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# Life strategies of 3 Perlodidae species (Plecoptera) in a Mediterranean seasonal stream in southern Europe

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**Abstract.** We studied aspects of the nymphal biology and ecology of 3 Perlodidae species (*Guadalgenus franzi*, *Hemimelaena flaviventris*, and *Isoperla curtata*) in a Mediterranean seasonal stream in the southern Iberian Peninsula. Their life-history strategies were greatly influenced by the characteristics of their environment, i.e., a summer dry period with relatively warm temperatures, but strategies differed among species. *Guadalgenus franzi* was semivoltine and probably underwent nymphal quiescence when the stream was dry. *Hemimelaena flaviventris* and *I. curtata* had relatively short univoltine life cycles that overlapped, but *I. curtata* was slightly ahead of *H. flaviventris*. Both species passed the dry period in the egg stage, probably with a diapause phase. Growth rates of *H. flaviventris* and *I. curtata* peaked before emergence, whereas growth rate of *G. franzi* peaked immediately before and after the dry period. The 3 species had relatively short flight periods compared with other species from seasonal streams. *Guadalgenus franzi* and *I. curtata* were mainly scrapers that fed on diatoms, whereas *H. flaviventris* was mainly predatory. Diet changed somewhat in relation to size, and prey electivity patterns differed among species. All 3 species preferred Chironomidae, but *G. franzi* preferred Chironomidae principally when smaller. All 3 species had high secondary production relative to other stonefly species from both temporary and permanent waters.

**Key words:** stoneflies, life history, secondary production, feeding, temporary stream, southern Iberian Peninsula, Spain.

Stoneflies are aquatic insects that are found in clean, fast-flowing waters with relatively low temperatures and high dissolved $O_2$ content (Fochetti and Tierno de Figueroa 2008). Temporary waters might be expected to be unsuitable habitats for stoneflies, but some species are successful inhabitants of these environments, despite the complete loss of a wet channel during dry periods (Williams 2006). These species use several strategies, including: migration to other streams with more suitable conditions, arrival at permanent waters in their immature stages, burrowing deep into the substrate to reach the hyporheic zone, modified life histories in which all immature development occurs within the wet period, or dormancy in temporary streams (Boulton et al. 1998, Williams 2006). During the wet period, growth is controlled mainly by temperature and food availability (Hynes 1970, Cummins and Klug 1979). Each species has an optimum temperature for development, and this difference contributes to the characteristic succession of species in the community (e.g., Hildrew and Edington 1979). Typical faunas of temporary waters seem to be opportunistic/generalistic feeders, but comprehensive dietary studies are rare (Williams 2006).

Secondary production is one of the most comprehensive measures of success for a population because

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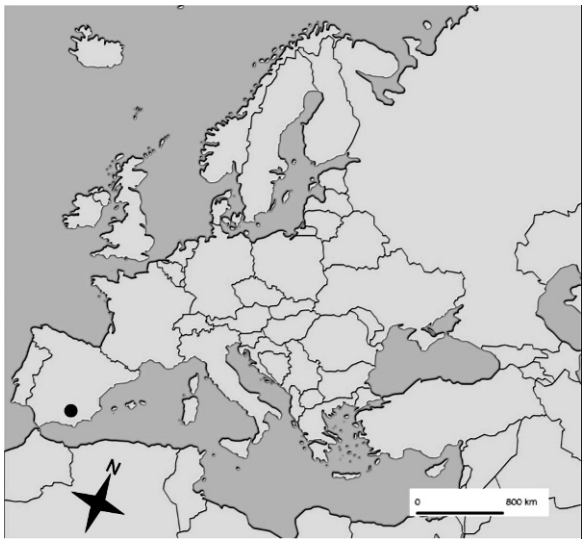


FIG. 1. Southwestern Europe and the sampling site marked with a circle.

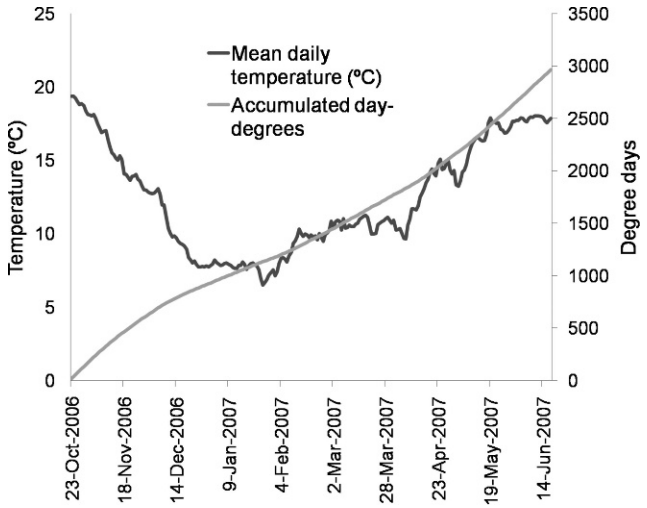


FIG. 2. Mean daily temperature and accumulated degree days during the wet period.

it is a composite of several other components of success: density, biomass, individual growth rate, reproduction, survivorship, and development time (Benke 1993). Thus, in seasonal streams, secondary production is an important clue to how well adapted a species is to its environment. Life-history information combined with data on secondary production and foodweb interactions can improve our understanding of the structure and function of communities and ecosystems (Huryn and Wallace 2000).

Our goal was to analyze the life histories, feeding behaviors, and secondary production patterns of 3 Plecoptera species (Perlodidae) that are found in temporary waters. We worked in a seasonal stream in the southern Iberian Peninsula. *Guadalgenus franzi* (Aubert, 1963) is endemic to the Iberian Peninsula, *Hemimelaena flaviventris* (Pictet, 1842) is found in the Iberian Peninsula and northern Africa, and *Isoperla curtata* Navás, 1924 is endemic to the Iberian Peninsula (Tierno de Figueroa et al. 2003). We discuss the strategies they use to inhabit this ephemeral environment and compare our results to what is known about these species. Few authors have studied these species because of their restricted distributions, so we also compare our results with those for other Perlodidae species found in seasonal and permanent streams.

## Methods

### *Study site and sample collection*

We worked in Río Despeñaperros (Sierra Morena, Jaén, Spain; lat 38°22′22.98″N, long 3°30′26.25″E, 560 m above sea level [asl]; Fig. 1), a Mediterranean-type seasonal stream, between October 2006 and September 2007. When water was present, the width of the stream varied from 2.95 to 5.35 m, and the depth ranged from 0.04 to 0.31 m. The substrate was composed of boulders and large cobbles (85%), gravels (10%), and sands and silt (5%), and some branches and trunks were present on the river bed. During spring and summer, Ranunculaceae and *Nasturtium* species were abundant in the main water course, but mosses were absent from the sampling site. Riparian vegetation was abundant along both sides of the stream, and it mainly included *Nerium oleander*, *Fraxinus* sp., *Berberis* sp., Poaceae, Umbelliferae, and Compositae.

In autumn 2006, we placed a data logger (HOBO® Water Temp Pro, 0.001°C accuracy; Onset Computer Corporation, Bourne, Massachusetts) in the river bed to record the temperature of the water hourly, and we visited the stream regularly to detect exactly when flow resumed. Temperature records showed that flow resumed at the end of October (Fig. 2). We sampled monthly from November 2006 to June 2007 when water was present. In mid-April, an extreme rain event led to a flood that delayed the sampling for that month until late April. In June, before the stream dried, we collected samples biweekly. In summer and part of autumn, the stream was completely dry, and no pools were present.

