

ORIGINAL ARTICLE

The unusual life history of a southern Iberian Peninsula population of *Torleya major* (Ephemeroptera: Ephemerellidae)

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Abstract The nymphal biology of a population of *Torleya major* (Klapálek) in southern Iberian Peninsula was studied. An atypical life cycle pattern is described, with eggs hatching in August producing a fast-developing cohort with adults emerging in autumn and a second slow-developing cohort with adults emerging in spring of the following year. Nymphal growth occurred primarily in summer–autumn (in the first cohort) and in spring (in the second). The origin of such a life history is discussed. Nymphs were collector-gatherers, consuming mainly detritus. Although ontogenetic shifts on the use of trophic resources were detected, similar food was utilized during the months when both cohorts cohabited, eliminating the possibility that the rapid growth of the first cohort could be related to the utilization of different food resources.

Key words collector-gatherer, life cycle, mayfly, nymphal feeding, southern Iberian Peninsula

Introduction

Aquatic insects exhibit great plasticity in life cycle patterns and strategies, many of them in relation to environmental conditions. This plasticity may even be present within a population as phenotypic plasticity, that is, alternative phenotypes produced by a single genotype depending on the environment during ontogeny (Nylin & Gotthard, 1998). One form of such plasticity is cohort splitting.

Cohort splitting, namely the variability in life cycle duration within populations, is a relatively uncommon life strategy in aquatic insects. It has been reported in some species of several orders, such as Ephemeroptera, Odonata, Plecoptera, Trichoptera and Diptera, (e.g., Butler, 1984; Alba-Tercedor, 1990a; Danks,

1992; Kozáčeková *et al.*, 2008; Lieske & Zwick, 2008). Within mayflies it has been mainly reported in species of the family Ephemeridae (particularly in the genera *Hexagenia* and *Ephemerella*), that are semivoltine (Butler, 1984; Alba-Tercedor, 1990a; Danks, 1992); although some Baetidae and Caenidae species may also exhibit this phenomena (Bengtsson, 1988; Taylor & Kennedy, 2003). The causes that originate this strategy in aquatic insects are not entirely clear. Lieske and Zwick (2008) pointed out for a stonefly species that interference competition (i.e., competition for space and resources) could enhance differences in size and development caused by other factors. This cohort splitting could also act as a mechanism to ensure the persistence of species living in unpredictable habitats (Danks, 1992).

Torleya Lestage is a genus of Ephemerellidae occurring in the Palearctic region (Thomas & Belfiore, 2004). Particularly, *T. major* (Klapálek) is widely distributed in Europe (Thomas & Belfiore, 2004). It is found both in fast-flowing waters, with substrate composed by pebbles and gravels, and in slow-flowing waters, with abundant detritus (Belfiore, 1983). The studied population morphologically fits in what Alba-Tercedor and Derka (2003)

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described as *T. nazarita*, recently synonymised with *T. major* by Jacobus et al. (2004).

Few studies have focused on the nymphal biology and life history of *Torleya* (e.g., Thibault, 1971; Rosillon, 1986a, b; Alba-Tercedor, 1990b). In the Atlantic Pyrenees, a population of *Torleya* (identified as *T. belgica* Lestage) is univoltine, and nymphs are present in the stream throughout the year, with a faster development period prior to the spring emergence (Thibault, 1971). In Belgium *T. major* (cited as *Ephemera major*) also exhibits a univoltine life cycle, with emergence synchronized and flight periods from mid-May to mid-June. Early instar nymphs occurred from June to late August, and total mortality from egg to adult was estimated >99%, although such high mortality is apparently compensated by a high fecundity (Rosillon, 1986a). In Sierra Nevada (southern Iberian Peninsula) the cycle of a population of *Torleya* (referred as *T. cf. belgica* and latter described as *T. nazarita*) is univoltine, with nymphs present from October to June. Growth is slow from October to March, and faster in the subsequent months (Alba-Tercedor, 1990b).

The objective of this study is to examine the nymphal biology of a population of *T. major*, both regarding its nymphal development and feeding. A relatively uncommon life strategy exhibited by this population is discussed, and several hypotheses for its explanation are proposed.

