Lac Noir". The highest section, "Cold Singine", includes stations 9 to 12 (870–1490 m). The stream system belongs to the salmonid region (Huet, 1949) and it presents all the possible longitudinal zonations from the eucrenal to the hyporhithral (Illies, 1961; Illies and Botosaneanu, 1963). The twelve stations investigated cover the whole altitudinal range.

Physico-chemical analysis

All stations investigated were characterized physico-chemically with the exception of station 3 which exhibited characters almost identical with those of station 2. pH, electrical conductivity (EC) and oxygen concentration (O_2) were measured potentiometrically with WTW pH 90, WTW LF 91 and WTW oxi 90 respectively. Alkalinity (Alk) and total (TH) and non-carbonate hardness (NCH) were determined by titration according to Höll (1979) and by complexometric titration according to Schwoerbel (1980). Biochemical oxygen demand for five days (BOD_5) was determined by the Winkler method and the concentrations of total phosphorus (P), ammonium (NH_4^+), nitrite (NO_2^-) and nitrate (NO_3^-) were measured photometrically using Merck-kits no. 14788, 14752, 14776 and 14773 respectively. Temperature was considered as annual amplitude.
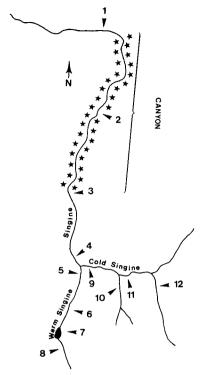
Figure 1. Geographical location of the stream system investigated, with the position of the twelve sampling stations

Sampling

a) Qualitative sampling

For the qualitative analysis of communities, kick samples (mesh size: 0.70 mm; surface 0.10 m^2) were collected monthly over three years (1987–1989). The sampling program took into consideration all ecological niches present at the stations in order to collect the maximum number of species. Larval material was preserved in 80% alcohol. Subimagines and imagines were collected in the field with an air net, and last larval instars were reared in the laboratory. The specimens were determined at species level with the aid of a binocular-magnifier or a microscope.

b) Quantitative sampling

Stations 2, 6 and 12 (one station from each of the three distinct sections) were chosen for quantitative analysis. Mayfly larvae were sampled during one year (monthly between April and September and bimonthly between October and March), using a modified surber net (mesh size: 0.70 mm; surface: 0.0625 m^2). Sampling units were randomly collected in the substrate at a depth of about 10 cm. The degree of precision

of the sample size was estimated for a 95% confidence limit (Elliott, 1983) and equals 20% for station 2, 10% for station 6 and 30% for station 12. The material was extracted alive by flotation with a 350 mg/l $MgSO_4^-$ solution and preserved in 80% alcohol for further analysis.

Analysis of data

The coefficient of interspecific association (*CA*) was calculated for each pair of species. This coefficient measures the strength of association between two species and has values ranging from −1 (absolute negative association) through 0 (no association) to 1 (absolute positive association) and was calculated from presence-absence data as follows (Cole, 1949):

$$CA = ((Npp\ Naa) - (Nap\ Npa))/((Npp + Nap)\ (Npa + Naa)$$
$$(Npp + Npa)\ (Nap + Naa))^{0.5} \tag{1}$$

where Npp is the number of times both species are present at the same station, Naa the number of times both species are absent at the same station, Npa the number of times the first species is present and the second one is absent.

α-diversity

The distribution of species in the community was calculated at the three stations sampled quantitatively (stations 2, 6 and 12). The quantitative sampling was repeated ten times during one year and the frequencies of the species were averaged over these ten samples. Two non-parametric indices were chosen because of being independent of any type of distribution (Southwood, 1978). The first index chosen was the Shannon-Weaver function (*H*), which determine the magnitude of diversity in a community (Shannon and Weaver, 1962):

$$H = -\Sigma\, p_i \log_2 p_i \tag{2}$$

where p_i equals the fraction of numbers of individuals belonging to the ith species.
    The second one was the Simpson index (*SI*), which describes the probability that a second individual drawn from a population should be of the same species as the first (Simpson, 1949):

$$SI = 1 - \Sigma\,(p_i)^2 \tag{3}$$

For a defined number of species (*S*), it is possible to determine a normalized diversity indice known as equitability or evenness. This factor defines the proportion of the maximum possible values that should be found by $H = (\log_2 S)$ and $SI = (1 - 1/S)$ when individuals are completely evenly distributed (Margalef, 1958; Pielou, 1966). The equitability index ranges from 0 in the case of the lowest diversity (one species present) to 1 in the case of even distribution of species (Pielou, 1969).

MacArthur (1957) showed that these distributions are never found in natural communities. Rather, he was able to describe tropical communities with the most highest diversity, giving the frequency of species according to its "broken-stick model". Lloyd and Ghelardi (1964) calculated an index ($E_{\text{MacArthur}}$) for the equitability of the actual species distribution taking the "broken-stick model" as a working hypothesis. They give a conversion table between E from Shannon and E from MacArthur ($E_{\text{MacArthur}}$). This table was used in the present study.

