

MOVEMENTS OF *RHITHROGENA LOYOLAEA* NAVÁS
AND *BAETIS ALPINUS* PICTET IN A HIGH MOUNTAIN STREAM
IN THE PYRENEES.

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ABSTRACT

Rhithrogena loyolaea and *Baetis alpinus* were studied at a station (altitude 2150 m, snow-cover for 5-7 months/year) in a fast flowing Pyrenean stream.

Under the snow, the drift is low. At lower water, drift presented several peaks related to the fluctuations in light but there was no clear day-night rhythm.

The biomass drifting over one year represented the production from an area of 1 and 30 m² for the young larvae and of 650 and 165 m² for the mature larvae of *B. alpinus* and *R. loyolaea* respectively.

Upstream movements did not compensate for downstream drift. The population stability is maintained by the young larvae which are numerous within the substratum and by the flight of reproductive females upstream.

INTRODUCTION.

Baetis alpinus and *Rhithrogena loyolaea* are two abundant and common species in mountain streams. Their embryonic and larval developments have been studied under various conditions (Humpesch 1979, Humpesch & Elliott 1980, Alba-Tercedor 1984, Weichselbaumer 1984). However little is known about the behaviour of the species in their natural environment.

The aim of this study was to characterize and quantify faunal movement throughout the year. Annual losses by drift were estimated for comparison with population dynamics (biomass, biological cycle and production) already known (Lavandier 1979, 1981, 1988) in a cold mountain stream where discharge is extremely variable and where the bed is regularly disturbed by floods.

MATERIALS AND METHODS

Study area: A detailed description of the Estaragne stream system, has been given elsewhere (Lavandier 1974). The sampling station was located

just above a glacial rise at an altitude of 2150 m. At the station, the stream is covered with snow for 5-8 months of the year and the water temperature ranged from 0°C under the snow to 10°C in summer.

Drift: The drift of invertebrates was sampled for six 24-hour periods in April, July, August, September, October and November 1971. Each drift collection consisted of 24 samples collected at 1-hr intervals. The bottom of the drift net (150 cm long, 50 cm wide, mesh size of 0.25 mm) was on the stream substratum. In April, the torrent ran under 4 m of snow-cover. The hole dug to reach the stream was covered with a black sheet to keep the station in permanent darkness during the sampling period. Drift density was calculated as the number of larvae caught per 100 m³ of water filtered, estimated from measurements of water velocity at the mouth of the net. Total drift was calculated by multiplying drift density by total discharge estimated from mean water velocity and cross-sectionnal area at the station. Hydrographs of the river are presented elsewhere (Lavandier 1974).

Upstream migration: Three experiments (August, September, November) were performed with two traps using Elliott's 1971 method. The traps (100 cm long, 50 cm wide, 10 cm deep) were placed at each sampling station for 72 h. Results are presented as total numbers moving upstream per day.

Density of the benthos within the substratum: Eight perforated pipes were driven into the bottom of the stream to a depth of about 15-30 cm, six months before the beginning of the study. With a manual pump fitted to the pipes, two liters of hyporheic water were pumped out weekly. Results are presented as percentage of the total fauna caught during the study period.

The population dynamics of the two species have been described earlier (Lavandier 1981, 1982, 1988). At this station, the population of *B. alpinus* is chiefly semivoltine whereas the larval development of *R. loyolaea* takes 3 years. In the text and figures, the larvae are called 0⁺, 1⁺, 2⁺, or 3⁺ according to whether they have passed 0, 1, 2, or 3 winters respectively. The corresponding mean sizes of the larvae are roughly 0.6, 3 and 6 mm for *B. alpinus* and 0.7, 2.1, 5 and 9 mm for *R. loyolaea*.

