Abundance, growth and production of three mayfly species (Ephemeroptera, Insecta) from the Swiss Prealps

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With 7 figures and 3 tables in the text

Abstract

A comparative study of three common mayfly species from the Swiss Prealps was carried out at two stations. Both localities exhibited quite similar temperature regimes but differences were recorded in the structure of substrate and in chemical characteristics of water. The first station was situated near a small lake and was influenced by the release of allochthonous nutrients due to local human activities. Significant differences in abundance between the two populations were recorded for *Rhithrogena semicolorata* (Curtis) and *Habroleptoides confusa* Sartori & Jacob but not for *Ephemerella ignita* Poda. These density differences were attributed mainly to the geomorphological nature of the substrate. Estimations of mean daily productions per m^2 for the three species were always higher at station near the lake and could be related to the high nutrients content of the station. The spatial distributions, the elimination rates and the growth rates of the species were not significantly different in the two populations.

Introduction

Most mayfly larvae are extremely sensitive to variations of their habitat (e.g. nature of substrate, bed topography) as well as physical parameters such as oxygen concentration (Jacob & Walther, 1981; Jacob et al., 1984) and the temperature regime (Humpesch, 1978; Elliott, 1978). The correlation with empirical saprobic system (Zelinka & Marvan, 1961) stimulated researchers to use the occurrence of mayfly larvae as a bioindicator for organic enrichment (Caspers, 1982). Nevertheless, the concept of faunistic composition alone, used in the management of water quality (Woodiwiss, 1964; Vernaux & Tuffery, 1967; Perret, 1977) is not systematically applicable because slight modifications of the environment produce only sublethal effects which are not sufficient to induce the complete disappearance of a taxon. Very often, natural or human disturbances produce subtle changes in the organization of the community, affecting only the numerical equitability of each taxon. The detection of such modifications is only possible when using quantitative methods.

In the present study, three common mayfly species from the Swiss Prealps have been chosen for a comparative study: *Rhithrogena semicolorata* (Curtis,

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1834), *Habroleptoides confusa* SARTORI & JACOB, 1986 and *Ephemerella ignita* (PODA, 1761). The ecological niches as well as the feeding behaviour of the first two species are clearly differentiated. *R. semicolorata* lives as a clinger on the surface of the stones, where large areas of riffles are predominant (HEFTI et al., 1985). According to the trophic classification of CUMMINS (1973) and CUMMINS & KLUG (1979), *R. semicolorata* is a mineral and organic scraper and collector-gatherer (ELLIOTT et al., 1988), grazing upon food that adheres to the stones, essentially periphyton. *H. confusa* is an interstitial species, living between heterogeneous elements of substrate (PLESKOT, 1953). Its feeding strategy is the one of a collector-gatherer utilizing chiefly detritus (PLESKOT, 1953). The specific habitat of *E. ignita* is difficult to specify. This opportunistic species is a clinger and sprawler (ELLIOTT et al., 1988), which does not seem to be bound to specific substrate requirements. Living equally on stony bottoms (BROOKER & MORRIS, 1978), on mosses or on macrophytes of running waters (BASS, 1976) the species has also been found on stony shores of lakes (MACAN, 1970). *E. ignita* is considered as a collector-gatherer and feeds on detritus and fine particulate organic matter (ELLIOTT et al., 1988).

The aim of the present study was to investigate quantitatively the population dynamic of the three mentioned species at two stations with different substrate structures and different chemical characteristics of the water.

Methods

Presentation of the stream and sampling sites

The river "Singine" near Fribourg (canton of Fribourg; Switzerland) is a typical calcareous prealpine stream with a catchment area equal to 352 km^2. Geographically, the stream flows on the north-western side of the Swiss Alps (Fig. 1) in a range of elevation from 1400 m to 490 m. The study was carried out at two stations. The first one lies 1003 m above sea-level in a wooded section of the stream, 2.3 km downstream from a small prealpine lake. It is located in a touristic area with strong human activities. The second station lies 650 m above sea-level in a wide meandering canyon with no direct access to touristic activities.

Abiotic factors

The substrate composition of both localities was analyzed using two methods. With the first one, the coarse size distribution of the substrate's elements was estimated qualitatively along several transects. The second method provided an indirect measure of the availability of interstitial habitat, e.g. the degree of clogging of substrate with fine mineral elements. It was estimated as follows: equivolumes of water were collected at the bottom together with fine mineral material in suspension, obtained by mixing the substrate. The water probes were filtered (filter paper Schleicher & Schuell no 589) and the amount of mineral material collected in the filter was dried and weighted.

Temperature was recorded continuously at both localities with an Elmes 12 instrument during the year 1988. Other edaphic parameters were measured regularly: electrical conductivity, pH, and oxygen concentration were recorded potentiometrically in
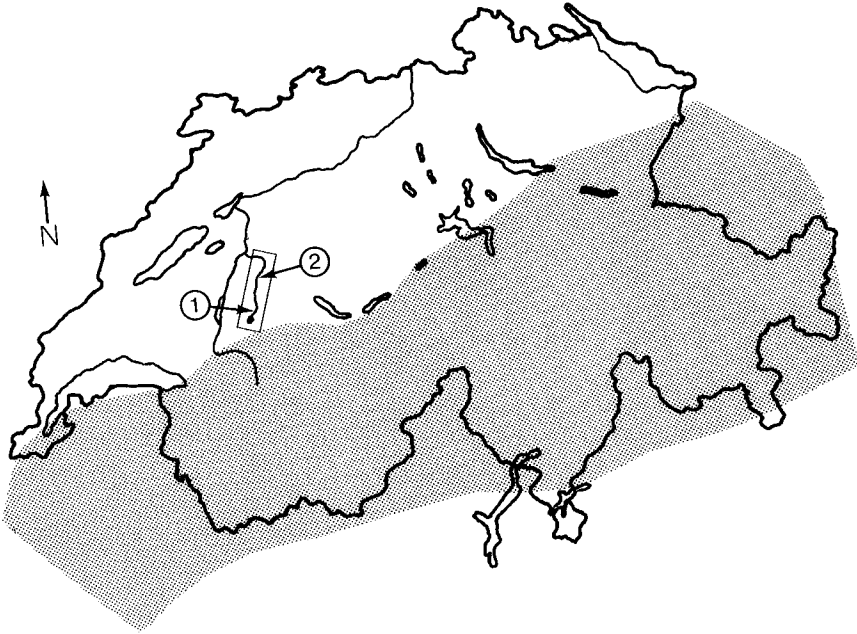
Fig. 1. Geographic location of the stream system investigated (in frame). 1 = Station 1; 2 = Station 2. The shaded area represents the Alps.