Materials and methods

The study site was the Río Fardes (Sierra de Huétor, Granada, Spain; Universal Transverse Mercator zone: 30SVG465413; 37°18'23"N, 3°25'17"W; 1 200 m a.s.l.), a permanent Mediterranean chalk stream. Samplings were carried out monthly from May 2006 to April 2007. Stream width varied from 1.15 to 3.02 m during the sampling period at the sampling site, and the depth ranged from 0.07 to 0.27 m. The composition of the substrate was approximately 15% silt, 35% pebble and 50% sand. Submerged vegetation was composed by *Nasturtium* sp. and Characeae. The riparian vegetation was abundant and was primarily Juncaceae or Ciperaceae, *Salix* sp., Poaceae, *Equisetum* sp., *Mentha* sp. and some *Carduus* sp. A data logger (HOBO[®] Water Temp Pro: Onset Computer Corp., Bourne, MA, US; 0.2°C accuracy) was placed in the stream to register the hourly water temperature. This allowed for the calculation of accumulated degree-days between two sampling dates (Fig. 1). On every sampling date dissolved oxygen, conductivity and discharge were recorded *in situ* and 1 L of water was collected and trans-

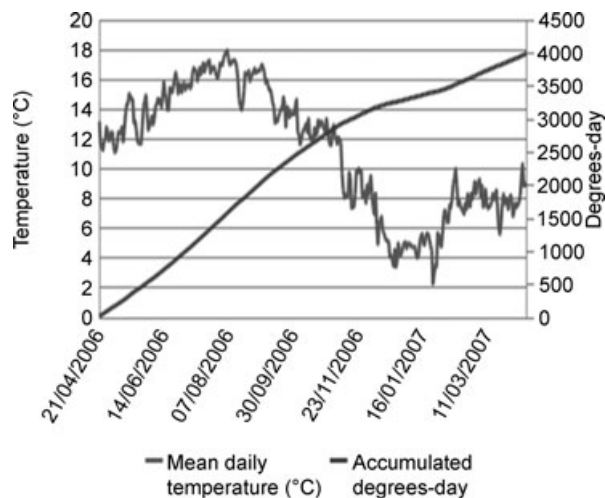


Fig. 1 Mean daily temperature and accumulated degree-days at Río Fardes (Sierra de Huétor, Granada, Spain) site during May 2006 to April 2007.

ported (on ice) to the laboratory to analyze chemical parameters (Table 1).

Macroinvertebrates were collected with a Surber sampler (0.09 m² area and 250 µm mesh size). Six replicates were taken to represent the different mesohabitats of the sampling site. Samples were preserved in 4% formalin and returned to the laboratory, where they were washed using a 150 µm mesh size sieve in order to remove excess preservative and fine detritus. Afterwards, organisms were sorted and identified to species.

For each monthly sample, 30 nymphs of *T. major* were measured for total body length and width of pronotum using an ocular micrometer to the nearest 0.01 mm. Measurements were standardized by placing each specimen between two slides. Because these two measurements were highly correlated (with a Gamma correlation of 0.87; $P < 0.05$), we used only total body length to depict nymphal growth. Afterwards, for representation purposes, individuals were classified into 1-mm intervals according to total body length. We used FiSAT II software (Gayaniolo et al., 2002) to generate the size-frequency graphs representing the life cycles.

Growth was calculated for each month as the weighted mean of the nymphal total body length. Mean was weighted by the number of individuals in each size class (Guisande González et al., 2006; López-Rodríguez et al., 2009).

The diet was studied according to the methodology described by Bello and Cabrera (1999) that has been also used in other studies of aquatic insect feeding habits (e.g., Tierno de Figueroa et al., 2006; Fenoglio et al., 2008; López-Rodríguez et al., 2008). For this analysis, the same

Table 1 Physicochemical parameters at the sampling site.

	Río Fardes				
	N	Mean	SD	Minimum	Maximum
pH	12	8.05	0.46	7.03	8.61
Ammonium (mg/L)	12	0.01	0.01	0.00	0.02
Phosphates (mg/L)	12	0.01	0.01	0.00	0.05
Nitrates (mg/L)	12	0.01	0.01	0.00	0.05
Nitrites (mg/L)	12	0.50	1.01	0.03	2.85
Sulphates (mg/L)	12	27.25	20.70	2.43	61.98
Chlorides (mg/L)	12	21.37	9.94	7.10	39.05
Alkalinity (meq/L)	12	51.04	21.73	31.96	114.68
Ss (mg/L)	12	18.78	52.66	1.00	185.80
Ca (mg/L)	12	78.13	49.44	3.90	140.00
Mg (mg/L)	12	43.50	18.12	20.90	82.62
Hardness (mg CaCO ₃ /L)	12	374.11	106.57	95.76	461.66
Turbidity (NTU)	12	2.31	1.74	0.00	6.51
O ₂ (% saturation)	12	85.08	5.43	76.00	95.00
O ₂ (mg/L)	12	8.11	0.74	7.10	9.20
Temperature (°C)	8 571	11.13	4.40	0.25	20.39
Conductivity (μS/cm)	12	428.08	102.73	104.00	474.00
Discharge (m ³ /s)	12	0.11	0.06	0.05	0.27

