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PRIMARY RESEARCH PAPER

Life history and larval feeding of some species of Ephemeroptera and Plecoptera (Insecta) in the Sierra Nevada (Southern Iberian Peninsula)

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Abstract We monitored two high mountain streams from the Sierra Nevada (Southern Spain) monthly throughout an annual cycle, measuring and analyzing physical and chemical parameters. Temperature was hourly registered. We studied life cycles and larval feeding of four mayfly species [*Serratella ignita* (Poda, 1761), *Serratella spinosa nevadensis* (Alba-Tercedor, 1981), *Alainites muticus* (Linnaeus, 1758), and *Baetis alpinus* Pictet, 1843] and two stonefly species [*Amphinemura triangularis* (Ris, 1902) and *Capnioneura mitis* Despax, 1932]. Some species changed their strategies (growth rate, life cycle duration, and/or voltinism) in accordance with different conditions (depending on the altitude and temperature). The gut content data showed that species fed mainly on detritus (as collector-gatherers or as shredders), except *B. alpinus* that behaved as a scraper in one of the streams. Differences in the larval diet of the same species in different streams, and even through its life, support the idea of not using general models to extrapolate the function of a species from a higher taxonomical level.

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Introduction

A life cycle is defined as the sequence of morphological stages and physiological processes that link one generation to the next. The components of this cycle will be the same for all members of a species, and can generally be described qualitatively. In contrast, the qualitative and quantitative details of the variable events that are associated with the life cycle make up a life history, which can vary between individuals or populations of one species (Butler, 1984; Humpesch, 1984). These variations are consequences of intrinsic factors, such as physiology, morphology, and behavior, and of extrinsic factors, such as temperature, photoperiod, nutrition, degree of habitat permanence, and relations with other animals (Giller & Malmqvist, 1998). Within the latter, food and temperature are the primary factors determining aquatic insect growth and life histories (Sweeney, 1984). This means that, when environmental conditions are different, life histories change and adapt to a particular situation. Such plasticity is found not only in different species, but also in different populations of the same species, and even within a population. This can be seen in the wide range of life history strategies. Some examples are the presence of a dormancy period (diapause, which is fixed in the life cycle, or quiescence, which appears mainly during adverse conditions), changes in the growth rate, or number of generations per year (Giller & Malmqvist, 1998).

This study focuses on four Ephemeroptera species, belonging to two different families: Ephemerellidae [*Serratella ignita* (Poda, 1761), *Serratella spinosa nevadensis* (Alba-Tercedor, 1981)] and Baetidae [*Alainites muticus* (Linnaeus, 1758) and *Baetis alpinus* Pictet, 1843], and two Plecoptera species, belonging also to two families: Nemouridae [*Amphinemura triangularis* (Ris, 1902)] and Capniidae [*Capnioneura mitis* (Despax, 1932)]. These species (except the ssp. *S. spinosa nevadensis*) are widespread throughout the West Paleartic region or in Western Europe (in the case of *C. mitis*), which allows comparison of our data with several other studies carried out in other geographical localities. The study was conducted in two high mountain streams of the Sierra Nevada (Southern Iberian Peninsula), with similar conditions to those found in other streams of more septentrional European localities. Furthermore, these species were also studied several years ago in the Sierra Nevada (Alba-Tercedor, 1983, 1986, 1990a, b; Sánchez-Ortega, 1986; Sánchez-Ortega & Alba-Tercedor, 1990), providing the possibility of having a wider vision of possible changes that may have occurred since then.

Thus, the aim of this work was to study the life cycles, growth, and feeding of these species, as well as the factors that influence them, and to make a comparison with previous available results.

Materials and methods

Study area

Samplings were carried out in two high mountain streams from the Sierra Nevada (Granada, Southern Spain): Poqueira stream (UTM 30SVF691942, 1540 m a.s.l.) and Válor stream (UTM 30SVF911009, 1840 m a.s.l.). We visited them monthly from December 2004 to December 2005. The Válor stream could not be reached in February 2005 due to snow accumulation.

The Poqueira stream belongs to the Guadalfeo river basin (Southern Iberian Peninsula) and, at the studied site, receives water from a watershed of approximately 33.25 km^2. It is a siliceous first-order stream (at 10 × 10 km^2 resolution). During the year, its width varied between 2.18 m and 6.75 m, and its depth between 0.05 m and 0.60 m. According to the Índice de Heterogeneidad Fluvial (Fluvial Heterogeneity Index) (IHF) index categories (Pardo et al., 2004), the substrate was composed mainly of more than 10% blocks and stones, more than 10% gravels, and less than 10% sands, the latter mainly in pools and shores. There was also some mud on the shores. The submerged vegetation was scarce and mainly composed by *Potamogeton* sp., mosses, and cyanobacteria masses. The riparian vegetation was composed of *Salix* spp., *Crataegus* sp., *Rubus* sp., and *Adenocarpus* sp.

The Válor stream belongs to the Adra river basin (South-Eastern Iberian Peninsula), and receives water from a watershed of 6 km^2 at the study site. It is also a siliceous first-order stream (at 10 × 10 km^2 resolution). During the sampling period the width ranged from 0.43 m to 2.20 m, and the depth fluctuated between 0.05 and 0.25 m. Its substrate was mainly composed of more than 10% blocks and rocks, more than 10% pebbles and gravels, less than 10% sands, and less than 10% lime and mud. Patches of mosses were common in rapids. Riparian vegetation was dominated by *Salix* spp., *Adenocarpus* sp., *Populus* sp., and some Poaceae.

Methodology

We recorded in situ physical parameters, such as dissolved oxygen, conductivity, and discharge, every sampling campaign, and we collected 1 l of water that was cold preserved in order to determine some chemical parameters in the laboratory (pH, ammonium, phosphates, nitrates, nitrites, sulfates, chlorides, alkalinity, suspended solids, calcium and magnesium content, hardness, and turbidity). Temperature was recorded hourly with the aid of a submerged thermometer datalogger sited in the studied streams (HOBO® Water Temp Pro, 0.001°C accuracy). These data were used in order to calculate the accumulated day-degrees of each stream per month.

We collected organisms by using a 300 μm mesh size kick net, and they were preserved with formalin (4%). In the laboratory, samples were sieved with a 150 μm mesh size sieve in order to remove the excess formalin and fine detritus. After this, we sorted out the six studied species.

For mayflies, we measured total length with the aid of an ocular micrometer mounted on a microscope. For Baetidae, developmental stage were counted following Alba-Tercedor (1983), where stage I means recently hatched larvae and stage VII means mature larvae. For stoneflies, pronotum width and femur length (at the outer side of the right hind femur, when possible) were measured. As these two measures were highly correlated in all Plecoptera species, we used pronotum width in order to represent their life cycles graphically. For Ephemeroptera, we used developmental stage for Baetidae and total length for Ephemerellidae.

In order to study the gut content, we introduced each specimen in a vial with Hertwigs' liquid and heated them in an oven at 65°C for 20–24 h, following the methodology of Bello and Cabrera (1999) used in other studies of larval feeding (e.g., Derka et al., 2004; López-Rodríguez & Tierno de Figueroa, 2006; Tierno de Figueroa et al., 2006; Fenoglio et al., 2007). By using a microscope with an ocular micrometer, we estimated the percentage of the absolute gut content (at 40×) as the total area occupied by the content in the whole digestive tract, and the relative gut content (at 400×) as the area occupied for each component within the total gut content.

Statistical methodology

For the life cycles study we used FiSAT II software (Gayanilo et al., 2002), and for statistical analysis we employed STATISTICA software (StatSoft, 2005). To decide on the suitability of data and to select which statistical test to run, we followed Guisande González et al. (2006).

None of the data analyzed agreed with the normality assumption needed to use parametric statistics, so nonparametric analyses were chosen.

For the physicochemical characterization of the streams, mean, standard deviation, minimum, and maximum were computed (Table 1). In order to detect differences in the physicochemical conditions between the two studied streams, we ran the Kolmogorov-Smirnov test (K-S). In both cases, February and April were not considered. In the first case, this was because in the Válor stream there were no data for this month. For April, there were no data because of technical problems.

