



Life cycle and secondary production of *Caenis luctuosa* (Ephemeroptera) in a semiarid stream (Southeast Spain)

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Abstract

Caenis luctuosa Bürmeister is a euryhaline species, which occurs throughout much of Europe. The study was carried out during 1994 in Chicamo stream, a spatially intermittent stream in Southeast Spain, with warm (7–30 °C) and hyposaline (5–12 g.l⁻¹) waters, and variable discharge (0.01–31 l. s⁻¹). Benthic samples were taken monthly in a perennial middle reach (354 m length). Larvae were separated, on the basis of body length, into nine size classes. Voltinism, and larval life span were determined from field data using a method for distinguishing cohorts proposed by the authors. Production was estimated using the Size-Frequency method. *Caenis luctuosa* reproduced continuously through the year and presented four overlapping cohorts with larval life spans ranging from three to seven months. The estimated annual production was 6.35 gDW m⁻² yr⁻¹ and the annual P/B ratio was 15.98. The production value was higher than previous records for this genus.

Introduction

In warm-water streams, such as those found in arid and semiarid zones, rapid growth rates and asynchronous development are common features of insect populations, especially among the Diptera and some of the Ephemeroptera (Gray, 1981; Fisher & Gray, 1983; Jackson & Fisher, 1986; Benke & Parson, 1990). Such organisms are often overlooked or ignored in production studies due to difficulties in recognising specific cohorts or estimating the cohort production interval (Benke, 1984).

Mayflies constitute a major part of macroinvertebrate biomass and production in freshwater habitats (Brittain, 1982). Seasonal variations in density and biomass and annual production are strongly influenced by life cycle parameters, indicating the importance of correct life cycle information in production studies. Many lotic production studies of mayflies have used laboratory-derived data to make generalisations concerning life histories or growth rates, but very few studies have used field-derived, species-specific

life-history data to examine secondary production (Christman & Voshell, 1992).

Caenis luctuosa Bürmeister, a species distributed throughout Europe (Illies, 1978), is a common inhabitant of temporary streams in the Mediterranean region. It is found in both lentic and lotic habitats with slow current, and it prefers warm waters and sand substrate with abundant detritus. It is tolerant to mineralised and organically polluted waters (Belfiore, 1983). Some life-history information is available. These show a highly flexible life cycle (Clifford, 1982). In northern and central Europe, the species is uni- and bivoltine, respectively (Landa, 1968; Brittain, 1974). In more southernly areas, the only data available is from high altitude streams in the Sierra Nevada Mountains (Alba-Tercedor, 1981), but there have been no life-history studies and production measurements in the semiarid streams of the Mediterranean region.

The purpose of this study was to determine the life cycle and to estimate the annual production of *C. luctuosa* in an intermittent, saline stream using field-derived life history data. The results are compared

to published life cycles and secondary production estimates of *Caenis* species.

Material and methods

The study was conducted in the Chicamo stream, a spatially intermittent stream in Southeast Spain (30SXH7029 UTM). The stream drains a watershed of 502 km². It is 59.4 km long, with approximately 22 km of steady flow separated by several discontinuous reaches, in which the flow is restricted to rainy periods. The climate is semiarid with a mean annual temperature of 18 °C and an annual precipitation of 300 mm. Although flooding usually occurs in early autumn and spring and low flows in summer, high flows may occur at anytime during the year. The study year (1994) was relatively dry (150.5 mm rainfall) with three precipitation peaks: 24.5 mm in April, 61.5 mm in September and 34.5 mm in October.

The study site was a middle reach 354 m long where the flow was continuous throughout the year. The maximum width of the channel was 53.5 m, although the stream ranged from 2 to 20.8 m in width. The major habitat types were runs and pools. Benthic sediments consisted of gravel and sand overlying consolidated marls in the erosional zones of the runs. Silts were abundant in pools and in the depositional zones of the runs. The water depth ranged from 14 to 22 cm in pools and 2–3 cm in runs. Mean annual discharge was 4.28 l/s with a range from 0.01 l s⁻¹ in July to 31 l s⁻¹ in February. Current velocity ranged from 0.37 m s⁻¹ in runs to 0 m s⁻¹ in pools. The mean water temperature was 18.6 °C, ranging from 7 °C in January to 30 °C in July. Salinity ranged from 5 to 12 g l⁻¹, the pH was fairly constant at around 8 and dissolved oxygen was rarely below saturation levels. Mean concentrations of nitrate and ammonium-N were high (2165.45 µg l⁻¹ and 322.42 µg l⁻¹, respectively) while the soluble reactive phosphorus concentration was low (7.44 µg l⁻¹).