β-diversity

Spatial comparison of the faunistic composition was investigated using the Sörensen coefficient (*SC*). This coefficient is a simple measure of the extent to which two habitats have species in common:

$$SC = 2J/(A + B) \tag{4}$$

where J equals the number of species present at both stations, A equals the number of species found at the first and B at the second station. It also ranges from zero (no affinity) to one (absolute identity).

Results

Abiotic factors

All stations investigated belong to the rhithral zonation, with the exception of station 7. The abiotic parameters recorded are listed in Table 1.

The first part of the stream system (stations 1 to 4 in Fig. 1) exhibits distinct geomorphological features. The mean slope of the section is low (0.6%) and the channel follows large meanders. Downstream the bed has dug a deep canyon between two high walls of sandstone (station 2). An annual thermal amplitude of 23 °C (-1 to 22 °C) was measured at station 2.

The physico-chemical components of the section "Warm Singine" (stations 5 and 6 in Fig. 1) are affected by the existence of the upper lake (station 7) and by local human activity at station 6 (cf. *P*-values in Table 1). An annual thermal amplitude of 20 °C (0 to 20 °C) was recorded at station 6. The geochemical parameters are not significantly different from the downstream section of the stream. Nitrification processes between stations 6 and 5 can be seen in changes in the ratio $N-NH_4^+/N-NO_3^-$ and reflect the good aeration and buffering capacities of the system (cf. % of O_2 saturation and alkalinity).

The section "Cold Singine" (stations 9 to 12 in Fig. 1) has a typical torrenticol character with cold water flowing through an heterogeneous substrate. An annual thermal amplitude of 13 °C (-1 to 12 °C) was measured at station 12. The geochemical parameters show the extremely calcareous character of the water at station 10 (EC = 742 μS/cm; TH = 157.90 mg/l). The nutrient parameters (BOD$_5$, P, $N-NH_4^+$, $N-NO_2^-$, $N-NO_3^-$) are low, explaining the poor productivity of this

Table 1. List of the abiotic parameters recorded for the twelve stations investigated, showing mean values (with their standard deviation in brackets) and the number of measurements. (* for a detailed analysis of the temperature see Hefti and Tomka, 1991)

Physical and geochemical factors :

Stations :	1.	2.	4.	5.	6.	7.	8.	9.	10.	11.	12.
Thermic amplitude over one year (°C)		23* (-1 to 22)			20* (0 to 20)					13 (-1 to 12)	
pH	8.30 (0.26) 8	8.25 (0.35) 27	8.50 (0.17) 6	8.50 (0.19) 4	8.20 (0.25) 25	8.10 (0.29) 10	8.20 - 1	8.50 (0.14) 5	8.20 (0.32) 15	8.10 (0.25) 10	8.20 (0.22) 24
Electrical conductivity EC (μS/cm)	375 (39) 9	370 (52) 27	404 (75) 6	403 (51) 4	415 (71) 28	370 (54) 10	360 - 1	418 (90) 5	742 (202) 16	340 (50) 10	444 (95) 23
Alkalinity Alk. (mVal/l)	3.20 (0.37) 8	2.80 (0.30) 21	3.00 (0.33) 5	3.00 (0.18) 2	2.70 (0.30) 19	2.70 (0.30) 8	2.80 - 1	2.90 (0.12) 3	2.80 (0.24) 10	2.70 (0.28) 8	2.80 (0.24) 14
Total hardness TH (mg/l)	80.90 (10) 8	82.40 (14) 14	88.50 (14) 5	87.80 (10) 2	94.40 (18) 18	88.10 (16) 16	- - -	83.60 (16) 3	157.90 (50) 9	72.10 (6) 8	102.60 (27) 14
Non carbonate hardness NCH (mVal/l)	0.85 (0.40) 8	1.35 (0.60) 21	1.45 (0.60) 5	1.30 (0.30) 2	2.00 (0.80) 19	1.75 (0.70) 8	- - -	1.30 (0.70) 3	5.00 (2.40) 9	0.85 (0.30) 8	2.35 (1.30) 14

Chemical factors :