RESULTS

Drift of Baetis alpinus: In April, under the snow, we observed no marked periodicity in drift (fig. 1). From July to November, there were several daily peaks whose position varied according to the length of the main periods of light following one another during the day. Thus we noticed (1) two main nocturnal peaks, of varying length depending on the duration of the night, (2) one peak after dawn, (3) another one when the stream was directly lit by the sun and (4) a minor one in August and September after the sun passed behind the western ridge of the valley. The generations 1⁺ and 2⁺ coexisting until September showed chiefly diurnal and quite synchronous drift. The mean number of larvae drifting in one hour during the day exceeded by 1.5 to 2 fold the mean number drifting in one hour at night. The drift of the new generation which had hatched massively since October showed a similar

variation in time, but most of the larvae drifted at night with two large peaks at the beginning and at the end of the night.

All the larval sizes were observed in the drifting fauna but large individuals showed a higher proportion in the drift than in the benthos (fig. 2). Quantitatively, total drift and drift density varied as did "standing crop" estimates. They increased from July to September (in spite of a decrease of stream discharge), and then decreased at the end of the year. From October, new hatched larvae (about 90% of the benthos) represented 75% of the drifting larvae. Expressed in terms of biomass, drift is at its highest in September, before the oldest individuals emerge: they constituted 2/3 of the drifting biomass. In October, the emergence of the old individuals caused a fall in the biomass transported downstream. The greatest daily losses are equivalent to the biomass of the benthos living on an area of 1 m² (larvae 0⁺) in October to over 6 m² (larvae 1⁺ and 2⁺) in September.

Drift of Rhithrogena loyolaea: The coexisting generations showed a synchronisation of daily drift characterized by 5 to 6 peaks whose position remained similar at all sampling periods (fig. 1). We can see one peak after dawn, when the stream is not directly lit, another one or two when the lighting is at its maximum, another at sunset and 2 peaks of the same size during the night. Whatever the size of the larvae, the number of individuals drifting during one hour was not significantly different during the day or the night.

Proportionally, slightly more mature larvae were taken in drift than in bottom samples. However the structure of the drifting population was close to that of the benthic communities, except for newly hatched larvae (fig. 2). The drift of the 0⁺ larvae seemed to be density-dependent and started only when they were numerous. However, it remained low probably because of low discharge at the end of the year. During the snow-melt flood, the young larvae whose size had not changed were carried downstream together with the older ones.

Daily mean drift densities were quite regular throughout the year, under 20 individuals per 100 m³. Total drift slowly decreased from July to November both because of the decrease of discharge and of the numbers of the larvae 1⁺, 2⁺ and 3⁺. When the water level dropped, at the end of the snow-melt, the daily biomass transported downstream was equivalent to the fauna living an area of 1 to 3 m². After September, the drifting fauna represented only about the benthic population living over an area of 0.25 m².

Upstream movements and distribution of the larvae within the substratum: Except for early instars, individuals of all size classes moved upstream. The rate of upstream movement was greatest in summer, but it remained relatively low (24 and 67 larvae per day for *R. loyolaea* and *B. alpinus* respectively). Most of the larvae collected by pumping the water below the gravel surface came from the top ten centimeters of the stream bed. They were especially larvae in early instars, mainly taken during the snow melt flood and at the end of the year when the new generation hatched massively.

DISCUSSION

The daily drift pattern of the two species is rather different. The drifting larvae of *R. loyola* were as numerous during the day as at night, while the drift of *B. alpinus* occurred mainly at night for the youngest larvae and during the day for the older ones. We had expected a much more distinct variation in the intensity of the drift between day and night, particularly for *B. alpinus* which belongs to a family which usually presents a clear day-night drift pattern. However, although the drift activity of *Baetis (bicaudatus ?)* was strongly nocturnal in a high Rocky Mountain stream (Allan 1987). Turcotte and Harper (1982) observed an absence of daily periodicity in the drift of *Baetis* larvae in the Andes.