The riparian vegetation of the study zone is sparse because of frequent floods. *Phragmites australis*, *Tamarix canariensis* and some species of reeds grow along the stream margins, but there are no trees. Periphyton, dominated by diatoms and Cyanobacteria, covered almost the entire stream area. Moreover, some patches of filamentous green algae (primarily *Cladophora glomerata*) and *Enteromorpha intestinalis* occurred in runs, while *Chara vulgaris* occurred in pools. Addi-

tional information about the study area can be found in Martínez et al. (1998).

Twelve benthic samples were collected monthly with a 298.6 cm² corer in a stratified pattern (six in runs and six in pools). The mesh size used to filter the samples was 250 µm. Samples were preserved in 80% ethanol. Mayflies were sorted and filmed with a video-camera in the laboratory. Larvae were then counted and measured (total body length without cerci) using an image analysis system (Microm 100). Larvae were sorted into nine size classes with an interval of 0.9 mm. Unpreserved groups of individuals of the different size classes were oven dried at 60 °C during 24 h to obtain mean individual dry weight (± 0.0001g). The length–mass equation obtained was:

$$W = 0.0231e^{0.6664L}, r^2 = 0.96 \quad p \leq 0.001. \quad (1)$$

Histograms of size-frequency distribution (percentage of each size class) were constructed. It was impossible to distinguish the different cohorts from these histograms, because of the asynchronous recruitment and development pattern shown. Therefore, we applied the procedure proposed by Perán (1997) for analysing asynchronous populations with indistinguishable and overlapping cohorts in order to estimate the voltinism and the larval life spans of the different cohorts. This procedure consists of several steps:

1. Calculation of the theoretical density of the underestimated first classes from the logarithmic equation obtained from the abundance plot of the 'average cohort'. Correction of density of underestimated classes by their catch probability (field estimated density/theoretical density).
2. Calculation of a mortality factor for each size class (size class density/mean annual density). The previously corrected data divided by this mortality factor gives a frequency distribution where the mortality is removed and the different peaks of the polymodal distributions are more obvious.
3. Calculation of modes using Battacharya's method (1967) which is included in the FISAT computer program (FAO-ICLARM STOCK ASSESSMENT TOOLS, ver. 1.01) to separate polymodal distributions into their constituents.
4. The final step consists of fitting the growth curve for the different cohorts through the modes that belong to the same cohort.

From the growth curves obtained, we estimated the cohort production interval (CPI) as the mean larval life span of the different cohorts. Secondary production was calculated using the Size–Frequency method

(Hynes & Coleman, 1968; Hamilton, 1969; Benke, 1979):

$$P = c \sum (N_j - N_{j+1}) (W_j W_{j+1})^{0.5} 365 / \text{CPI}, \quad (2)$$

where P is the annual-production, c is the number of size classes ($j=1$ to c), N_j is the mean number of individuals of size-class j during the year, W_j is the mean mass of size-class j and CPI is the cohort production interval (mean time from hatching to the final size class).

Confidence intervals of production were not calculated because they are only reliable when aggregation is weak and sampling effort is high (Morin et al., 1987), but we provided estimates of the standard error for mean density and mean standing stock biomass. The ratios between production and average standing biomass (cohort and annual P/B) were also calculated. Accumulated degree-days for each generation were calculated from mean daily air temperature registered at a nearby weather station.

Results

Diptera, Coleoptera, Heteroptera, Odonata and Ephemeroptera are the principal components of the macroinvertebrate community of the Chicamo stream. Ephemeroptera were second in order of abundance (8%) after Diptera, and the fifth in order of richness, with three species, *C. luctuosa*, *Cloeon inscriptum* and *Baetis lutheri*, represented in order of abundance (Guerrero et al., 1996).

Seasonal changes in density and biomass of *Caenis luctuosa*

Caenis luctuosa was present throughout the year and was especially abundant during the warm months, but numbers dropped greatly in autumn (Figure 1). Mean annual density was 1234 ± 579 ind m^{-2} . The major peaks of density occurred in May and July, with secondary peaks in late winter. The lowest density was registered in September after the rainy period. In spite of good replication ($n=12$), standard errors were still quite high (averaging 44.45% of the mean), reflecting a high degree of clumping.

