Research Article

The life history of *Serratella ignita* (Poda, 1761) (Insecta: Ephemeroptera) in a temporary and permanent Mediterranean stream

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Abstract. In mid latitudes, such as the Mediterranean region, one consequence of global climate change will be a progressive shift of permanent to temporary water courses, altering the life histories of present species or making them disappear. Presented here is a study on the life history of a mayfly species, *Serratella ignita*, in two Mediterranean streams, one permanent and one temporary. The research focuses on life history parameters such as life cycle, nymphal growth pattern, feeding type, biomass and secondary production. The life cycle was univoltine, showing a fast seasonal nymphal growth during four months in the permanent stream and five months in the temporary stream, with a long egg stage with diapause. The cumulated day-degrees during nymphal growth were similar between streams. Both populations behaved mainly as gatherer-collectors, but the population from the temporary stream also played an important role as a scraper. Animal matter was also consumed by nymphs from both populations. Gut content analysis showed that both *S. ignita* populations were opportunist/generalists, where changes in diet were correlated with size. Biomass and secondary production were notably higher in the permanent stream, but they were also high in the temporary stream. These data show that *S. ignita* had a high fitness in both streams. Our results support the idea that species such as this one may cope with future global climate change by maintaining, or even increasing, their populations at the expense of more stenoecic species.

Keywords: *Serratella ignita*; mayfly; life cycle, feeding; secondary production; Southern Iberian Peninsula.

Introduction

It is widely accepted that an increase in temperature over the past century has occurred, and that additional warming is expected to occur during the present century, as well as regional and seasonal variations in precipitation (Allan and Castillo, 2007). The direct effects on aquatic ecosystems will be due to changes in temperature and flow regimes (Allan et al., 2005). Future climatic scenarios predict more frequent and extended droughts, especially in the mid-latitudes (Boulton and Lake, 2008), resulting in a progressive shift from permanent to temporary water bodies. This will be more evident in Mediterranean-type streams, where flow is mainly influenced by rainfall, exhibiting a strong seasonal and annual variability (Gasith and Resh, 1999). Drought is a severe disturbance because it results in community changes and may introduce different stresses on ecosystem functioning (Grimm, 1993). Other consequences of this global change will

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be rising temperatures, which will also greatly affect lotic ecosystems by decreasing the oxygen solubility, thus affecting species having high oxygen requirements (Grimm, 1993). Apart from migration, phenology and life history changes are means of coping with higher temperatures, associated changes in food quality (Sweeney et al., 1992), and drought. The impact of these extended dry periods on the life histories of organisms can be harmful for some species but advantageous for others, increasing their overall fitness (Ladle and Bass, 1981; Harper and Peckarsky, 2006). Within this context, at the species level, some life history characteristics are particularly advantageous under expected future climatic conditions, such as long egg development, asynchronous egg hatching and nymphal development, temperature independence and flexibility in the life cycle, as well as being a generalist (Brittain, 2008).

Permanent and temporary waters differ greatly in the factors that control the development and behaviour of aquatic species. Sometimes it is difficult to elucidate the factors that control life histories in different habitats, such as permanent and temporary streams, because strategies frequently valid for some species are not present in both environments. In our study, we have taken as a model a species of mayfly that is widely found in these two types of stream and is also widely distributed throughout the Palaearctic region, *Serratella ignita* (Poda, 1761) (Ephemeroptera, Ephemerellidae) (Thomas and Belfiore, 2004). This model organism allows us to draw conclusions on several aspects of its life history in both environments, such as growth, the impact of temperature on growth, feeding, and ecological fitness under the given conditions as estimated from secondary production. Using the permanent stream as a model of current climatic conditions and the temporary stream as a model of possible future conditions, we can draw some consequences of this new scenario on this and similar species. The aim of this work is to make a comparison between permanent and temporary waters (as models of current and future climatic conditions) by using a mayfly that is widely found in these two types of stream, and to discuss the influence of abiotic and biotic factors on the species' life history.

Methods

The study was performed in two Mediterranean streams with different hydrological regimes: Río Despeñaperros (Sierra Morena, Jaén, Spain; UTM: 30SVH558476, 560 m a.s.l.), a temporary stream that carried water from the end of October 2006 to June 2007 (after which it dried out completely), and Río

Fardes (Sierra de Huétor, Granada, Spain; UTM: 30SVG465413, 1200 m a.s.l.), a permanent stream. Río Despeñaperros had a width during the wet period that ranged from 3 to 5.4 m, and a depth that varied from 0.04 to 0.31 m. The substrate composition was around 85 % blocks and stones, 10 % gravel and 5 % sand and silt. There were some tree branches and trunks on the riverbed. During the spring and summer there were abundant *Nasturtium* sp. and Ranunculaceae, but mosses were absent at the sampling station. Riparian vegetation was abundant on both sides of the stream, mainly represented by *Nerium oleander*, *Fraxinus* sp., *Berberis* sp., Poaceae, Umbelliferae and Compositae. Río Fardes had a width of 1.2 to 3.0 m during the sampling period, and the depth varied from 0.07 to 0.27 m. The substrate was mainly composed of 50 % sand, 35 % pebbles and 15 % mud. Mosses were absent, but *Nasturtium* sp. and Characeae were abundant. Riparian vegetation was well represented by Juncaceae or Cyperaceae, *Salix* sp, Poaceae, *Equisetum* sp., *Mentha* sp. and some *Carduus* sp.