It is always difficult to distinguish between "catastrophic drift" "constant drift" and "behavioural drift" which interact in a stream (Waters 1972) particularly when the water velocities are high. In the river Estaragne variations in drift rates were obviously related to change in light fluxes as is shown by the comparison of drift rates in April and November. Indeed, at these times larval populations, temperatures and water levels were quite similar, whereas lighting conditions were very different since, in April, the stream was covered by 4 meters of snow. Under continuous darkness, drift rates were low and fairly constant whereas they were greater and variable in November. Note that in April, the small peaks observed in the drift of *R. loyola* occurred at the same time as the peaks occurring when there was no snow-cover. This pattern suggests that under the snow, either very low changes in light intensity may act on larval activity, or the larvae have an endogenous rhythm. During the snow melt, larvae move to "refuge-habitats" : large individuals maintain themselves between rocks, pebbles or under banks and the early instars are numerous in the surface layers of the substratum.

As a result, the "standing crop" is low and the drift is dependent upon the distribution of the larvae. During this period of high discharge *R. loyola*, which is caught in greater numbers than *B. alpinus* by surber sampling, probably remained more exposed to the flow and drifted more easily.

When the discharge decreased the two species colonized the bottom of the stream progressively. The drift of *R. loyola* decreased even though the apparent population density increased; it was the opposite for *B. alpinus* whose drift increased together with the standing crop.

Daily averages of drift density are variable but are in the range of numerous estimates (Bournaud & Thibault 1973, Armitage 1977). However, some much higher values had been recorded for *Baetis* (Pearson & Franklin 1968, Zelinka 1976, Allan 1987).

The drift rates of the two species have been extrapolated to the whole year, taking account of the estimates of discharge (Allan 1987) and compared with the population dynamics data (Lavandier 1979, 1981). The surface area needed for the production of the biomass of young larvae transported was small (30 m² for *B. alpinus*, less than 1 m² for *R. loyola*). On the other hand, it was very high for the oldest larvae reaching 650 and 165

m² for *B. alpinus* and *R. loyolaea* respectively (fig. 3). At this altitude, this means a length of stream of more than 200 and 60 m. Upstream movements did not compensate for downstream drift. The permanence in time and the stability of the populations were maintained by young larvae which drift little, and by the eggs deposited by females flying up from downstream. Adult migration upstream, as a compensating mechanism for drift (Müller 1954, Pearson & Kramer 1972) was clearly demonstrated for both the species (Lavandier 1981-1982) particularly for *B. alpinus* using the difference in size of subimagines and imagines along the torrent (fig. 4).

These results emphasize the role of species behaviour on the population dynamics of the benthic invertebrates under the difficult conditions of a high mountain stream.

