

APPLIED ISSUES

Influence of hypolimnetic hydropeaking on the distribution and population dynamics of Ephemeroptera in a mountain stream

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SUMMARY

1. The Ephemeroptera assemblage of the River Oriège (Pyrenees, France) was studied up- and downstream of a hydroelectric power plant with hypolimnetic releases from a nearby high altitude reservoir. The life histories and larval growth of the six dominant species (*Rhithrogena semicolorata*, *R. sp. gr. hercynia*, *R. kimminsi*, *Baetis alpinus*, *B. rhodani*, *Ephemerella ignita*) were studied 700 m upstream (site A) and 700 and 3500 m downstream (sites B and C, respectively) of the power plant. Their drift patterns were studied at sites A and B.
2. The natural flow of the river was preserved when the plant was inoperative. During power generation, flow and temperature were the two main environmental factors modified. The natural flow in the river below the outlet may be enhanced several times a day from 1 to 11 m³ s⁻¹ in summer and winter, and from 5 to 15 m³ s⁻¹ during spring spates. During hydropeaking, the water was cooled in summer and slightly warmed in winter, but this was attenuated 3500 m downstream from the plant.
3. The density and biomass of the species studied at the three sites reflected both the impact of hydropeaking and the natural longitudinal zonation of the fauna. The lowest density and biomass was estimated at 700 m downstream from the plant (site B), consistent with a prominent role for hydropeaking. Site A showed constant mayfly drift caused by accidental dislodgement plus behavioural drift that was mainly nocturnal. Below the plant, the flushing action of peaking flows added to this a catastrophic drift, which was highest in autumn when the difference between natural and peak flows was greatest.
4. Environmental change caused only slight modifications in the life history patterns, affecting the hatching and/or emergence period and growth of several species. For instance, *R. semicolorata* grew through the winter below the outlet, when growth was slight upstream from the power plant. Under this kind of river regulation (natural discharge and temperature except during periods of power generation, and intermittent hydropeaking from a separate reservoir) modifications of the thermal regime had a minor effect on the population dynamics of mayflies, unlike hydraulic disturbances which strongly influenced the abundance and structure of the benthic community. Frequent (at least daily) high flow disturbances caused depletion of mayfly populations, despite daily renewal and colonization (drift) from undisturbed upstream locations.

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Introduction

Many ecological studies have dealt with the impact of hydroelectric facilities on the lotic environment (see reviews in Armitage, 1984; Brittain & Saltveit, 1989) but few studies have focused on the effect of intermittent hydropeaking on invertebrate communities. Hydropeaking operations result in sudden physical and chemical changes in the receiving stream (Cushman, 1985). Flow and temperature alterations are common when peak flows result from hypolimnetic releases (Hilsenhoff, 1971; Ward & Stanford, 1979; Raddum, 1985; Moog, 1993). Because temperature and flow are important ecological factors, such river regulation can modify the structure and dynamics of invertebrate populations, either directly by removing the fauna (Troelstrup & Hergenrader, 1990) and by acting on the energetics of stream insects (Sweeney, 1978, 1984; Sweeney, Vannote & Dodds, 1986; Pritchard & Zloty, 1994), and/or indirectly by increasing spatiotemporal variability (Feminella & Resh, 1990; Robinson, Reed & Minshall, 1992) and by modifying available food resources (Anderson & Cummins, 1979; Moog & Janecek, 1991). River regulation can cause significant changes in the density and richness of invertebrate assemblages (e.g. Kraft & Mundahl, 1984; Bretschko & Moog, 1990; Cobb & Flannagan, 1990). The effects of stream regulation can also alter life history patterns (Benke, Van Arsdall & Gillespie, 1984; Butler, 1984), but there are few data concerning the influence of artificial peak flows and altered temperature regimes on larval development (e.g. Mundahl & Kraft, 1988; Raddum & Fjellheim, 1993).

Environmental conditions in the receiving stream result from operation and construction characteristics (position of the outlet, purpose of the reservoir, frequency of releases) (Ward & Stanford, 1979). Stream water below most hydroelectric facilities generally consists entirely of reservoir water and thermal variability is reduced (e.g. Ward & Stanford, 1983a,b). The setting for the study reported here is quite different; a dam does not disrupt the natural flow of the river, so natural discharge and temperature regimes are preserved when the plant is inoperative. During periods of power generation (often several times a day), the natural flow is supplemented by hypolimnetic

water from a high-elevation reservoir. The purpose of the present work was to compare the composition, abundance and biomass of mayflies, including impact on drift and life histories of six dominant species, upstream and downstream from the outlet of the hydroelectric power plant. Specifically, the aims of the study were to: (i) document the effects of intermittent hydropeaking, a topic little studied under this kind of river regulation; and (ii) examine changes caused by this type of facility, which subjects mayflies alternatively to natural and then highly variable thermal and flow regimes. The results are discussed taking into account the natural altitudinal distribution of Ephemeroptera in the Pyrenees mountains (Vinçon & Thomas, 1987) with respect to temperature and discharge, which are the two factors altered in many river regulation schemes (Crisp, 1987; Brittain & Saltveit, 1989; Saltveit, Bremnes & Brittain, 1994).

Study area

The River Oriège is a torrential stream in the French Pyrenees (Fig. 1). A detailed description of the study area has been given in Céréghino, Boutet & Lavandier (1997). The natural mean flow of the Oriège varied from $1 \text{ m}^3 \text{ s}^{-1}$ in winter and summer to $15 \text{ m}^3 \text{ s}^{-1}$ during the spring thaw (Fig. 1). Flow in the Oriège River (912 m a.s.l.) is supplemented by discharge from the Orlu hydroelectric plant (by $5 \text{ m}^3 \text{ s}^{-1}$ in spring to $10 \text{ m}^3 \text{ s}^{-1}$ in winter or summer), which is fed by hypolimnetic water from a high altitude reservoir (Lake Naguilles 1855 m a.s.l.). Three sampling sites were selected, a reference site upstream of the discharge point from the hydrostation (site A), and two sites below the outlet (sites B and C). Their characteristics are given in Table 1. During hydropeaking, the input of hypolimnetic water slightly increased downstream winter temperatures (by about 2–3 °C) and strongly reduced summer stream temperatures (by about –6 °C, see examples in Fig. 2). Total degree-days (dd) accumulated monthly at sites B and C were 109 and 46 dd lower, respectively, than at site A from August to October 1991 (Fig. 2), and 61 and 215 dd higher from November 1991 to July 1992. During winter, hypolimnetic releases accentuated the natural increase