Stations :	1.	2.	4.	5.	6.	7.	8.	9.	10.	11.	12.
Oxygen concentration O_2 (mg/l) % saturation	11.80 (2.30) 5 104	11.50 (1.85) 12 101	10.40 (0.90) 2 105	- - - -	10.00 (1.20) 19 98	9.90 (0.85) 8 90	11.30 - 1 -	11.40 - 1 107	10.10 (0.95) 4 98	10.20 (0.80) 5 95	10.30 (0.75) 11 98
Biochemical oxygen demand BOD_5 (mg/l)	1.00 (0.65) 5	1.00 (0.40) 17	- - -	- - -	1.80 (0.40) 19	1.60 (0.70) 7	- - -	- - -	0.70 (0.70) 6	- - -	0.50 (0.40) 11
Phosphorus total P (μg/l)	16 (6) 3	14 (17) 17	7 (9) 6	6 (7) 4	26 (15) 16	8 (5) 11	4 - 1	3 (3) 5	7 (4) 8	3 (1) 4	9 (10) 14
$N-NH_4^+$ (μg/l)	65 (25) 3	367 (560) 13	40 (23) 6	35 (39) 4	109 (104) 16	154 (226) 10	20 - 1	53 (41) 5	29 (13) 6	27 (23) 3	38 (59) 13
$N-NO_2^-$ (μg/l)	6 (5) 3	6 (5) 12	8 (8) 6	5 (5) 4	16 (12) 17	6 (3) 11	1 - 1	4 (2) 5	4 (3) 7	1 (1) 4	2 (2) 13
$N-NO_3^-$ (μg/l)	1100 (834) 3	691 (270) 13	401 (208) 6	537 (312) 4	297 (125) 16	287 (134) 11	250 - 1	320 (92) 5	462 (236) 7	378 (375) 3	391 (334) 14

section. Station 8 exhibits physico-chemical properties similar to those of this section, despite its distinct topographical localization.

Community structure and longitudinal zonation

Thirty-five species of mayflies have been found at the twelve stations investigated (Table 2). On the basis of their respective longitudinal distribution, it is possible to group the taxa in several faunistic groups with different ecological requirements:

Group 1:
The first group includes eurybiontic species with a common longitudinal distribution but always associated with running water (stations 1–6 and 8–12): *Ecdyonurus venosus, Rhithrogena hercynia, R. hybrida, R. semicolorata, Baetis alpinus, B. rhodani and Habroleptoides confusa* (the latter not being recorded at station 8).

Group 2:
The second group includes species restricted to definite sections of the stream:

Sub-group 2.1:
The two limnophilic species *Leptophlebia marginata* and *Siphlonurus lacustris* are present only in the lake (station 7).

Sub-group 2.2:
Centroptilum luteolum, Ephemera danica and *Caenis beskidensis* are restricted to the "warm" sections of the stream system (stations 1 to 6) and to the lake (station 7). The distribution of *Habrophlebia lauta* in running water is exclusively restricted to the "Warm Singine".

Sub-group 2.3:
a) *Ephemerella ignita* and *E. major* are temperature dependent (stations 1 to 6) but only associated with running waters and are absent from the lake.
b) *Baetis fuscatus, B. lutheri, B. melanonyx, B. scambus,* and *B sinaicus* are distributed along the warm lowing sections of the Singine (stations 1 to 6) as well as the lowest part of the cold section (station 9), reflecting a slight torrenticol character.

Sub-group 2.4:
a) *Epeorus alpicola* (stations 8 to 12) is typically associated with a cold and torrenticol habitat. *E. sylvicola* has the same habitat but replaces *E. alpicola* downstream.
b) *Ecdyonurus parahelveticus* and *Habroleptoides auberti* are also found in the cold section, specifically in tributaries of high calcium content (stations 8, 10 and 12).

Sub-group 2.5:
Ecdyonurus torrentis, Ephemerella mucronata and *Oligoneuriella rhenana* exhibit the lowest altitudinal distribution and are the characteristic species of the hyporhithron (stations 1 and 2).

Table 2. List of the taxa recorded in the twelve stations investigated. A sign in brackets indicates an imaginal catch but that no larvae were sampled