Monthly macroinvertebrate samples were collected with a Surber sampler (0.09 m^2 area, 250 μm mesh size) from May 2006 to April 2007. Six replicates were taken to represent the different mesohabitats at each sampling site. They were preserved in 4 % formalin and taken to the laboratory, where they were sieved with a 150 μm mesh size sieve to remove excess formalin and fine detritus. Afterwards, organisms were sorted and identified to species level. In Río Despeñaperros, monthly sampling was carried out just during the wet period (from the end of October 2006 to June 2007) and with biweekly sampling in June due to the nearness of the dry period. In mid April, it was not possible to sample because of a flood caused by extreme rain, and we sampled at the end of this month.

A datalogger (HOBO® Water Temp Pro, 0.001 °C accuracy) was placed in the riverbed to register hourly temperature, and used to calculate the cumulated day-degrees between two sampling dates (Fig. 1). On each sampling date, we recorded physical parameters in situ (oxygen, conductivity and discharge, the latter by means of a propeller-meter) and collected one litre of water that was cooled and transported to the laboratory for analyzing selected physicochemical parameters (Table 1). Each month we measured the total body length and pronotum width of 30 nymphs of *S. ignita* using a micrometer of a binocular microscope (0.01 mm accuracy). Because these two measures were highly correlated (Gamma correlation = 0.88 in Río Despeñaperros and 0.87 in Río Fardes; p < 0.05 in both cases), we used total length to represent the life cycles of the mayfly. Nymphs were classified into 0.5 mm intervals. Measures were standardized by
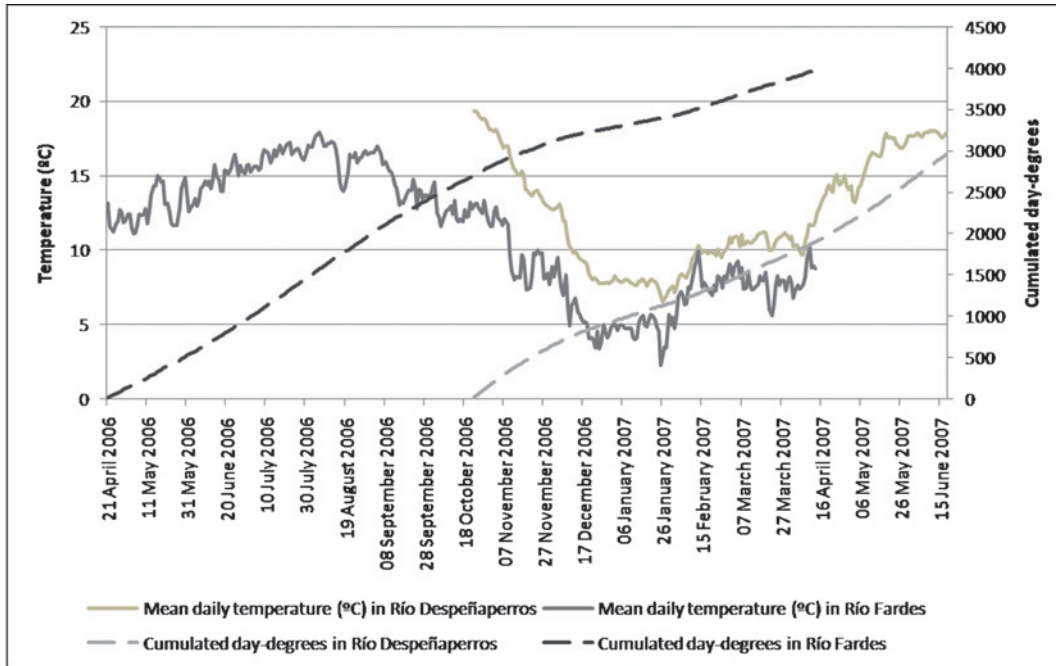
Fig. 1. Mean daily temperature and cumulated day-degrees at both sampling sites during the sampling period.

putting every individual between two slides. We used FiSAT II software (Gayanilo et al., 2002) to generate the size-frequency graphs representing the life cycles. Growth was calculated each month as the weighted mean of nymphal total length, where mean total length was weighted by the number of individuals in each size class.