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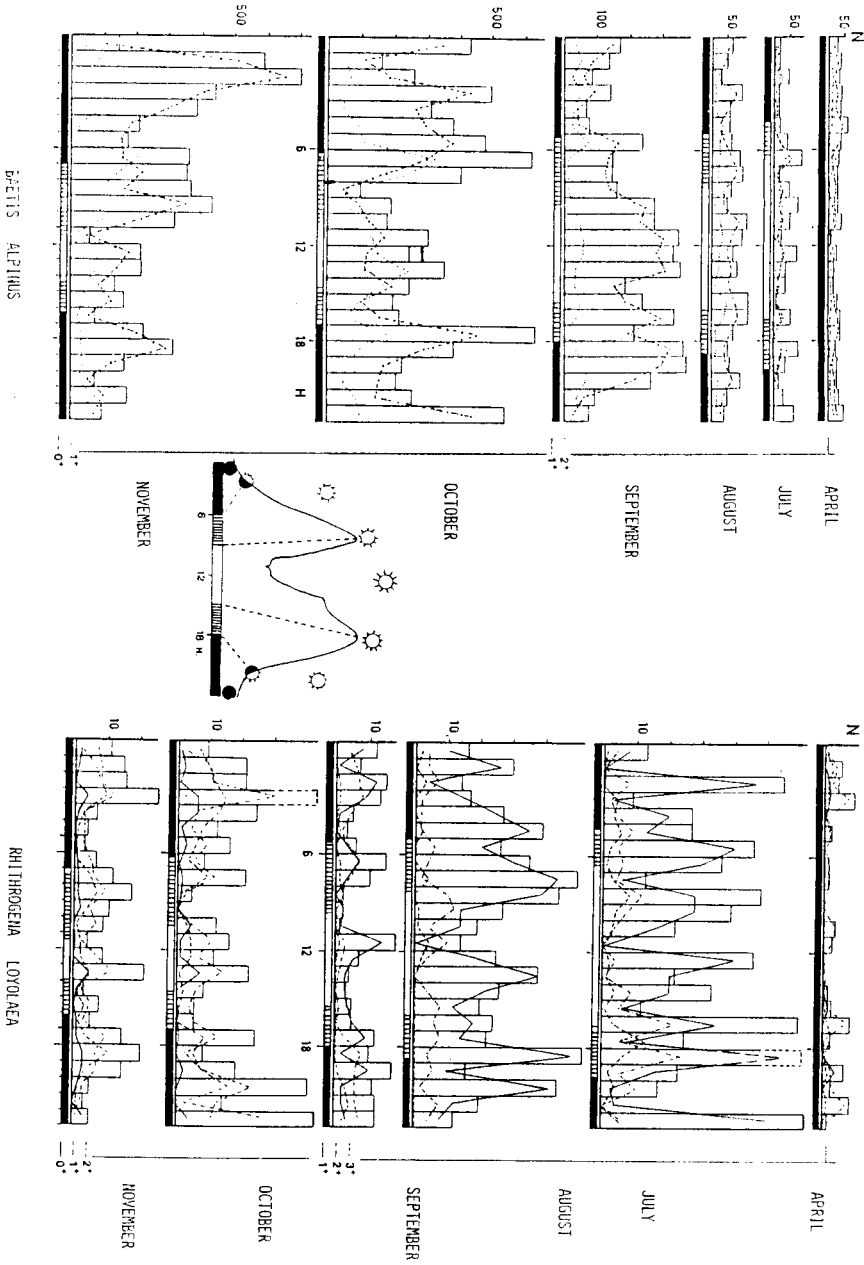


Fig.1. Diel periodicity in the drifting of *B. alpinus* (a) and *R. loyolaea* (b). The histograms indicate the total numbers of larvae taken in each sample over 1 hour at the six sampling periods. The different lines (continuous, dotted, dashed etc...) show the changes in the numbers of drifting larvae of different age : O⁺, 1⁺, 2⁺, 3⁺ = larvae respectively hatched 1, 2, 3 and 4 years before. Variations in light intensity are shown at the bottom of the figure.