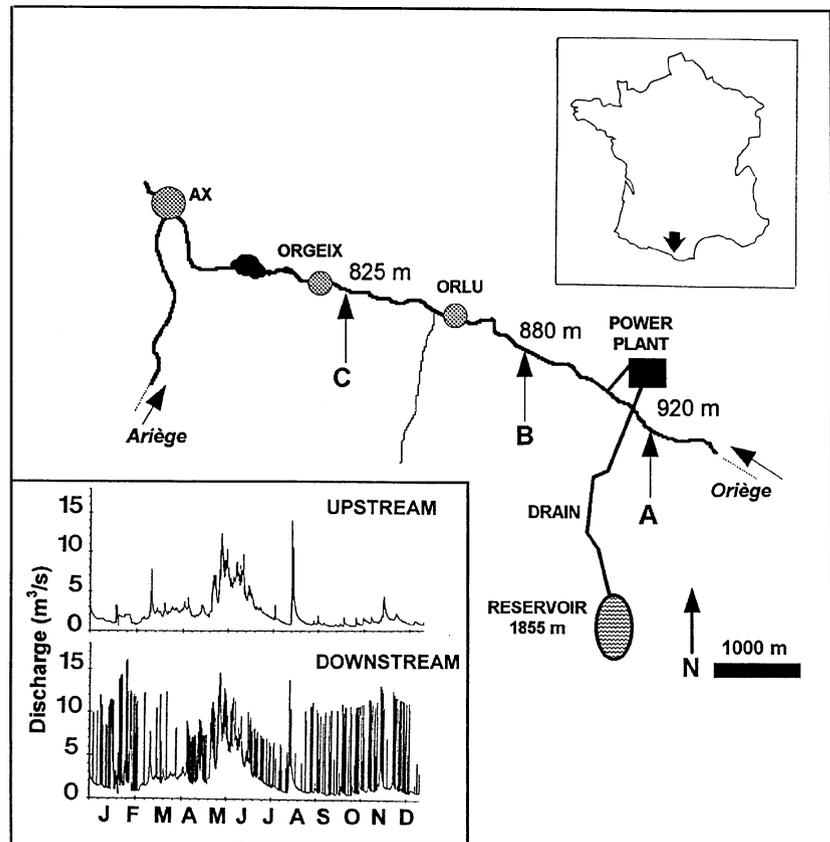


Fig. 1 Map of the River Oriège, location of the three sampling sites (A, B, C), and hourly discharge ($\text{m}^3 \text{s}^{-1}$) recorded upstream at site A and 1500 m downstream from the Orlu power plant.

of temperature at downstream sites. As a result, site B had the lowest total number of degree-days calculated for the study period (June 1991–July 1992), but the annual thermal sums were similar (Table 1).

Methods

At least five benthic sample-units were collected each month from June 1991 to July 1992 using a standard Surber sampler (0.3-mm-mesh size). Samples were taken from various substrata [gravel (2–20 mm); pebbles (20–200 mm); and cobbles (>200 mm)] and were distributed in proportion to the relative abundance of these substrata. This scheme provided the best qualitative (all substrata were sampled, thus maximizing the species list) and quantitative (Surber sampler, replicate sample-units) estimates. However, because of a low number of sample-units each month and as a result of mayfly seasonality, confidence limits of mean annual estimates are large. Therefore, the lower and upper density and biomass observed during the sampling period are indicated. Inverte-

Table 1 Main characteristics of the three sampling sites (A, B, C)

	A	B	C
Distance from the outlet (m)	-700	700	3500
Altitude (m a.s.l.)	920	880	825
Stream width (m)	8	17	21
Water temperature (min–max, °C)	0–13.5	0.4–13.8	0.7–14.5
Total degree-days (June 1991–July 1992)	2917	2877	3144

brates were preserved in the field in 5% formalin, identified in the laboratory and preserved in 70% ethyl alcohol.

Drift was collected for 24 h in June and October 1991, at sites A and B using a standard drift net (0.3-mm mesh size) at 1-h intervals. Because of clogging, the sampling period was reduced to 30 min during hydropeaking. Drift abundance was expressed as number of individuals per volume of water filtered (individuals 100 m^{-3}).

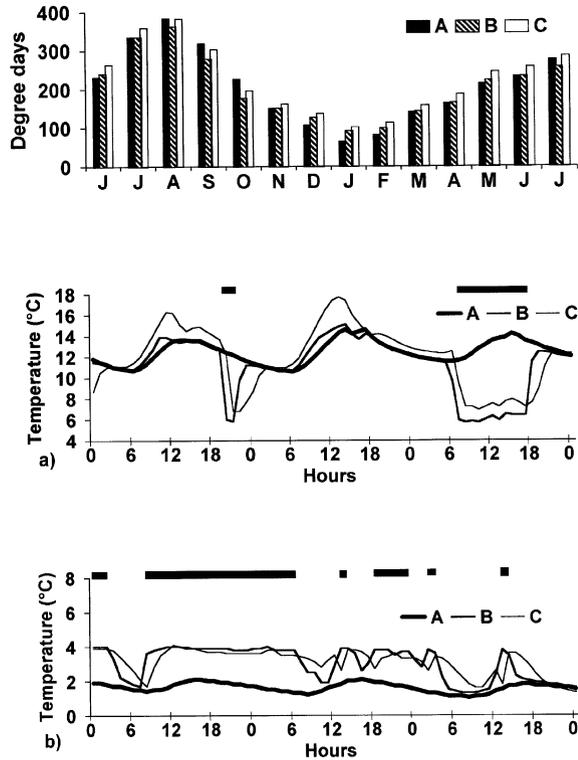


Fig. 2 Thermal regime of the River Oriège and influence of hypolimnetic releases (June 1991–July 1992) showing examples of diel fluctuations in stream water at sites A, B and C over 3 days in summer (a) and winter (b). Solid bars at the top of the graph indicate periods of power generation.

All larvae were divided into 0.1-mm-interval size classes based on head capsule width or tibia length of the third leg. This last size criterion reduced the variability resulting from sexual dimorphism in *Rhithrogena* species. Measurements were used to construct size-frequency plots for life cycle determination. Differences in the mean annual frequency distribution of larval size (upstream vs. downstream) for each species was compared using Kolmogorov–Smirnov two-sample tests.