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
Heptageniidae												
1. Ecdyonurus helveticus	-	+	+	+	+	+	-	+	+	+	+	+
2. E. parahelveticus	-	-	-	-	-	-	-	+	-	+	-	+
3. E. picteti	-	+	+	+	+	-	-	+	+	+	+	+
4. E. torrentis	+	+	-	-	-	-	-	-	-	-	-	-
5. E. venosus	+	+	+	+	+	+	-	+	+	+	+	+
6. Electrogena lateralis	+	+	+	+	+	+	-	-	+	-	+	-
7. Epeorus alpicola	-	-	-	-	-	-	-	+	+	+	+	+
8. E. sylvicola	+	+	+	+	+	+	-	-	(+)	-	+	-
9. Rhithrogena alpestris	-	+	-	-	-	-	-	-	-	-	-	+
10. R. dorieri	-	+	-	-	-	+	-	-	-	+	-	-
11. R. hercynia	+	+	+	+	+	+	-	+	+	+	+	+
12. R. hybrida	+	+	+	+	+	+	-	+	+	+	+	+
13. R savoiensis	+	+	+	+	-	-	-	-	+	-	-	-
14. R. semicolorata	+	+	+	+	+	+	-	+	+	+	+	+
Baetidae												
15. Baetis alpinus	+	+	+	+	+	+	-	+	+	+	+	+
16. B. fuscatus	+	+	+	+	+	+	-	-	+	-	-	-
17. B. lutheri	+	+	+	+	+	+	-	-	+	-	-	-
18. B. melanonyx	+	+	+	+	+	+	-	-	+	-	-	-
19. B. muticus	+	+	+	+	+	+	-	-	+	-	+	+
20. B. rhodani	+	+	+	+	+	+	-	+	+	+	+	+
21. B. scambus	+	+	+	+	+	+	-	-	+	-	-	-
22. B. sinaicus	+	+	+	+	+	+	-	-	+	-	-	-
23. Centro. luteolum	+	+	+	+	+	+	+	-	-	-	-	-
Ephemerellidae												
24. Ephemerella ignita	+	+	+	+	+	+	-	-	-	-	-	-
25. E. major	+	+	+	+	+	+	-	-	-	-	-	-
26. E. mucronata	+	+	-	-	-	-	-	-	-	-	-	-
Ephemeridae												
27. Ephemera danica	+	+	+	+	+	+	+	-	-	-	-	-
Oligoneuriidae												
28. Oligo. rhenana	+	+	-	-	-	-	-	-	-	-	-	-
Leptophlebiidae												
29. Habrolept. auberti	-	-	-	-	-	-	-	-	-	+	-	+
30. H. confusa	+	+	+	+	+	+	-	-	+	+	+	+
31. Habrophlebia lauta	-	-	-	-	+	+	+	-	-	-	-	-
32. Para. submarginata	-	-	-	-	-	+	-	-	-	-	-	-
33. Lepto. marginata	-	-	-	-	-	-	+	-	-	-	-	-
Caenidae												
34. Caenis beskidensis	+	+	+	+	+	+	+	-	-	-	-	-
Siphlonuridae												
35. Siphlonurus lacustris	-	-	-	-	-	-	+	-	-	-	-	-

Sub-group 2.6:
This group includes several species with a large range of longitudinal distribution but which tend to disappear downstream (*Ecdyonurus helveticus, E. picteti*).

Sub-group 2.7:
Paraleptophlebia submarginata is present only at station 6, where high concentrations of nutrients were recorded.

Sub-group 2.8:
This group includes one species related to the combination of morphological and thermal conditions (*Rhithrogena savoiensis*).

Group 3:
Discontinous longitudinal zonation was found for the remaining species which had distributions that were essentially related to local factors. *Electrogena lateralis* and *Baetis muticus* are located in running water with silty substrates and aquatic vegetation respectively. Stations 7, 8 and 10 are lacking in such habitats although *E. lateralis* was not found in station 12 which did possess the required habitat as demonstrated by the presence of *B. muticus*. *Rhithrogena alpestris* and *R. dorieri* are two rare species in this stream system and their low abundances prevent the establishment of a clear longitudinal zonation.

Coefficients of interspecific association

The coefficient of interspecific association calculated for each pair of species (Eq. 1) has been combined with tests for significance using a contingency table with Yates' correction for continuity (Bailey, 1981). Results are shown in Table 5 where the associations are listed for different levels of precision. Three groups of species show an absolute negative correlation ($CA = -1$): *Epeorus alpicola – Centroptilum luteolum, E. alpicola – Ephemera danica* and *E. alpicola – Caenis beskidensis*. In contrast there are many species-pairs which are always found together at the same station ($CA = +1$).

α-diversity

α-diversity and equitability have been calculated for the three stations investigated quantitatively (stations 2, 6 and 12) using the indices discussed above (Eqs. 2 and 3). The highest diversity and equitability were recorded at station 6 (Table 3). Differences in diversity (H and SI) between the three communities are highly significant (*t*-test, $P < 0.001$). The Shannon (H) and Simpson (SI) diversity indices are correlated with each other but are independent from the richness (S) of the communities.

Another attempt to describe a community makes use of the frequency of each taxon by plotting it against rank on a logarithmic scale. This parametric method allows a direct comparison of species distribution in a community. The rank

Table 3. Species richness (S), index of diversity of Shannon (H) and of Simpson (S), equitability of Shannon $(E_{Shannon})$ and of Simpson $(E_{Simpson})$ as well as that of MacArthur $(E_{MacArthur})$ for the three stations investigated quantitatively

	Station 2		Station 6		Station 12	
S :	28		24		14	
H :	2.58	(±0.52)	3.03	(±0.30)	0.98	(±0.29)
SI :	0.68	(±0.14)	0.83	(±0.08)	0.25	(±0.07)
E Shannon :	0.54	(±0.11)	0.66	(±0.07)	0.26	(±0.08)
E.Simpson :	0.71	(±0.14)	0.87	(±0.09)	0.27	(±0.08)
E.McArthur :	0.30	(±0.06)	0.48	(±0.05)	0.18	(±0.05)