Table 1 Physicochemical characterization of the sampling sites

	Poqueira stream					Válor stream				
	N	Mean	SD	Min.	Max.	*N*	Mean	SD	Min.	Max.
pH	10	7.849	0.356	7.110	8.270	10	7.109	0.687	6.230	8.250
Ammonium (mg/l)	10	0.019	0.027	0.000	0.090	10	0.012	0.020	0.000	0.062
Phosphates (mg/l)	10	0.010	0.009	0.000	0.024	10	0.017	0.018	0.000	0.060
Nitrates (mg/l)	10	0.089	0.061	0.000	0.177	10	0.134	0.083	0.000	0.284
Nitrites (mg/l)	10	0.007	0.011	0.000	0.030	10	0.002	0.003	0.000	0.007
Sulfates (mg/l)	10	9.476	7.446	1.370	27.010	10	4.301	3.667	0.910	12.200
Chlorides (mg/l)	10	41.250	5.000	31.950	46.900	10	52.070	11.303	35.500	80.400
Alkalinity (meq/l)	10	0.816	0.215	0.400	1.140	10	0.314	0.257	0.120	0.980
Ss (mg/l)	10	9.580	14.850	0.600	48.900	10	17.296	37.614	0.800	122.600
Ca (mg/l)	10	20.480	7.647	7.200	29.600	10	12.320	7.334	4.800	25.600
Mg (mg/l)	10	6.415	3.412	1.944	10.692	10	3.256	3.031	0.486	8.748
Hardness (mg $CaCO_3$/l)	10	77.544	31.516	25.980	115.919	10	44.166	29.366	21.987	99.930
Turbidity (NTU)	10	2.588	5.310	0.000	17.330	10	2.479	3.587	0.000	11.640
O_2 (% sat)	10	87.900	7.992	70.000	97.000	10	88.500	8.449	70.000	98.000
O_2 (mg/l)	10	8.470	1.291	6.500	10.100	10	7.760	1.018	6.100	9.000
Temperature (°C)	8,827	9.102	4.424	0.079	18.319	8,830	8.823	4.043	0.273	18.224
Conductivity (μS/cm)	10	107.640	13.302	84.200	123.900	10	33.110	2.586	29.900	38.200
Discharge (m^3/s)	10	0.199	0.162	0.060	0.494	10	0.055	0.036	0.007	0.115

To assess differences in the temperature regimes of both streams, we used a Wald-Wolfowitz runs test (W-W). Growth was studied in relation to accumulated day-degrees (Table 2) by selecting those species and streams in which a clear growth period could be identified. We estimated growth for each month as the difference between the mean size of the species in a given month and the mean size in the previous month. Daily mean growth was calculated by dividing such growth by the days between the two sampling dates. Mean growth rate was also estimated as the species percentage of growth per day. In several species some periods with negative growth appear, corresponding to the widely accepted decrease in mean size of the Ephemeroptera and Plecoptera populations at the end of the life cycle (Sweeney & Vannote, 1978; Vannote & Sweeney, 1980; Tierno de Figueroa & Sánchez-Ortega, 2004).

For the study of diet, we calculated the mean, standard deviation, minimum, and maximum for each single species. To study the variations of diet throughout the growth period (i.e., in relation to the size), we ran a gamma correlation test.

Results

Both streams showed similar patterns in temperature regimes (Fig. 1). However, we found significant differences in the thermal regime of the two streams (W-W, $Z = -29.178$; $P < 0.05$). Water temperature of the site located at lower altitude, in the Poqueira stream, was higher (mean = 9.10 ± 4.42°C) than in the Válor stream (mean = 8.82 ± 4.04°C) (Fig. 1). Both studied sites had similar physicochemical conditions (Table 1), although in some variables (pH, chlorides, alkalinity, and conductivity) significant differences were found (K-S $P < 0.05$).

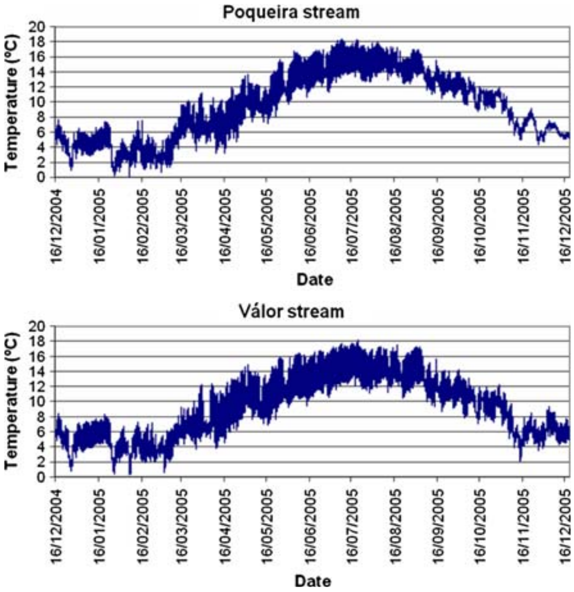


Fig. 1 Temperature records during the sampling period

Table 2 Monthly accumulated day-degrees in each sampling site (months represent periods between sampling dates)

	Monthly accumulated day-degrees	
	Poqueira stream	Válor stream
January–February	87.628	102.597
February–March	91.435	204.106
March–April	255.040	168.061
April–May	268.831	283.341
May–June	342.409	326.479
June–July	490.641	466.145
July–August	451.854	424.220
August–September	433.216	408.771
September–October	338.796	310.289
October–November	340.095	300.030
November–December	209.597	191.939
Total	3309.542	3185.977

Serratella ignita

This species showed a univoltine cycle, in both the Poqueira and Válor streams (Fig. 2), with several cohorts. Larvae were present from June to August in the Poqueira stream, and from May to August in the Válor stream, i.e., for 3 months in the former and for 4 months in the latter period. Nevertheless, we punctually found some of them in October and January at the Poqueira stream and in September at the Válor stream. We found mature larvae during July–August, when oviposition occurred. Laid eggs remained in the stream during the whole autumn and winter, until the next spring.

Growth was higher in the Poqueira stream in the periods when accumulated day-degrees were higher, showing a relation between growth rate and temperature (Table 3). In Válor no clear pattern can be concluded.

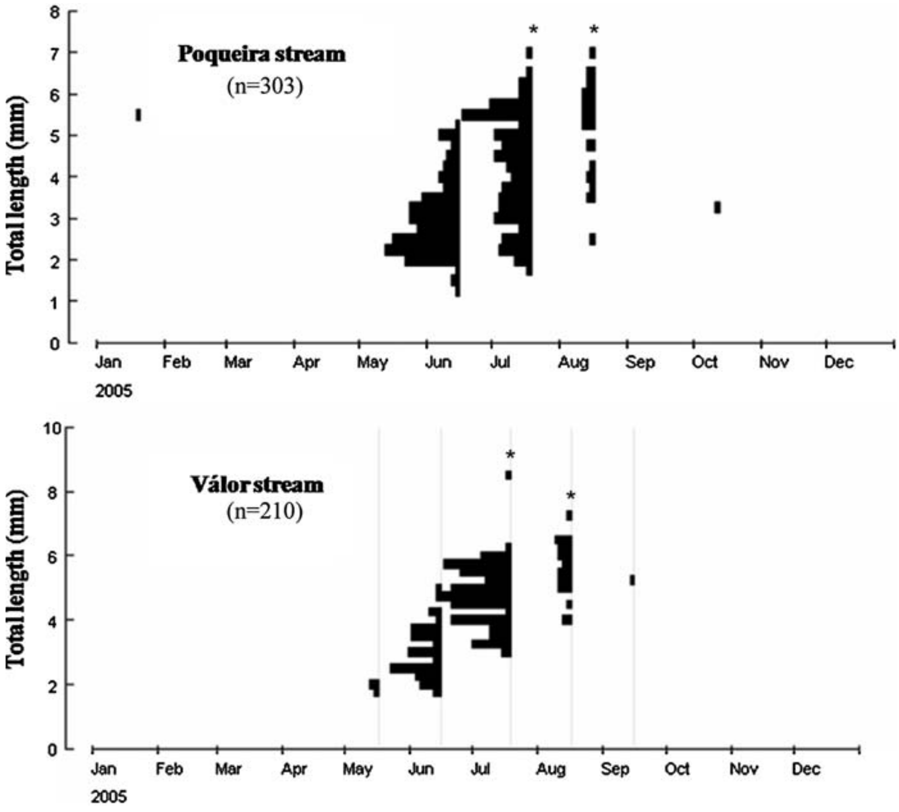


Fig. 2 Life history of *S. ignita* in the two sampling sites. Asterisks indicate the presence of mature larvae