We measured dissolved $O_2$ with an oximeter (Oxi 320/set Best-Nr 200 212, Wissenschaftlich-Technische Weerkstätten, Weilheim, Germany), conductivity with a conductimeter (Ecoscan handheld series, Euteoh Instrument Technology, Singapore), and discharge

TABLE 1. Physicochemical parameters of the sampling site.

| Variable | *n* | Mean | SD | Minimum | Maximum |
|---|---|---|---|---|---|
| pH | 9 | 8.24 | 0.34 | 7.61 | 8.79 |
| $NH_4^+$ (mg/L) | 9 | 0.65 | 1.84 | 0.00 | 5.55 |
| $PO_4^{3-}$ (mg/L) | 9 | 0.01 | 0.01 | 0.00 | 0.03 |
| $NO_3^-$ (mg/L) | 9 | 0.03 | 0.04 | 0.00 | 0.11 |
| $NO_2^-$ (mg/L) | 9 | 0.04 | 0.05 | 0.00 | 0.13 |
| $SO_4^{2+}$ (mg/L) | 9 | 22.55 | 7.26 | 10.14 | 33.24 |
| $Cl^-$ (mg/L) | 9 | 49.10 | 8.70 | 36.40 | 68.25 |
| Alkalinity (meq/L) | 9 | 39.85 | 7.86 | 24.64 | 50.02 |
| Solids in suspension (mg/L) | 9 | 4.02 | 4.17 | 0.60 | 12.60 |
| Ca (mg/L) | 9 | 65.96 | 12.80 | 50.40 | 88.00 |
| Mg (mg/L) | 9 | 29.70 | 7.77 | 20.90 | 40.34 |
| Hardness (mg $CaCO_3$/L) | 9 | 286.94 | 54.13 | 213.87 | 379.77 |
| Turbidity (NTU) | 9 | 1.33 | 0.87 | 0.40 | 3.20 |
| $O_2$ (% saturation) | 9 | 69.11 | 23.75 | 13.00 | 92.00 |
| $O_2$ (mg/L) | 9 | 7.03 | 2.73 | 1.10 | 9.70 |
| Temperature (°C) | 5908 | 12.54 | 3.86 | 5.90 | 25.87 |
| Conductivity (μS/cm) | 9 | 454.89 | 69.43 | 359.00 | 553.00 |
| Discharge ($m^3$/s) | 9 | 0.10 | 0.11 | 0.00 | 0.32 |

with a propeller meter (Global Water Model FP101, Global Water Instrumentation, Gold River, California) in situ during each sampling event. We collected 1 L of water, cool-preserved it, and transported it to the laboratory where we measured the physicochemical conditions of the site (Table 1). We determined pH by means of a pH meter (CyberScan PH 510, Graintec Scientific Pty Ltd., Toowoomba, Australia), $NH^{4+}$, $PO_4^{3-}$, $NO^{3-}$, $NO^{2-}$, and $SO_4^{2+}$ with molecular absorption spectrophotometry, $Cl^-$ by means of the Mohr method, alkalinity by means of the potentiometric method, solids in suspension by filtration through a membrane, Ca, Mg, and hardness by means of the complexometric method, and turbidity with a turbidimeter (Hanna HI 93703-11, Hanna Instruments, Eibar, Spain) (Rodier 1998).

We collected macroinvertebrates with a Surber sampler (area = 0.09 $m^2$, 250-μm-mesh size). We took 6 samples on each sampling date to represent the diversity of mesohabitats encountered at sites (e.g., the fast-flowing zone, the submerged vegetation zone), preserved animals in 4% formalin, and brought them to the laboratory. We rinsed samples in a 150-μm-mesh sieve to remove excess formalin and fine detritus. We sorted stoneflies and identified them to species. We sorted the rest of the animal community and identified individuals to the family level, except for Ostracoda, Hydracarina, Nematomorpha, Nematoda, and Copepoda (Table 2).

We collected adults of the 3 stonefly species on each sampling date by beating the riparian vegetation with an insect net and picking adults directly from the stones. We preserved adults in 70% ethanol and used them, together with the information obtained from collection of mature nymphs, to establish the flight period.

*Individual size and secondary production*

We measured total body length and pronotum width of each nymph with the micrometer of a binocular microscope. To avoid measurement errors produced by curvature in the body, we placed nymphs between 2 slides before measuring them. Total body length and pronotum width were highly correlated ($\gamma$ correlation $> 0.77$ for every case, $p < 0.05$), and we did subsequent analysis using only total body length. We distributed nymphs in 1-mm-length size classes and represented their life cycles by means of size–frequency graphs with FiSAT II software (version 1.2.0; www.fao.org/fi/statist/fisoft/fisat/index.htm). We calculated mean growth between sampling dates as the difference in mean dry mass of the species between successive months.

We used the size–frequency method to evaluate secondary production because nymphs of different size classes were present at the same time (Hynes and Coleman 1968, Hamilton 1969, Benke 1979, Benke and Huryn 2006). We applied a correction for the cohort production interval (CPI = mean development time from hatching to final size; Benke 1979) for each species. We estimated CPI relative to the period when flowing water was present (8 mo), as in Chadwick and Huryn (2007). We estimated nymphal biomass with the equation:

Table 2. Densities (individuals/$m^2$) of macroinvertebrate taxa collected on each sampling date. Taxa are identified to the level used when calculating Ivlev's Index.