Fig. 2. Rank-abundance diagram of station 12. The sigmoid curve indicates the optimum "MacArthur's distribution". Numbers on the abscissa refer to the species numerotation (cf. Table 2)

Figure 3. Rank-abundance diagram of station 6. The sigmoid curve indicates the optimum "MacArthur's distribution". Numbers on the abscissa refer to the species numerotation (cf. Table 2)
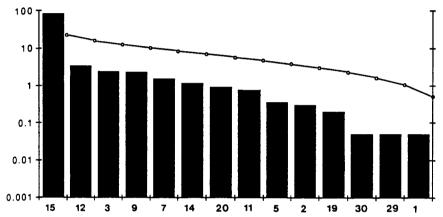
Figure 4. Rank-abundance diagram of station 2. The sigmoid curve indicates the optimum "MacArthur's distribution". Numbers on the abscissa refer to the species numerotation (cf. Table 2)
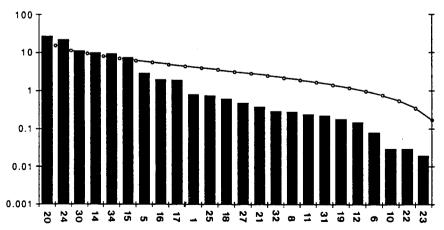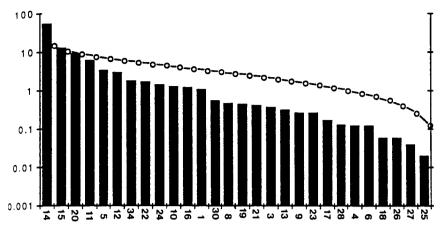
abundance diagrams of stations 2, 6 and 12 are presented on Figs. 2–4. Station 6 has the profile most similar to that proposed by MacArthur and accordingly the station has the highest diversity (H, SI).

β-diversity

The pairwise faunistic affinities of the twelve stations have been calculated using the Sörensen coefficient (Eq. 4). The results, summarized in a matrix (Table 4), show the absolute faunistic identity between stations 3 and 4 ($SC = 1$) and the absolute faunistic dissimilarity between station 7 and the stations 8 to 12 ($SC = 0$). The matrix has been clustered according to the unweighted pair-group arithmetic average (UPGMA) method (Ferguson, 1980) to obtain a hierarchical classification based on faunistic affinities. The classification obtained is shown, in the form of a dendrogram, in Fig. 5.

Discussion

Longitudinal zonation

Thirty five species of mayfly are present in the three branches of the Singine system. According to the faunistic surveys of Zurwerra and Tomka (1984), Sartori and Dethier (1985) and Sartori (1988), this number represents more than one third of the total Swiss mayfly fauna. The faunistic richness of the system can be explained by the diversity of the natural habitats of the stream (e.g. the existence of three distinct topographical "axes") and by the relative good quality of the water. With the exception of four rare taxa (*E. parahelveticus*, *R. dorieri*, *B. sinaicus* and *O. rhenena*), all other species are quite common faunistic elements in Switzerland. The most
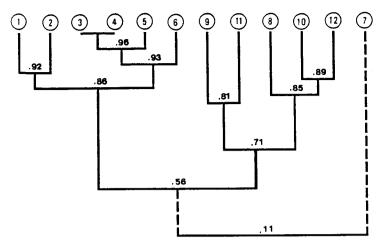
Figure 5. Dendrogram showing the faunistic classification of the twelve stations investigated

abundant taxa belong to the families Heptageniidae and Baetidae, both typical fauna elements of prealpine and alpine streams.

The changes in taxonomic composition recorded between the different stations show the existence of a longitudinal gradient regulated by abiotic factors, independent from local specific characteristics like substrate structure, current velocity (etc.) which belong to the description of the niche. These factors are responsible for the longitudinal distribution of mayflies and can be considered as limiting factors. Apart from the eurybiontic species (group 1) and those of low abundance (group 3), the occurrence of the other mayfly species is mainly related to the temperature regime (sub-groups 2.2; 2.3; 2.4a), to the fluvial character (sub-group 2.1) or to a subtle combination of morphological and thermal conditions (sub-groups 2.5; 2.6; 2.8). These factors were also recognized as the determinant in the distribution of mayfly communities in a stream system in the Atlantic Pyrenees (Vinçon and Thomas, 1987). Temperature is evidently an essential limiting factor which acts directly at the embryonic or post-embryonic development level (Humpesch, 1980a, b, 1981). As a consequence, each species is restricted physiologically to definite sections of a stream. The "fluvial character" or the "stream hydraulics" emphasized by Stazner and Higler (1986) are also important factors which determine different types of environments. In the present study, two species (*S. lacustris* and *L. marginata*) are restricted to a limnic habitat. Despite the fact that the first of these species can also be found in running water (Elliott et al., 1988; Zurwerra and Tomka, 1984), none were collected in lentic sections of the stream in the present study. This demonstrates the specific ecological characteristics of limnic habitat in contrast with those of lentic portions of the stream.