Mean annual standing stock was 343 ± 131 mgDW m^{-2} . The seasonal pattern of biomass was similar to density variation, although the biomass peaked in February and March (Figure 2).

Life cycle: analysis of cohorts

Monthly size-frequency histograms for *C. luctuosa* in the Chicamo stream are shown in Figure 3. Almost all the size classes were present on most dates and no cohort patterns were apparent. The smallest and the largest larvae were both present between March and July, indicating an extended period of emergence and recruitment. The species appears to be multivoltine with asynchronous hatching and development, although based on this frequency distribution it was impossible to determine the number of generations made by *C. luctuosa* and the larval development time. We applied the procedure for estimating the voltinism of populations with indistinguishable cohorts as described above.

Figure 4 shows an abundance plot of the density of the different length classes. The abundance of classes I and II was largely underestimated, due to their small size (Pauly, 1983) and short duration (Morin et al., 1987). The logarithmic equation obtained excluding the first two classes accounted for 98.55% of the variability of N :

$$N = -4179.1 \ln(L) + 8227.5, \quad p \leq 0.001, \quad (3)$$

where N is the number of individuals $\times \text{m}^{-2}$ and L the body length.

According to Equation (3), the sampling probabilities for classes I and II were 0.24%, and 24.05%, respectively. These probabilities were used to correct the abundance of these classes. The mortality factor (f_m) calculated for each size class is depicted in Table 1. The size-frequency distributions, obtained after correcting the sampling and mortality effects, are shown in Figure 5, together with the modes and growth curves fitted.

Caenis luctuosa is multivoltine and four overlapping cohorts were produced by the above analysis. Larval spans ranged from three to seven months depending principally on temperature. A slowly developing winter generation with a larval span of about seven months was followed by a spring generation, with a larval development period of about four months, one fast summer generation that completed their development in three months, and one autumn generation of four months of larval development period. Degree-day developmental rates (Figure 6) were similar for all generations, being the mean degree-day developmental rate of 2742 ± 85 .

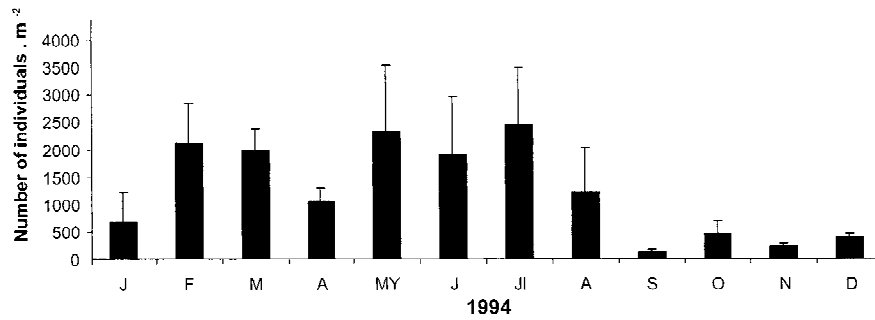


Figure 1. Temporal changes in the mean density (\pm SE) of *C. luctuosa* larvae in Chicamo stream.

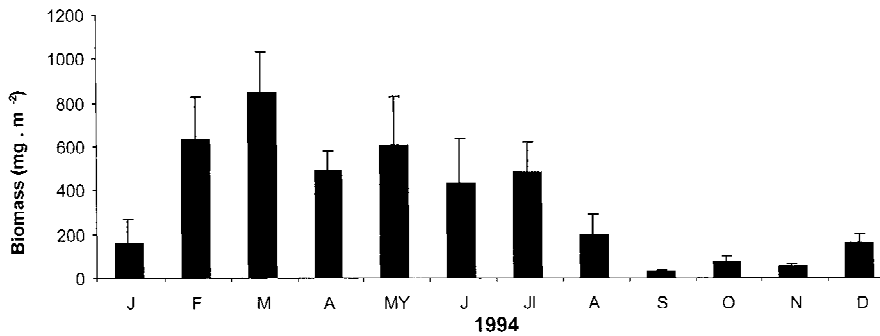


Figure 2. Temporal changes in the mean biomass (\pm SE) of *C. luctuosa* larvae in Chicamo stream.