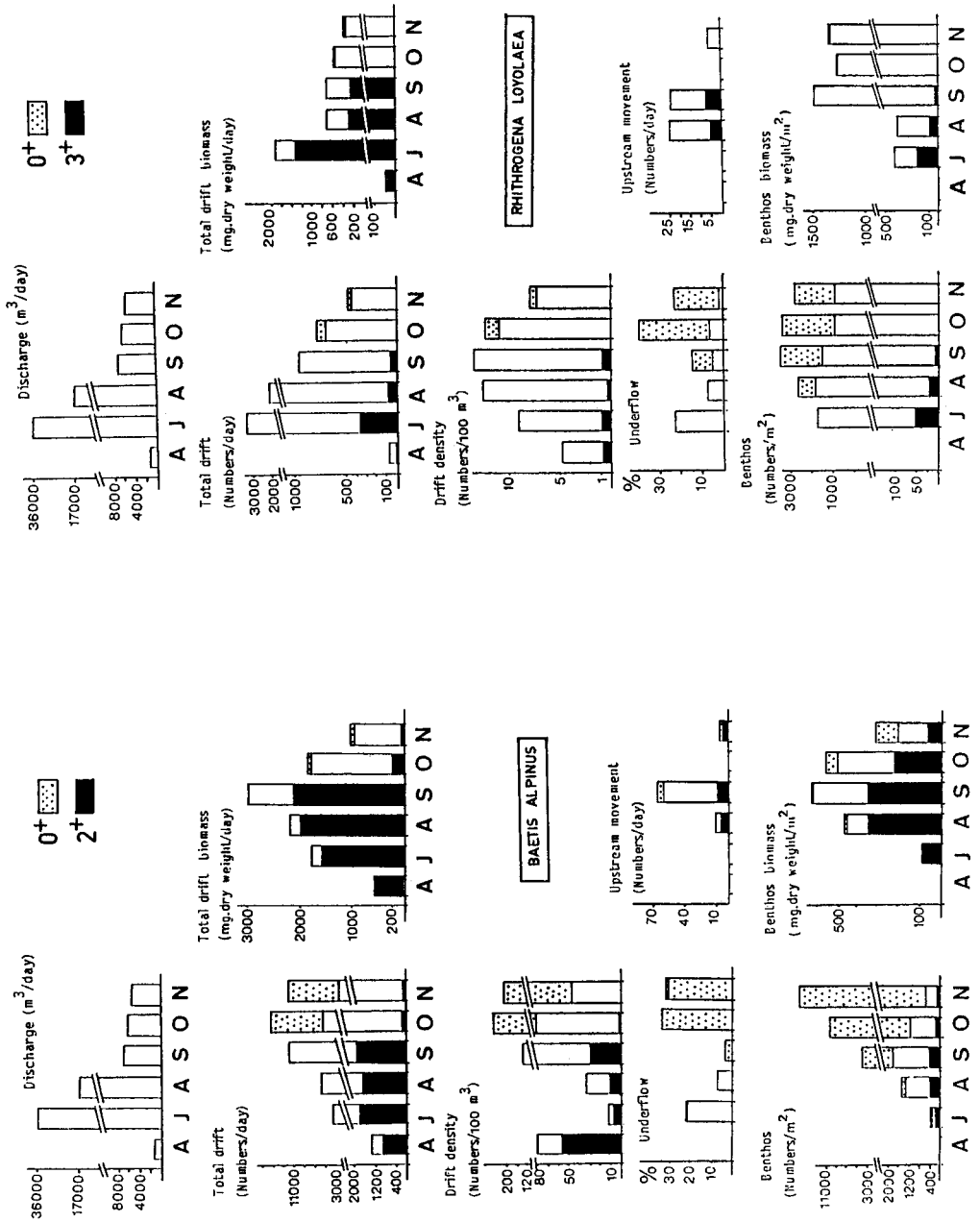


Fig. 2. Movements of the fauna. Total drift (numbers and biomass carried down per day), drift density (numbers per 100 m³), upstream movements (numbers per day) and numbers of larvae within the substratum (expressed as percent of the total number caught during the study). The results are compared to discharge and to benthic populations (numbers and biomass). 0⁺ new hatched larvae, 2⁺ and 3⁺ old larvae of *B. alpinus* and *R. loyolaea* respectively.