Sets of larvae (at least ten individuals) of different size classes were dried at 60°C for 24 h and weighed. Larval mean individual dry weights (mg) were deduced from linear regressions (with 95% CL) between the natural log of weight (LnW) and tibia length or head capsule width (*L*). Mean individual dry weights of cohorts from each site were natural log transformed to generate a series of subsegment linear regressions that represent a cohort’s seasonal growth patterns over the year. The relationship between the mean individual dry weight of the larvae of each cohort and time was calculated as: $W_t = W_{t_0} e^{kT}$, where W_t = weight at instant t , W_{t_0} = weight at instant t_0 , $T = t - t_0$ days, k ($\text{mg mg}^{-1} \text{day}^{-1}$) = instantaneous growth rate (Humpesch, 1979, 1981). Growth of individuals

Table 2 Mean annual densities (ind m^{-2} and dry weight biomasses (mg m^{-2}) of Ephemeroptera species from the River Oriège (France) at three samplings sites (A, B, C). Minimum and maximum monthly estimates are indicated in brackets

	A		B		C	
	ind m^{-2}	mg m^{-2}	ind m^{-2}	mg m^{-2}	ind m^{-2}	mg m^{-2}
Baetidae						
<i>Baetis alpinus</i>	667 (8–2750)	534 (12–2420)	578 (5–2568)	488 (4–1823)	429 (15–1196)	549 (6–1662)
<i>B. rhodani</i>	61 (5–407)	44 (4–273)	74 (0–482)	54 (0–416)	321 (17–2370)	231 (11–1896)
<i>B. catharus</i>	177 (3–1023)	57 (7–225)	40 (0–216)	14 (0–56)	27 (0–146)	8 (0–41)
<i>B. muticus</i>	5 (0–15)	2 (0–6)	–	–	–	–
Heptageniidae						
<i>Rhithrogena semicolorata</i>	311 (80–862)	500 (49–1207)	154 (20–506)	566 (74–2110)	589 (80–1748)	548 (107–556)
<i>R. sp. gr. hercynia</i>	88 (0–317)	311 (0–268)	24 (0–86)	166 (0–468)	10 (0–50)	95 (0–281)
<i>R. kimminsi</i>	43 (10–150)	74 (15–259)	10 (0–30)	20 (0–108)	3 (0–27)	2 (0–6)
<i>Ecdyonurus angelieri</i>	14 (0–49)	7 (0–265)	6 (0–27)	3 (0–46)	59 (3–150)	28 (1–998)
<i>Epeorus torrentium</i>	18 (5–70)	34 (9–161)	5 (0–13)	20 (0–40)	166 (7–478)	184 (16–1968)
Ephemerellidae						
<i>Ephemerella ignita</i>	24 (0–69)	11 (0–18)	68 (0–735)	36 (0–272)	263 (0–2050)	210 (0–1086)
Leptophlebiidae						
<i>Habroleptoides berthelemyi</i>	8 (0–67)	4 (0–9)	–	–	2 (0–11)	1 (0–2)
Caenidae						
<i>Caenis sp.</i>	1 (0–10)	0.1 (0–1.5)	1 (0–3)	0.1 (0–0.6)	11 (0–79)	2 (0–5)
Total	1417	1578	960	1367	1880	1859

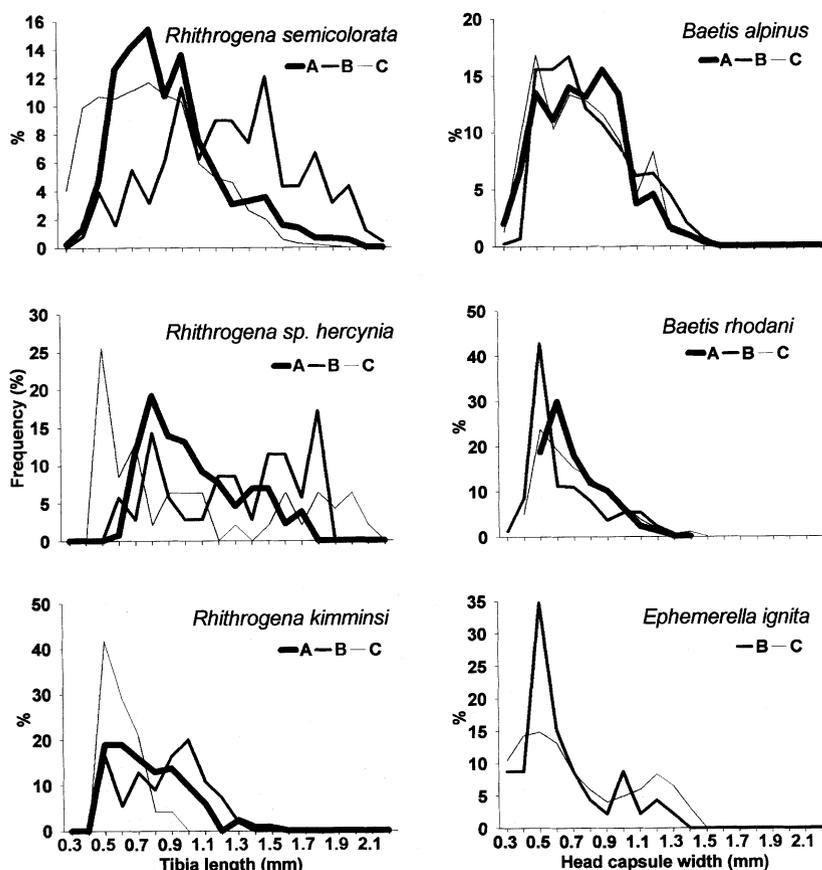


Fig. 3 Frequency distribution of size measurements for larvae of six Ephemeroptera species at sites A, B and C over the whole study period.

was expressed as specific growth rate, K , with $K = 100k$ (% dry weight per day \pm 95% CL).