the current (apparatus: WTW LF91, WTW pH 90; WTW oxi 91). Alcalinity and total hardness were determined by titration after Höll (1979) and Schwoerbel (1980) respectively (apparatus: Methrom E 485). Biochemical oxygen demand for five days was determined chemically using the Winkler procedure. P-orthophosphate concentration was measured photometrically using α-phosphomolybdic acid to form a heteropoly-acid (Merck 14788-RM-1) and total organic carbon concentration was determined by a TOC-analyzer.

Sampling and samples evaluation

The benthos of both localities was quantitatively sampled using a modified surber net (mesh size 0.7 mm; surface 0.0625 m^2). The sampling units were collected randomly in the substrate at a depth of about 10 cm. The frequence of prospections (samples) as well as the number of replicates taken at each occasion (sampling units) were variable. The total number of individuals (x) was determined per sampling unit and mean value ($\bar{x}$) was calculated per sample for one m^2 (density). Further qualitative samples were collected for the determination of the length of the larvae. Specimens were extracted alive in the laboratory by flotation with a 350 g/l MgSO$_4$ solution and preserved in 80 % alcohol for further analysis.

Growth in length and in weight

The lengths of the larvae (L) were measured from the head to the tip of the abdomen and the geometric mean ($\bar{L}$g) was determined for each sample (Humpesch, 1979).
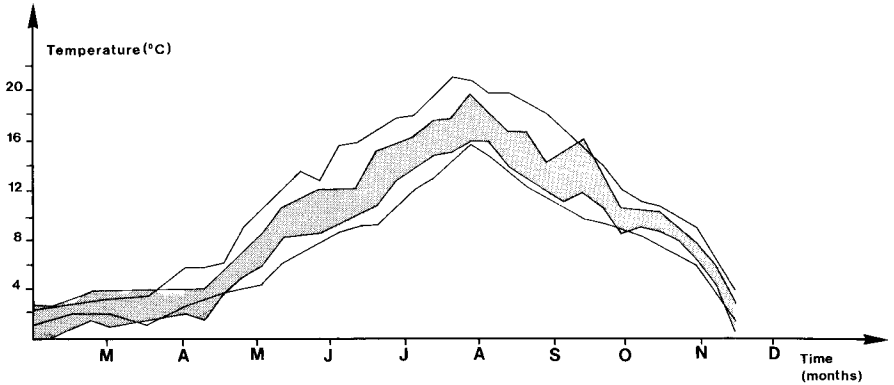
Fig. 2. Water temperature range (Tmin – Tmax) recorded automatically with Elmes 12 instruments during the year 1988 at station 1 (shaded area) and at station 2 (non shaded area).
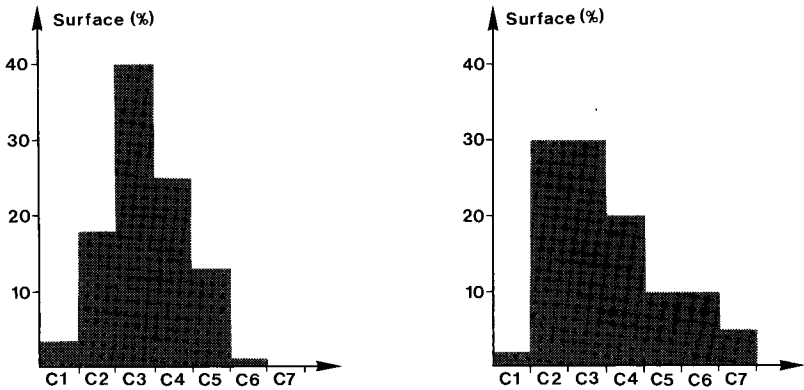

Fig. 3. Surface (in %) occupied by different categories of substrate elements along several transects at station 1 (right) and at station 2 (left). C1: rocks unmovable; C2: boulders > 100 mm in diameter; C3: large gravel 100 to 20 mm in diameter; C4: fine gravel 20 to 2 mm in diameter; C5: sand 2–1 mm in diameter; C6: silt < 1 mm in diameter; C7: mudd.

The mean dry weights of the larvae ($\bar{W}$) and the respective mean biomasses were estimated using the length-weight relationship of Smock (1980):

$$\log_e \bar{W} = \log_e a + b \log_e \bar{L}g \tag{1}$$

where $\log_e a = -5.021 \pm 0.095$ and $b = 2.88 \pm 0.070$.

Results

Abiotic parameters

The temperature regimes of both localities were almost similar (Fig. 2). Station one exhibited a narrow thermic amplitude of daily variation which expressed the typical regulation effect of the upper lake.

Table 1. Geomorphological, geochemical and chemical characteristics of the two stations investigated with standard deviations (in brackets) and number of measurements (n) at station 1 and station 2 as well as geochemical and chemical characteristics of the littoral zone of the upper lake.