| | Sampling date | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Taxon | 16 November 2006 | 15 December 2006 | 17 January 2007 | 12 February 2007 | 12 March 2007 | 26 April 2007 | 17 May 2007 | 4 June 2007 | 18 June 2007 |
| Ancylidae | 338.89 | 307.41 | 151.85 | 303.70 | 151.85 | 227.78 | 272.22 | 164.81 | 0.00 |
| Anthomyidae (larvae) | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 7.41 | 0.00 |
| Anthomyidae (pupae) | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 11.11 | 3.70 |
| Athericidae | 0.00 | 7.41 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Ceratopogonidae | 0.00 | 0.00 | 1.85 | 0.00 | 0.00 | 0.00 | 5.56 | 11.11 | 0.00 |
| Chironomidae (larvae) | 418.52 | 50.00 | 68.52 | 188.89 | 42.59 | 20.37 | 455.56 | 1846.30 | 2642.59 |
| Chironomidae (pupae) | 1.85 | 1.85 | 0.00 | 3.70 | 0.00 | 1.85 | 7.41 | 170.37 | 142.59 |
| Dixidae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.70 | 0.00 |
| Dugesiidae | 42.59 | 142.59 | 46.30 | 53.70 | 9.26 | 22.22 | 64.81 | 116.67 | 5.56 |
| Dytiscidae (adult) | 1.85 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Dytiscidae (larvae) | 33.33 | 0.00 | 5.56 | 3.70 | 0.00 | 0.00 | 3.70 | 7.41 | 1.85 |
| Elmidae (adult) | 9.26 | 5.56 | 11.11 | 16.67 | 35.19 | 12.96 | 9.26 | 0.00 | 1.85 |
| Elmidae (larvae) | 85.19 | 122.22 | 94.44 | 27.78 | 1.85 | 24.07 | 24.07 | 50.00 | 12.96 |
| Ephemeroptera | 0.00 | 7.41 | 31.48 | 38.89 | 83.33 | 140.74 | 1000.00 | 4100.00 | 227.78 |
| Gammaridae | 0.00 | 0.00 | 0.00 | 1.85 | 0.00 | 0.00 | 0.00 | 1.85 | 0.00 |
| Gerridae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 22.22 |
| Glossiphoniidae | 12.96 | 25.93 | 7.41 | 18.52 | 3.70 | 7.41 | 5.56 | 11.11 | 9.26 |
| Glossosomatidae | 0.00 | 1.85 | 1.85 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Haliplidae (larvae) | 0.00 | 3.70 | 5.56 | 1.85 | 0.00 | 0.00 | 0.00 | 0.00 | 12.96 |
| Haplotaxidae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.85 | 0.00 | 0.00 |
| Hydracarina | 0.00 | 0.00 | 3.70 | 0.00 | 0.00 | 0.00 | 0.00 | 3.70 | 0.00 |
| Hydraenidae (adult) | 1.85 | 0.00 | 0.00 | 1.85 | 0.00 | 0.00 | 0.00 | 24.07 | 0.00 |
| Hydrobiidae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.85 | 0.00 | 0.00 | 0.00 |
| Hydrophilidae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 5.56 | 1.85 |
| Hydropsychidae | 0.00 | 3.70 | 9.26 | 7.41 | 1.85 | 0.00 | 3.70 | 40.74 | 0.00 |
| Libellulidae | 0.00 | 0.00 | 0.00 | 1.85 | 0.00 | 0.00 | 0.00 | 0.00 | 1.85 |
| Limnephilidae | 0.00 | 0.00 | 0.00 | 7.41 | 1.85 | 0.00 | 0.00 | 0.00 | 0.00 |
| Limoniidae | 3.70 | 1.85 | 20.37 | 55.56 | 44.44 | 59.26 | 16.67 | 20.37 | 0.00 |
| Lumbriculidae | 151.85 | 220.37 | 81.48 | 75.93 | 103.70 | 162.96 | 677.78 | 303.70 | 259.26 |
| Nematoda | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.70 | 0.00 | 0.00 | 0.00 |
| Nematomorpha | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.85 | 0.00 | 0.00 | 0.00 |
| Neritidae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.85 | 0.00 | 0.00 | 0.00 |
| Notonectidae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.85 | 7.41 |
| Planorbidae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 7.41 |
| Plecoptera | 972.22 | 461.11 | 396.30 | 416.67 | 292.59 | 366.67 | 62.96 | 66.67 | 0.00 |
| Psychomyiidae | 0.00 | 1.85 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.85 |
| Rhyacophilidae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.85 | 0.00 |
| Scirtidae (adult) | 9.26 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Simuliidae (larvae) | 661.11 | 16.67 | 20.37 | 12.96 | 0.00 | 0.00 | 972.22 | 5953.70 | 0.00 |
| Simuliidae (pupae) | 1.85 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.70 | 0.00 |
| Tabanidae | 20.37 | 29.63 | 22.22 | 18.52 | 14.81 | 14.81 | 33.33 | 27.78 | 3.70 |
| Tipulidae | 0.00 | 3.70 | 0.00 | 0.00 | 0.00 | 1.85 | 1.85 | 1.85 | 16.67 |
| Veliidae | 1.85 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

$$DM = aX^b$$

or, in natural logarithmic form:

$$\ln(DM) = \ln(a) + b\ln(X),$$

where DM = individual dry mass, X = total length, $a$ = constant, and $b$ = slope of the regression.

To construct the regression line, we measured 30 formalin-preserved specimens of *G. franzi* and *H. flaviventris* and 29 *I. curtata* specimens, dried them at 60°C for 24 h, and placed them in a desiccator for 1 h. We weighed the dried specimens to the nearest 0.001 mg with a Mettler model M3 microbalance (Mettler Instrumente AG, Zürich, Switzerland).

*Diet analysis*

For the diet study, we analyzed the smallest nymphs with methods proposed by Bello and Cabrera (1999) (López-Rodríguez and Tierno de Figueroa 2006, Tierno de Figueroa et al. 2006, Navarro-Martínez et al. 2007, Bo et al. 2008, Fenoglio et al. 2008). We placed each individual in a vial with Hertwigs liquid and heated it in an oven at 65°C for ~24 h before mounting individuals on slides for study under the microscope. We dissected larger nymphs through the ventral right side of the thorax to remove the gut. We spread gut contents on a slide to remove the prey, if present, and mounted the remaining contents in Hertwigs liquid. In both cases, we used a compound microscope equipped with an ocular micrometer to estimate the % absolute gut content (at 40× as % total area occupied by the contents in the whole digestive tract) and the relative abundances of food items in the gut content (at 400× as % area occupied by each component of the total gut contents). We calculated the mean, standard deviation, minimum and maximum, presence (number of individuals whose guts contained a given item), and % presence (% individuals in which a given item was found with respect to the total number of individuals sampled). We classified the species to functional feeding groups (FFG) on the basis of their food sources and mechanisms of food acquisition (Cummins 1973, Merritt and Cummins 2006).

To study the correlation between nymphal size and gut contents, we measured up to 30 nymphs/mo (when sufficiently abundant) to the nearest 0.01 mm. We used Ivlev's index (Ivlev 1961) to calculate prey electivity for each species as $E = (r_i - p_i)/(r_i + p_i)$, where $r_i$ = the relative abundance of a particular taxon in the diet, and $p_i$ = the relative abundance of the same taxon in the benthic community. This index ranges from −1 to 1. A value of −1 means total rejection, 1 indicates complete specialization, and 0 indicates that the species eats the resource in equal proportion to the proportion in which it is found in the community.

*Statistical analyses*

We used STATISTICA software (version 7.1; StatSoft, Tulsa, Oklahoma) for data analysis. We assessed normality of each variable distribution with a Kolmogorov–Smirnov test and found that none was normally distributed. Therefore, we used nonparametric statistics. We used Spearman's correlation to assess whether growth and accumulated degree days (dd) were correlated because it outperforms other tests when there are few data (Guisande González et al. 2006). We used γ correlation to test for an association between total length and protonum width, and size and percentages of diet components because γ correlation is thought to be the most appropriate statistic when a high degree of range overlap exists among variables (Guisande González et al. 2006).

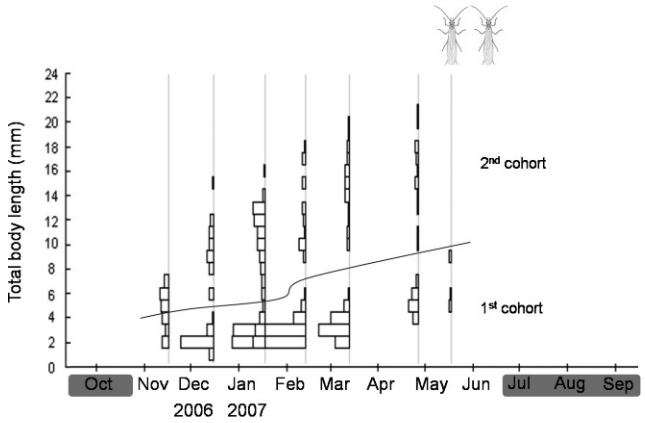


FIG. 3. Size–frequency graph representing the life cycle of *Guadalgenus franzi* ($n$ = 498). Adults were present on sampling dates marked with an image of a macropterous adult. Shaded labels on the $x$-axis indicate the period in which the stream was dry. Curved line separates the 2 cohorts.

## Results

*Life cycles*

*Guadalgensu franzi* was semivoltine, and 2 different cohorts inhabited the site simultaneously (Fig. 3). The 1st cohort (represented by the smallest nymphs in Fig. 3) was collected from November to May. No nymphs were collected in June, even though water remained in the stream. Nymphs probably had migrated to the hyporheic zone by this time because they disappeared prior of the dry period and reappeared after it without signs of further development. The nymphs of the 2nd cohort were collected from November to late April, when adults started flying. The flight period of this species extended into June, when the stream began to dry. Eggs were laid in the last pools found in the stream in May and June. Eggs probably remained in the river bed without hatching until the next wet period because nymphs collected in November were early instars.