Results

Species distribution

Twelve species from five families were captured among the three sites, with all species occurring at the reference site A (Table 2). Species identification of *Epeorus* and *Ecdyonurus* requires adults. No *Epeorus* adults were caught, but *E. torrentium* Eaton is normally dominant in the Pyrenees at this altitude (Vinçon & Thomas, 1987). *Ecdyonurus angelieri* Thomas was the only species caught in the adult stage. Table 2 helped to identify four different spatial distribution patterns: (i) the mean annual density and biomass of *Baetis catharus* Thomas, *Rhithrogena* sp. gr. *hercynia* (Landa), and *R. kimminsi* Thomas decreased from sites A to C; (ii) the mean annual density and biomass of *B. rhodani* (Pictet), *Ephemerella ignita* (Poda) and *Caenis* sp. increased from sites A to C; (iii) the mean annual

density and biomass of the two Heptageniidae *Epeorus torrentium*, *E. angelieri* and of the Leptophlebiidae *Habroleptoides berthelemyi* (Thomas) decreased from site A to B then increased at C; and (iv) *B. muticus* (Linné) was only found at site A. A somewhat more variable pattern occurred for two species: in *B. alpinus* (Pictet), density decreased from site A to C but biomass was the highest at site C, and in *R. semicolorata* (Curtis), density decreased from site A to B then increased at C, but its highest biomass occurred at site B. *Habroleptoides berthelemyi* was absent at site B and scarce at site C.

There were differences in the biomass to density ratio between site A and each of the downstream sites for the six most common species (Table 2). This resulted from differences in the mean annual distribution of size classes (Fig. 3). Thus, significant differences ($P < 0.05$, Kolmogorov–Smirnov two-sample tests) in the frequency distribution of size classes occurred for the three *Rhithrogena* species, with a shift towards larger larvae at site B. Only *R. semicolorata* recovered to the reference population structure at site C. The frequency distribution of size classes at both

downstream sites did not differ significantly ($P > 0.05$) from the upstream sites for baetids. *Ephemerella ignita* occurred mainly at sites B and C, and no comparison was possible with site A.

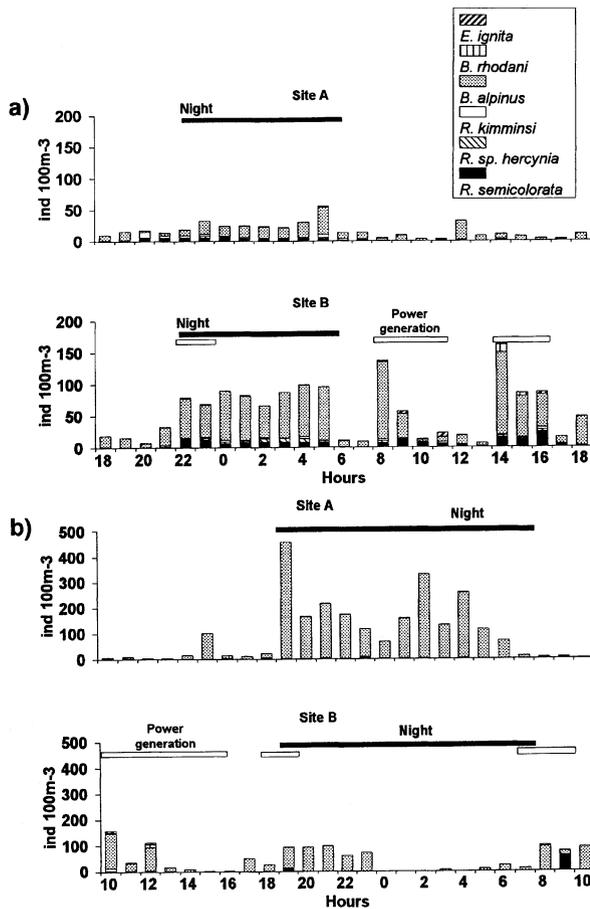


Fig. 4 Drift of six dominant Ephemeroptera species (individuals 100m^{-3}) over 24 h at sites A and B in (a) June 1991 and (b) October 1991.

Table 3 Values for the constants a and b , with 95% confidence intervals, obtained from equation $\text{Ln}W = a + bL$ (see text). W = dry weight (mg), L = tibia length of the third leg (*Rhithrogena* species) or head width (other species) (mm). All correlation coefficients (r) were highly significant ($p < 0.01$)

Species	a	b	r
<i>Rhithrogena semicolorata</i>	-2.26 ± 0.37	2.38 ± 0.27	0.95
<i>R. sp. gr. hercynia</i>	-2.16 ± 0.47	2.99 ± 0.34	0.95
<i>R. kimminsi</i>	-2.53 ± 0.69	3.59 ± 0.7	0.94
<i>Baetis alpinus</i>	-2.84 ± 0.33	3.38 ± 0.39	0.97
<i>B. rhodani</i>	-2.55 ± 0.31	3.32 ± 0.32	0.98
<i>Ephemerella ignita</i>	-4.8 ± 0.93	4.86 ± 1.02	0.91

Drift

Upstream from the plant, drift exhibited a clear diel periodicity, and was almost exclusively nocturnal, particularly during low-flow periods in October (Fig. 4). In June, drift rates were about twice as high during the night as during the day, but they remained moderate over the 24-h period. *Baetis alpinus* was the dominant drifting mayfly, and few other species were caught in October. In June, all species were caught, mainly at night.

Downstream from the plant, each peak flow added catastrophic drift to the daily pattern. Most larvae were flushed at the beginning of peak flows, and the disturbance was higher when the difference between natural and peak flow was greatest. In October, the natural periodicity disappeared and drift was chiefly a result of hydropower generation. Natural levels of drift during the day were low, so the impact of catastrophic flows (elevated drift) was easily detected. However, it is interesting to note that natural drift rates during the night at the unregulated site were only slightly elevated (Fig. 4a) or lower (Fig. 4b) than catastrophic drift rates at the regulated site. *Baetis alpinus* was always the most abundant mayfly in the drift. All other species were regularly taken during the day in June, and during peak flows in October.

Life histories and growth

A simple regression ($\text{Ln}W = a + bL$) provided the best fit for the relationship between dry weight (W) and tibia length or head width (L). Table 3 presents values for constants a and b ($\pm 95\%$ CL) obtained for the six studied species. ' r ' values ranged from 0.91 to 0.98 and were highly significant for each species ($P < 0.01$).

Specific growth rates, based on biomass and length for these six species ranged from 0.10 ± 0.08 to $6.05 \pm 1.54\% \text{ day}^{-1}$, and from 0.027 ± 0.02 – $1.24 \pm 0.31\% \text{ day}^{-1}$, respectively. The relationship between growth (K) and mean water temperature (T) for all species combined and for each *Rhithrogena* species was described by $K=a+bT$, where b is the slope or increase in biomass per unit increase in temperature (Table 4).