	Station 1	Station 2	Lake*
Geomorphological parameters			
Mean breadth (m)	5	15	–
Mean depth (m)	0.30	0.30	–
Mean current velocity (m/s)	0.60	0.40	–
Mean slope (%)	3.00	1.20	–
Length of the period (m)	15–30	40–50	–
Interstitial mineral material (mg/l)**	180	230	–
Geochemical parameters			
pH	8.22 (0.25) n=25	8.25 (0.35) n=27	8.13 (0.29) n=10
Electrical conductivity (μS/cm)	415 (71) n=28	370 (52) n=27	401 (54) n=10
Alcalinity (mVal/l)	2.70 (0.30) n=19	2.80 (0.30) n=21	2.65 (0.30) n=8
Total hardness (mg/l)	94.40 (18) n=19	82.40 (14) n=12	88.13 (16) n=8
Chemical parameters			
Oxygen concentration (mg/l)	10.05 (1.20) n=19	11.50 (1.85) n=12	9.90 (0.85) n=8
Oxygen percent saturation (%)	98	101	90
Total organic carbon (mg/l)	4.70 (2.60) n=4	4.00 (2.30) n=4	3.90 (2.50) n=4
Biochemical oxygen demand (mg/l) (5 days)	1.80 (0.40) n=19	1.00 (0.40) n=17	1.60 (0.40) n=7
Total P-orthophosphate (μg/l)	26 (15) n=16	14 (17) n=17	8 (5) n=11

 * Measurements on the litoral zone.
** Definition cf. method (abiotic factors).

The substrate composition of both localities is summarized in Fig. 3. Station one was characterized by the presence of mud and station two by the net
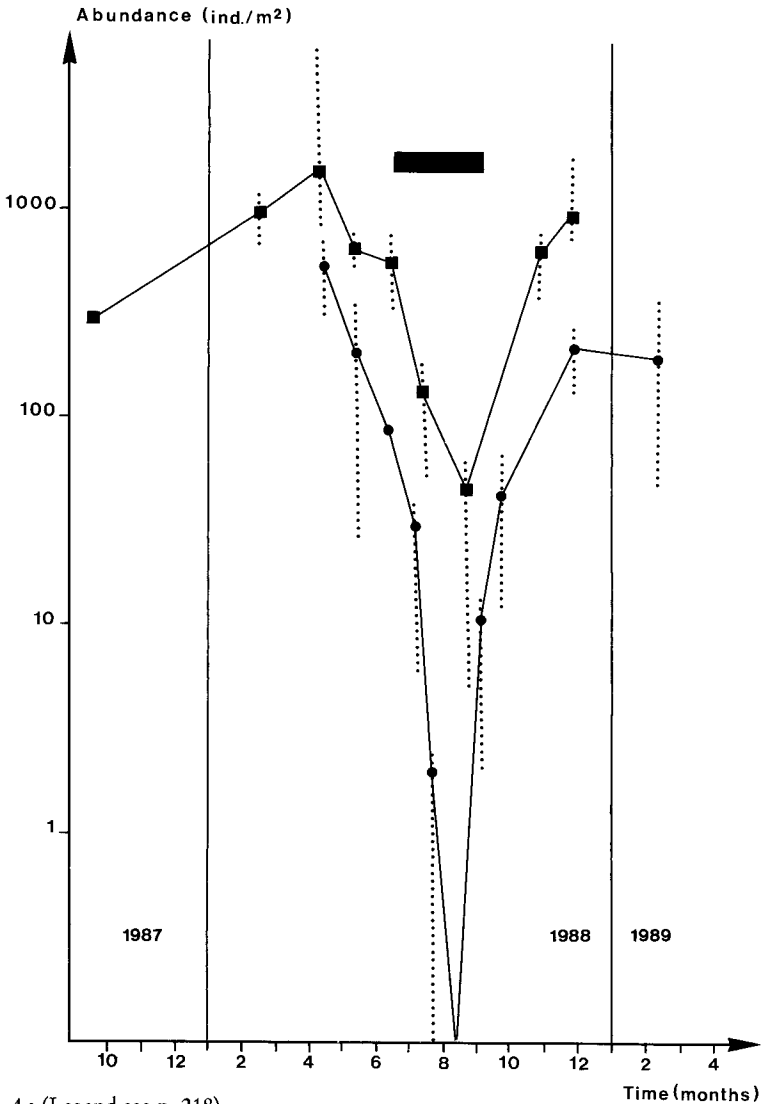
Fig. 4 a (Legend see p. 218).

predominance of gravels from 100 to 20 mm in diameter. Other differences were related to the spatial assemblage of the substrate's elements and to the amount of fine mineral material accumulated at the bottom (Table 1).

Other abiotic divergencies were of chemical nature. The mean concentrations of total organic carbon, of P-orthophosphate and the mean values for biochemical oxygen demand were higher at station one than at station two, reflecting a moderate organic enrichment due to local human activities (Table 1).
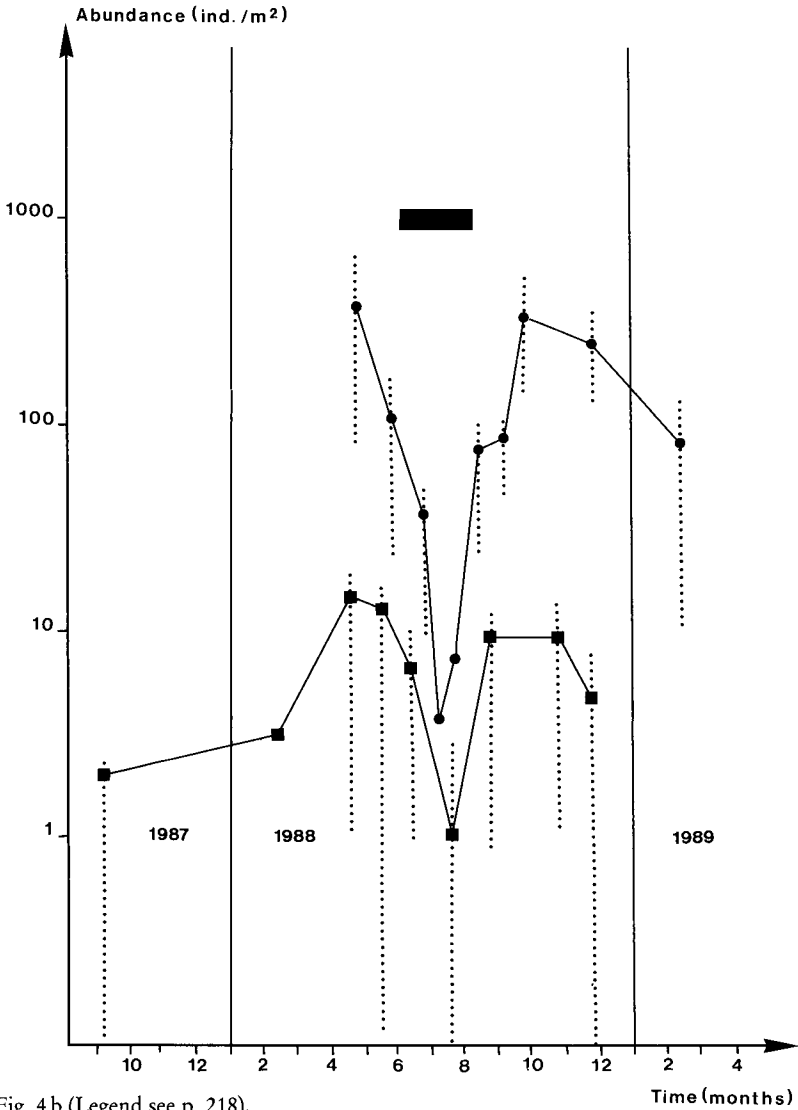
Fig. 4 b (Legend see p. 218).