A diet study was performed according to the methodology used by Bello and Cabrera (1999), as in other studies of mayfly feeding (e.g. Fenoglio et al., 2008; López-Rodríguez et al., 2008). Each individual was put in a vial with Hertwigs′ liquid and then heated in an oven at 65 °C for approximately 24 hours. Afterwards, specimens were mounted on slides for study under the microscope. We estimated the percentage of the absolute gut content (at 40x) as the total area occupied by the content in the whole digestive tract, and also estimated the relative gut content (at 400x) as the area occupied for each component within the total gut content, using a microscope with an ocular micrometer. Animal matter was quantified by number of consumed individuals (from isolated sclerotized parts, e.g. heads, legs) and not by the occupied area. The mean, standard deviation, minimum and maximum were calculated for non-animal matter.

From these data, the species were classified into functional feeding groups (FFG) according to food source and mechanism of food acquisition (Cummins, 1973; Merritt and Cummins, 2006). We studied the correlation between the size of the nymphs and percentage of the different gut contents.

Secondary production was calculated by means of the size-frequency method (Hynes and Coleman, 1968; Hamilton, 1969; Benke, 1979; Benke and Huryn, 2006), due to the presence of many size classes on the same date. As a non-cohort method, its use is appropriate for populations where no cohort can be clearly followed, where nymphal recruitment is continuous and size spread is high, as in our case. Using this method, when nymphal development period is different than a year, as in our case, a correction must be applied. This correction factor is known as cohort production interval (CPI), and it is the mean development time from hatching to final size (Benke, 1979). Thus, annual production was calculated multiplying the total production previously obtained by 12/CPI, with CPI representing the number of months that the species spends in the nymphal stage. Estimation of larval biomass was made according to the equation:

$$DW = aX^b$$

or, in natural logarithmic form:

$$Ln\ DW = Ln\ a + b\ LnX$$

where DW = individual dry weight, X = total length, a = constant, and b = slope of the regression. For calculating the regression equation, 29 formalin-preserved specimens from each site were measured, dried at 60 °C for 24 h and placed in a desiccator for 1 hour. Afterwards, they were weighed to the nearest

Table 1. Physicochemical parameters of the sampling streams.

	Despeñaperros					Fardes				
	N	Mean	S.D.	Minimum	Maximum	N	Mean	S.D.	Minimum	Maximum
pH	9	8.24	0.34	7.61	8.79	12	8.05	0.46	7.03	8.61
Ammonium (mg/l)	9	0.65	1.84	0.00	5.55	12	0.01	0.01	0.00	0.02
Phosphate (mg/l)	9	0.01	0.01	0.00	0.03	12	0.01	0.01	0.00	0.05
Nitrate (mg/l)	9	0.03	0.04	0.00	0.11	12	0.01	0.01	0.00	0.05
Nitrite (mg/l)	9	0.04	0.05	0.00	0.13	12	0.50	1.01	0.03	2.85
Sulfate (mg/l)	9	22.55	7.26	10.14	33.24	12	27.25	20.70	2.43	61.98
Chloride (mg/l)	9	49.10	8.70	36.40	68.25	12	21.37	9.94	7.10	39.05
Alkalinity (meq/l)	9	39.85	7.86	24.64	50.02	12	51.04	21.73	31.96	114.68
Ss (mg/l)	9	4.02	4.17	0.60	12.60	12	18.78	52.66	1.00	185.80
Ca (mg/l)	9	65.96	12.80	50.40	88.00	12	78.13	49.44	3.90	140.00
Mg (mg/l)	9	29.70	7.77	20.90	40.34	12	43.50	18.12	20.90	82.62
Hardness (mg CaCO$_3$/l)	9	286.94	54.13	213.87	379.77	12	374.11	106.57	95.76	461.66
Turbidity (NTU)	9	1.33	0.87	0.40	3.20	12	2.31	1.74	0.00	6.51
O$_2$ (% sat)	9	69.11	23.75	13.00	92.00	12	85.08	5.43	76.00	95.00
O$_2$ (mg/l)	9	7.03	2.73	1.10	9.70	12	8.11	0.74	7.10	9.20
Temperature (°C)	5908	12.54	3.86	5.90	25.87	8571	11.13	4.40	0.25	20.39
Conductivity (μS/cm)	9	454.89	69.43	359.00	553.00	12	428.08	102.73	104.00	474.00
Discharge (m^3/s)	9	0.10	0.11	0.00	0.32	12	0.11	0.06	0.05	0.27

0.001 mg using a Mettler model M3 microbalance. We calculated a single equation for each population. For statistical analysis, STATISTICA software (StatSoft, 2005) was employed. None of the variables studied were normally distributed, so non-parametric statistics were used in all cases. For selection of the proper statistical tests, we followed Guisande González et al. (2006).