Rhithrogena semicolorata was univoltine at the reference site A (Fig. 5), its flight period extended from June to October. Newly hatched larvae appeared in August. Their growth continued during autumn ($K=0.63 \pm 0.18\% \text{ day}^{-1}$), slowed in winter ($K=0.15 \pm 1.3\% \text{ day}^{-1}$), and increased during spring ($K=1.37 \pm 0.71\% \text{ day}^{-1}$). At site B, hatching occurred in September, and growth continued until February; growth rates were $K=0.55 \pm 0.5\% \text{ day}^{-1}$ in

autumn, $K=0.92 \pm 0.01\% \text{ day}^{-1}$ in winter, and $K=2.23 \pm 1.3\% \text{ day}^{-1}$ in summer. At site C, emergence extended from June to August. There was a large pulse of early instars in September. Larval growth

Table 4 Regression coefficients (a and b), with 95% confidence intervals, obtained from the positive linear relationship between temperature and growth ($K=a+bT$). K is specific growth rate (% dry weight per day), T is mean water temperature ($^{\circ}\text{C}$), and b is the slope or increase in growth per increase in temperature

Taxa	a	b	r
<i>Rhithrogena semicolorata</i>	-1.11 ± 1.04	0.53 ± 0.23	0.75*
<i>Rhithrogena</i> sp. gr. <i>hercynia</i>	-1.21 ± 1.6	0.65 ± 0.38	0.85**
<i>Rhithrogena kimminsi</i>	-1.29 ± 0.9	0.38 ± 0.18	0.82**
All species combined	-1.69 ± 0.8	0.63 ± 0.15	0.74*

* $P < 0.01$; ** $P < 0.05$.

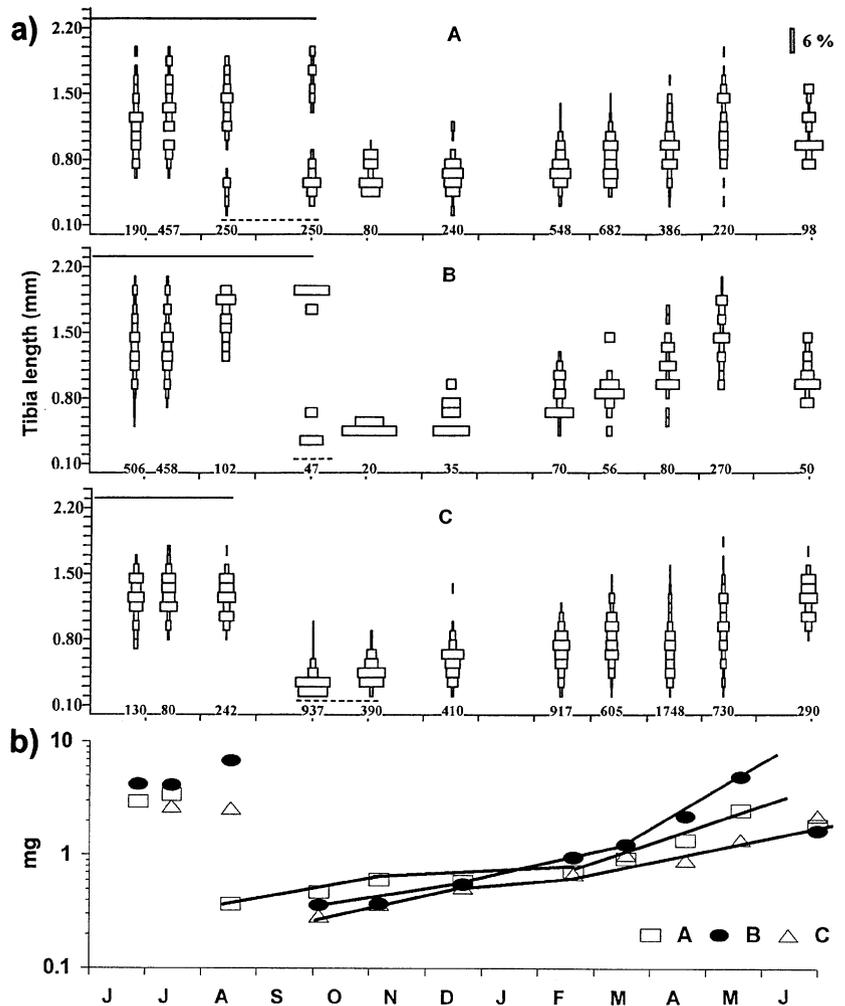


Fig. 5 Life history and growth of *Rhithrogena semicolorata* at sites A, B and C based on size class frequency distributions (a). Horizontal lines indicate the approximate times of hatching (dotted line) and emergence (solid line), and numbers indicate the mean density (individuals m⁻²). (b) The mean individual dry weight (mg) throughout the life cycle at each sites.