Life cycles

At both stations, the respective life cycles of each species were not different (Fig. 4). The species investigated were univoltine, characterized by distinct specific pattern. *R. semicolorata* (Figs. 4 a and 5) and *H. confusa* (Figs. 4 b and 6) exhibited a seasonal univoltine winter cycle (following the code of CLIFFORD, 1982: "Uw"). After hatching, the young larvae grew during autumn months and overwintered at larval stage. The emergence took place the following year.
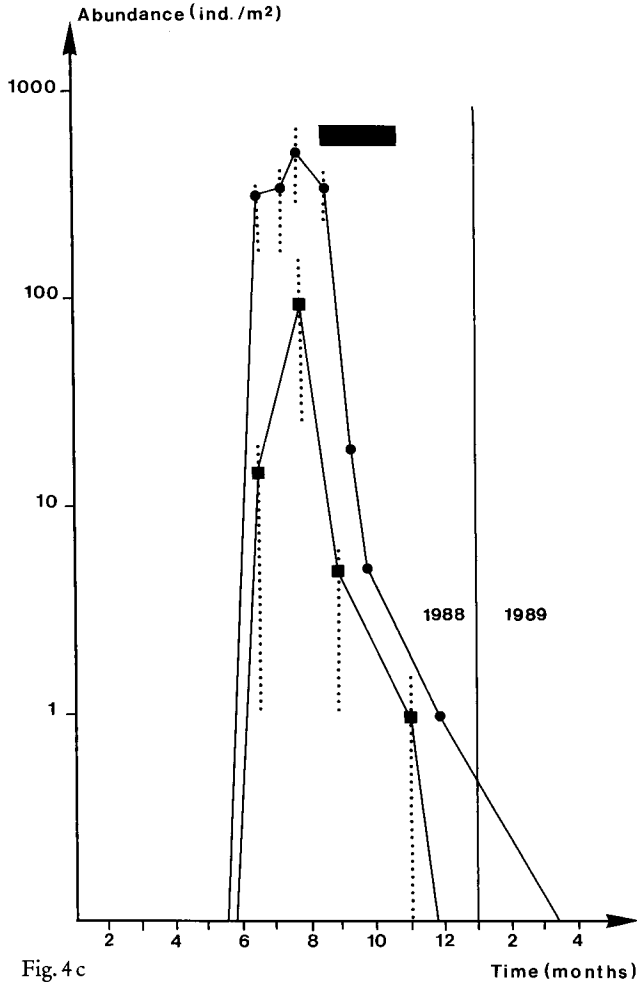
Fig. 4c

Fig. 4. Density (ind/m²) of *Rhithrogena semicolorata* (4a). *Habroleptoides confusa* (4b) and *Ephemerella ignita* (4c) with corresponding 95 % confidence limit at station 1 (●) and at station 2 (■). Emergence period: ▬▬

The larval development of *E. ignita* (Figs. 4 c and 7) was typical for a summer species where hatching, growth and emergence took place during late spring and summertime of the same year (following the code of CLIFFORD, 1982: "Us"). Population densities were higher at station one for *H. confusa* (Fig. 4 b) and for *E. ignita* (Fig. 4 c) but were lower for *R. semicolorata* (Fig. 4 a). Density differences between populations of each species have been investigated using Students t-tests after a $\log(x + 1)$ transformation (as to normalize the frequency distribution of the counts). Density differences were highly significant

between the two populations of *H. confusa* (P < 0.001), significant between the two populations of *R. semicolorata* (P < 0.05), but not significantly different between the two summer populations of *E. ignita* (P > 0.05).

Spatial distribution

For all species and populations investigated, the arithmetic mean ($\bar{x}$) and the variance (s^2) of the number of larvae per sampling unit was calculated for each sample. The relation between the two variables followed a Taylor power law, where variance was proportional to a fractional power of the mean (TAYLOR, 1961):

$$s^2 = c\bar{x}^d \tag{2}$$

where c and d are constants, the last one characterizing the dispersion of the population. The different values of the constants have been calculated by regression analysis with the obtained data:
— for *R. semicolorata*: c = 0.19; d = 1.41 ± 0.16 (r^2 = 0.98; n = 9) at station 1 and c = 0.43; d = 1.32 ± 0.59 (r^2 = 0.80; n = 9) at station 2,
— for *H. confusa*: c = 0.41; d = 1.48 ± 0.18 (r^2 = 0.98; n = 10) at station 1 and c = 0.25; d = 1.24 ± 0.58 (r^2 = 0.79; n = 9) at station 2 and
— for *E. ignita*: c = 0.33; d = 1.40 ± 0.25 (r^2 = 0.98; n = 7) at station 1 and c = 0.26; d = 1.29 ± 0.54 (r^2 = 0.96; n = 4) at station 2.