Some authors (Avery, 1970; Minshall and Minshall, 1978; Ormerod et al. 1987; Townsend et al., 1983, 1987) describe the occurrence of significant modifications in aquatic communities induced by geo- or chemical factors. In the present study, these factors do not seem to strongly influence the natural distribution of mayfly species, with some exceptions:

- *H. lauta* and *P. submarginata* are only present in discrete sections of the "Warm Singine", their occurrence showing no apparent relationship to temperature or to fluvial or geomorphological factors. This singular distribution is correlated with the heterotrophic activities recorded at stations 6 and 7, as suggested by the BOD_5-values (Table 1) and by the high nutrient input at station 6 (cf. P-concentration on Table 1), probably due to human activity. The specific localization of both species can be explained by their detritivorous diet (Pleskot, 1953) and is in agreement with our own observation on their geographical distribution in Switzerland, where both taxa colonize only eutrophic streams.
- *E. parahelveticus* and *H. auberti* also exhibit a restricted distribution which is related to both the temperature, and to the high concentration of calcium dissolved in the water (cf. station 10 and 12 in Table 1). This ion has been recognized as an important abiotic factor in the distribution of mayflies (Hefti et al., 1985, 1986) and aquatic organisms (Tucker, 1958; Macan, 1974).

Coefficients of interspecific association (CA)

The measure of interspecific association between taxa is a further step in the characterization of communities. Groups of species with high positive correlation have partially identical ecological requirements or species with high negative correlation are mutually excluded because of ecological incompatibility. The significant absolute negative correlation recorded between *E. alpicola* and *C. luteolum*, *E. danica* and *C. beskidensis* illustrate their different temperature requirements. *E. alpicola* is a cold stenotherm, living exclusively in a torrenticol habitat. In the present study, its occurrence was found to be restricted to sections of the stream where the mean temperature never exceeds 12 °C.

The coefficients used in the present study are slightly biased because they are influenced by the species frequencies (Hurlbert, 1969). Furthermore, the establishment of a significant positive association between species should not necessarily be interpreted as a causal relationship based on interspecific interactions (Wratten and Fry, 1980).

α-diversity

Description of α-diversity using non-parametric indices like those of Shannon-Weaver (H) or Simpson indices (SI) is mainly based on theoretical considerations and is complicated by conceptual difficulties (Hurlbert, 1971). Relative indices, such as those of Lloyd and Ghelardi (1964) compare the equitability of the distribution with the assumption that the species are distributed according to the MacArthur model ($E_{MacArthur}$ in Table 3). These values of equitability express a more realistic situation than those of Shannon and Simpson where maximum diversity implies an absolutely even numerical distribution of species.

The lowest diversity was recorded at station 12 and it confirms the general assumption that headwaters have a moderate or low diversity (Vannote et al., 1980). Despite high allochthonous input at the head water, mainly in the form of fallen leaf,

the energy content is only processed and released downstream because the temperature regime is too low in the upper section. The extreme conditions of such environments allow only a few specialists, typical of pioneer communities, to live (Patrick, 1970).

Because of the natural gradient of mean temperature elevation, the diversity and equitability of communities tend to increase downstream. In the present study the fact that the values of these parameters are higher at station 6 than at station 2 (despite a lower richness) can be explained by the presence of a lake above station 6 which regulates its temperature regime, providing a stable thermic environment and affecting its energy input by the release of detritus and organic material. As a consequence, the abundance of the detritivorous species (*H. lauta*, *H. confusa*, *P. submarginata*), normally present at low densities in prealpine streams, is enhanced, providing a more even numeric distribution among the species. This is typically the case for the species *H. confusa* (Hefti and Tomka, 1991), which is much more abundant at station 6 than downstream (Fig. 3). A similar observation has also been made by Townsend et al. (1983) on benthic invertebrates, and it is reinforced by some personal observations of species of Trichoptera in the Singine, where net-spinning species (detritivorous), abundant at station 6, become significantly scarcer downstream and are progressively replaced by predator species.