*Hemimelaena flaviventris* was univoltine. Nymphs were collected from February to June (Fig. 4), mature nymphs (with black wingpads) were found from late April to June, and adults were collected from May to June. After mating, eggs were laid in the water, and they hatched at the beginning of the next wet period.

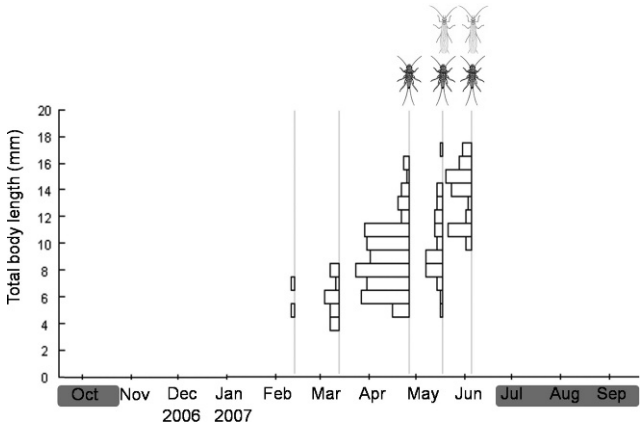


FIG. 4. Size–frequency graph representing the life cycle of *Hemimelaena flaviventris* ($n$ = 197). Mature nymphs were present on sampling dates marked with an image of a nymph. Adults were present on sampling dates marked with an image of a macropterous adult. Shaded labels on the $x$-axis indicate the period in which the stream was dry.

Eggs might have been dormant during the dry period. No 1st-instar nymphs were collected, but nymphs belonging to several other size classes inhabited the site at the same time. Development of this species was relatively fast (~5–6 mo). Eggs were observed in mature nymphs collected in April and June.

*Isoperla curtata* was univoltine. Nymphs were collected from January to May (Fig. 5), mature nymphs were collected in May, and adults were collected in May and June. As in *H. flaviventris*, the eggs probably remained unhatched until the next wet period and might have been dormant during the dry period. Nymphs probably hatched before the 1st collections in January because no 1st-instar individuals were collected.

*Growth*

The highest growth rate of *G. franzi* nymphs occurred in the months immediately before and after the dry period (Fig. 6). No growth was observed during the dry period. Thus, the dry mass of the nymphs of the smaller cohort in May was similar to the dry mass of nymphs from the larger cohort in November. Mass gain of the 2nd cohort was much higher than that of the 1st cohort. Development required ~4477.67 dd for completion, but growth and degree day were not significantly correlated (Spearman's $R$, $p > 0.05$). Growth rate of *H. flaviventris* was very fast. Most growth occurred in May and June before the dry period (Fig. 6). Nymphs accumulated 1647.69 dd, but growth and degree day were not significantly correlated (Spearman's $R$, $p > 0.05$). Growth of *I. curtata* also was very fast (Fig. 6).

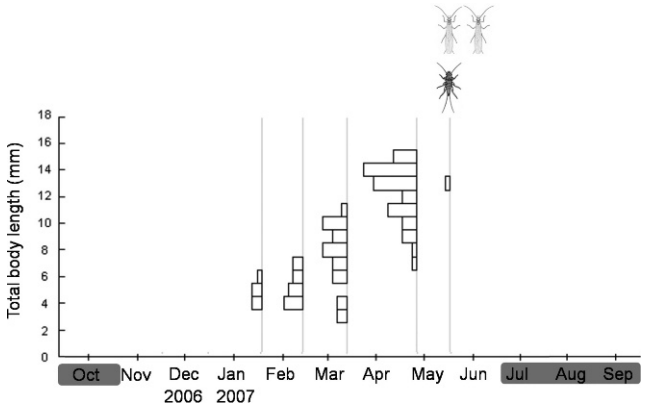


FIG. 5. Size–frequency graph representing the life cycle of *Isoperla curtata* ($n$ = 83). Mature nymphs were present on sampling dates marked with an image of a nymph. Adults were present on sampling dates marked with an image of a macropterous adult. Shaded labels on the $x$-axis indicate the period in which the stream was dry.

Nymphs accumulated 1696.29 dd, but growth and degree day were not significantly correlated (Spearman's $R$, $p < 0.05$).

*Feeding*

The 3 species fed primarily on epilithic diatoms, most of which belonged to the genus *Melosira* (Sánchez-Castillo, University of Granada, Granada, Spain, personal communication), followed by detritus (measured by % absolute gut content and relative abundance in gut contents) (Table 3). A large percentage of *H. flaviventris* had animal prey in their guts,

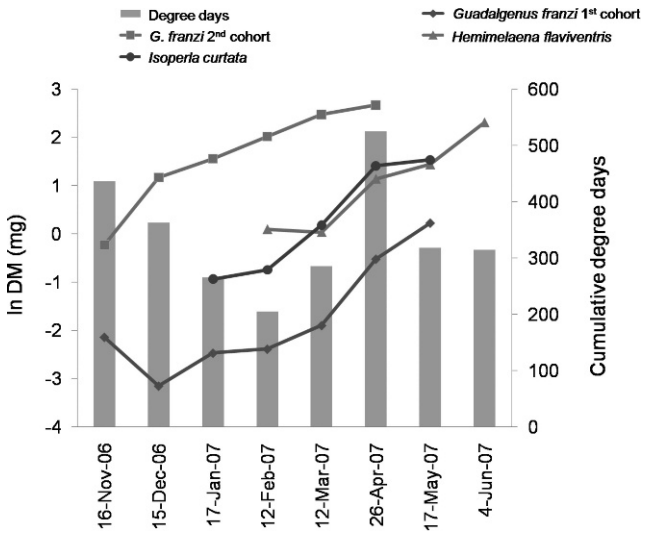


FIG. 6. Growth patterns of each species and accumulated degree days during the intervals between sampling dates. Note that the $y$-axis is in logarithmic form.

TABLE 3. Gut contents of nymphs of *Guadalgenus franzi*, *Hemimelaena flaviventris*, and *Isoperla curtata* in the sampling site. Functional feeding group (FFG) designations in bold font indicate the most important functional group to which the species can be assigned. Pres = number of individuals with taxon in the gut, % pres = % of individuals with taxon in the gut, % absolute = % total digestive tract occupied by food items, RA = % of food item in the gut contents, CPOM = coarse particulate organic matter.