The most abundant component of the diet was detritus, both in Poqueira and Válor, so the species behaved as collector-gatherers, although an important scraper function was also detected, mainly in the Poqueira stream, due to the relatively high quantity of epilithic and epiphytic diatoms found in the gut (Table 4). When analyzing the changes in the diet in relation with the larval size, we observed that detritus consumption was reduced in favor of other components (Table 6).

Serratella spinosa nevadensis

This species had a univoltine life cycle, which lasted 4 months (from April to July) in the Poqueira stream and 7 months (from the end of March to September) in the Válor stream (Fig. 3). As for its co-generic species, there were several cohorts. We found mature larvae just in July in the Poqueira stream and from June to September in the Válor stream. After oviposition, eggs remained in the stream until the next spring.

As for *S. ignita*, the higher the accumulated day-degrees, the higher the growth rate in the Poqueira stream (Table 3). In Válor there was not a clear relation between growth and accumulated day-degrees. In the second middle of the cycle, a period with negative growth rate was observed, probably by chance in the collection of individuals and possibly related to the fact that many individuals had emerged in the previous month. Thus, we considered this case as a null growth period.

In the two streams, the main component found in the gut was detritus (Table 4). Thus, this species could be catalogued as a collector-gatherer, although it could also play a certain role as scraper, and even as a shredder in the Válor stream, due to the approximately equal presence of material coming from the biofilm (epilithic and epiphytic diatoms, hyphae) and phyllidia. The detritus intake in the Poqueira increased with increasing size, while in Válor it decreased (Table 6).

Alainites muticus

This species showed a univoltine life cycle in the Poqueira stream and a bivoltine cycle in the Válor

Table 3 Growth, daily mean growth, mean growth rate, and day-degrees for each species, for the two sampling sites and months

Species	Stream	Date	Period (days)	Growth (mm)	Mean daily growth (mm/day)	Mean growth rate (%/day)	Day-degrees (accumulated)
S. ignita	Poqueira	15/06/05–18/07/05	34	1.374	0.040	1.705	490.641
		18/07/05–16/08/05	29	0.996	0.034	1.449	451.854
	Válor	19/05/05–15/06/05	28	1.039	0.037	1.003	326.479
		15/06/05–18/07/05	33	1.782	0.054	1.459	466.145
		18/07/05–16/08/05	29	0.879	0.030	0.819	424.220
		16/08/05–15/09/05	30	*	*	*	408.771
S. spinosa nevadensis	Poqueira	21/04/05–19/05/05	29	0.804	0.028	0.601	268.831
		19/05/05–15/06/05	27	1.164	0.043	0.934	342.409
		15/06/05–18/07/05	33	2.646	0.080	1.738	490.641
	Válor	30/03/05–21/04/05	23	0.392	0.017	0.412	168.061
		21/04/05–19/05/05	28	1.317	0.047	1.139	283.341
		19/05/05–15/06/05	27	1.855	0.069	1.663	326.479
		15/06/05–18/07/05	33	**	**	**	466.145
		18/07/05–16/08/05	29	0.329	0.011	0.275	424.220
		16/08/05–15/09/05	30	0.237	0.008	0.192	408.771
A. triangularis	Válor	15/09/05–12/10/05	28	0.088	0.003	0.352	310.290
		12/10/05–17/11/05	36	0.077	0.002	0.241	300.030
		17/11/05–19/12/05	32	0.108	0.003	0.378	191.939
		20/01/05–30/03/05	70	0.350	0.005	0.562	306.703
		30/03/05–21/04/05	22	0.189	0.009	0.967	168.061
		21/04/05–19/05/05	28	0.078	0.003	0.312	283.341
C. mitis	Válor	15/09/05–12/10/05	28	0.076	0.003	0.598	310.290
		12/10/05–17/11/05	36	0.246	0.007	1.500	300.030
		17/11/05–19/12/05	32	0.133	0.004	0.914	191.939
		20/01/05–30/03/05	70	*	*	*	306.703
		30/03/05–21/04/05	22	*	*	*	168.061

For Ephemeroptera, the employed measures are total length, and for Plecoptera pronotum width

* Period in which there was negative growth, coinciding with the end of the cycle

** Period in which there was negative growth in the middle of the cycle. See the “Materials and methods” section for details

stream, with several cohorts in both cases (Fig. 4). Almost every larval stage (*sensu* Alba-Tercedor, 1983) was present during all the year, mainly in Válor. Mature larvae were present in May in the Poqueira stream and in May, July, August, and September in the Válor stream.

In both streams, the species behaved mainly as a collector-gatherer (detritus being the most consumed resource), but it also acted as scraper, principally in the Poqueira stream, where we found a high quantity of epilithic and epiphytic diatoms (Table 4). The detritus was less consumed for bigger larvae from Poqueira (in Válor there was not a significant correlation), while simultaneously the other components were more frequently found in the gut (Table 6).

Baetis alpinus

The life cycle of *B. alpinus* was probably bivoltine in the Poqueira stream, but due to the problems mentioned in the “Material and Methods” section for sampling in Válor during February, we were not able to clearly determine if in this stream the cycle was univoltine or bivoltine (Fig. 5). Larvae of several stages were present almost the whole year in both cases. We found mature larvae in February, April,

Table 4 Larval gut contents of the studied Ephemeroptera species in the two sampling sites

Species	Stream		% absolute	% detritus	% diatoms	% hyphae	% fungi spores	% pollen	% phyllidia	FFG
S. ignita	Poqueira	*N*	275	261	261	261	261	261	261	**Collector-Gatherer/ Scraper**
		Mean	60.150	82.830	13.830	1.540	0.550	0.780	0.510	
		SD	28.390	26.560	24.640	2.720	1.400	1.410	5.620	
		Min.–max.	0–100	4–100	0–90	0–15	0–12	0–10	0–88	
	Válor	*N*	184	175	175	175	175	175	175	**Collector-Gatherer/** Scraper
		Mean	68.420	83.360	1.470	6.650	1.680	2.680	4.530	
		SD	27.000	13.630	4.110	8.160	2.030	2.810	9.670	
		Min.–max.	0–100	20–100	0–30	0–98	0–15	0–20	0–70	
S. spinosa nevadensis	Poqueira	*N*	89	86	86	86	86	86	86	**Collector-Gatherer/** Scraper
		Mean	66.520	88.030	10.100	0.940	0.480	0.350	0.090	
		SD	20.410	19.310	19.150	1.920	1.500	0.860	0.630	
		Min.–max.	10–100	3–100	0–95	0–10	0–10	0–5	0–5	
	Válor	*N*	382	366	366	366	366	366	366	**Collector-Gatherer/** Scraper/Shredder
		Mean	64.330	90.700	0.760	2.960	0.980	0.980	3.180	
		SD	24.280	14.790	2.340	3.950	2.170	1.960	9.280	
		Min.–max.	0–100	0–100	0–20	0–20	0–25	0–15	0–90	
A. muticus	Poqueira	*N*	335	330	330	330	330	330	330	**Collector-Gatherer/ Scraper**
		Mean	53.809	70.460	26.620	1.240	0.810	0.830	0.050	
		SD	17.524	24.110	24.250	1.970	2.800	2.010	0.480	
		Min.–max.	0–100	0–100	0–100	0–15	0–40	0–15	0–5	
	Válor	*N*	906	881	881	881	881	881	881	**Collector-Gatherer/** Scraper
		Mean	55.010	88.230	6.910	2.950	0.950	0.870	0.040	
		SD	18.910	13.530	12.500	3.290	1.810	1.720	0.410	
		Min.–max.	0–100	0–100	0–100	0–25	0–15	0–12	0–6	
B. alpinus	Poqueira	*N*	150	130	130	130	130	130	-	**Scraper/Collector-Gatherer**
		Mean	34.570	43.190	53.430	1.400	1.780	0.120	-	
		SD	21.170	38.080	37.550	7.330	8.820	0.580	-	
		Min.–max.	0–80	0–100	0–100	0–80	0–80	0–5	-	
	Válor	*N*	402	339	339	339	339	339	339	**Collector-Gatherer/ Scraper**
		Mean	34.380	71.720	24.810	1.990	1.020	0.440	0.020	
		SD	25.780	31.020	30.760	2.980	4.660	1.160	0.290	
		Min.–max.	0–100	0–100	0–100	0–25	0–50	0–10	0–5	