Elimination rate

From mid-april 1988 to the respective emergence periods, the rates of elimination were estimated for both populations of *R. semicolorata* and *H. confusa*. The decrease in mean number of individuals ($\bar{N}$) was described by an exponential relationship over time (t in days):

$$\log_e \bar{N} = \log_e g - ft \tag{3}$$

where g and f are constants. The elimination rate (E, % day^{-1}) was defined as 100f and are given in Table 2. For both species, the highest rate of elimination was recorded at station 1 but the differences were not significant (P > 0.05).

Growth in length and in weight

The experimental (length) and derived (weight) data were fitted to an exponential growth function:

$$\bar{L}g_t = \bar{L}g_o \exp ((G_l/100)t) \tag{4}$$
$$\text{and}$$
$$\bar{W}_t = \bar{W}_o \exp (G_w/100)t) \tag{5}$$

where $\bar{L}g_o$ and $\bar{W}_o$ are the mean initial length and weight, $\bar{L}g_t$ and $\bar{W}_t$ are the corresponding mean length and weight after an interval of time t (in days). The

Table 2. Instantaneous growth rates in length (G_l) in % mm/day and in weight (G_w) in % mg/day, maximum theoretical growth in lenght (G_{max}) in % mm/day, elemination rate (E) in %/day and mean daily production (P_d) in mg/m² for the three species at station 1 and at station 2. Standard deviation (in brackets), coefficient of determination (r^2) and number of measurements (n).

Stations		G_l 1.	G_l 2.	G_w* 1.	G_w* 2.	$G_{l\,max}$ 1.	$G_{l\,max}$ 2.	E 1.	E 2.	P_d 1.	P_d 2.
R. semicolorata	1)	0.45 (0.15) $r^2=0.88$ n=3	0.31 (0.10) $r^2=0.97$ n=6	1.30 (0.20) $r^2=0.88$ n=3	0.90 (0.15) $r^2=0.97$ n=6	–	0.86	5.70 (2.5) $r^2=0.90$ n=6	2.60 (0.9) $r^2=0.97$ n=5	7.90	6.90
	2)	0.50 (0.10) $r^2=0.99$ n=6	0.54 (0.10) $r^2=0.99$ n=4	1.45 (0.10) $r^2=0.99$ n=6	1.56 (0.10) $r^2=0.99$ n=4	0.95	1.20				
H. confusa	1)	0.28 (0.08) $r^2=0.97$ n=4	0.28 (0.02) $r^2=0.99$ n=6	0.81 (0.40) $r^2=0.97$ n=4	0.81 (0.05) $r^2=0.99$ n=6	–	–	4.69 (3.4) $r^2=0.86$ n=5	2.64 (1.5) $r^2=0.83$ n=4	1.60	0.10
	2)	0.28 (0.15) $r^2=0.87$ n=6	0.28 (0.20) $r^2=0.99$ n=3	0.79 (0.10) $r^2=0.87$ n=6	0.84 (0.20) $r^2=0.99$ n=3	0.85	–				
E. ignita	3)	0.68 (0.15) $r^2=0.98$ n=5	0.50 (0.25) $r^2=0.92$ n=3	1.96 (0.10) $r^2=0.98$ n=5	1.40 (0.60) $r^2=0.92$ n=3	3.00	–	–	–	7.60	0.60

1) January to August 1988.
2) September 1988 to Mai 1989.
3) Mai to December 1988.
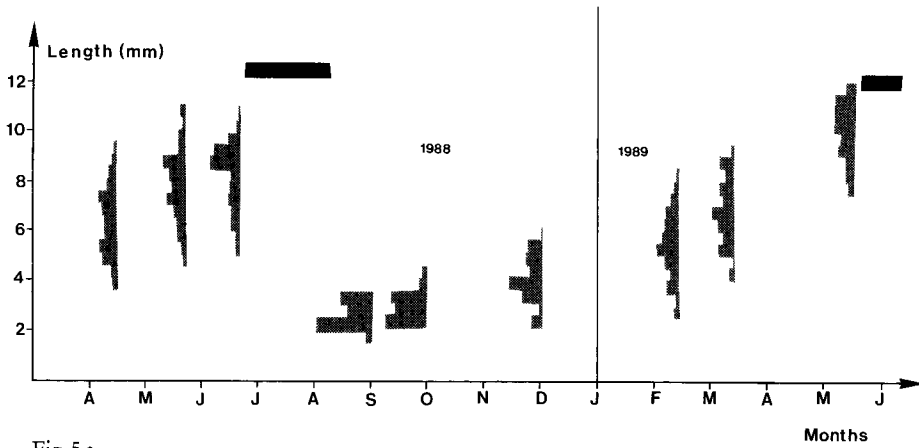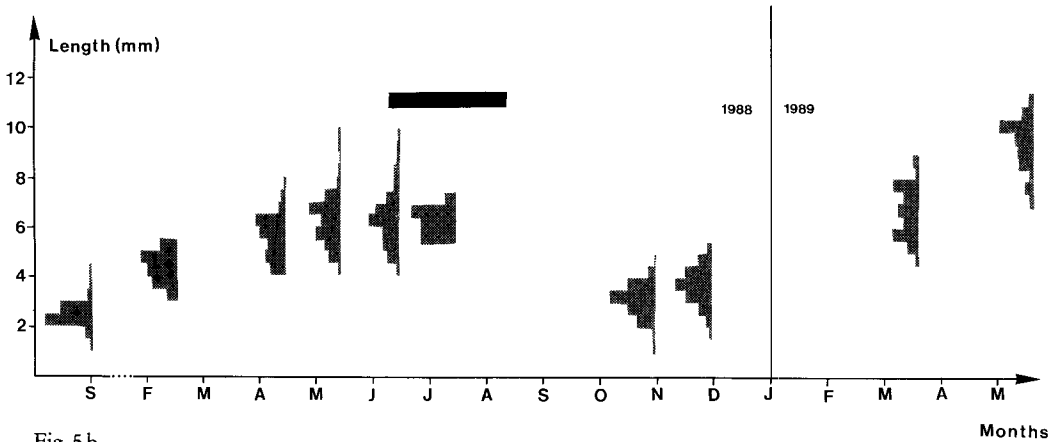* Calculated from G_l (SMOCK, 1980).