A more complete description of species abundances in a community is obtained when the frequency of each taxon is plotted against rank (parametric method). From a theoretical point of view, linear relationships between log abundance and rank correspond to a geometric series distribution (Motomura, 1947), mainly recorded in pioneer communities (Whittaker, 1970; Meijer, 1980). This model assumes that the most successful species fills up a fraction k of the total niche space, the next species a fraction k of the remainder and so on. Successive stages exhibit more a even distribution like the log-normal one (Preston, 1948), a purely statistical model with no evident biological meaning (May, 1975) or the more equitable "Broken Stick" distribution (MacArthur, 1957), predicting an intrinsically even division of the environment among the species. This latter distribution presents slightly sigmoidal ranked abundance plots on a semi-log scale. Despite some problems in the fitting of

Table 4. Matrix of the faunistic affinity recorded between the twelve stations investigated using the Sörensen coefficient

	2	3	4	5	6	7	8	9	10	11	12
1	.92	.89	.89	.85	.83	.20	.35	.74	.38	.54	.42
2		.90	.90	.86	.85	.18	.42	.76	.49	.58	.52
3			1	.96	.89	.21	.48	.86	.50	.67	.54
4				.96	.89	.21	.48	.86	.50	.67	.54
5					.94	.28	.48	.81	.50	.67	.54
6						.27	.41	.74	.49	.59	.47
7							0	0	0	0	0
8								.62	.87	.78	.83
9									.62	.81	.67
10										.77	.89
11											.81

Table 5. Coefficient of interspecific association ranging from -1 through 0 to 1 ($*P<0.05$; $**P<0.01$) between each pair of species

	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)	(22)	(23)	(24)	(25)	(26)	(27)	(28)	(29)	(30)	(31)	(32)	(33)	(34)	(35)
E. helv. (1)	.26	.77	-.40	.67	.16	.38	.16	.20	.26	.67	.67	-.08	.67	.67	.08	.08	.08	.26	.67	.08	.08	-.38	0	0	-.40	-.38	-.40	.20	.40	-.26	.13	-.67	-.38	-.67
E. para. (2)		.33	-.26	.17	-.82*	-.68	-.82	.26	-.11	.17	.17	-.49	.17	.17	-.68	-.68	-.68	-.56	-.17	-.68	-.68	-.68	-.58	-.58	-.26	-.68	-.26	.77	-.26	-.33	-.17	-.17	-.68	-.17
E. pict. (3)			-.26	.52	0	.49	0	.26	-.11	-.52	-.52	.10	-.52	.52	-.10	-.10	-.10	.11	.52	-.10	-.10	-.49	-.19	-.19	-.26	-.49	-.26	.26	.26	-.56	-.52	-.52	-.49	-.52
E. torr. (4)				.13	.32	-.38	.32	.40	.26	.13	.13	.52	.13	.13	.38	.38	.38	.52	.13	.38	.38	.38	.45	.45	1*	.38	1*	-.20	.20	-.26	-.13	-.13	-.38	-.13
E. veno.(5)					.43	.25	.43	.13	.17	1	1	.53	1	1	.36	.36	.36	.52	1	.36	.36	.38	.71	.30	.13	-.25	.13	.13	.67	-.52	.09	-1	.48	-1
E. lut. (6)						.48	1*	-.16	0	.43	.43	.60	.43	.43	.84*	.84*	.84*	.82*	.43	.84*	.84*	.48	.71	.71	.32	.48	.32	.13	.63	0	.21	-.43	.48	-.43
E. alp. (7)							-.48	.08	-.10	.25	.25	-.37	.25	.25	-.66	-.66	-.66	-.29	.25	-.66	-.66	-.1**	-.84*	-.84*	-.38	-.1**	-.38	-.63	.08	.49	-.25	-.25	-.1**	-.25
E. sylv. (8)								-.16	0	.43	.43	.60	.43	.43	.84	.84	.84	.82	.43	.84	.84	.48	.71*	.71*	.38	.48	.38	.53	.63	0	.21	-.43	.48	-.43
R. alpe. (9)									.26	.13	.13	.08	.13	.13	-.08	-.08	-.08	.26	.13	-.08	-.08	-.08	0	0	.13	-.08	.13	.53	.20	-.49	-.13	-.13	.48	-.13
R. dorl. (10)										.17	.17	-.10	.13	.17	-.10	-.10	-.10	-.11	.17	.10	.10	.10	.19	.19	.13	.10	.13	-.10	.26	0	.52	-.17	.10	-.17
R. bere. (11)											1	.17	1	1	.36	.36	.36	.52	1	.36	.36	-.25	.30	.30	.13	-.25	.13	.13	.67	-.26	.09	-1	-.25	-1
R. hybr. (12)												.17	1	1	.36	.36	.36	.52	1	.36	.71	.37	.30	.30	.13	-.25	.13	.13	.67	.11	.09	-.25	-.25	-.25
R. savo. (13)													.25	.25	.71	.71	.71	.49	.25	.71	.71	.37	.51	.51	.13	.37	.13	.13	.38	-.52	-.25	-1	.37	-1
R. semi. (14)														1	.36	.36	.36	.52	1	.36	.36	-.25	.30	.30	.13	-.25	.13	.13	.67	-.52	.09	-1	-.25	-1
B. alpi. (15)															.36	.36	.36	.52	1	.36	.36	-.25	.30	.30	.13	-.25	.13	.13	.67	-.49	.09	-.36	-1	-.36
B. fusc. (16)																1**	1**	.68	.36	1**	1**	.66	.84*	.84*	.38	.66	.38	.13	.67	-.52	.09	-.36	-.25	-.36
B. luth. (17)																	1**	.68	.36	1**	1**	.66	.84*	.84*	.38	.66	.38	.13	.67	-.52	.09	-.36	-.25	-.36
B. mela. (18)																		.68	.36	1**	1**	.66	.84*	.84*	.38	.66	.38	.13	.67	-.52	.09	-.52	-.25	-.52
B. mutl. (19)																			.52	.68	.68	.29	.58	.58	.26	.29	.26	.13	.67	-.11	.17	-.52	-.25	-1
B. rhod. (20)																				.36	.36	-.26	.30	.30	.13	-.25	.13	-.53	.53	-.52	.09	-.36	-.25	-.36
B. scam. (21)																					1**	.66	.84*	.84*	.38	.66	.38	.13	.53	.10	.25	-.36	.66	-.36
B. sina. (22)																						.66	.84*	.84*	.38	.66	.38	.13	.53	.10	.25	-.52	.66	-.52
C. lute. (23)																							.84	.84	.45	.66	.45	-.20	.77	-.11	.09	-.36	.66	.25
E. igni. (24)																								1**	.45	.84*	.45	-.45	.53	.10	.25	-.52	1*	-.30
E. majo. (25)																									.45	.84*	.45	-.45	.45	.19	.30	-.30	.84*	-.30
E. macr. (26)																										.38	1*	-.20	.45	.19	.30	-.30	.84*	-.30
E. danic. (27)																											.38	-.53	.20	-.26	.25	-.13	.38	-.13
O. rhen. (28)																												-.20	.08	.49	-.13	-.25	1**	-.25
H. mbe. (29)																													.20	-.26	-.13	-.13	.38	-.13
H. conf. (30)																														-.26	.13	-.67	-.53	-.13
H. lent. (31)																															.13	-.67	.08	-.67
P. sabm. (32)																																-.09	.49	.52
L. marg. (33)																																	.25	-.09
C. beati. (34)																																		.25
S. lacu. (35)																																		