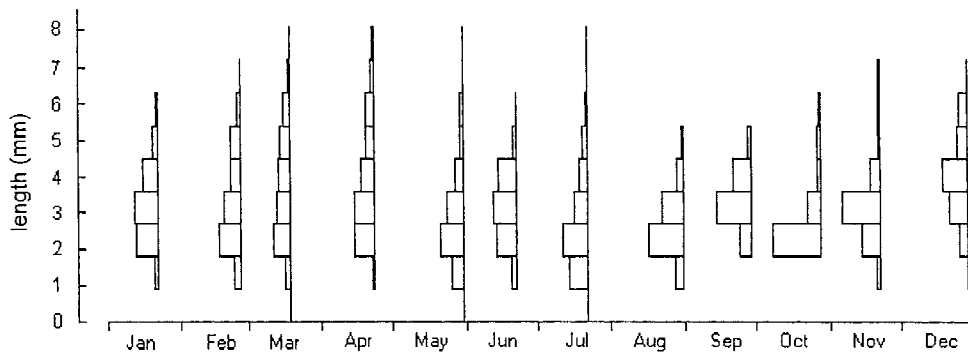


Figure 3. Monthly size-frequency histograms for *C. luctuosa* larvae from Chicamo stream.

Annual production

Using the Size-Frequency method, the cohort production estimated was 2.35 gDW m⁻² and the annual production was 6.35 gDW m⁻² yr⁻¹, based on an average cohort production interval of 135 days. The cohort P/B ratio was 5.91, which is within the range of values predicted for benthic insects (Waters, 1979). The annual P/B ratio was 15.98. Other production parameters are presented in Table 2.

Discussion

Mayflies show a remarkable variation in life history even at the species level (Clifford, 1982). Temperature, food, habitat and photoperiod are factors that contribute to the observed variability. In most species that have been studied in detail, temperature, in terms of mean values, the scale of diel fluctuations, or total degree-days, is the major growth regulator (Brittain, 1982).

Table 1. Mortality factor of each size class

Size classes	I	II	III	IV	V	VI	VII	VIII	IX
Mortality factor	3.31	1.99	1.36	1.06	0.68	0.35	0.20	0.05	0.01

Table 2. Production parameters of *C. luctuosa* in Chicamo stream

Size class	Mean density (No m ⁻²)	Mean length (mm)	Indv. mass (W mg)	Biomass (mg m ⁻²)	ΔN	Mass at loss (W _j W _{j+1}) ^{0.5}	Biomass lost (W _j W _{j+1}) ^{0.5} × ΔN	(W _j W _{j+1}) ^{0.5} × ΔN × No. sizes
I	*968.75	0.45	0.031	30.17				
II	*581.17	1.35	0.057	32.90	387.58	0.04	16.27	146.47
III	397.69	2.25	0.103	40.93	183.48	0.08	14	126.04
IV	310.48	3.15	0.187	58.08	87.21	0.14	12.10	108.90
V	198.38	4.05	0.356	70.67	112.09	0.26	28.93	260.40
VI	103.72	4.95	0.618	64.11	94.66	0.47	44.42	399.76
VII	58.61	5.85	1.123	65.85	45.12	0.83	37.60	338.39
VIII	13.95	6.75	2.042	28.50	44.65	1.51	67.64	608.75
IX	1.63	7.65	3.712	6.04	12.33	2.75	33.94	305.45
					1.63	3.71	6.04	54.38
			Biomass = 397.25				Cohort P = 2348.56	
			Cohort P/B = 5.91				CPI mean = 135.00	
			Annual P/B = 15.98				Annual P = 6349.81	

*Mean density corrected for their catch probability.

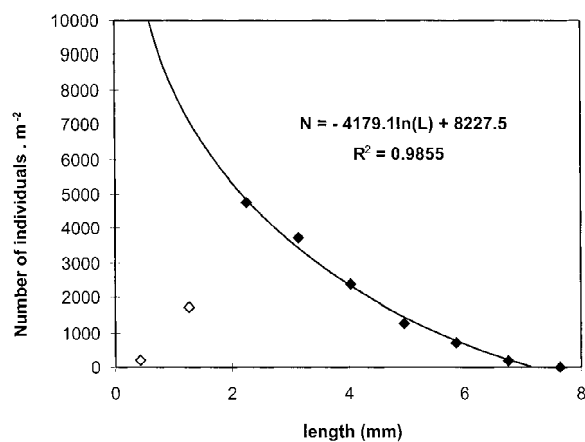


Figure 4. Abundance plot of the length classes of *C. luctuosa* larvae. The logarithmic equation excludes the I and II classes (open diamonds).