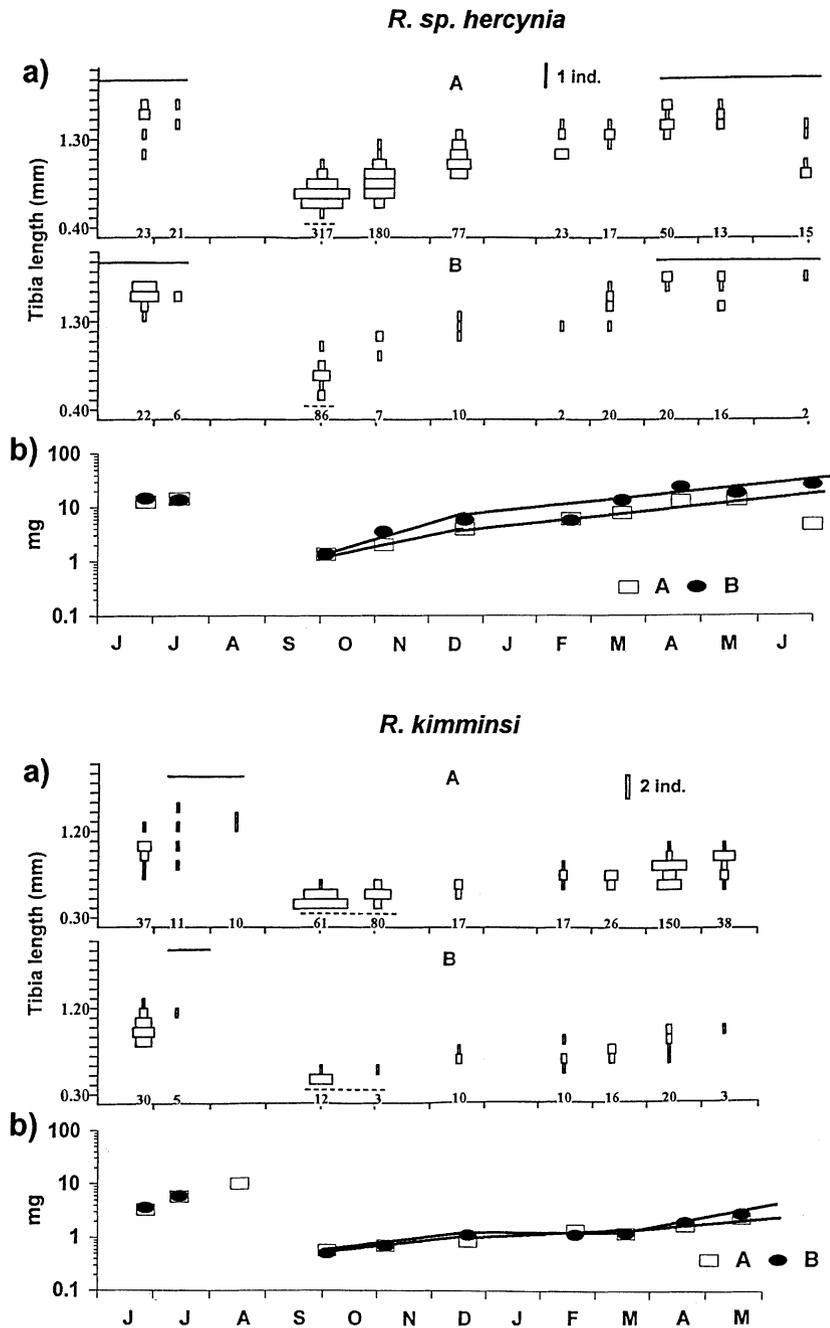


Fig. 6 Life history and growth of *Rhithrogena* sp. gr. *hercynia* and *R. kimminsi* at sites A and B (see legend to Fig. 5).

was $K = 0.75 \pm 0.01\% \text{ day}^{-1}$ in autumn, and slowed in winter to $K = 0.45 \pm 0.01\% \text{ day}^{-1}$. In spring, the growth rate was similar to that in autumn ($K = 0.78 \pm 0.39\% \text{ day}^{-1}$).

This is the first description of the larval development of *Rhithrogena* sp. gr. *hercynia* (Fig. 6). Few *R. sp. gr. hercynia* larvae were caught, but their size distribution suggested one generation per year. The flight period extended from April to July at sites A

and B. No larvae were found in the stream during August. Hatching probably occurred in September, and larvae of various size classes were caught in October. Larval growth was rapid during autumn ($K = 1.39 \pm 1.1\% \text{ day}^{-1}$ at site A, $K = 1.87 \pm 1.3\% \text{ day}^{-1}$ at site B), but slowed during winter at site A and continued until spring emergence ($K = 0.80 \pm 0.3\% \text{ day}^{-1}$). Similar growth patterns were observed at site B, where the winter to spring

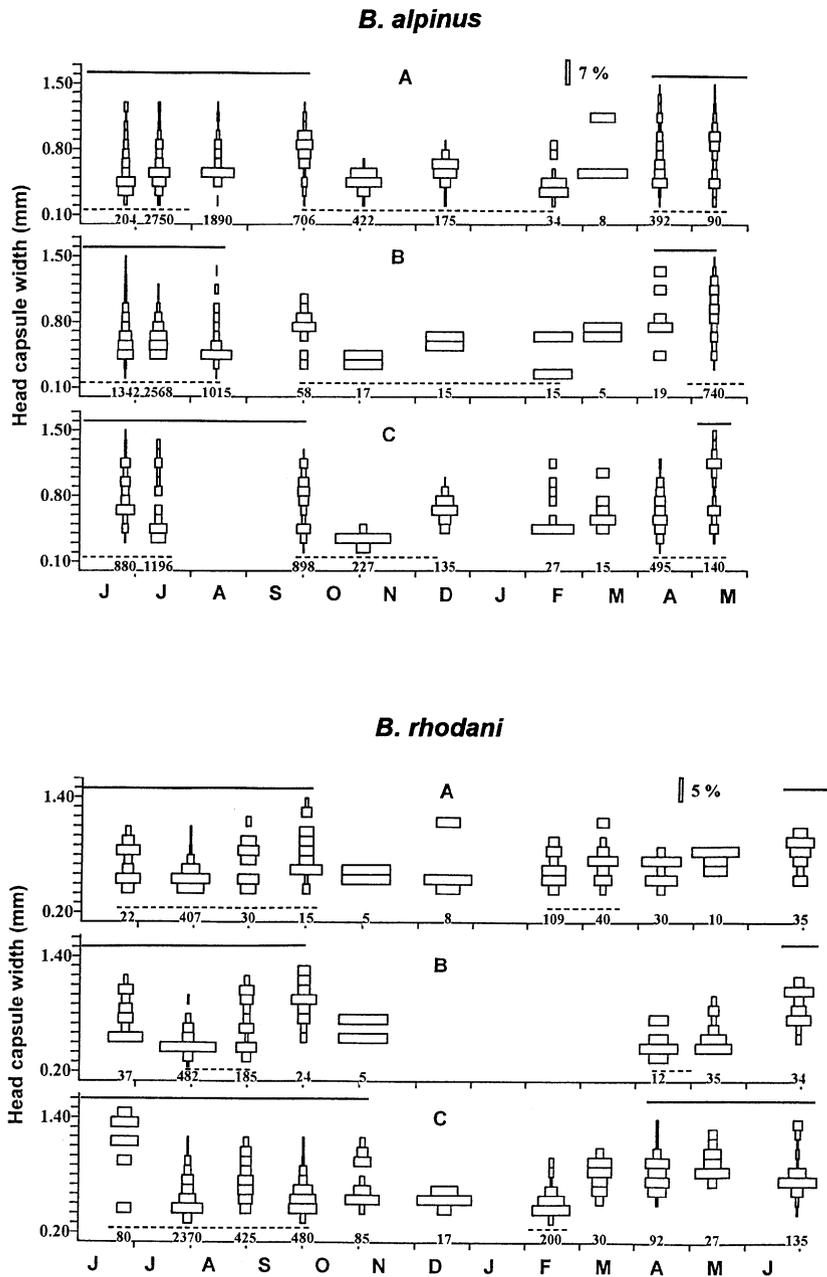


Fig. 7 Life history of *Baetis alpinus* and *B. rhodani* at sites A, B and C (see legend to Fig. 5). Growth calculations were not possible (see text).

instantaneous growth rate was $K = 0.75 \pm 0.6\% \text{ day}^{-1}$. The extreme scarcity of larvae at site C prevented study of life history patterns.