these models to real data (Pielou, 1975), comparisons of the results show that the communities studied exhibit straight to slight sigmoidal curves. The low value of MacArthur's equitability (Table 3) recorded at station 12 suggests a linear relationship (Fig. 2), characterizing a pioneer community composed of a few "specialists", strongly competing with each other to exploit the rare resources of the biotope. The downstream communities investigated (stations 2 and 6) show a more even partition of the resource and their distributions are closer to the optimum MacArthur model (Figs. 3 and 4; Table 3). Furthermore, the higher temperature regime allows the existence of potentially more taxonomic elements (24 at station 6 and 28 at station 2) and the spatial extension of the biotope furnishes additional micro-habitats (like lentic zones, presence of macrophytes, etc.).

β-diversity

According to Southwood (1978), β-diversity is concerned with "change in species diversity from habitat and the comparison of the quantitative and qualitative make-up of different communities". As a consequence, β-diversity is mainly a spatial concept. The Sörensen coefficient allows us to compare the different stations spatially in terms of faunistic affinities. Nevertheless, it does not take account of the relative abundance of each species and, as a consequence, tends to overestimate rare species (Southwood, 1978).

The faunistic classification obtained in the present study (Table 4 and Fig. 5) reflects the main abiotic properties of the stream system and gives important indications about the limiting factors affecting mayfly communities.

Station 7 stands clearly apart from the other localities because of its limnic character. The absence of a current determines the existence of specific and isolated populations of mayfly species (*L. marginata* and *S. lacustris*).

Stations 9 to 12 share identical temperature characteristics and are grouped faunistically. Station 8 also belongs to this group even though topographically completely separated from the "Cold Singine". A clear faunistic division appears in this section between the tributaries with high calcium content (stations 10 and 12) and the "main stream" (stations 9 and 11).

The last group (stations 1 to 6) includes communities belonging to the "warm" sections of the stream system. Its influence below the confluence with the "Cold Singine" is dominant at stations 3 and 4. The faunistic compositions of stations 3 and 4 are affected by the "Warm Singine".

Stations 1 and 2 are segregated from the others, both being located in the canyon.

Conclusions

Thirty five species of mayfly were found at twelve stations of a prealpine stream system in Switzerland. A descriptive analysis of the communities allows the identification of some of the factors that control the longitudinal zonation of mayfly species. The occurrence of more than 55 % of the species recorded could be related to

the temperature and to the flow characteristics of the stations, while the occurrence of 11 % of species could be related to chemical factors. Diversity and equitability were highest at the station with high allochthonous detritus input, allowing detritivorous species to increase their abundance. The faunistic classification of the communities is spatially correlated with the abiotic parameters mentioned.

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