Fig. 5 a

Fig. 5 b

Fig. 5. Size distribution (in %) of larvae of *Rhithrogena semicolorata* for each sample at
station 1 (5a) and at station 2 (5b). Emergence period: ▬

instantaneous growth rates in length (G_l) and in weight (G_w) were estimated by
regression analysis and are summarized in Table 2 for the species and the popu-
lations studied.

Maximum theoretical growth rates (G_{lmax}) were calculated for each species
when the elaboration of a size frequency distribution was possible (Figs. 5—7).
G_{lmax} values were established between the smallest size category recorded and
the largest size category of the sample preceding the emergence period. Results
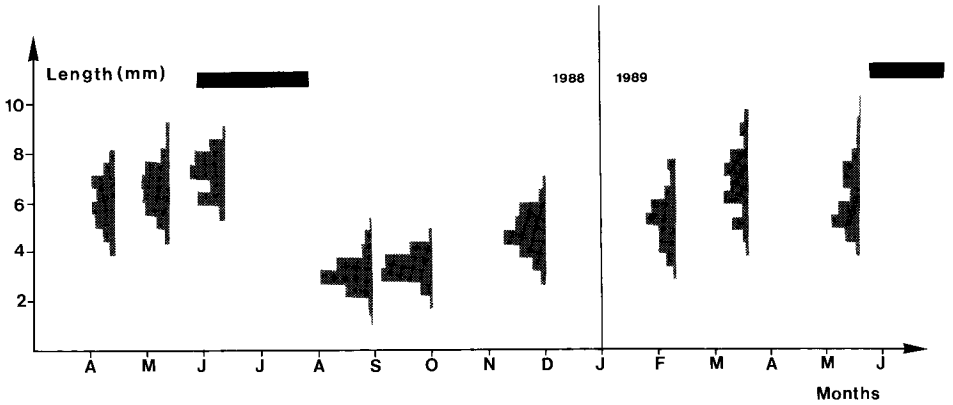are listed in Table 2.

Fig. 6. Size distribution (in %) of larvae of *Habroleptoides confusa* for each sample at station 1. Emergence period: ■
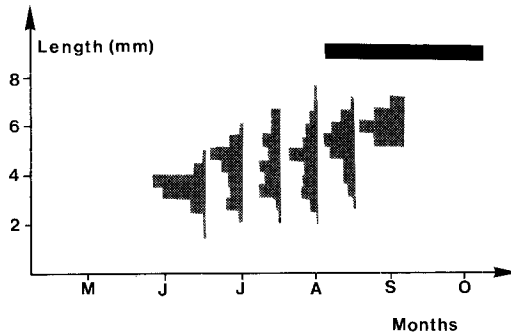

Fig. 7. Size distribution (in %) of larvae of *Ephemerella ignita* for each sample at station 1. Emergence period: ■

Biomass and production

The biomass of each sample (b) as well as the estimation of the mean annual biomass per m² (B) have been determined for each species (Table 3). The mean annual biomass corresponds to the first central moment of the timely distribution of the biomass calculated over one year.

Estimation of the annual production (P) was calculated using the formula of RICKER (1946):

$$P = \Sigma \bar{\beta} \gamma_w \tag{6}$$

where $\bar{\beta}$ = arithmetic mean population biomass (dry weight in mg per m²) of two consecutive samples and γ_w = growth rate between two consecutive samples. As the calculations of production did not always involve the entire larval developmental cycle, the obtained values were reduced to a mean daily

Table 3. dates, number of replicates (n), biomass of each sample (b) and mean annual biomass (B) of the three species investigated.

Date	n	R. semicolorata Biomass (b) (mg/m²)	H. confusa Biomass (b) (mg/m²)	E. ignita Biomass (b) (mg/m²)
Station 1				
21. 04. 88	10	660	360	0
26. 05. 88	11	525	132	0
24. 06. 88	24	239	57	73
6. 07. 88	24	110	7	106
25. 07. 88	24	9	15	213
17. 08. 88	24	0	11	220
5. 09. 88	24	1	14	21
22. 09. 88	12	6	57	6
29. 11. 88	12	68	84	4
13. 02. 89	12	169	51	0
Mean annual biomass (B)		177	107	32
Station 2				
21. 04. 88	10	1117	11	0
26. 05. 88	10	795	13	0
15. 06. 88	10	706	9	7
21. 07. 88	12	178	2	58
30. 08. 88	12	152	1	3
3. 09. 87	20	23	0	33
30. 10. 88	12	112	2	3
29. 11. 88	10	269	1	0
18. 02. 88	20	428	1	0
Mean annual biomass (B)		355	3	10

estimation per m² (P_d) according to the period of time investigated. The mean values of daily production were clearly higher at station one for *H. confusa* and *E. ignita* and slightly higher for *R. semicolorata* (Table 2).

Discussion

Life cycles and abundances

The larval developments of *R. semicolorata* and *H. confusa* as well as their respective emergence periods did not exhibit significant differences between the two localities. This can be explained by the closely related temperature regimes of the two localities. Significant differences in density were nevertheless recorded. As already mentioned, abiotic differences appeared in the qualitative set up of the substrate and in the nutrients content of the water. These factors are suggested to play a role in the quantitative regulation of both populations (e.g. density, growth and production).