This is also the first account of the larval development of *R. kimminsi*. Although few larvae were caught, the specimens collected suggest a univoltine life cycle with a short flight period extending from July until August (Fig. 6). The youngest larvae appeared in September and October. At site A, larval growth rate was $K = 0.53 \pm 0.5\% \text{ day}^{-1}$ in autumn, $K = 0.42 \pm 0.26\% \text{ day}^{-1}$ in winter and $K = 1.08 \pm$

$0.34\% \text{ day}^{-1}$ in spring. At site B, growth was greater in autumn ($K = 1.04 \pm 0.53\% \text{ day}^{-1}$) and spring ($K = 1.37 \pm 1.3\% \text{ day}^{-1}$) and slowed in winter ($K = 0.10 \pm 0.08\% \text{ day}^{-1}$). As was the case for *R. sp. gr. hercynia*, no difference was found in the life history patterns between sites A and B.

The range in sizes of *B. alpinus* was great throughout the year (Fig. 7), indicating the possibility of a bivoltine life cycle with long periods of flight, egg laying and hatching. At the reference site (A), early instars appeared in August and September and

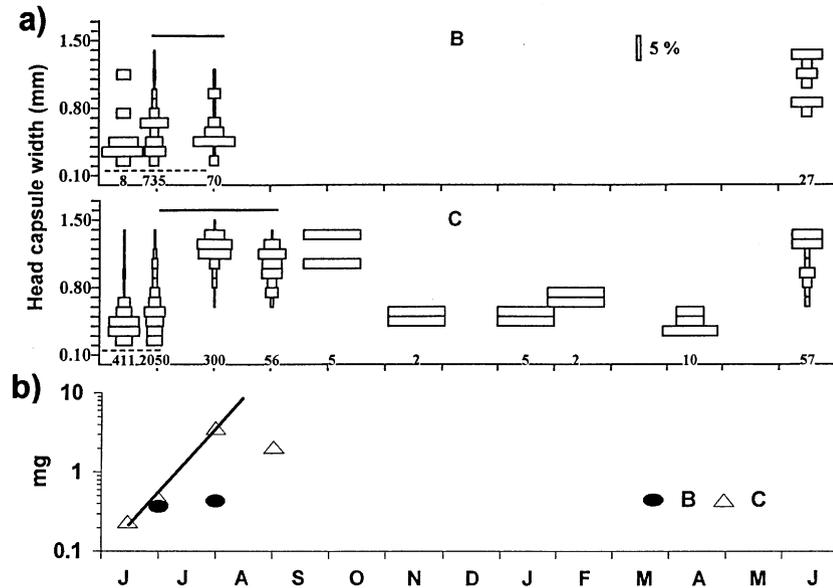


Fig. 8 Life history and growth of *Ephemera ignita* at sites B and C (see legend to Fig. 5).

showed continuous development until spring. Hatching continued until February and thus all larval sizes were present simultaneously in spring. Emergence occurred from April to October. The number of young larvae in April suggested the hatching of a new generation, which yielded the last emerging adults of the flight period following rapid larval development. Development patterns were quite similar at both downstream sites. Delayed recruitment and the notable overlap of different generations prevented growth calculations.

Baetis rhodani also appeared to have a bivoltine life cycle (Fig. 7). At sites A and C, hatching occurred mainly in February and lasted until April. Larval growth was quick and emergence extended from April to October at site C, and from July to October at site A. A large number of newly hatched larvae appeared in July, some of which probably yielded the last emerging adults at the end of the flight period in October. At site B, no larvae were caught during winter and the larval development patterns were clearer: two distinct cohorts developed successively between April and July ($K = 1.4 \pm 0.52\% \text{ day}^{-1}$) and between July and October ($K = 2.5 \pm 2.3\% \text{ day}^{-1}$). With the exception of site B, the overlap of cohorts prevented calculation of the growth of *B. rhodani* larvae.

Ephemera ignita occurred mainly at downstream sites (B and C), and had a univoltine life cycle with a long egg diapause between November and June (Fig. 8). Growth was rapid in summer

($K = 6.05 \pm 1.54\% \text{ day}^{-1}$ at site A; $K = 4.04 \pm 8.03\% \text{ day}^{-1}$ at site B) and emergence occurred from August to October.

Discussion

Assessing the effect of hydroelectric facilities in mountain rivers requires the longitudinal distribution of aquatic insect populations along the stream studied to be taken into account (Hauer & Stanford, 1982; Ward & Stanford, 1983a). The study section of the River Oriège is a zone of transition, where the distributions of high, moderate and low altitude species overlap (Vinçon & Thomas, 1987). Previous studies of various types of hydropeaking operations have chiefly reported a decrease in species richness and/or abundance below outlets, and/or discontinuities in the longitudinal zonation of lotic insects (summarized in Ward & Stanford, 1979, 1983a). The Orlu hydroelectric facility did not modify the qualitative composition of the mayfly community, but clearly affected the densities and biomasses of several populations; for example, *R. semicolorata* was abundant at all sites but its density was reduced by 50% 700 m downstream from the plant. On the other hand, the low abundance of several species below the outlet reflected the impact of both hydropeaking and zonation. These species were high mountain species, the density of which naturally decreases towards downstream sites in the Pyrenees (e.g. *R. sp. hercynia*, *R. kimminsi*), and

low mountain species, the density of which naturally decreases towards upstream sites (e.g. *B. rhodani*, *Ephemerella ignita*, *Epeorus torrentium*).

Three *Rhithrogena* species, *R. sp. hercynia* and *R. kimminsi* (of which life cycles have not been previously reported) and *R. semicolorata*, coexist in the Oriège. They show slow univoltine seasonal cycles, but slight temporal segregation of larval development patterns and differences in the size of coexisting larvae may have reduced any interspecific competition for space and food.