Results

Both streams had similar physicochemical characteristics (Table 1), with only significant differences in nitrate, chloride and hardness (Kolmogorov-Smirnov test, $p < 0.05$). The maximum value of ammonium found in Río Despeñaperros is also high, a consequence of nitrogen-rich compounds on the riverbed when it is dry. The minimum value of oxygen content is also low in this stream due to some measurements taken in small pools with little dissolved oxygen when the river was in the process of drying.

Life histories
The nymphal development period lasted five months in Río Despeñaperros and four months in Río Fardes, although in the latter two individuals were collected in September and another two in December 2006. Thus, the life cycle was univoltine and with several cohorts in both streams.

In Río Despeñaperros, the first small larvae were collected in February 2007 and emergence ended in June 2007, prior to the dry period (Fig. 2). Mature nymphs were collected in May and June, indicating a flight period occurring mainly in the spring. The range

of nymph sizes was high in the last months, with individuals of different size classes coexisting at the same time. After mating and oviposition, eggs persisted in the stream until the next year. Thus, this species remained in the egg stage for up to seven months. For its entire development, the nymphs needed a total amount of 1648 day-degrees.

In Río Fardes, nymphs were present in the stream from May to August 2006, with scarce presence in September (Fig. 3). Only two nymphs were collected in December 2006. Mature nymphs were present from May to August, indicating a long flight period. There was also a large range in the size of nymphs, and an increasing mortality over time, reflected in the lower number of individuals collected in the last months of the nymphal development period. For reaching the adult stage, the nymphs cumulated a total of 1725 day-degrees.

When studying the relation between growth and cumulated day-degrees in each period, no significant correlation was found in either population (Spearman $r = 0.7$ in Despeñaperros population, and Spearman $r = 0.4$ in Fardes population; $p > 0.05$ in both cases), although some trends could be observed during some parts of the nymphal development (Fig. 4). On average, nymphal development took place between 10 and 18 °C in Despeñaperros and between 11 and 18 °C in Fardes.

Feeding
Individuals of *S. ignita* of both populations fed mainly on detritus (Table 2), with diatoms also highly consumed by the Despeñaperros population. In both cases, the mayfly consumed a relatively low percentage of coarse particulate organic matter (CPOM), but
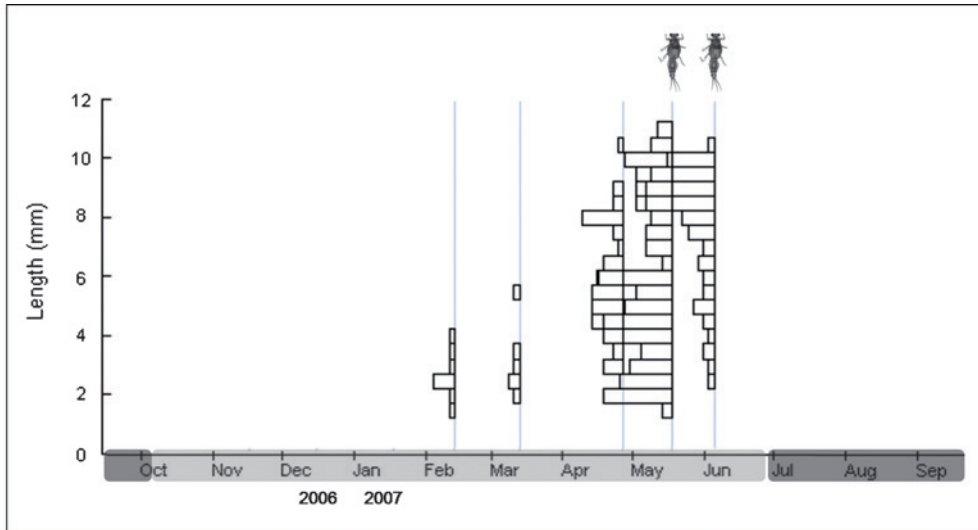
Fig. 2. Size-frequency graph representing the life cycle of *Serratella ignita* in Río Despeñaperros (N = 295). Presence of mature nymphs is marked with nymph pictures. The period in which the stream was dry is marked darker in the horizontal axis.
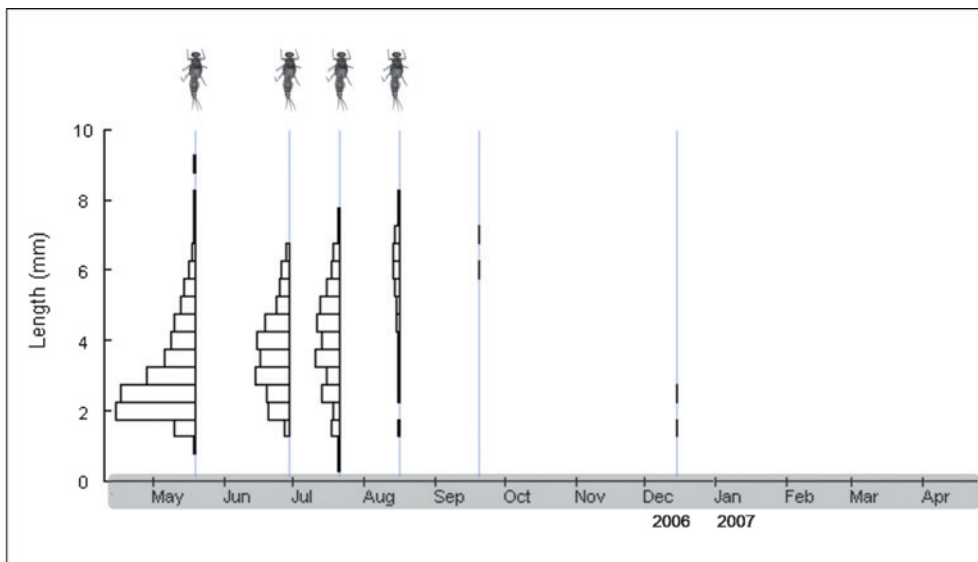