| | *G. franzi* | | | | | | *H. flaviventris* | | | | | | *I. curtata* | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Item | *n* | Mean | SD | Range | Pres | % pres | *n* | Mean | SD | Range | Pres | % pres | *n* | Mean | SD | Range | Pres | % pres |
| % absolute | 180 | 31.25 | 28.97 | 0–100 | – | – | 99 | 33.03 | 32.54 | 0–100 | – | – | 50 | 44.10 | 37.32 | 0–100 | – | – |
| RA | | | | | | | | | | | | | | | | | | |
| % detritus | 175 | 19.26 | 22.52 | 0–95 | 144 | 82.29 | 68 | 26.07 | 29.57 | 0–95 | 61 | 89.71 | 47 | 22.70 | 21.77 | 0–100 | 43 | 91.49 |
| % diatoms | 175 | 78.27 | 23.82 | 0–100 | 174 | 99.43 | 68 | 71.50 | 30.58 | 0–100 | 67 | 98.53 | 47 | 76.66 | 21.81 | 0–100 | 46 | 97.87 |
| % hyphae | 175 | 0.18 | 0.68 | 0–5 | 15 | 8.57 | 68 | 0.03 | 0.17 | 0–1 | 2 | 2.94 | 47 | 0.11 | 0.43 | 0–2 | 3 | 6.38 |
| % fungi spores | 175 | 0.12 | 0.54 | 0–4 | 10 | 5.71 | 68 | 0.04 | 0.36 | 0–3 | 1 | 1.47 | 47 | 0.13 | 0.74 | 0–5 | 2 | 4.26 |
| % CPOM | 175 | 0.65 | 2.17 | 0–15 | 20 | 11.43 | 68 | 0.94 | 3.37 | 0–20 | 8 | 11.76 | 47 | 0.38 | 1.07 | 0–5 | 6 | 12.77 |
| % Cyanobacteria | 175 | 0.87 | 6.14 | 0–70 | 19 | 10.86 | 68 | 0.04 | 0.36 | 0–3 | 1 | 1.47 | 47 | 0.02 | 0.15 | 0–1 | 1 | 2.13 |
| % pollen | 175 | 0.09 | 0.52 | 0–5 | 7 | 4.00 | 68 | 0.01 | 0.12 | 0–1 | 1 | 1.47 | – | – | – | – | – | – |
| Number | | | | | | | | | | | | | | | | | | |
| Chironomidae | 175 | 0.19 | 0.67 | 0–5 | 22 | 12.57 | 68 | 2.90 | 6.37 | 0–28 | 29 | 42.65 | 47 | 0.06 | 0.25 | 0–1 | 3 | 6.38 |
| Simuliidae | 175 | 0.08 | 0.36 | 0–3 | 10 | 5.71 | 68 | 2.81 | 6.74 | 0–40 | 26 | 38.24 | – | – | – | – | – | – |
| Plecoptera | 175 | 0.07 | 0.28 | 0–2 | 12 | 6.86 | – | – | – | – | – | – | – | – | – | – | – | – |
| Ephemeroptera | 175 | 0.01 | 0.08 | 0–1 | 1 | 0.57 | 68 | 0.13 | 0.42 | 0–2 | 7 | 1.47 | 47 | 0.02 | 0.15 | 0–1 | 1 | 2.13 |
| Ancylidae | 175 | 0.07 | 0.60 | 0–7 | 4 | 2.29 | – | – | – | – | – | – | – | – | – | – | – | – |
| Lumbriculidae | 175 | 0.01 | 0.08 | 0–1 | 1 | 0.57 | – | – | – | – | – | – | – | – | – | – | – | – |
| Hydracarina | – | – | – | – | – | – | 68 | 0.01 | 0.12 | 0–1 | 1 | 1.47 | – | – | – | – | – | – |
| Ostracoda | – | – | – | – | – | – | – | – | – | – | – | – | 47 | 0.02 | 0.15 | 0–1 | 1 | 2.13 |
| Unidentifiable animal matter | 175 | 0.05 | 0.22 | 0–1 | 8 | 4.57 | 68 | 0.04 | 0.21 | 0–1 | 3 | 4.41 | 47 | 0.02 | 0.15 | 0–1 | 1 | 2.13 |
| FFG | **Scraper**/Gatherer–collector/Predator | | | | | | **Predator**/Scraper/Gatherer–collector | | | | | | **Scraper**/Gatherer–collector/Predator | | | | | |

TABLE 4. Relative abundance of food items in the gut contents of *Hemimelaena flaviventris* nymphs without prey in their guts. CPOM = coarse particulate organic matter.

| Item | *n* | Mean | SD | Range | Presence | % presence |
|---|---|---|---|---|---|---|
| % detritus | 18 | 18.28 | 22.59 | 0–60 | 18 | 100.00 |
| % diatoms | 18 | 81.06 | 22.40 | 40–100 | 18 | 100.00 |
| % hyphae | – | – | – | – | – | – |
| % fungi spores | – | – | – | – | – | – |
| % CPOM | 18 | 0.61 | 1.97 | 0–8 | 18 | 100.00 |
| % Cyanobacteria | – | – | – | – | – | – |
| % pollen | 18 | 0.06 | 0.24 | 0–1 | 18 | 100.00 |

and some individuals had >40 ingested animal prey. Some of the nonanimal items in the guts of *H. flaviventris* could have come from the guts of its prey, but the guts of *H. flaviventris* that contained no animal prey also contained considerable amounts of diatoms and detritus (Table 4). Animal prey was rare in the guts of *G. franzi* and *I. curtata*, as was coarse particulate organic matter (CPOM), fungi, pollen, and Cyanobacteria (Table 3).

Percent Chironomidae decreased and % Ancylidae and % Plecoptera in gut contents increased as the length of *G. franzi* individuals increased (Table 5). The number of animal prey items in the gut contents was not significantly correlated with *G. franzi* specimen length ($\gamma$ correlation = 0.11, $p > 0.05$). Percent Chironomidae and % Simuliidae in gut contents increased as the length of *H. flaviventris* individuals increased. The number of animal prey items was positively correlated with *H. flaviventris* specimen length ($\gamma$ correlation = 0.34, $p < 0.05$). Percent hyphae in gut contents decreased as the length of *I. curtata* increased (Table 5). The number of animal prey items was positively correlated with *I. curtata* specimen length ($\gamma$ correlation = 0.51, $p < 0.05$). However, this result must be interpreted with caution because few individuals had animal prey in their guts. For *I. curtata*, the strong positive correlation between the relative abundance of Ostracoda in the gut and length probably was an artifact caused by the presence of only one Ostracoda (probably ingested accidentally when collecting detritus) in the gut of a large nymph.

TABLE 5. Gamma correlations between total length and food items in the gut contents of nymphs of *Guadalgenus franzi*, *Hemimelaena flaviventris*, and *Isoperla curtata*. CPOM = coarse particulate organic matter. Values marked with an asterisk are statistically significant ($p < 0.05$).

| | Total length (mm) | | |
|---|---|---|---|
| Item | *G. franzi* | *H. flaviventris* | *I. curtata* |
| Relative abundance | | | |
| % detritus | 0.05 | 0.13 | 0.03 |
| % algae | −0.05 | −0.10 | −0.03 |
| % hyphae | −0.03 | −0.07 | −0.75* |
| % fungi spores | 0.03 | −0.85 | 0.12 |
| % CPOM | 0.19 | 0.14 | 0.00 |
| % Cyanobacteria | −0.09 | −0.18 | −0.74 |
| % pollen | 0.17 | −0.76 | – |
| Number | | | |
| Chironomidae | −0.23* | 0.25* | 0.01 |
| Simuliidae | 0.20 | 0.44* | – |
| Plecoptera | 0.41* | – | – |
| Ephemeroptera | 0.29 | 0.19 | 0.91 |
| Ancylidae | 0.65* | – | – |
| Lumbriculidae | 0.86 | – | – |
| Hydracarina | – | −0.52 | – |
| Ostracoda | – | – | 1.00* |
| Unidentifiable animal matter | −0.10 | −0.64* | 0.77 |

Ivlev's electivity index revealed that *G. franzi* nymphs in the 1st cohort preferred Chironomidae and rejected Plecoptera and Ephemeroptera (although mayflies were found in their guts during 1 mo) (Fig. 7A). Simuliidae were preferred in February but rejected in May (Fig. 8A). Nymphs of the 2nd cohort preferred Ancylidae, Chironomidae (although to a lesser degree than the 1st-cohort nymphs), Simuliidae, and Lumbriculidae, but Simuliidae and Lumbriculidae were found in guts only occasionally (Fig. 7B). Plecoptera were preferred in January and February but rejected in November, December, and March (Fig. 8B).