30 specimens previously measured to study the correlation between total body length and pronotum width were used. Each individual specimen was placed into a vial with Hertwig's fluid and then heated in an oven at 65°C for approximately 24 h. Individual specimens were mounted on slides for study under the microscope. 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 also estimated the relative gut content (at 400×) as the area occupied for each component within the total gut content, using an ocular micrometer. Mean, standard deviation, minimum and maximum area occupied for each component were calculated. Functional feeding groups (FFG) were identified following Cummins (1973) and Merritt and Cummins (2006). We also studied the correlation between the nymphal size classes and percentage of gut contents.

STATISTICA software (StatSoft, 2005) was used for statistical analyses. None of the variables were normally distributed, therefore non-parametric statistical measures were used in all cases (Guisande González *et al.*, 2006).

Results

Nymphs of *T. major* were present in the stream from August to May. Two cohorts can be differentiated in the same

population (Fig. 2): eggs hatching in August, with nymphs of the first cohort reaching maturity in September to December, and those of the second cohort reaching maturity in April into May of the following year. The density of individuals of the first cohort and second cohort were approximately 298 individuals/m² and 444 individuals/m², respectively.

Mature nymphs (with black wingpads) of both generations had a total body length greater than 6.45 mm. The flight period of the first cohort was relatively long, starting in September and extending into December, whereas

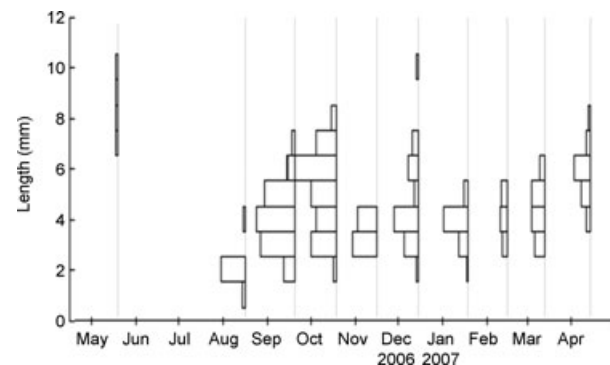


Fig. 2 Size-frequency graph representing the life cycle at Río Fardes (Sierra de Huétor, Granada, Spain) ($n = 457$).

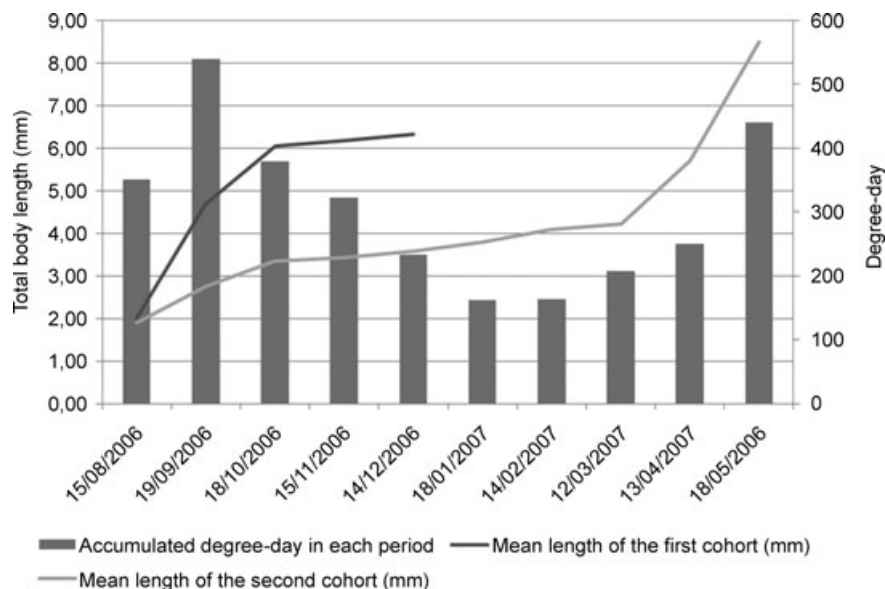


Fig. 3 Growth pattern of the *Torleya major* nymphs and accumulated degree-days between two consecutive sampling dates during the sampling period, Río Fardes (Sierra de Huétor, Granada, Spain). Note: the last column of the graph corresponds to the previous year, and so it should be at the left of the graph, but for representation purposes, the column has been placed to the right to allow a clearer depiction of nymphal development.

the flight period of the second cohort was shorter, from April into May.