Fig. 3. Size-frequency graph representing the life cycle of *Serratella ignita* in Río Fardes (N = 4865). Presence of mature nymphs is marked with nymph pictures.

this was the second most-consumed resource in Fardes. Some ontogenetic shifts were detected when correlating total length with the percentage of the different consumed resources (Table 3). In Despeña-perros, the percentage of hyphae decreased as the nymphs increased in size, whereas the percentage of fungi spores and CPOM increased. In Fardes, large nymphs consumed less detritus but more hyphae, fungi spores, CPOM and pollen. In individuals from both populations, animal remains were detected (Simuliidae and other nonidentifiable animal matter), but were notably higher in Río Despeñaperros (9.4 % of the individuals studied versus 2.4 % in the Río Fardes). These were always present in the gut together with non-animal matter. The presence of animal remains in the gut contents was not significantly correlated with nymphal size (p >0.05 in both cases).

Secondary production

For *S. ignita*, dry weight (DW) at each site was correlated with body length (X) by the following equations:

$$Ln\ DW = -6.22 + 3.40\ LnX,\ (r^2 = 0.92,$$
$$F_{1,27} = 312.47,\ p< 0.05)\ for\ Río\ Despeñaperros$$

$$Ln\ DW = -6.19 + 3.35\ LnX,\ (r^2 = 0.83,$$
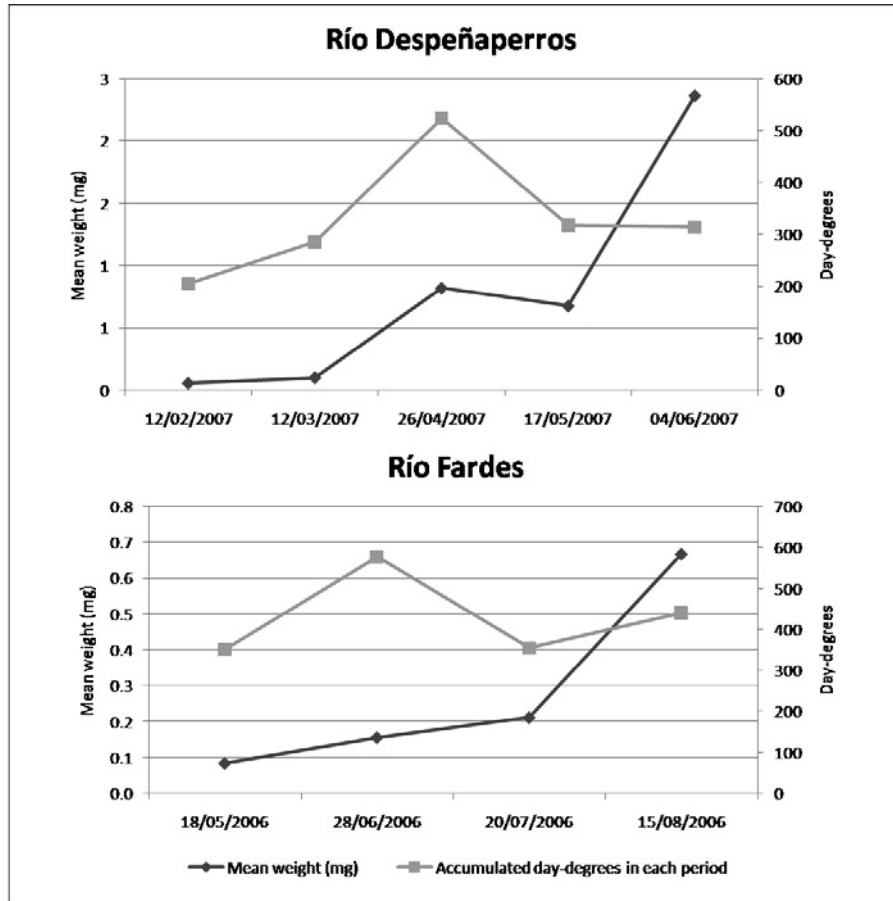$$F_{1,27} = 133.38,\ p< 0.05)\ for\ Río\ Fardes.$$