Bold face in the functional feeding group (FFG) column represents the most important functional group into which the species can be assigned

and May in the Poqueira stream and in January, March, and April in the Válor stream.

In the Poqueira stream, this species fed mainly on epilithic and epiphytic diatoms and detritus, being a scraper and collector-gatherer, but in Válor the principal component of the diet was the detritus, followed by epilithic and epiphytic diatoms (Table 4). Larger larvae consumed less detritus (Table 6).

Amphinemura triangularis

Due to the lack of small larva collections in several months in the Poqueira stream, we do not comment on the life cycle in this site, although the data appears in Fig. 6. In the Válor stream, the cycle was univoltine, with larvae present from September to May, when mature larvae started appearing.

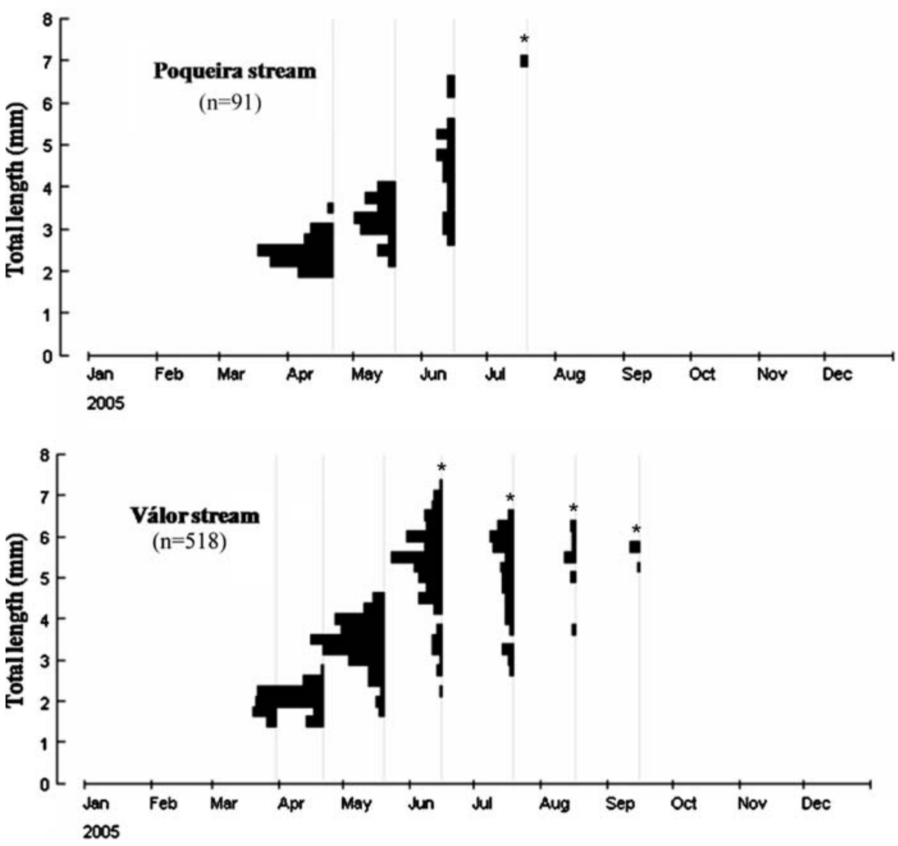


Fig. 3 Life history of *S. spinosa nevadensis* in the two sampling sites. Asterisks indicate the presence of mature larvae

When studying the growth of the species in relation with accumulated day-degrees in the Válor stream no patterns could be inferred from the results (Table 3). As can be seen, there were periods with high growth rate and low accumulated day-degrees and vice versa.

The diet of this species, both in Poqueira and Válor, was mainly composed by detritus, with the other components being found more rarely (Table 5). Therefore, this species could be grouped principally as a collector-gatherer. Larger larvae in the Válor stream fed more on detritus than did smaller ones (Table 6).

Capnioneura mitis

We do not comment the cycle in the Poqueira stream due to the lack of information about the earlier stages, as occurred for *Amphinemura triangularis*. In Válor this species had a univoltine life cycle, with larvae present from September to April, although those appearing in March and April were very scarce (Fig. 7). We found mature larvae in November and December.

The study of the growth of this species in Válor did not show any relationship with accumulated day-degrees (Table 3).

In *C. mitis*, the main component found in the gut was detritus, but this came from fragmented leaves (Table 5). Thus, the species could be catalogued as a shredder. Nevertheless, in the Poqueira stream, there were a high amount of epilithic and epiphytic diatoms in the gut, indicating that this species was also an important scraper in this site. In the Válor stream there was a decrease in detritus intake of bigger larvae (Table 6).

Discussion

Life histories

Serratella ignita

Due to the wide distribution of this species throughout the Paleartic region, it has been studied by many authors. Maitland (1965) describes in Scotland a life