At station one, the spatial variation of substrate size was high because the conglomerates of stones were distributed spatially with no apparent structure. This arbitrarily assemblage of inhomogeneous geo-elements allowed the establishment of a net of interstitial holes at the bottom, which provided an optimum habitat for *H. confusa*.

From theoretical considerations, LEOPOLD et al. (1964) predicted that the most probable energetic state of low slope rivers is realized with the meandering pattern. In this case, the topography of the system is near to equilibrium and is composed of successive sequences of pools and riffles with differential current velocities. The bed topography of station two was typical for a meandering channel. The different size elements of substrate were regularly clumped, building distinct surfaces of stones of quite similar size and with quite homogeneous flow. Furthermore, the meandering pattern maximalized the occurrence of large zones of riffles, which provided the optimum habitat for *R. semicolorata*. The amount of fine mineral material sedimented at station two could be one of the reasons for the low abundance of *H. confusa* recorded, reducing the availability of interstitial habitat by clogging.

The developmental pattern of *E. ignita* was identical in both populations but the density difference recorded was not significant, illustrating the opportunistic character of the species concerning substrate requirements.

The relative high trophic level of station one (see TOC, P and BOD_5 values in Table 1) could also explain the densities recorded for *H. confusa* and *E. ignita*, both species being partially detritivorous. This allochthonous nutrients input in the system, originated from the upper lake and from the surrounding human activities, was correlated with the proliferation of large areas of filamentous algae, not present downstream. Other mayfly taxa belonging to the detritivorous trophic level were also clearly more abundant than downstream (HEFTI & TOMKA, 1990).

Spatial distribution

The spatial distributions of larvae on the benthos have been investigated for each population using the mentioned power law (2). This one was found to apply to a wide range of organisms and has the advantage to be independent from any specific frequency distribution and densities (TAYLOR et al., 1978). The constant c from equation (2) is largely an arbitrary factor, depending upon the size of the sampling unit. The constant d can be considered as an index of aggregation and is particularly useful to compare the distribution of different species. The last mentioned index ranges from 0 (for a maximum regularity) over one (for a random pattern) to infinity (for a maximum contagious distribution) (TAYLOR, 1961). In the present study, the values obtained for d were always higher than unity and showed that larvae exhibited an aggregated

spatial distribution on the benthos. This type of spatial distribution was valid for the whole range of densities recorded ($c > 0$) and, as a consequence, showed that the dispersion pattern of the investigated species were density independant and mainly determined by external factors (substrate, flow).

Growth rates

HUMPESCH (1979, 1981) and ELLIOTT (1978) showed experimentally that embryonic and larval growths of mayflies are mainly affected by the temperature of water. In the present study, this assumption could not be confirmed for *H. confusa*, which exhibited a constant growth rate during all the year despite some temperature variations. The determinations of growth rates were probably biased because of temporary continuous recruitments of young larvae due to delayed eggs hatching. This assumption is revealed by the broad size distribution of the three species (Figs. 5—7) and explained the low growht rate values recorded. As a consequence, growth rates calculated in the present study, were not a measure of individual growth but characterized the mean growth of the population around its geometric mean. Nevertheless they can be used to compare populations growing under different conditions.

In addition, maximum theoretical growth rates (G_{Imax}) were also estimated and used as a measure of individual growth. The obtained values were clearly higher than growth rates of populations (Table 2) and are comparable with the one of WELTON et al. (1982) for *E. ignita*: working in an experimental recirculating stream (for a temperature range of 9.7 to 15.1 °C), the authors found a mean individual growth rate of 3.26 % mm/day.

Biomass and production

The biomass and production of the species investigated were probably underestimated because the calculations did not involve the youngest larval stages (not sampled because of their small size). Our results (Table 3) concerning mean annual biomass per m² (B) are nevertheless comparable with the variation range of other authors:
— For *R. semicolorata*: B = 345 mg/m² (ZELINKA, 1973); B = 455 mg/m² (ZELINKA, 1977); B = 115 mg/m² (RUSSEV & DOSHKINOVA, 1985); B = 55—103 mg/m² (BROOKER & MORRIS, 1978).
— For *E. ignita*: B = 82 mg/m² (BASS, 1976); B = 36—120 mg/m² (BROOKER & MORRIS, 1978); B = 104 mg/m² (ZELINKA, 1980); B = 83 mg/m² (RUSSEV & DOSHKINOVA, 1985).

The release of allochthonous nutrients or energy in an aquatic system induces an increase in production of the primary consumers (SCHWOERBEL, 1974). This assumption was illustrated in our results by the fact that mean daily productions per m² (P_d) were always higher at station one, suggesting that

organic enrichment affected significantly the production of mayfly communities. The production levels recorded at both stations were correlated with the biomasses of *H. confusa* and *E. ignita* but not with the ones of *R. semicolorata*. In this situation, one can argue that daily production per m² was mainly controlled by the amount of allochthonous nutrients input in the system, which could act directly or indirectly (via the primary production) on the production of primary consumers.

Conclusions

The productivity of *R. semicolorata* was higher at station one than at station two in spite of a lower abundance and biomass recorded at station one. The high abundance recorded at station two could be explained by substrate preference and the high productivity at station one by the release of nutrients in the stream.

H. confusa exhibited a higher abundance and productivity at station one than at station two. The same argument can be used as for *R. semicolorata* for productivity but the high availability of intestitial habitat recorded at station one determined the high density of the species.

The abundances of *E. ignita* were not significantly different because of the opportunistic substrate relationships of the species. Differences of productivity could also be explained by the high nutrient contents recorded at station one.

These conclusions were possible to derive because the two stations investigated were situated at two distinct altitudinal levels of the same river system with practically identical temperature regime but different substrate structures and nutrients input.

Acknowledgements

References

BASS, J. A. B. (1976): Studies on *Ephemerella ignita* (PODA) in a chalk stream in southern England. — Hydrobiologia **49**: 117—121.