Fig. 4. Growth pattern of *Serratella ignita* and cumulated day-degrees between two consecutive sampling dates in each stream.

Table 2. Nymphal gut contents of *Serratella ignita* at the sampling sites (animal matter has not been considered; see Methods). Bold letter in FFG column (Functional Feeding Group) represents the most important functional group at the two sites.

		Despeñaperros				Fardes		
N	Mean	SD	Min-Max	N	Mean	SD	Min-Max	
% absolute	106	58.98	33.00	0–100	124	63.15	30.81	0–100
% detritus	93	60.52	31.53	5–100	114	88.30	12.36	10–100
% diatoms	93	29.83	30.65	0–95	114	2.37	4.74	0–25
% hyphae	93	0.19	0.49	0–2	114	0.71	1.25	0–5
% fungi spores	93	0.26	0.71	0–5	114	0.22	0.70	0–5
% CPOM	93	8.02	17.14	0–80	114	8.23	10.69	0–90
% pollen	93	0.68	2.23	0–20	114	0.22	0.68	0–4
% Cyanobacteria	93	0.44	2.81	0–25	–	–	–	–
FFG		**Gatherer-collector/scraper**				**Gatherer-collector/**shredder		

The cohort production interval (CPI) was 5 in Río Despeñaperros and 4 in Río Fardes, due to the fact that only two nymphs were collected in September in Río Fardes, which were insignificant. In Río Despeñaperros, we obtained a secondary production equal to 4.67 gDWm^{-2}. When corrected assuming a CPI of 5 months, this yields an annual secondary production of 11.21 gDWm^{-2}year^{-1}, with a cohort production/biomass ratio (P/B) of 4.14 and a biomass turnover (or annual P/B rate) of 9.92 year^{-1}. On the other hand, in

Río Fardes, the secondary production was 16.32 gDWm^{-2}. Thus, using a CPI of 4 months, the annual secondary production was equal to 48.95 gDWm^{-2}year^{-1}, the cohort P/B ratio was 6.12 and the annual P/B rate was 18.37 year^{-1}.

Table 3. Gamma correlations between total length and the percentage of the different food items (animal matter not included) in *Serratella ignita*. Values marked with an asterisk are significant at $p < 0.05$.

	S. ignita total length (mm)	
	Despeñaperros	**Fardes**
% detritus	–0.12	–0.31*
% diatoms	0.05	0.09
% hyphae	–0.29*	0.28*
% fungi spores	0.29*	0.33*
% CPOM	0.23*	0.33*
% pollen	0.12	0.26*
% Cyanobacteria	0.47	–

Discussion

The two studied populations of *S. ignita* showed similar, short nymphal development and rapid growth periods, lasting four or five months in Fardes and Despeñaperros, respectively. There was little growth in the Río Despeñaperros population, probably conditioned by the proximity of the dry period at the end of the nymphal growth. We observed a particularly large spread in size in the last months, probably due to both sexual dimorphism and the recruitment of newly-hatched individuals. Some of these small nymphs probably did not have enough time to complete their development due to the arrival of the dry period. The flight period occurred just before dry period, when adults started oviposition. The eggs probably remained in the stream until the following year, passing the dry period and part of the wet period in diapause. This diapause has been already pointed out by several authors for this species in permanent streams (e.g. Maitland, 1965; Zelinka, 1984; Sowa, 1975; Bohle, 1972).

Although it seems that the main growth occurs from May to August (probably corresponding to the main cohort) in Río Fardes, the presence of mature nymphs in the first few months implies a rapid growth of some individuals, which probably hatched some months before. Nymphs from December 2006 in Río Fardes were probably those that had an unsynchronized development. The two nymphs collected in September corresponded to a small proportion of individuals that usually do not reach the normal mature nymphal size when the emergence period occurs (Sweeney and Vannote, 1978; Vannote and Sweeney, 1980). The presence of these nymphs several months after the flight period (corresponding to a second failed generation) has been already pointed out by several authors (Pleskot, 1959; Hynes, 1961, 1970; Elliott, 1967, 1978; Alba-Tercedor, 1990; López-Rodríguez et al., 2008).