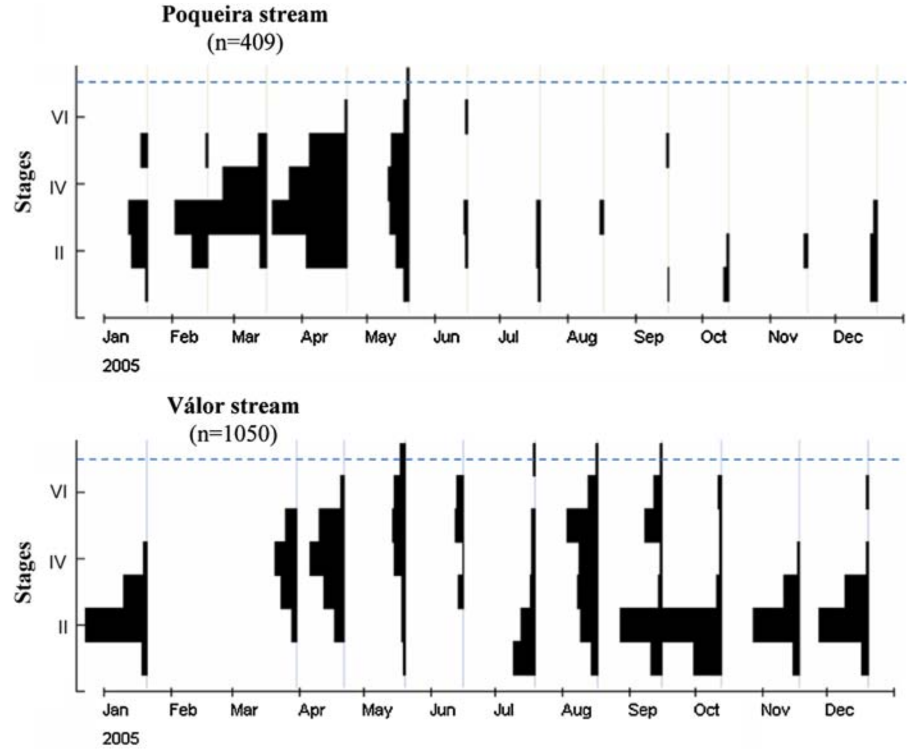
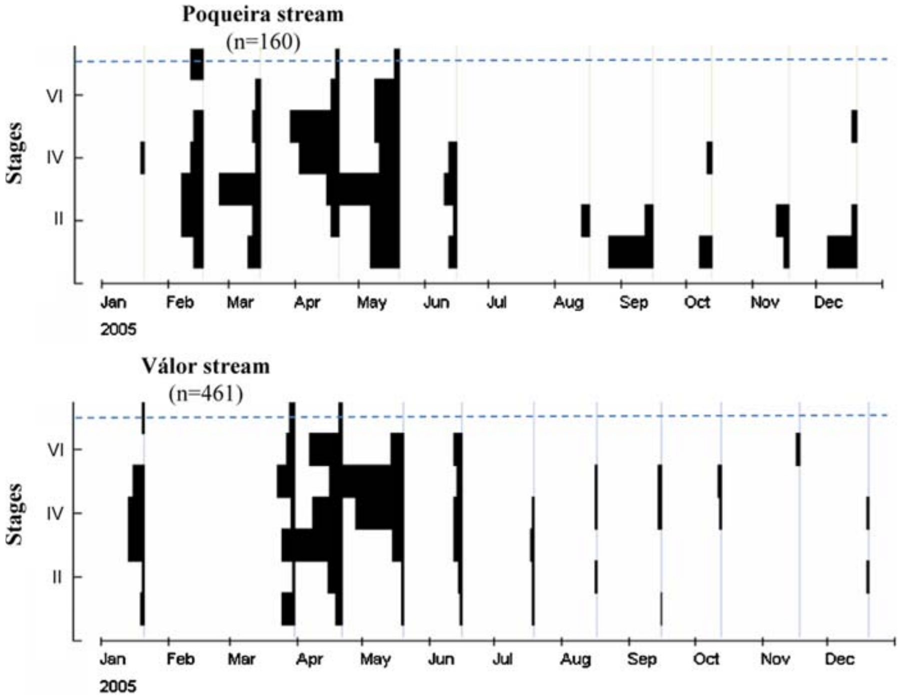


Fig. 4 Life history of *A. muticus* in the two sampling sites. The dotted line indicates stage VII (i.e., mature larvae)

Fig. 5 Life history of *B. alpinus* in the two sampling sites. The dotted line indicates stage VII (i.e., mature larvae)



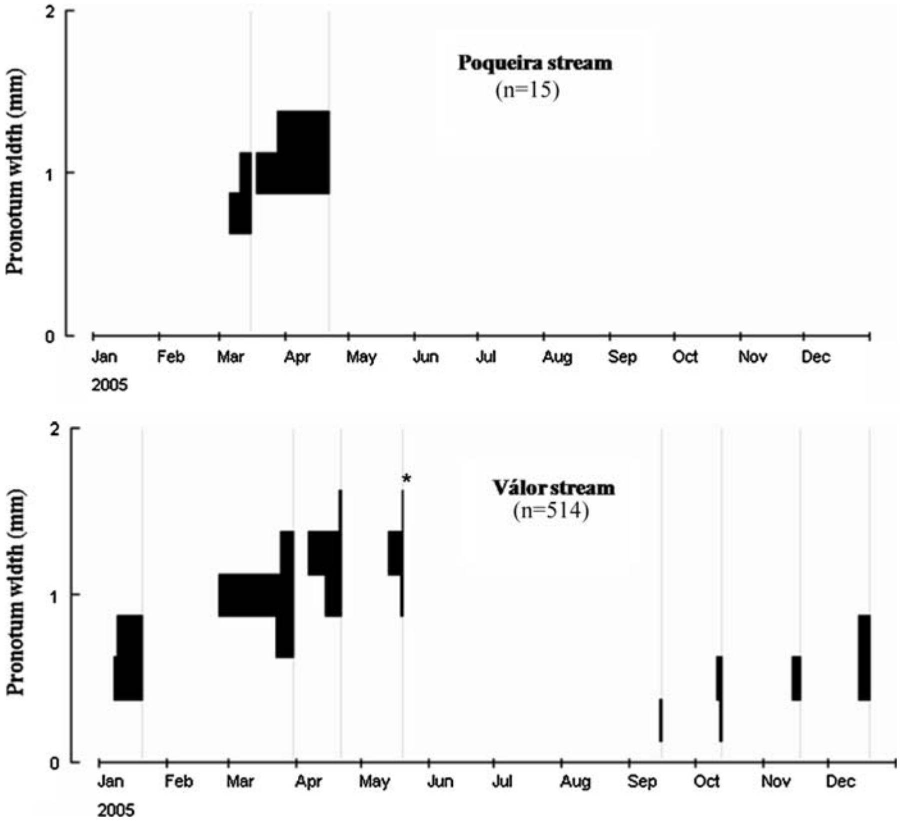


Fig. 6 Life history of *A. triangularis* in the two sampling sites. Asterisk indicates the presence of mature larvae.

cycle for this species similar to the one we found: annual, with eggs lying dormant over winter, and hatching in April and May. Larvae develop rapidly thereafter to emerge and lay the eggs in July and August. Hynes (1970) pointed out that eggs would wait for approximately 6 months to hatch. The larvae would experiment a rapid growth during summer, with some of them remaining small for several months after the flight period, as occurs in the Poqueira stream. In the Central Pyrenees, the cycle is more extended, with larvae present throughout all the year, and adults flying from April to October (Lavandier & Dumas, 1971). In Southern England, larvae are present in all months except October (Bass, 1976). Jazdzewska (1980) found a univoltine cycle in a population of a Polish stream, with larvae from the end of March to September, similar to but wider than those found by us. In a study carried out in Central Wales, Cowx et al. (1984) found that *S. ignita* passed from being present in the stream from May to September in 1 year, to being present from April to August in the next, after a drought period. Zelinka (1984) describes the cycle as univoltine, with eggs passing through a winter diapause and hatching at the end of May. Larvae grow very fast, until they emerge in July–August (with some subimagines collected in September). In Great Britain, the species is also univoltine, overwintering in the egg stage. Its growth is very fast, with about 85% of the larvae developing in about 3 months (Elliott, 1967, 1978). Small larvae are also found in October and November long after the flight period, although these larvae probably do not survive the winter. In the warmer waters of Southern England, larvae are found during the whole year, making possible the existence of two separate, winter and summer, generations. The main flight period is between April and September, although adults have been sighted in January. In some populations, parthenogenetic eggs have been recorded (Elliott et al., 1988), although their development is slower and they have less hatching success (Elliott & Humpesch, 1980). Deván (1993) also found a univoltine life cycle in two localities of Slovakia, with a development period of 4 months, from May to August, similar to that found in our study.