The life history of *C. luctuosa* in Chicamo stream reflects the non-seasonal multivoltine type suggested by Clifford (1982). This type usually has four to six generations during the course of a year and is typical of mayfly populations from tropical and subtropical

regions, where temperature does not limit hatching and larval development (Brittain, 1982).

The life cycles of many *Caenis* populations seem quite flexible. About half the *Caenis* cycles summarised by Clifford (1982) were univoltine, mainly univoltine winter, while about half were multivoltine, mainly bivoltine winter–summer. *Caenis luctuosa* displays a considerable degree of life cycle flexibility throughout its distributional range. It has been reported as univoltine in high latitudes and mountain areas (Brittain, 1974; Alba-Tercedor, 1981; Mol, 1983), while in Central Europe it is bivoltine with a winter and a summer generation (Landa, 1968). In Britain, Elliot et al. (1988) described both univoltine and bivoltine cycles. In our study area, we observed almost four generations with shorter development times (90–210 days). A similar flexibility is found in *C. horaria* and many of the Baetidae species (Brittain, 1982). Flexibility in the number of generations per year may be a response to thermal differences between habitats at different latitudes or altitudes (Ward & Stanford, 1982).

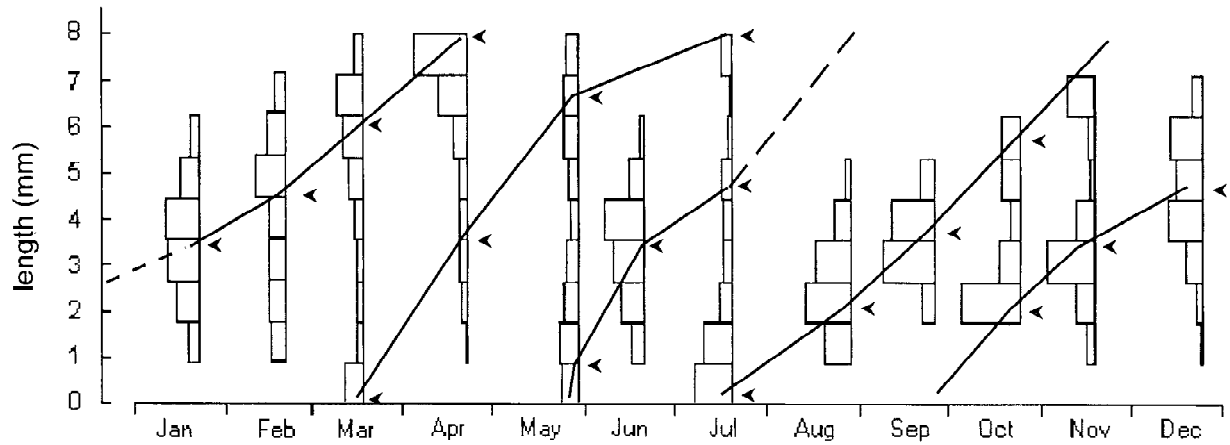


Figure 5. Monthly size-frequency histograms for *C. luctuosa* larvae from Chicamo stream after correcting for sampling and mortality effects. Modal values of the polymodal size-frequency distributions and growth pattern of the different cohorts are also represented.