In both streams, the life cycle fulfils the characteristics of a "fast-seasonal" cycle according to Hynes'

(1970) classification. Within Landa's (1968) classification, it is of the "A2" category, corresponding to species with a long egg stage and diapause, which hatch during spring or summer. Nevertheless, in Río Despeñaperros the nymphal development is expected to occur a bit sooner due to the presence of a dry period during summer, with diapause occurring mainly during this period. Following Sowa's (1975) classification, our data fit the "B1" category, which takes into account the long egg development and the presence of a diapause stage during development.

The Río Fardes population has a life cycle similar to that found by the same authors in two nearby, high mountain streams of the Sierra Nevada, with different thermal regime (López-Rodríguez et al., 2008). In these streams, the nymphal development period extended from May to August in the stream at higher altitude (Río Válor), and from June to August in the stream at lower altitude (Río Poqueira). In comparison with Río Fardes, the mayfly cumulated fewer day-degrees at these higher sites (1500 in Río Válor and 1285 in Río Poqueira) for nymphal development, despite that they coincided in time (although in Río Poqueira, the stream with less day-degrees cumulated by nymphs, the nymphal development had a duration of only three months). Furthermore, in Río Despeñaperros, where the nymphs as a whole cumulated the highest number of day-degrees in comparison with the other three streams, nymphal development was the longest. It is expected that the development of the nymphs was fastest in streams where the species was able to reach the necessary cumulated day-degrees, because the development of mayflies is temperature dependent (Brittain, 1990); this is not completely supported by our data. This could be a consequence of the wide thermal requirements of the mayfly during the nymphal stage (Belfiore, 1983). Thus, the life cycle could be mainly determined by the time the mayfly spends in the egg stage, which seems to be an important stage of the life cycle of this mayfly, as well as in many others, given its lifespan (Clifford, 1982). We also found intraspecific differences in egg hatching in relation to temperature in both populations, as pointed out by Elliott and Humpesch (1980), reflected in the presence of small and mature nymphs throughout the nymphal development period, which probably is due to eggs that were subject to different temperatures. Nevertheless, the temperature at which hatching must take place is included in the range pointed out by Elliott and Humpesch (1980) and Humpesch (1984).

The presence of a diapause in these populations is not necessarily an adaptation to environmental stress such as drying, but is a necessary prerequisite to complete embryonic development, as pointed out by

Bohle (1972) for some German populations. However, it preadapts the species for survival in changing and harsh environments, such as temporary streams, and could contribute to its widespread distribution throughout the Palaearctic region. Nevertheless, in some other populations, or under experimental conditions, this diapause stage was not found (Bohle, 1972; Elliott, 1978); this fact has been discussed in other studies (Elliott et al., 1988). When comparing the flight period of the two populations, we realize that the flight period is longer in the permanent stream than in the temporary stream. A priori this could be seen as a contradiction with the typical patterns found in these types of environments (Dieterich and Anderson, 1995). Nonetheless, the presence of a long flight period in species of aquatic insects that inhabit temporary waters that dry out during summer is uncommon in spring species (authors personal observation), where a synchronic and short emergence period could be a better strategy to find mates before the dry period. Another typical characteristic of temporary water fauna is small size, which would imply a faster development (Jacobi and Cary, 1996; Williams, 1996, 2006); but we found the opposite in the studied populations. The temporary stream population had a mean mature nymphal total length of 9.39 mm ± 0.89 mm, while in the permanent stream population the mean was equal to 6.02 mm ± 0.53 mm; the developmental time was approximately the same (see Figs. 2 and 3). Furthermore, if we compare these data with those of the high mountain stream populations previously mentioned (López-Rodríguez et al., 2008), we find that the sizes are surprisingly similar between those populations and that of Río Fardes (the mean total length of the mature nymphs in those streams was 6.10 mm ± 0.47 mm and 6.10 mm ± 0.17 mm, respectively).

Another characteristic related to temporary stream populations is high fecundity (Jacobi and Cary, 1996; Williams, 1996, 2006), typical of r strategists that usually also have high population densities. Nevertheless, in the temporary stream, the total number of captured individuals in the same area was 295 (i.e., 647.4 ind/m^2), while in the permanent stream it was 4865 (i.e., 9425.9 ind/m^2).

Regarding feeding behaviour, both populations can be classified as gatherer-collectors. In Río Despeñaperros, the species would also perform an important function as a scraper and, to a lesser extent, as a shredder. These results coincide with those found by López-Rodríguez et al. (2008) in two different populations of *S. ignita* in the Sierra Nevada mountains. The great amount of diatoms found in the gut contents of the Despeñaperros population is probably due to their high abundance in this site, and suggests

opportunistic feeding, as usually pointed out for aquatic insects in general (Cummins, 1973; Monakov, 2003). The Fardes population also played a minor role as a shredder of CPOM, similar to that of the Despeñaperros population. Animal matter was not a main component of the gut content, and therefore was not considered for the functional feeding group classification.