Table 5 Larval gut contents of the studied Plecoptera species in the two sampling sites

Species	Stream		% absolute	% detritus	% diatoms	% hyphae	% fungi spores	% pollen	% phyllidia	FFG
A. triangularis	Poqueira	*N*	14	10	10	10	10	10	10	**Collector-Gatherer/** Scraper
		Mean	43.570	90.500	5.800	0.800	0.200	0.200	2.500	
		SD	31.340	14.710	12.900	1.620	0.630	0.630	7.910	
		Min.–max.	0–95	60–100	0–40	0–5	0–2	0–2	0–25	
	Válor	*N*	453	305	305	305	305	305	305	**Collector-Gatherer/** Scraper
		Mean	41.610	94.630	0.830	2.350	1.110	0.280	0.810	
		SD	32.670	10.130	3.820	6.200	4.740	0.770	4.260	
		Min.–max.	0–100	15–100	0–50	0–70	0–50	0–6	0–40	
C. mitis	Poqueira	*N*	28	16	16	16	16	16	–	**Shredder/Scraper**
		Mean	38.570	64.000	32.440	2.620	0.690	0.250	–	
		SD	37.340	34.800	35.450	3.140	1.700	0.580	–	
		Min.–max.	0–100	8–100	0–90	0–10	0–5	0–2	–	
	Válor	*N*	250	185	185	185	185	185	185	**Shredder/**Scraper
		Mean	45.340	85.160	5.740	5.260	2.320	1.420	0.100	
		SD	34.080	16.330	10.740	10.500	7.050	2.480	0.820	
		Min.–max.	0–100	0–100	0–80	0–100	0–80	0–20	0–10	

Bold face in the functional feeding group (FFG) column represents the most important functional group into which the species can be assigned

Table 6 Correlations between larval size (total length for Ephemeroptera and pronotum width for Plecoptera) and diet components in the two study sites

Species	Stream	% detritus	% diatoms	% hyphae	% fungi spores	% pollen	% phyllidia
S. ignita	Poqueira	−0.272*	0.243*	0.453*	0.449*	0.369*	0.672*
	Válor	−0.339*	−0.045	0.350*	0.052	0.300*	0.379*
S. spinosa nevadensis	Poqueira	0.328*	−0.391*	−0.178	0.135	−0.240	0.224
	Válor	−0.253*	0.092	0.185*	0.240*	0.296*	0.596*
A. muticus	Poqueira	−0.156*	0.122*	0.183*	0.244*	0.176*	0.369
	Válor	−0.034	−0.043	0.122*	0.115*	0.325*	0.198
B. alpinus	Poqueira	−0.154*	0.210*	−0.115	−0.048	−0.152	–
	Válor	−0.101*	0.067	0.151*	0.215*	0.232*	0.762*
A. triangularis	Poqueira	0.310	−0.130	0.043	0.556*	−0.556*	0.250
	Válor	0.098*	−0.168*	−0.138*	−0.177*	−0.119	0.530*
C. mitis	Poqueira	0.000	0.000	−0.450*	−0.706*	−0.437	–
	Válor	−0.245*	0.225*	0.180*	0.082	0.221*	0.400

Values marked with * are significant at $P < 0.05$

The studied cycle is similar to that drawn by Alba-Tercedor (1990a) also in the Poqueira stream, although in that survey larvae were only present from the beginning of July to the end of August, with mature individuals found in August. In the same study, larvae were collected in other streams with different temperature regimes, showing a more expanded cycle, but always univoltine, and with an emergence period going from late June to September. The author suggested the presence of a failed second generation in some studied streams [as was previously pointed out by Pleskot (1959), Hynes (1961),

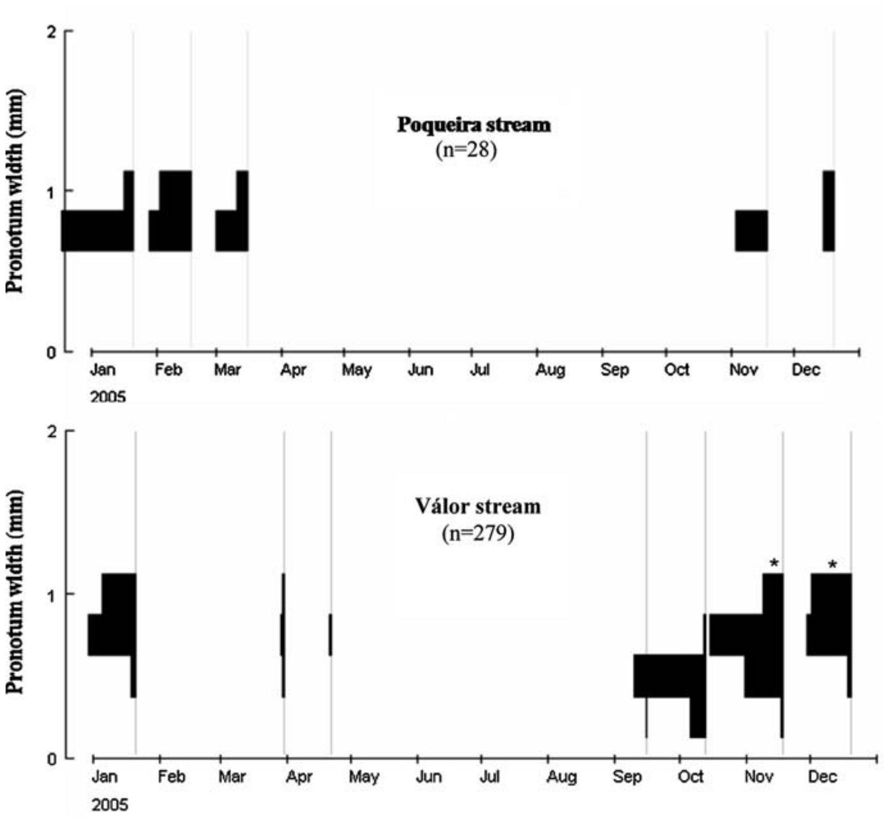


Fig. 7 Life history of *C. mitis* in the sampling sites. Asterisk indicates the presence of mature larvae

Elliott (1967, 1978), Wise (1980), and Rosillon (1986)]. Nevertheless, this second generation was not present in the Poqueira stream, as it was not in our study. Under other environmental conditions in the Northern Iberian Peninsula, the cycle lasts 8, 9 or 10 months, with first larvae appearing in autumn and emergence occurring in spring and summer (Riaño et al., 1997; González et al., 2000).

In our study area we found a single generation with several cohorts. Small larvae would hatch in spring. Humpesch (1984) found in *S. ignita* that there are not intraspecific differences in the temperature range within which eggs hatch, and that the duration of hatching decreases with increasing temperature, which would explain the short hatching period found in our survey, and the almost coincidence of it in both streams.

Hatching was quite synchronous, despite the presence of some larvae in autumn and winter, mainly in the Poqueira stream. These larvae would not survive the winter, as pointed out by several authors (Elliott et al., 1988; Alba-Tercedor, 1990a). In our study area, hatching started before in the Válor stream, with a lower average temperature, although in some months more accumulated day-degrees were recorded than in the Poqueira stream (Table 2).

Growth would take place rapidly during the spring and summer, and the flight period would occur in July and August in Poqueira and Válor. The species would spend the rest of the year in the egg stage, probably passing through a diapause period, as pointed out by Sowa (1975) and Böhle (1972). The latter author suggested that diapause was obligatory in Germany, but not in other European populations. Nevertheless, Elliott (1978), in an experimental study, did not found a diapause in a population of the English Lake District, so more studies should be carried out in order to clarify what happens during this period.

According to Hynes (1970), we could classify this cycle as fast seasonal, given that growth was very fast during the few months that the larvae were present in the streams. Following Landa's (1968) classification, it would fit within the A2 category mentioned for some populations of the same species in Central Europe by the author, i.e., species in which, after oviposition, the eggs remain in diapause until the spring or summer of the next year. It could be also classified under the B1 category of Sowa (1975), in which those species with a long egg development period in which diapause occurs are grouped.

Serratella spinosa nevadensis

In several streams of the Sierra Nevada (the Poqueira stream included), Alba-Tercedor (1990b) found a more expanded cycle, going from October to the end of June, and with an increase in growth during spring and summer. This coincides with the period of growth of the population in the Poqueira stream in our study.

Thus, hatching would occur within a few months, indicating an approximately synchronous hatching period. Mature larvae appeared earlier in the Válor stream than in the Poqueira. In the former stream the flight period seemed to be longer, going from June to September. Oviposition took place in those months. The species would probably pass the rest of the year in a diapause stage, as pointed out by Alba-Tercedor (1990b).

This was also a fast seasonal cycle according to the classification of Hynes (1970), and would fulfil the characteristics of the A2 class pointed out by Landa (1968) for Central European species, and the B1 category mentioned by Sowa (1975).