BROOKER, M. P. & MORRIS, D. L. (1978): Production of two species of Ephemeroptera (*Ephemerella ignita* PODA and *Rhithrogena semicolorata* (CURTIS)) in the upper reaches of the R. Wye, Wales. — Verhandlungen Internationale Vereinigung Limnologie **20**: 2600—2604.

CASPERS, N. (1982): Steinfliegen, Eintagsfliegen und Zweiflügler als Indikatoren der Gewässergüte. — Decheniana, Beihefte **26**: 114—119.

CLIFFORD, H. F. (1982): Life cycle of mayflies (Ephemeroptera) with special reference to voltinism. — Quaestiones Entomologicae 18: 15—90.
CUMMINS, K. W. (1973): Trophic relations of aquatic insects. — Annual Review of Entomology 18: 183—206.
CUMMINS, K. W. & KLUG, M. J. (1979): Feeding ecology of stream invertebrates. — Annual Review of Ecology and Systematic 10: 147—172.
ELLIOTT, J. M. (1978): Effect of temperature on the hatching time of eggs of *Ephemerella ignita* (PODA) (Ephemeroptera, Ephemerellidae). — Freshwater Biology 8: 51—58.
ELLIOTT, J. M., HUMPESCH, U. H. & MACAN, T. T. (1988): Larvae of the British Ephemeroptera. A key with ecological notes. — Freshwater Biological Association. Scientific Publication No 49.
HEFTI, D. & TOMKA, I. (1990): Mayfly communities in a prealpine stream system from Switzerland. In preparation.
HEFTI, D., TOMKA, I. & ZURWERRA, A. (1985): Recherche autoécologique sur les Heptageniidae (Ephemeroptera, Insecta). — Bulletin de la Société Entomologique Suisse 58: 87—111.
HÖLL, K. (1979): Wasser. — Walter De Gryuter. Berlin — New York 1—515.
HUMPESCH, U. H. (1978): Preliminary notes on the effect of temperature and light-condition on the time of hatching in some Heptageniidae (Ephemeroptera). — Verh. Internat. Verein. Limnol. 20: 2605—2611.
— (1979): Life cycles and growth of Baetis spp. in the laboratory and in two stony streams in Austria. — Freshwater Biology 9: 467—479.
— (1981): Effect of temperature on larval growth of *Ecdyonurus dispar* (Ephemeroptera: Heptageniidae) from two English lakes. — Freshwater Biology 11: 441—457.
JACOB, U. & WALTHER, H. (1981): Aquatic insect larvae as indicators of limiting minimal contents of dissolved oxygen. — Aquatic Insects 4: 219—224.
JACOB, U., WALTHER, H. & KLENKE, R. (1984): Aquatic insect larvae as indicators of limiting minimal contents of dissolved oxygen — part II. — Aquatic Insects 3: 185—190.
LEOPOLD, L. B., WOLMAN, M. G. & MILLER, J. P. (1964): Fluvial processes in geomorphology. — W. H. Freeman and Company, San Francisco 1—522.
MACAN, T. T. (1970): A key to the nymphs of the British species of Ephemeroptera, with notes on their ecology. — Freshwater Biological Association, Scientific Publication No 20.
PERRET, P. (1977): Zustand der Schweizerischen Fließgewässer in den Jahren 1974/75 (Projet Mapos). — Eidgenössisches Amt für Umweltschutz und eidgenössische Anstalt für Wasserversorgung, Abwasserreinigung und Gewässerschutz.
PLESKOT, G. (1953): Zur Ökologie der Leptophlebiidae (Insecta, Ephemeroptera). — Österr. Zool. Z. 4: 45—107.
RICKER, W. E. (1946): Production and utilization of fish populations. — Ecological Monographs 16: 373—391.
RUSSEV, B. K. & DOSHKINOVA, M. G. (1985): On the development and productivity of mayfly larvae (Ephemeroptera, Insecta) in a stretch of the Iskar River. — Hydrobiology 25: 3—16.
SCHWOERBEL, J. (1974): Einführung in die Limnologie. — Gustav Fischer, Stuttgart — New York 1—177.
— (1980): Methoden der Hydrobiologie, Süßwasserbiologie. — Gustav Fischer, Stuttgart — New York 1—261.
SMOCK, L. A. (1980): Relationships between body size and biomass of aquatic insects. — Freshwater Biology 10: 375—383.

TAYLOR, L. R. (1961): Aggregation, variance and the mean. — Nature **189**: 732—735.

TAYLOR, L. R., WOIWOD, I. P. & PERRY, J. N. (1978): The density-dependence of spatial behaviour and the variety of randomness. — J. Anim. Ecol. **47**: 343—406.

VERNAUX, J. & TUFFERY, G. (1967): Une méthode zoologique pratique de détermination biologique des eaux courantes. Les indices biotiques. — Annales scientifiques de l'Université de Besançon **3**: 79—90.

WELTON, J. S., LADLE, M. & BASS, J. A. B. (1982): Growth and production of five species of Ephemeroptera larvae from an experimental recirculating stream. — Freshwater Biology **12**: 103—122.

WOODIWISS, F. S. (1964): The biological system of stream classification used by the trent river board. — Chemistry and Industry **14**: 443—447.

ZELINKA, M. (1973): Die Eintagsfliegen (Ephemeroptera) in Forellenbächen der Beskiden II. — Produktion. — Hydrobiologia **42**: 13—19.

— (1977): Production conditions of the polluted trout brook. — Folia Facultatis Scientiarum Naturalium Universitatis Purkynianae Brunensis, Biologia **18**: 7—105.

— (1980): Differences in the production of mayfly larvae in partial habitats of a barbel stream. — Archiv für Hydrobiologie **90**: 284—297.

ZELINKA, M. & MARVAN, P. (1961): Zur Präzisierung der biologischen Klassifikation der Reinheit fließender Gewässer. — Archiv für Hydrobiologie **57**: 389—407.