*Hemimelaena flaviventris* nymphs strongly rejected Ephemeroptera (Fig. 7C). Chironomidae were preferred at the beginning of its life cycle in March, April, and May and were rejected in June (Fig. 8C). Simuliidae were rejected in May and preferred in June (Fig. 8C). Hydracarina had an Ivlev's index value of 1 (indicating total preference), but this result was an artifact caused by ingestion of 1 Hydracarina by an individual in a month when no Hydracarina had been recorded in the community. *Isoperla curtata* preferred Ostracoda, Chironomidae, and Ephemer-

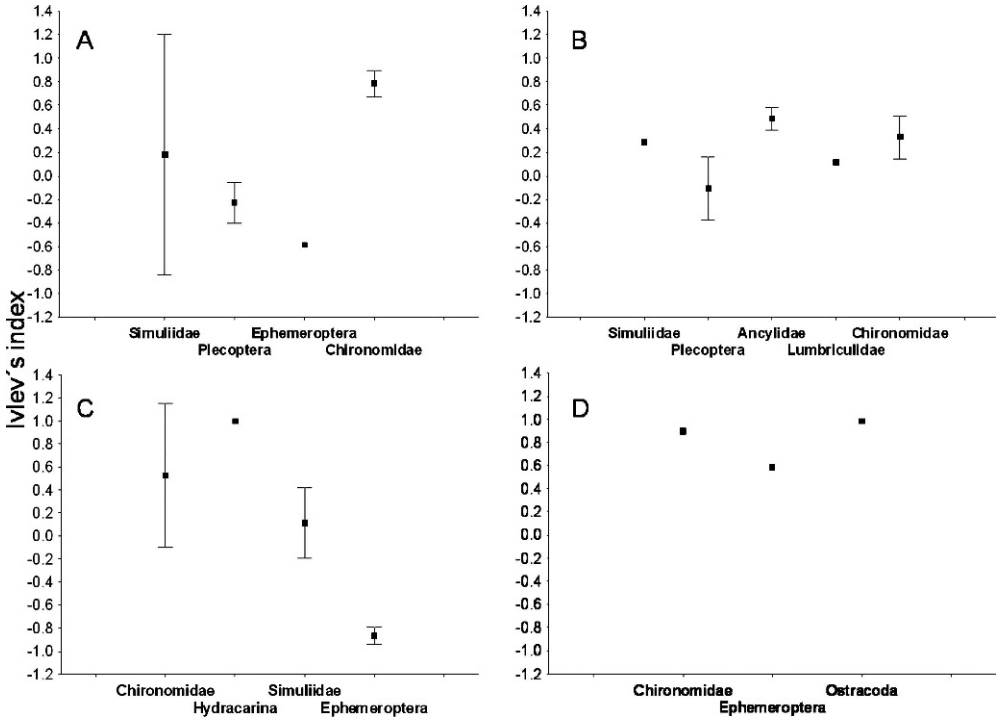


FIG. 7. Mean (±[0.95SD]) Ivlev's index for prey taxa consumed by *Guadalgenus franzi* 1st cohort (A), *G. franzi* 2nd cohort (B), *Hemimelaena flaviventris* (C), and *Isoperla curtata* (D).

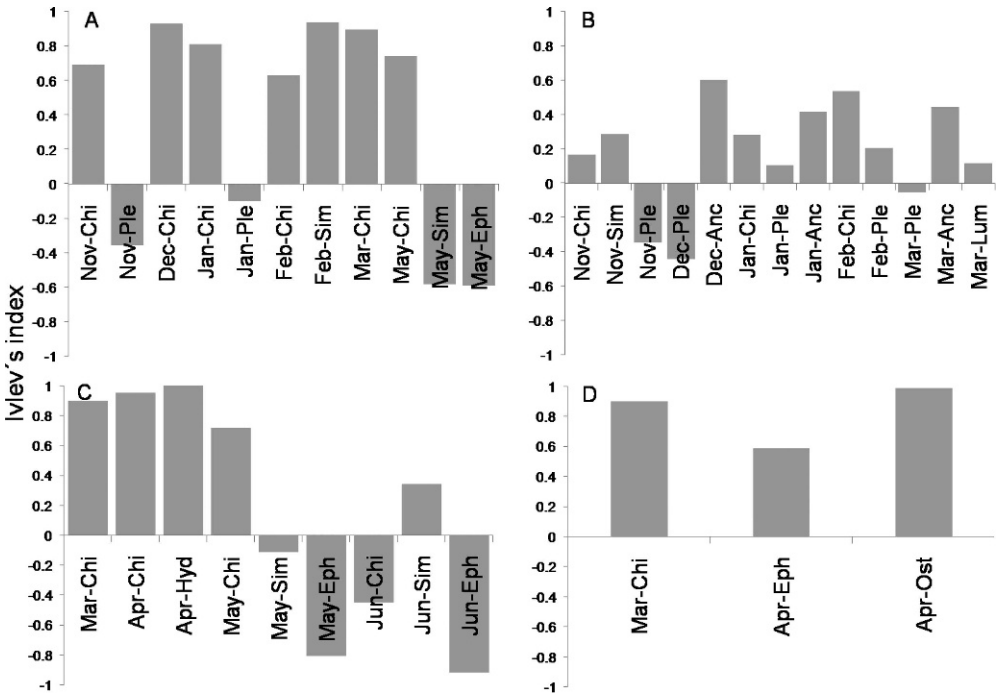


FIG. 8. Monthly Ivlev's electivity index for prey taxa consumed by *Guadalgenus franzi* 1st cohort (A), *G. franzi* 2nd cohort (B), *Hemimelaena flaviventris* (C), and *Isoperla curtata* (D). Bars represent values of the index for a given date and a given prey taxon. Bar labels are in the format month–taxon. Multiple prey items occur on some dates, and no prey on others. Anc = Ancylidae, Chi = Chironomidae, Eph = Ephemeroptera, Hyd = Hydracarina, Lum = Lumbriculidae, Ost = Ostracoda, Ple = Plecoptera, Sim = Simuliidae.

Table 6. Secondary production parameters of *Guadalgenus franzi*, *Hemimelaena flaviventris*, and *Isoperla curtata*. CPI = cohort production interval. P/B = production to biomass ratio.

| Species | Secondary production (g DM $m^{-2}$) | CPI (mo) | Annual secondary production (g DM $m^{-2}$ $y^{-1}$) | Annual P/B | Cohort P/B |
|---|---|---|---|---|---|
| *G. franzi* (1st cohort) | 0.11 | 7 | 0.12 | 7.91 | 6.92 |
| *G. franzi* (2nd cohort) | 1.32 | 6 | 1.76 | 5.00 | 3.75 |
| *H. flaviventris* | 1.19 | 5 | 1.91 | 5.52 | 3.45 |
| *I. curtata* | 0.24 | 5 | 0.38 | 4.37 | 2.73 |

optera (Figs 7D, 8D), but these results should be taken with caution because only a small number of individuals had animal prey in their guts during our observations.

*Secondary production*

DM was related to body length (X) by the following equations: 1) *Guadalgenus franzi*: ln DM = −5.31 + 2.89(ln X), $r^2 = 0.95$, $F_{1,28} = 513.57$, $p < 0.05$; 2) *Hemimelaena flaviventris*: ln DM = −4.74 + 2.68(ln X), $r^2 = 0.94$, $F_{1,28} = 421.40$, $p < 0.05$; and 3) *Isoperla curtata*: ln DM = −4.80 + 2.48(ln X), $r^2 = 0.71$, $F_{1,27} = 65.33$, $p < 0.05$.