As can be observed from the present results, *S. ignita* and *S. spinosa nevadensis* cycles almost do not overlap, i.e., larvae of the same size belonging to different species are not found at the same time. This has been also found within populations of *S. ignita* and *Ephemerella mucronata* (Bengstsson, 1909) in Central Europe (Sowa, 1975). Such differences in the life history, as egg biology or timing of hatching, may be a cue factor for avoiding resource competition (Elliott, 1995; Giller & Malmqvist, 1998).

Alainites muticus

There are several studies focused on this species throughout Europe. Ulfstrand (1968) studied it in North Sweden and found a univoltine cycle, overwintering in the egg stage. In the French Pyrenees, the species presents three generations that overlap (Thibault, 1971). Elliott et al. (1988) recorded a bivoltine life cycle in the British Isles, with a winter generation and a fast-growing summer generation, coinciding with that found in our study in the Válor population. In Northwest Slovakia, Deván (1992) found a univoltine life cycle, from September to August, with a long flight period, going from the end of April to August. More recently, in a study carried out in a pre-Alpine stream of the Italian Alps, Erba et al. (2003) found a univoltine life cycle, with a probable egg diapause from June to October or even December. It is likely that all these differences reflect the differences in the conditions of the streams where these studies were carried out.

Alba-Tercedor (1986) pointed out, from data coming from several streams in the Sierra Nevada range (where the Poqueira stream was included), a three-generation cycle for the species: the first going from October to February–March, the second from March to April–May, and the third from May–June to July–August. Nevertheless, in the Poqueira stream, it had two generations (Alba-Tercedor, 1986, Fig. 8) as we found in this study. There were small larvae from the beginning of October to March, when they grew. Mature larvae appeared from the beginning of June to the end of August, coinciding with the beginning of the emergence in our study.

In the Poqueira stream we could differentiate a single generation, probably hatching in late summer and beginning of autumn (September or October), growing during winter and spring, and emerging around May. Larvae were also present in other months, but in a lower quantity, probably representing intra-population differences in the hatching time or slow growth of the larvae of first instars. This could also be interpreted as a second generation that would not have success. In the Válor stream we could distinguish two generations: the first would start hatching in September–October. Larvae grow during the winter, and emergence takes place around May. Eggs are laid in this month and hatched larvae grow very fast in summer, coinciding with a high-temperature period. This second generation emerged from July to September. Mature larvae of this generation were smaller than those belonging to the first generation, due to their rapid and short growth period (mean mature larva size for the first generation = 6.96 ± 0.44 mm, maximum = 7.56 mm; mean mature larva size for the second generation = 5.46 ± 0.71 mm, maximum = 6.28 mm), supporting a bivoltine life cycle.

The species presented a fast-seasonal cycle (F1 type) in the Poqueira stream, according to Hynes

(1970), owing to the rapid development of the larvae, which hatch in autumn and mature in spring. In the Válor stream, the cycle was slow seasonal for the winter generation and fast-seasonal for the summer generation. Following Landa's (1968) classification, this species belongs partially to the A1 class (as recorded by the author) in the Poqueira stream (i.e., the eggs hatch approximately 1 month after oviposition and larvae grow until emergence occurs in spring or summer, depending on the altitude), and to the B1 class in the Válor stream (two generations in the year, one long and one fast growing). In Sowa's (1975) classification, the species in the Poqueira stream did not fall within any clear category. In the Válor stream this species would belong to the C2 category (species with two generations, one going from the end of summer to spring, and another developing very fast in summer), as pointed out by the author for the Central European populations.

Baetis alpinus

In Europe it is possible to find a wide diversity in the life histories of this species. Thus, Lavandier (1988) found that it had a univoltine cycle at 1,920 m.a.s.l. and a semivoltine cycle at 2,190 m.a.s.l., and higher mature larvae in the latter populations. In Poland, the life cycle also showed a marked plasticity, being bivoltine at low altitudes and univoltine or bivoltine at higher altitudes (Kukula, 1997). A study carried out in a glacial stream of the Austrian Alps showed that there was a different size distribution at snow-covered and snow-free sites. Under the snow, development was slower. Larvae were found throughout the year, but the highest densities were recorded at the open site in winter (Schütz et al., 2001). In the Italian Alps, *B. alpinus* had a trivoltine or bivoltine life cycle depending on environmental conditions, such as probably the temperature or the hydrological instability (Erba et al., 2003).

Alba-Tercedor (1986) described three generations for the same species in the Poqueira stream: the first going from February to May, the second from August to October, and the third from November to January, approximately.

We found first-stage larvae during nearly every month, indicating an asynchronous hatching or slow growth of the smallest larvae, and probably several cohorts, as pointed out by Humpesch (1979). Mature larvae started appearing in February in the Poqueira stream, and in January in the Válor stream, probably showing an advance of the flight period in the Válor site. Thus, in the Poqueira stream we could distinguish two generations. The first would grow slowly throughout the autumn (from September to December, approximately) and faster in January. It would emerge in February, and oviposition would take place within a few weeks. The eggs would hatch almost immediately, originating the second generation, which would grow until April–May, when emergence would occur. These two generations were, as occurred in the case of *A. muticus* in the Válor stream, different in mature larva size (mean mature larva size for the first generation = 7.57 ± 0.64 mm, maximum = 8.22 mm; mean mature larva size for the second generation = 6.83 ± 0.94 mm, maximum = 7.50 mm). In the Válor stream, due to the absence of data in February, there are two possibilities: (1) a univoltine cycle, with one generation hatching at the end of summer and growing until January, when emergence started and lasted until April, or (2) a bivoltine cycle, with the first generation going from the end of summer to January, and a second fast-growing generation, with eggs laid in January that would hatch and grow very fast during winter, with emergence taking place in March and April. The first hypothesis is supported by the fact that mature larvae of the supposed first generation were not higher than those of the second generation (mean mature larva size for the first generation = 7.58 ± 0.68 mm, maximum = 8.06 mm; mean mature larva size for the second generation = 8.48 ± 1.06 mm, maximum = 9.56 mm). Furthermore, the months in which the second generation would develop are those in which the minimum temperatures of all the year are recorded (Fig. 1). In addition, in the literature, we find references to the change of a bivoltine cycle to a univoltine one when we go up in altitude (e.g., Landa, 1968; Sowa, 1975), which would support our findings in the Sierra Nevada.

If we compare the cycle in Alba-Tercedor (1986) and that found in this study we can observe a reduction of one generation after more than two decades, which could be a reflection of changes in the environmental conditions, mainly in temperature; but due to the low number of temperature records in Alba-Tercedor study, no reliable conclusions can be drawn.

We can classify this cycle in the Poqueira stream as slow seasonal for the winter generation and fast seasonal for the summer generation, and fast-seasonal (F1 type) in the Válor stream according to the classification of Hynes (1970). Following Landa's (1968) classification, this species belongs either to the A1 class or to the B1 class, depending on the altitude. Sowa (1975) classifies this species into the group C2, coinciding with the type of cycle of the Poqueira stream. In the Válor stream this species would not fit into any particular category.

Amphinemura triangularis

We did not collect small larvae in the Poqueira stream. This site suffered a high input of sludge from September that made possible the existence of migratory movements of the smaller larvae to other parts of the stream or other mesohabitats in order to avoid this unfavorable situation, as pointed out in some studies (e.g., Chutter, 1969). These changes in substrate may act selectively on individual species and on individual life history stages (Lehmkuhl, 1979), and would be responsible for this lack of information.

The only study of the life history of this species in the rest of Europe is that of Raušer (1963) in the former Czechoslovakia, in which the cycle was more extended, going from May to April, when the flight period began.

This species was also studied in the Poqueira stream by Sánchez-Ortega (1986), who found a univoltine life cycle with small larvae in November and growing until June. This author supposed that the hatching period started at the end of the spring or at the beginning of summer, and lasted until the end of autumn. Nevertheless, larvae of first stages were not collected in that study. In the Sierra de Huétor, a mountain range next to the Sierra Nevada, the cycle of the species lasted 7 months, from October to April, with a higher growth period from February to April (López-Rodríguez & Tierno de Figueroa, 2004).