As hypolimnetic releases caused no chemical pollution or oxygen depletion, flow and temperature were the two main environmental factors modified by hydropeaking in the River Oriège. Peak flows are known to decrease both the density and biomass of aquatic insects downstream from hydroplant outlets (Gore, 1977; Boles, 1980; Gersich & Brusven, 1981; Hauer & Stanford, 1982; Cushman, 1985; Irvine, 1985; Moog, 1993) by increasing the frequency and intensity of bed scour (Newbury, 1984; Rader & Ward, 1988; Cobb, Galloway & Flannagan, 1992; Death & Winterbourn, 1994; Gore *et al.*, 1994), which leads to a high catastrophic drift (Pearson & Franklin, 1968; Brooker & Hemsworth, 1978; Crisp & Robson, 1979; Gore, Nestler & Layzer, 1989). This was particularly true of the River Oriège, where great amounts of mineral particulates and invertebrates were flushed downstream during hydropeaking. Catastrophic drift was highest in autumn when the difference between natural and peak flows was the greatest. Intermittent discharges were primarily responsible for the observed depletion of the benthos. Behavioural drift almost disappeared, suggesting it is related to density-dependent factors (Waters, 1965; Ghetti & Ravanetti, 1984; Ciborowski, 1987). Hydropeaking may also modify the population structure of species; for instance, Raddum (1985) reported a shift towards smaller individuals in several mayfly and stonefly species in Norway as a result of the drift of the largest individuals out of the area. In the Oriège, species responded to environmental changes in two different ways, depending on their larval development. In *B. alpinus*, *B. rhodani* and *Ephemerella ignita*, most larval instars were present at all times during the development period. The population structure remained similar at the three sites, suggesting that all instars were similarly

affected by hydropeaking. In *Rhithrogena* species, which had slow seasonal cycles, only few larval instars were simultaneously present during the life cycle. During the short hatching period, most of the newly hatched larvae were flushed downstream by peaking flows, and the shift of the mean population structure towards larger larvae at site B probably resulted from the enrichment of the benthos by larvae drifting in from the unregulated zone, chiefly during snowmelt floods, i.e. when the natural drift remained extensive over the day.

Temperature is a major ecological factor affecting the seasonality and development of mayflies (Vannote & Sweeney, 1980; Ward & Stanford, 1982; Sweeney *et al.*, 1986; Newbold, Sweeney & Vannote, 1994) and influences Ephemeroptera densities through growth, adult size and fecundity (Kondratieff & Voshell, 1981; Rader & Ward, 1990; Giberson & Rosenberg, 1992; Pritchard & Zloty, 1994). Below most hydroelectric impoundments, stream water consists entirely of reservoir water, and thermal effects observed downstream are either a higher thermal constancy or an increased thermal variability, depending on operation characteristics (reviewed by Ward & Stanford, 1979). In the regulation scheme in the present study, hypolimnetic releases had no thermal effects during snowmelt flood periods, because hypolimnetic water and stream water had similar temperatures. On the other hand, they caused a slight winter warming and a strong summer cooling of the stream water, which slightly reduced the annual thermal sums and the annual range of temperatures downstream from the hydroplant. In these conditions, life history patterns showed only slight differences between the three sites and were close to those already described for the same species under similar natural conditions in Europe (Landa, 1968; Ulfstrand, 1968; Langford, 1971; Lavandier & Dumas, 1971; Thibault, 1971; Sowa, 1975; Bass, 1976; Humpesch, 1979; Macan, 1979; Wise, 1980; Alba-Tercedor, 1984, 1990; Elliott, Humpesch & Macan, 1988; Lavandier, 1988; Ouahsine & Lavandier, 1988). The present study and previous research (summarized in Brittain, 1990) showed that the growth of Ephemeroptera is temperature dependent. In the Oriège, there was a significant linear relationship between the growth rates of *Rhithrogena* species and mean water temperatures (at each site and at all sites combined) suggesting that larvae react rapidly to changes in temperature, as shown by Sweeney (1978)

in his study of the mayfly *Isonischia bicolor*. This growth/temperature relationship also indicates that high current velocities, which tend to increase physiological demands for position maintenance (see Hynes, 1970; Kovalak, 1978; Mundahl & Kraft, 1988), did not decrease growth sufficiently to be detected from the field data obtained in the present study. Similarly, in winter, when warmer water and increased current velocities may have antagonistic effects on larval growth, *R. semicolorata* showed a slight increase in growth downstream of the outlet, whereas growth nearly stopped upstream. This suggests that when species are able to withstand harsh hydrological conditions, the positive influence of increased winter temperature on larval growth overcomes the negative effects of hydropeaking flows. Even though the results obtained here indicated that mean temperatures were a suitable parameter to interpret larval development patterns of mayflies in both the regulated and unregulated zones of the Oriège, it would be interesting to determine the precise influence of temperature fluctuations on larval growth, particularly comparing stenothermic and eurythermic species. Indeed, according to theoretical relationships between activity and temperature (Pradhan, 1945 in Sweeney, 1984), changes in temperature may have different consequences when they occur near the upper or near the lower temperature limits for a species; for example, an increase in minimum temperature chiefly stimulated the growth of stenothermic species having a low threshold temperature, whereas a decrease in maximum temperature had a minor effect on their growth rate. Thus, in the River Oriège, winter warming and summer cooling could be advantageous to cold-water species, but detrimental to warmer-water species, especially when they reach their altitudinal limits. As a result, temperature reductions could favour the expansion of cold-water species towards downstream sites (e.g. *R. kimminsi*), but restrict the movement of low mountain species towards upstream sites (e.g. *B. rhodani*, *Ephemerella ignita*). Further studies, based on both laboratory and field experiments, are needed to confirm this hypothesis which cannot be directly verified from the data obtained in the present study.

In conclusion, in the Oriège, where natural discharge and temperature are preserved when the hydroplant is inoperative, mayfly abundance and population structure are mainly governed by the

hydraulic regime. Peak flows generate catastrophic drifts, leading to a significant depletion of the benthos, and to a modification of population structures, depending on the timing of the species' development. Larval growth was temperature dependent, but the low magnitude of thermal modifications had a minor effect on mayfly population dynamics. The main consequence would be the expansion of cold stenothermic species towards downstream sites. Brittain & Saltveit (1989) reviewed the impact of river regulation on mayflies, particularly below deep-release dams. They reported that: (i) increased thermal constancy reduced the average number of mayfly taxa, although their mean density often increased; and (ii) widely fluctuating daily flows and current velocities lead to lower benthic densities and richness. In the Oriège, hydropeaking reduced the benthic abundance of most species, underlining the prominent role of current velocities through drift patterns, but did not affect the diversity of the Ephemeroptera community, probably because the river returned to 'normal' conditions when the plant was inoperative, and because daily artificial fluctuations in flow and temperature remained within the limits of natural seasonal variations.

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