We studied the secondary production of the 2 cohorts of *G. franzi* separately. Thus, secondary production of the 1st cohort of *G. franzi* was 0.12 g DM $m^{-2}$ $y^{-1}$ (CPI = 7 mo), and cohort production/biomass (P/B) was 6.92 (Table 6). Secondary production of the 2nd cohort was 1.76 g DM $m^{-2}$ $y^{-1}$ (CPI = 6 mo), and cohort P/B was 3.75. For this species, CPI values corresponded to the months in which nymphs were collected and during which development occurred. The dry period was not included because nymphs were thought to pass it in a quiescent phase during which no development (and no secondary production) occurred. CPI corrections were made relative to the 8-mo period when water was present in the stream. The great difference in production between the 1st and 2nd cohorts of *G. franzi* was probably related to the higher growth rate of the 2nd cohort (Fig. 6).

Secondary production of *H. flaviventris* was 1.91 g DM $m^{-2}$ $y^{-1}$ (CPI = 5 mo), and cohort P/B was 3.45 (Table 6). Secondary production of *I. curtata* was 0.38 g DM $m^{-2}$ $y^{-1}$ (CPI = 5 mo), and cohort P/B was 2.73 (Table 6). In these 2 species, CPI values corresponded to the months in which nymphs were active in the benthos. CPI corrections were made relative to the 8-mo period when water was present in the stream. The CPI values might actually be higher because nymphal development could have begun some months before nymph collection began. However, we prefer to err on the conservative side, and, thus, we report the lower numbers here.

## Discussion

*Life histories*

The life cycle of *G. franzi* is nonseasonal (Hynes 1970). Two years are needed for its complete development, and different cohorts overlap. This species had a similar life cycle in 2 seasonal streams from the same mountain range, and the authors hypothesized that nymphs of the 1st cohort survived the dry period by burrowing into the hyporheic zone (Agüero-Pelegrín and Ferreras-Romero 2002). *Calliperla luctuosa* (Banks, 1906), a perlodid species from North America, had a similar life cycle in a temporary stream (Dieterich and Anderson 1995). In our study, growth was close to 0 during the dry period (Fig. 6); this result indicates that this species undergoes a period of dormancy. Two types of dormancy are known to exist in Plecoptera: 1) diapause, in which a programmed (delayed) response with suppressed development lasts longer than the adverse conditions, and 2) quiescence, in which an immediate direct response to a limiting factor occurs while adverse conditions persist (Danks 1987). Both types of dormancy can occur either in the egg or in the nymphal stage. Nymphal diapause is not common among Plecoptera in general and among Perlodidae in particular (Harper and Hynes 1970, Pugsley and Hynes 1985, Stewart and Stark 2002), so quiescence might be the strategy *G. franzi* uses. Several of our observations support this idea. First, nymphs began to disappear at the time the dry period began and reappeared when flow resumed. Diapause usually precedes and lasts through adverse conditions (Danks 1987). Thus, nymphs should have disappeared before and reappeared after the adverse conditions, but not simultaneously with the changes. Second, nymphal diapause in Plecoptera has been reported only in the 1st stages of development (e.g., Harper and Hynes 1970), and the dry period arrives when *G. franzi* is midsize. Last, when other aquatic insects dehydrate

as a consequence of high temperatures, they enter a quiescent period during which they can survive extremely high temperatures (Hinton 1951, 1960). Therefore, middle-instar nymphs of *G. franzi* might have migrated to the hyporheic zone when the dry period began. There, they either remained in the wet zone within the hyporheic zone or in the substrate interstices until flow resumed (Harper and Hynes 1970). This proposition is supported by the fact that nymphs were collected in the 1st sampling events, when they would have just reactivated their development. Moreover, nymphs from the end of the 1st (smaller) cohort and those from the beginning of the 2nd (bigger) cohort were approximately equal in length and dry mass, indicating that no growth occurred during the summer dry period. Subsequently, nymphs of the 2nd cohort grew to 2× the length of nymphs in the 1st cohort and increased greatly in mass to reach their maximum size and dry mass in April, when the flight period started. After mating and reproduction, females probably laid eggs in May to June, just before the stream dried. Thus, the eggs also must have passed through a dry period, either with normal development or with an embryonic diapause stage. Eggs of Systellognatha, the group to which *G. franzi* belongs, typically posses an anchor plate that adheres firmly to the substrate (Hynes 1976). However, the eggs of *G. franzi* and some other species do not possess this plate (Tierno de Figueroa et al. 2003). The lack of an anchor structure on eggs of perlodid species in other temporary waters might enable them to slide into the substrate and avoid exposure to the air when the stream dries (Berthélemy 1973, Tierno de Figueroa et al. 1998).

Both *H. flaviventris* and *I. curtata* had fast-seasonal life cycles (Hynes 1970). However, completion of their entire cycles requires more time than we recorded because we did not find the smallest nymphs of both species. Recently hatched nymphs of *Isoperla libanica* Aubert, 1964 in a seasonal stream migrated to the hyporheic zone and appeared in the benthos later (Alouf 1989). Such a migration might explain why we did not find small nymphs of *H. flaviventris* and *I. curtata*. Furthermore, the life cycle described by Alouf (1989) is very similar to the life cycle we found for *I. curtata* (nymphs collected February–May). The mean growth pattern of *H. flaviventris* and *I. curtata* can be extrapolated from Fig. 6. We estimate, with a certain error margin, that hatching must have taken place 1 or 2 mo before our collections. During the dry period, eggs probably passed through a diapause period, as has been found in other Perlodidae species (Hynes 1976). Experiments will be needed to confirm this supposition. Eggs of other *Isoperla* species can remain in diapause for 7 to 8 mo (Lillehammer et al. 1989). If this were the case for *I. curtata*, eggs laid in May and June would hatch from December to February, which would coincide with the beginning of the life cycle we propose here. Something similar also might occur in *H. flaviventris*. As in *G. franzi*, the absence of the anchor plate in the eggs could help them to slide into deeper zones of the river bed (Berthélemy 1973, Tierno de Figueroa et al. 1998). Thus, the absence of an anchor plate might be an adaptation that helps the species cope with the dry period and high temperatures of the summer.

If an embryonic diapause exists in both species, the fact that nymphs of many size classes were present in the stream at the same time indicates that its end must be very asynchronous. Alternative explanations for the presence of a wide rage of size classes do exist. Hynes (1970) associated a wide size range among nymphs and a fairly short emergence period with carnivorous behavior in several species of *Isoperla*. We observed marked sexual dimorphism in size among mature nymphs of *H. flaviventris* in June, when males and females could be clearly differentiated. However, asynchrony is a key strategy for coping with unpredictable dry periods in temporary waters (Dieterich and Anderson 1995). Dieterich and Anderson (1995) proposed a prolonged adult emergence for species inhabiting temporary streams.

We did not observe prolonged emergence, possibly because we worked with spring species in which emergence occurred a few weeks before the dry period began. Thus, a better strategy might be synchronous emergence and a short flight period for rapid mating and oviposition followed by embryonic diapause with asynchronous hatching of eggs. At our study site, the Plecoptera species with earlier emergence had relatively long flight periods (personal observations), as recorded for *Tyrrhenoleuctra* cf. *minuta* (Klapálek, 1901), *Brachyptera vera* Berthélemy and González del Tánago, 1983, and *Capnioneura gelesae* Berthélemy and Baena, 1984.

Growth and degree days were not significantly correlated in any of the species we studied. Growth of some stonefly species is relatively temperature independent within a certain temperature range, but this pattern typically is found in those species in which nymphal development occurs during winter at low temperatures (Hynes 1970, Brittain 1990). In our study, nymphs grew during winter but were not exposed to very low temperatures because of the thermal characteristics of the stream (Fig. 2, Table 1). Moreover, *H. flaviventris* and *I. curtata* accumulated almost the same number of degree days despite the fact that the life cycle of *H. flaviventris* was delayed

1 mo with respect to the life cycle of *I. curtata*. This result might indicate an equal degree-day requirement for the complete development of both species, but laboratory rearing experiments would be needed to confirm this hypothesis.