In the Válor stream we could clearly differentiate a single cohort, with a very synchronous hatching time, taking approximately 2 months. Mature larvae began emerging in May, coinciding with the flight period recorded in the same river by Tierno de Figueroa et al. (2001).

As can be seen in the different studies, mature larvae are always found in the spring months (from April to June). Thus, differences in the life cycle are mainly related to the time the eggs spend for hatching. The population studied by Raušer (1963) seems to hatch immediately after being laid, while the populations from the Southern Iberian Peninsula remain in the riverbed during the summer months. It could be possible that during this period the species passed through a diapause (in order to avoid high temperatures).

Following the classification of Hynes (1970), this life cycle could be classified as fast seasonal, although it was not clear that a diapause during the egg stage occurred.

Capnioneura mitis

Sánchez-Ortega and Alba-Tercedor (1990) found a univoltine cycle in other streams in the Sierra Nevada mountains, going from October, when the first larvae appeared (although these authors pointed out that these larvae did not belong to the first instars), to March. This would coincide with our data, although we did find larvae of first instars in October (including some larvae without completely developed compound eyes). It is also pointed out that the species present an egg diapause [as also recorded by several authors for other species of the same genus (Lavandier, 1975; Navarro-Martínez et al., 2007)]. This is likely in the population studied by us, and would allow the species to avoid the high temperatures of the summer.

In the Poqueira stream, larvae belonging to the first instars were not caught for the same reasons mentioned for *A. triangularis*, so no pattern can be derived from these data. In the Válor stream the cycle is univoltine. Larvae of the first instars were found from September to November, but mainly in October, indicating relatively synchronous hatching. Some larvae remained in the stream until March–April, probably representing the larvae that came from the eggs that hatched last. Mature larvae appeared in November, coinciding with the beginning of the flight period described by Tierno de Figueroa et al. (2001) in this site. The occurrence of mature larvae already in autumn indicated a very fast growth, completing their development in only 3–4 months.

This cycle can be catalogued as fast seasonal according to the classification of Hynes (1970).

Growth patterns and their relationships with temperature

Only for *S. ignita* and *S. spinosa nevadensis*, both in the Poqueira stream, there is a clear positive relation between growth and accumulated day-degrees. This relationship between growth and temperature has also been pointed out by different authors (e.g., Alba-Tercedor, 1981; Brittain, 1982; Huryn, 1996; Fenoglio et al., 2005). In all the other cases this relation does not appear, maybe due to the influence of some other natural factors on growth. Furthermore, in the period in which the Válor stream reached nearly 0°C (February–March), *A. triangularis* experienced a high growth rate. In fact, Illies (1952a) indicated that, in this genus, the temperature does not influence larval growth, and that the emergence takes place in a constant manner. In general, this author pointed out that growth in Ephemeroptera is stopped by cold weather, while the developmental temperature threshold of Plecoptera is very low, even near 0°C (Raušer, 1962). This was also observed in Central Norway for some species of Ephemeroptera, which passed a large part of their growth period under the ice (Arnekleiv, 1996). In the case of *C. mitis*, which feeds mainly on leaf remains, there is an important growth period coinciding with the autumn, due to the input of good-quality food in the stream.

Feeding behavior

Detritus was the main component in all studied species except for *B. alpinus* in the Poqueira stream, where epilithic and epiphytic diatoms were the principal component, agreeing with the scraper-gatherer feeding behavior found by Galas and Dumnicka (2003) for this species. The general dominance of detritus instead of diatoms in all the other species does not agree with the pattern found in an experimental study carried out by Rosillon (1988), who observed that starved larvae of *S. ignita* prefer a diatom-rich diet rather than a detritus diet, and that at a given temperature, growth rate was significantly higher on the diatom diet than on the detritus diet.

Moss phyllidia were particularly important in some cases, such as in *S. ignita* and *S. spinosa nevadensis*, both in the Válor stream, compared with the percentages found in other species and/or places. This could be related to the high density of moss present in the Válor stream and in the particular mesohabitats where the animals were caught. From studies on several Ephemerellidae species, some authors have pointed out that the consumption of high quantities of mosses would have some kind of benefit but without specifying which one (Hawkins, 1985).

Some individuals of each species, except *A. triangularis*, had some punctual animal remains in their guts (as pointed for *S. ignita* by Riaño et al., 1997), probably representing accidental ingestion when feeding on other sources. Nevertheless, these items did not represent a significant part of the diet in any case.

From a functional point of view, most species have an important role as collector-gatherers, and some of them as scrapers too. Only *C. mitis* is mainly a shredder (in the sense of Palmer & O'Keefe, 1992), although in the Poqueira stream it acts as a scraper to a lower degree. In other studies, Elliott et al. (1988) classified *A. muticus* as a scraper-gatherer and *S. ignita* as a collector-gatherer, similar to that found by Murphy and Giller (2000).

The feeding behavior of both *Serratella* species was quite similar. Thus, they do not have coincident life cycles, but a displacement of one cycle with respect to the other, avoiding in this way resource competition between the two species. The existence of temporal segregation between closely related species has been associated with a mechanism for resource competition avoidance in many aquatic insect groups (Illies, 1952b; Danks, 1979; Butler, 1984).

When analyzing the possible correlation between larval size and the percentage of each component found in the guts, it was observed that the general trend is to feed less on detritus, and to incorporate another kind of component when larvae grow, except for *S. spinosa nevadensis* in the Poqueira stream and *A. triangularis* in the Válor stream, for which there is a tendency to increase the percentage of detritus (although in the case of *A. triangularis* the correlation was extremely low). Most larvae that feed on moss phyllidia do so when they are larger. In fact, as Arnekleiv (1996) pointed out, small changes in feeding may result in considerable changes of mesohabitats, allowing different habitats opportunities to the larvae of different sizes.

We found differences by comparing the components of the diet of species in both studied streams. This may reflect differences in the availability of a given resource. This agrees with Coffman et al. (1971), who suggested that availability of food is the dominant factor influencing diet composition.

Conclusions

There is great plasticity in the species life histories and strategies for coping with environmental conditions. This reflects the intrinsic factors that also play an important role in their success, together with extrinsic factors such as temperature, photoperiod, nutrition, etc. (Giller & Malmqvist, 1998). Temperature affects the growth rate of some species more than others, as occurs with *S. ignita* and *S. spinosa nevadensis* in the Poqueira stream. For mayflies, environmental factors such as temperature seem to be more determinant than for stoneflies, in which the life history patterns are more stable. We may conclude this by observing the life histories found by some authors (also in the Sierra Nevada or in other mountain ranges) and those found by us in two streams in the same mountains, with different temperature conditions. As shown, some species of mayflies (e.g., *A. muticus* and *B. alpinus*) suffered great ontogenetic changes (passing from univoltine to bivoltine, and some of them having several cohorts in a very short period) depending on the stream (and consequently on the temperature). In the stoneflies this comparison was not possible due to the lack of data from the Poqueira stream. However, by comparison with others studies, it is clear that temperature does not affect them by changing the number of generations, but just advancing, delaying or displacing the cycle some months. For mayflies in general, if we take into account the time, and we compare with studies carried out in the same stream several years ago, we realize that this plasticity continues to be higher. This high plasticity in the life history of the species is one of the most important factors that preadapt them to different environments and allow them to be widespread in the Paleartic region, as indeed they are. Thus, once again, the use of general patterns at the species or higher taxonomical category level turns out to be inadequate. It is not appropriate to use information from a given population to assume that the species as a whole behaves in the same manner, due to differences in the environmental conditions that determine their life histories.

In relation to feeding behavior, no general pattern (at the genus or family level) can be used to catalogue a given species in a particular site. Furthermore, as we have seen, several changes in the diet may occur in the same population, so generalizations such as their grouping in functional feeding groups (FFG), even for a single species, must be treated with caution. One of the major inconveniences of the classification following FFGs is that spatial, developmental, and temporal dietary variability make the actual sorting of macroinvertebrate taxa into FFGs very difficult (King et al., 1988; Mihuc, 1997), as has also been shown in the present study.

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