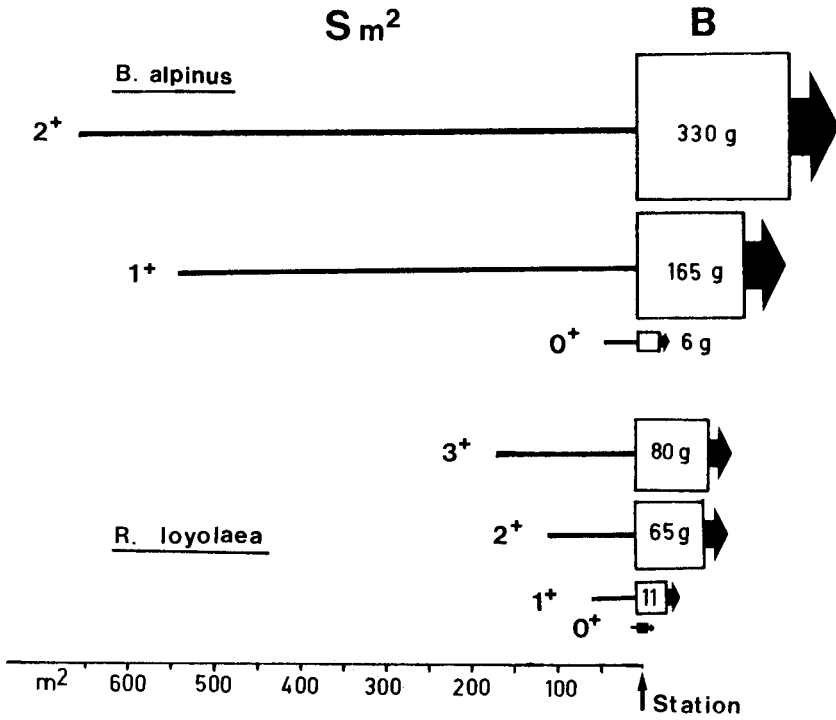


Fig. 3. Drifting biomass (B, g dry weight per year) and corresponding surface area (S) needed for the production of the biomass transported downstream. $S = \text{drifting biomass} : \text{biomass production per } m^2 \text{ per year}$ (from Lavandier 1979, 1982).

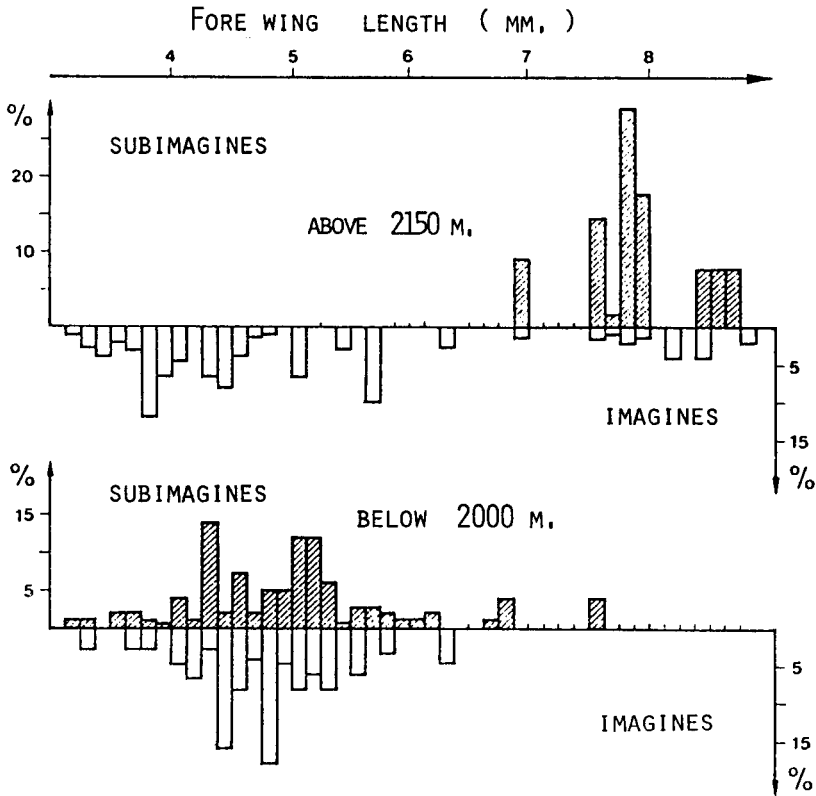


Fig. 4. Upstream migration by female adults of *Baetis alpinus*. The subimagines whose size depends on the characteristics of development (Lavandier 1988) are smaller downstream than upstream. The size of adult females collected in a drift net after oviposition shows the same changes according to altitude, but the size range is larger upstream. Aerial movements may be deduced by comparing the size of subimagines at the localities where they emerge (starting place of the migration) with the size of imagines at the localities where they lay their eggs (end of the migration). Downstream, the size of adult females corresponds to the size of subimagines which have emerged there. Upstream, the size range of adults corresponds to the size of the subimagines which have emerged both up and downstream. This demonstrates an obvious upstream migration.