*Feeding behavior*

Aquatic insects tend to be generalist feeders (Cummins 1973), but Perlodidae (and Perlidae) are among the major macroinvertebrate predators in stream ecosystems (Merritt and Cummins 1996). However, all of the species we studied fed on diatoms and detritus, probably the most abundant resources in the stream, in addition to animal prey. Our results show that *G. franzi* and *I. curtata* are mainly primary consumers (scrapers and gatherer–collectors), and they serve only a minor role as predators. A similar trophic role has been reported in other species of *Isoperla* that consumed large quantities of diatoms (Frison 1935, Shapas and Hilsenhoff 1976, Jop and Szczytko 1984, Lancaster et al. 2005). The food habits of *Isoperla* are highly diverse and range from predatory to detritivorous–herbivorous or omnivorous (Stewart and Stark 2002), and our results confirm that the feeding habits of an unstudied species cannot be inferred from studies of congeners (Stewart and Stark 2002). In contrast, *H. flaviventris* was a voracious predator that also was a scraper and collector–gatherer. Azzouz and Sánchez-Ortega (2000) found that Chironomidae were the main prey of this species, but that it also ate a high proportion of vegetable matter (mainly diatoms), especially the smallest nymphs. Our gut content data indicate that Chironomidae were the primary prey of all 3 species. Some of the other prey species were present only occasionally: Ephemeroptera and Lumbriculidae in *G. franzi*, Hydracarina in *H. flaviventris*, and Ephemeroptera and Ostracoda in *I. curtata*.

Diets of the 3 species changed in relation to body size (Table 5), and dietary shifts were reflected in changes in electivity indices over the sampling period (Fig. 8A–D). Ontogenetic shifts in diet have been found in other species of Perlodidae stoneflies (Fuller and Stewart 1977, Jop and Szczytko 1984, Malmqvist et al. 1991, Azzouz and Sánchez-Ortega 2000, Fenoglio et al. 2005, Céréghino 2006). Despite their status as important predators in stream ecosystems (Merrit and Cummins 1996), vegetable matter can be important for some species or during certain stages of their lives (Stewart and Stark 2002). We were unable to sample the smallest instars of *H. flaviventris* and *I. curtata*, so nothing can be said about their feeding habits. However, prey preference of *H. flaviventris* varied among the instars we did sample (Fig. 8C). *Guadalgenus franzi* specimens fed primarily on diatoms and detritus, but they were opportunistic predators on the most abundant prey in the community. *Isoperla curtata* individuals ingested few animals, so no conclusion can be drawn regarding prey preferences or dietary shifts.

Changes in diet composition over the life cycle can be a consequence of prey size or mobility. Predatory aquatic invertebrates often are undiscriminating and capture whatever they encounter that is small enough to subdue (Allan and Castillo 2007). The smallest life stages of *G. franzi* and *H. flaviventris* preferred Chironomidae (Figs 7C, 8C), which are small and slow-moving, and rejected bigger or more mobile prey, such as Plecoptera, Ephemeroptera, or Simuliidae, which are large. Some of the larger nymphs preferred these larger prey species (e.g., Simuliidae; Figs 7A, 8A). Similar patterns of prey selection by Plecoptera have been documented by other authors (e.g., Allan and Castillo 2007).

Large *G. franzi* nymphs ingested Ancylidae, which are very slow-moving, but the shells of which should make them an unattractive prey, at several times during their life cycle (Figs 7A, B, 8A, B). Nymphs might have ingested Ancyclidae incidentally while feeding on diatoms, which also are eaten by Ancyclidae (Monakov 2003). Incidental ingestion might have been the source of several other prey items, such as Lumbriculidae, in the diet of *G. franzi*. We suspect that incidental ingestion explains why Hydracarina was found in *H. flaviventris* and Ostracoda was found in *I. curtata*. Haphazard carnivory might provide additional high-quality protein needed by many invertebrates to complete their life cycles (Anderson 1976).

*Secondary production*

All 3 species had intermediate to low values of annual secondary production and annual P/B compared with the minimum and maximum values compiled by Huryn and Wallace (2000) for stream macroinvertebrates. However, their annual P/B values were similar to those most frequently observed across species (Benke 1993). Although intermediate when compared with other macroinvertebrates in general, the value of annual production for the 2$^{nd}$ cohort of *G. franzi* was relatively high compared to values for other scrapers, and the value for *H. flaviventris* was comparable to values for other predators. Annual production of the 2$^{nd}$ cohort of *G. franzi* and *H. flaviventris* was higher than values reported for other Perlodidae species, even when compared with populations from permanent water

(e.g., Short and Ward 1980, Céréghino 2006). However, *I. curtata* had low production values when compared with values for congeneric species in other systems (e.g., Lavandier 1982, Jop and Szczytko 1984).

Only a few studies of secondary production have been done in temporary streams. Chadwick and Huryn (2007) found low values of annual secondary production for the entire macroinvertebrate community in different habitats in an intermittent-stream system. They explained these values on the basis of the absence of large-bodied taxa. The 3 species in our study were large, and their size might help explain the relatively high production values reported here, particularly for the 2nd cohort of *G. franzi* and for *H. flaviventris*. Jop and Stewart (1987) reported production values of 5.07 to 7.14 g DM $m^{-2}$ $y^{-1}$ for a stonefly assemblage of 13 species in a 2nd-order stream in the Ozarks (USA), and our values in Despeñaperros compare favorably. Our results might indicate that our study species are quite successful in this temporary stream, but further comparisons with other populations of the same species in different habitats or under different environmental conditions are necessary to confirm the conclusions reached here.

Assimilation efficiencies and information on dietary enzymatic complexes are not available for these species. Therefore, we estimated the production derived from each dietary component as described by Benke and Wallace (1980) and assumed a net production efficiency of 40% (Benke and Jacobi 1994). Much of the production (>70%) of *G. franzi* and *I. curtata* was the result of their consumption of diatoms. Diatoms also contributed to the diet of *H. flaviventris*, but animal matter was more important. Animal matter accounted for an extremely low percentage of production in *G. franzi* and *I. curtata*, but it was the main contributor to production in *H. flaviventris*. More must be known of digestion processes in these species before more detailed results can be presented.

### *Life-history adaptations*

Stoneflies are not common in temporary waters, but they have developed several strategies that enable them to occupy an important niche in these habitats. The most commonly cited traits for organisms in temporary habitats are small size (and faster development), egg or nymphal diapause, high fecundity, staggered hatching of long-diapause eggs, and opportunistic/generalistic feeding (Jacobi and Cary 1996, Williams 1996, 2006). The species we studied have some of the typical characteristics of fauna of temporary waters. *Hemimelaena flaviventris* and *I. curtata* appear to have long embryonic diapause and staggered hatching of eggs, fast nymphal development, and generalistic feeding, but they are large. *Guadalgenus franzi* has a nymphal dormancy during the dry period, indicated by its long, semivoltine life cycle. This strategy appears to be less adaptive than embryonic diapause because eggs are probably the stage in which species more easily survive dry periods (Hynes 1970). The feeding behavior of these species appears to be the result of an opportunistic/generalistic strategy that enables them to take advantage of the abundant diatom resources in the stream. The relatively high values of annual secondary production of these species when compared with other Perlodidae suggest that these species are able to live successfully in this temporary stream.

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