The presence of some animal remains in the guts of the nymphs could be a consequence of accidental ingestion, as Riaño et al. (1997) suggested for *S. ignita*, but the presence of several animals in the same gut could also suggest active ingestion. This carnivore behaviour (likely unintentional) may provide high-quality protein needed by many invertebrates to complete their life cycles (Anderson, 1976). In fact, Simuliidae were one of the more abundant macro-invertebrates in the Despeñaperros stream and could have been easily ingested by the nymphs when collecting detritus or scraping the diatoms on the stones' surface where the blackflies live. This would also support the opportunistic/generalistic feeding habit mentioned above (Cummins, 1973; Monakov, 2003), which is also noted by some authors for temporary stream fauna (Jacobi and Cary, 1996; Williams, 1996, 2006).

As shown before, there were some changes in the gut content composition in relation to size. In both populations there was an increase in CPOM presence with size, probably related to the higher chewing capacity of larger nymphs that have more powerful mouthparts. This could be related with the increase of fungi hyphae and spores in larger nymphs (mainly in the Fardes population), due to the fact that these are largely associated with biofilm on the surface of leaves. This would lead to a higher efficiency in resource use because many aquatic insects obtain their nutrients from fungi and bacteria metabolism (Cummins, 1973).

In relation to the secondary production of the studied populations, both yield high values for being mainly gatherer-collectors species (Benke, 1993). It is notable that the great amount of biomass produced by the Fardes population is almost four times higher than that of the Despeñaperros population. This was probably a consequence of the great number of individuals present in Río Fardes (9425.9 ind/m^2 versus 647.4 ind/m^2 in Río Despeñaperros). Nevertheless, if we take into account the cohort P/B ratio, the difference is not so marked. Both values are around five, which is the mean value usually found in freshwater invertebrates in general. If we observe the annual P/B, we can see that the values are relatively high for gatherer-collectors (Benke, 1993), but appear intermediate if we compare them with other fresh-

water macroinvertebrates (Huryn and Wallace, 2000). Some authors have studied the secondary production of this species in other parts of Europe (see review in Elliott et al., 1988; González et al., 2000), providing a wide range of values for the species. Our values are very high compared to them, even that of the temporary stream, which can be related to the fitness of the species in this habitat.

As has been pointed out by several authors (e.g. Butler, 1984; Hynes, 1970), the main factors controlling growth in aquatic insects are temperature and food supply. In temporary waters, water level is also important in regulating growth (Williams, 2006). As we have seen, the studied populations of *S. ignita* developed in a similar range of temperatures in both streams (between 10 °C and 18 °C in Río Despeñaperros and 11 °C and 18 °C in Río Fardes), and cumulated approximately the same quantity of day-degrees to complete nymphal development, which was slightly higher in the permanent stream. On the other hand, both populations acted mainly as gatherer-collectors, although the Despeñaperros population also fed on diatoms, a more energyrich and easily assimilated resource (Benke and Wallace, 1980). This should be reflected in a higher secondary production for the population of Río Despeñaperros, and also in a shorter life cycle; but this is not supported by our results. In the contrary, we found a longer nymphal development period and a lower secondary production in the temporary stream, where the nymphs also fed on a higher energy-producing resource.

This can be related to the relatively harsh conditions imposed by the dry period in temporary streams compared with those found in permanent streams. Nevertheless, we found relatively high values of secondary production in the Río Despeñaperros population, indicating that this population is well adapted to this environment, given that secondary production is the most comprehensive measure of success for a population (Benke, 1993). When compared to the population of the permanent stream, we realize that this fitness must be constrained by some environmental factor other than temperature or food and water level and oxygen content variations were good candidates for such constraints (Table 1). Thus, this comparative study gives a wider picture on factors that control life histories and the success of species in different environments, and may provide a natural experiment for assessing conditions to which some species will be subject under a likely global climate change scenario in the future, as well as how such species will be able to adapt. With droughts occurring more frequently, some species, such as *S. ignita*, will achieve a relatively high fitness under the new conditions, as has been already pointed out by Ladle

and Bass (1981). Furthermore, as we have mentioned previously, the typical characteristics of temporary water fauna are present in the permanent stream population, which will also preadapt it to supposed future conditions of seasonality. It is important to note that these conclusions can be only applied to a reduced group of species which, as the species studied here, present a number of preadaptations to drought, such as egg diapause, long egg development and/or a short nymphal stage. For other species that have longer cycles or lack resistance stages, the consequences will not be so gentle.

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