Eggs laid by adults of each cohort apparently exhibited different incubation times, taking into account that eggs hatched around August. Those of the first cohort hatched after approximately 8 months, accumulating about 2 507 degree-days, and eggs of the second cohort hatched after about 3 months, accumulating approximately 1 373 degree-days.

Growth was considerably faster in nymphs from the first cohort, completing nymphal development in 3–5 months (Fig. 3), during which period approximately 1 917 degree-days were accumulated. Nymphs belonging to the second cohort developed over 8–10 months, with a slower growth during the autumn and winter and a faster growth rate in spring, prior to emergence. These nymphs accumulated approximately 3 050 degree-days. In both cohorts there was no significant correlation (Spearman correlation with $P > 0.05$ in both cases) between growth and accumulated degree-days between two consecutive sampling dates.

The main trophic resource was detritus (Table 2). Other ingested food items included coarse particulate organic matter (CPOM), diatoms, fungal hyphae or pollen, but these items contributed a small percentage of the total gut contents of examined nymphs. There was a significant negative correlation between total body length and the

percentage of detritus found in their guts, and a significant positive correlation between total body length and content of diatoms, fungal hyphae and CPOM (Table 3). Mineral particles representing 23.63% of the studied nymphs also occurred in the guts.

Discussion

The studied population of *T. major* exhibited an atypical life cycle as compared with previously reported studies (e.g. Thibault, 1971; Rosillon, 1986a; Alba-Tercedor, 1990b). There may be two possible interpretations of the

Table 2 Nymphal gut contents of the *Torleya major* nymphs at the sampling site.

	N	Mean	SD	Minimum	Maximum
% absolute	233	48.69	24.69	0.00	100.00
% detritus	209	94.75	9.32	10.00	100.00
% diatoms	209	0.68	2.68	0.00	20.00
% hyphae	209	0.56	1.60	0.00	15.00
% fungi spores	209	0.14	0.45	0.00	3.00
% CPOM	209	3.52	4.92	0.00	50.00
% pollen	209	0.04	0.44	0.00	6.00

CPOM, coarse particulate organic matter.

Table 3 Gamma correlations between total body length and the percentage of the different food items in the nymphal diet.

	Total length (mm)
% detritus	-0.21*
% diatoms	0.77*
% hyphae	0.44*
% fungi spores	0.14
% CPOM	0.16*
% pollen	-0.08

Values marked with an asterisk are significant at $P < 0.05$. CPOM, coarse particulate organic matter.

life cycle: (i) a univoltine life cycle with cohort splitting; and (ii) a bivoltine life cycle. This study supports the first interpretation because a bivoltine cycle would imply: (i) the presence of small nymphs in February and March resulting from eggs laid by the first cohort (under this hypothesis, the first generation); and (ii) a faster egg hatching when temperatures are lower, that is, a faster hatching of eggs laid in winter than of those laid down in spring, when the opposite would be expected, as temperature is the major factor determining the length of the period of egg development in mayflies (Brittain, 1982). Although in *T. major* this relationship has not been determined, in many other mayflies there is a clear relationship between water temperature and the length of egg development (Brittain, 2008), usually with a shorter hatching developmental time when temperature is higher (Elliott & Humpesch, 1980). Moreover, in populations that are bivoltine, the generation with faster development generally occurs in the warmest months (e.g. López-Rodríguez *et al.*, 2008), and in our population the first cohort developed when water temperatures were decreasing.

Cohort splitting may have evolved when the initial longer nymphal developing population reached maturity and emerged prior to decreasing winter water temperature. The eggs of offspring of these individuals would then diapause through the winter, and then have a faster nymphal development period in the spring.

The slower-developing nymphs that remained in the stream during the winter months under colder water temperatures would not develop, as pointed out by Hynes (1970). Under this hypothesis some nymphs (probably those that hatched later, when water temperatures were decreasing) would become dormant during low water temperatures. On the other hand, those that hatched first would be able to develop under warmer water temperatures.

Eggs of different cohorts would also pass through different embryonic developmental stages. Those of the first

cohort would probably enter diapause, whereas those of the second cohort would have a direct development. Eggs in diapause would not accumulate degree-days during these resting months, and would start to develop during the warmest months of summer, together with the eggs recently laid down by adults from the second cohort. This would explain the synchronous hatching of nymphs in August. Also water temperature by itself could act as a clue for hatching which was supported by the fact that hatching started in August, when the maximum annual water temperature was reached (Fig. 1).