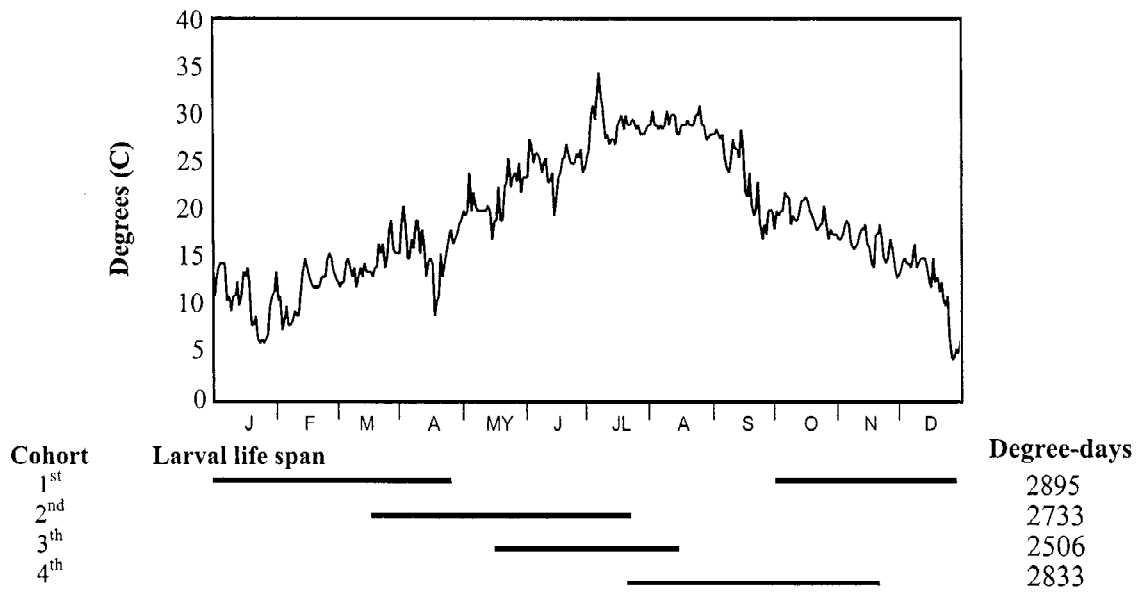


Figure 6. Variation of the mean daily air temperature in the study area, and accumulated degree-days for the different cohorts of *C. luctuosa*.

Table 3. Comparisons of secondary production and biomass turnover with other studies of *Caenis* species

Species	P (mgDW m ⁻²)	P/B	Habitat (Location)	Source
<i>C. luctuosa</i>	6349.81	15.98	Mediterranean semiarid stream (Murcia, Spain)	This study
<i>C. amica</i>	445.05	13.00	Experimental ponds (Virginia, U.S.A.)	Christman & Voshell, 1992
<i>C. amica</i>	676.00	12.72	Experimental stream (Alabama, U.S.A.)	Rodgers, 1982
<i>C. simulans</i>	4200.00	4.20	Cold/mesic plains stream (Minnesota, U.S.A.)	MacFarlane & Waters, 1982
<i>Caenis</i> spp.	82.10	59.1	Humid/mesic plains stream (Georgia, U.S.A.)	Benke & Jacobi, 1994

Multivoltine cycles and asynchronous recruitment and development patterns shown by the species in Chicamo stream are common characteristics of the life history of aquatic insects in desert streams (Gray, 1981). Rapid development may be advantageous in streams subjects to flash floods and periodic drying. Emergence and reproductive period extending throughout the year permit rapid recolonization of the stream if catastrophic events occurs. Other adaptations would include the food partitioning among different sizes of larvae and a reduction in the predation on larvae (Clifford, 1982).

Relatively few estimates of *Caenis* production exist, and not one concerns *C. luctuosa*. The estimated annual production in our study represents the highest values ever reported for *Caenis* species (Table 3). The annual P/B ratio measured in Chicamo stream was also substantially higher than that reported for northern temperate populations, where cooler temperatures result in slower development rates and fewer cohorts. On the other hand, our annual P/B value was lower than those reported by Benke & Jacobi (1994) for three *Caenis* species (*C. diminuta*, *C. hilaris* and *C. maccafferti*) in a subtropical blackwater stream. High annual P/B values are characteristic of insects with rapid development and multiple cohorts (Benke et al., 1984; Benke, 1993), and, as such, have been found in both hot and cold desert streams in the United States (Fisher & Gray, 1983; Jackson & Fisher, 1986; Gaines et al., 1992).

Despite the high production and turnover values found in Chicamo stream compared to those of temperate zones, they were lower than those estimated for mayfly species in a Sonoran Desert stream (Fisher & Gray, 1983; Jackson & Fisher, 1986). This stream had the highest production of any studied natural stream (Benke, 1993) because of extremely high growth rates among the gathering collector functional group. Differences in production estimates may be due to higher temperatures and a more predictable disturbance regime than in Chicamo stream. Although lower than those recorded in desert streams, our values must still be considered quite high.

In summary, our data support the hypothesis than in warm-water environments, the high growth rates and extensive periods of reproduction and emergence provide a high degree of resilience to these populations in adjusting to unpredictable variations in water level and habitat availability (Benke & Jacobi, 1994).

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