Each cohort exhibited a differential response to water temperature. At the same sampling date, with similar temperatures and accumulated degree-days, a portion of the population (the first cohort) grew very rapidly, whereas the second cohort had no growth (see grow pattern of both cohorts from August to October in Fig. 3). This is also reflected in the differences between accumulated degree-days of both cohorts and could be a consequence of the presence of the previously mentioned dormant nymphal stage.

The growth pattern of the second cohort in our study was similar to what was reported for a population of *T. major* in a stream of the Atlantic Pyrenees (Thibault, 1971), for a Belgian population (Rosillon, 1986a) and for a population in a nearby mountain stream (just a few kilometres from our sampling site and with similar characteristics, although with a warmer temperature regime) of Sierra Nevada (southern Iberian Peninsula) (Alba-Tercedor, 1990b).

A longer nymphal development pattern seems to be characteristic in other populations of *T. major*. Alba-Tercedor (1990b) described a univoltine life cycle with nymphs present from October to August, and a late spring–early summer adult activity period. Hynes (1970) also classified *Torleya* as univoltine, within the slow seasonal cycle category. This author reported that growth of nymphs occurred principally in autumn and winter and that nymphs exhibited nymphal diapause, and he indicated a category “S₂d” (i.e., a slow seasonal cycle of type two with a diapause in a stage other than the egg). In our population, the second cohort would exhibit a slow seasonal cycle, but the first cohort would be classified as fast seasonal. Nevertheless, in this population, nymphal growth primarily occurred at the end of summer and the beginning of autumn (in the first cohort) and in spring (in the second cohort), but not in the colder months of autumn and winter, as pointed out by other authors (Pleskot, 1958, 1961). The pattern of the second cohort of our population coincides with the type of life cycle pointed out for this species by Landa (1968) in Central Europe and by Thibault (1971) in the Atlantic Pyrenees. Sowa

(1975) found that this species exhibited a univoltine life cycle with nymphs present in the stream practically all the year (with the highest percentage of young nymphs occurring in autumn) and with a long emergence period from May–June to July–August. Clifford (1982) also recorded a univoltine life cycle for *T. major*, with overwintering nymphs.

Thus, the ancestral population dynamics of the studied population was probably a univoltine life cycle, with nymphal development lasting approximately from August to May. This is supported by the highest density of individuals during this development period. Some individuals from an initial population with longer nymphal development may have an ecological advantage by developing faster and reaching maturity in autumn. Thus the progeny of those adults would pass the coldest months in the egg stage.

In these conditions a genetic isolation could occur if members from the first cohort always entered a nymphal dormancy stage. This would lead to an incipient speciation phenomenon, given that adults from the first and the second cohort were temporally separated (if this pattern is maintained).

In regard to feeding behavior, the studied population are considered collector-gatherers, with relatively low ingestion of other food items. The relatively high number of nymphs with mineral particles in the guts supports a collector-gatherer guild, as these mineral particles would be mainly consumed when feeding on detritus. This functional group rejects the possibility that the rapid growth of the first cohort is the result of utilization of some other energy-rich trophic resource. Furthermore, during the months that both cohorts coexisted, they shared the same feeding pattern. Neither intraspecific competition, as pointed out by Lieske and Zwick (2008), seemed to explain the pattern found in our population of *T. major*, since the density of individuals in our study site was much lower than that reported by the above authors and detritus did not seem to be a limiting factor.

Conclusions

The studied population of *T. major* exhibited an atypical life cycle pattern. There seem to be two differentiated cohorts, one with fast nymphal development lasting 3–5 months and other with a slower nymphal development period of 8–10 months. Since hatching was relatively synchronized and took place approximately in August, both cohorts would exhibit different embryonic development. This splitting of cohorts is probably due to phenotypic plasticity due to nymphs facultatively entering into dor-

mancy. The possibility of this differentiation being genetically controlled exists, and would lead to an incipient speciation or, at least, a genetic differentiation between members of both cohorts. Differences in the nymphal development of the cohorts are difficult to explain, taking into account that the only possible advantage of the first cohort for developing so fast could be the avoidance of the winter low temperatures. Differences in growth rate due to variations in feeding cannot be argued, because all the individuals of the entire population fed mainly on detritus. These differences do not seem to be a consequence of intraspecific competition, as the density of individuals was not especially high at the sampling site.

Thus, phenotypic plasticity could explain the behavior of this population if the factor that regulates the duration of the nymphal development is the entrance into a dormancy stage as consequence of temperature. If this would not be the case, a genetic basis appears as the most probable explanation.

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