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ORIGINAL ARTICLE

The influence of floods on the life history of dominant mayflies (Ephemeroptera) in a subtropical mountain stream

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The larval life cycles and annual production of two mayfly (Ephemeroptera) species were studied in a subtropical low-order mountain stream. The relationship between precipitation and nymphal density, biomass (B) and secondary production was also investigated. Surber samples were taken weekly during a period of two years. Life spans were estimated from size-class frequency graphs and, independently, from nymphal length and environmental data. Annual production (P) was calculated using the size-frequency method. *Thraulodes consortis* (Leptophlebiidae) and *Leptohyphes eximius* (Leptohyphidae) showed asynchronous and continuous multivoltine life cycles. Mean life spans were 74 days for *L. eximius* and 124 days for *T. consortis*. Annual production values ranged from 1.4 to 4.05 g/m² year in *T. consortis*, and from 0.28 to 0.93 g/m² year in *L. eximius*. Annual P/B ratio ranged from 9 to 15 in *T. consortis*, and from 15 to 17 in *L. eximius*. Nymphal density and biomass declined abruptly after heavy storms but recovered quickly. Daily production was much higher in the dry than in the wet season for both species.

Los ciclos de vida y la producción anual de dos especies de Ephemeroptera fueron investigados en un arroyo de montaña de bajo orden. Se estudió también la relación entre la precipitación y la densidad, biomasa (B) y producción secundaria de las ninñas. Muestras Surber fueron tomadas semanalmente durante un período de dos años. La longitud del ciclo de vida se estimó a partir de gráficos de frecuencias de clases de talla, e independientemente, a partir de datos de longitud ninfal y datos ambientales. La producción anual (P) se calculó a través del método de frecuencia de talla. *Thraulodes consortis* (Leptophlebiidae) y *Leptohyphes eximius* (Leptohyphidae) mostraron ciclos de vida multivoltinos, asincrónicos y continuos. La longitud media del ciclo de vida fue de 74 días para *L. eximius* y 124 días para *T. consortis*. La producción anual varió entre 1.4–4.05 g/m² en *T. consortis*, y 0.28–0.93 g/m² en *L. eximius*. La razón P/B anual estuvo en el rango 9–15 en *T. consortis*, y 15–17 en *L. eximius*. La densidad y biomasa ninfal decayó abruptamente después de tormentas fuertes, pero se recuperaron rápidamente. La producción secundaria diaria para ambas especies fue mucho mayor en la época seca que en la húmeda.

**Keywords:** biomass; density; floods; production; seasonality

Introduction

Known life cycles of Neotropical mayflies are mainly multivoltine with asynchronous growth, and life spans range from 26 to 165 days (Jackson & Sweeney 1995; Huryn & Wallace 2000; Miserendino 2001; Jacobsen et al. 2008). Nevertheless, semivoltine and univoltine life patterns have also been reported (Sweeney et al. 1995; Añón Suárez & Albariño 2001, respectively). Life spans constitute key data to estimate secondary production, but they are difficult to obtain from field studies on seasonal aquatic insects (Marchant & Yule 1996). Secondary production estimates from Neotropical streams are thus rare. Only Ramírez & Pringle (1998) reported the annual production for three mayfly species from Costa Rica (range 0.0022–0.1388 g m⁻² year ash-free dry mass).

It is supposed that in warm-water environments, the high growth rates and extensive periods of reproduction provide a high degree of resilience to aquatic insect populations in adjusting to unpredictable variations in water level (Benke & Jacobi 1994). Information on how secondary production is affected by seasonal variations in stream discharge is completely unknown in the region.

The present paper has the following objectives: (1) to describe the life histories of *Thraulodes consortis* Dominguez and *Leptohyphes eximius* Eaton, the most abundant mayfly species present in Las Conchas stream, NW Argentina; (2) to estimate their secondary production using the size-frequency method; and (3) to relate changes in density, biomass and production with the seasonal variations in precipitation.

Material and methods

Study site

Las Conchas is a third-order mountain stream, flowing through subtropical rain forest in NW Argentina
This humid evergreen forest is part of the Yungas biogeographical province ranging from Venezuela and Colombia to Tucumán province in Argentina (Cabrera & Willink 1973). Almost the entire stream basin is protected by a natural reserve, without large settlements or other human-related activities. Stream width varied between 0.5 and 4 m, but was less than 1 m for most of the year. Marginal vegetation prevented direct sunlight reaching the stream (oriented N–S) except for a few hours around midday. Abundant allochthonous plant material is present in the stream, the period of greatest leaf fall occurring from March to September (Brown 1995). Boulders and rocks (>100 mm) dominate the bed substrate. Water depth reached 10 cm in riffles, and 30 cm in pools. The study site is at 700 m a.s.l., 26°47′9″S, 65°20′13″W. Seasonality (Figure 1) is evident in precipitation (from an annual mean of 1500 mm, 80% fall in the six warmest months, Figure 1) and in temperature (mean Summer temperature 28°C, Winter 12°C).

From the 12 mayfly species recorded during the study period, only L. eximius (Leptohyphidae) and T. consortis (Leptophlebiidae) were abundant and frequent enough in the samples to further analyze their life cycles and secondary production.

Samples consisted of one, two, or most commonly three Surber samples (0.09 m², pore size 1 mm) taken weekly from the stream, during a period of two years (from April 1994 to April 1996). Mayfly adults were obtained from mature nymphs that were reared in small cages in the stream. Additional adults were caught with aerial nets or picked from the water surface of pools and spider webs. Samples were fixed with 4% formalin, mayflies were sorted under magnification and preserved in 70% ethanol. All rainfall events, especially those large enough to produce spates in the stream, were recorded during the study period. These records were confirmed with daily precipitation graphs at the study area (Hunzinger 1997), and at a nearby weather station (Figure 1).

**Life cycles**

The presence of mature nymphs (with black wingpads) and emerging adults were recorded for each sampling date. All nymphs of each species obtained in the Surber samples were counted and the results expressed as numbers per m². Individuals were allocated into six size classes based on their body length which was measured to the nearest 0.10 mm (Table 1). Size classes were used to construct histograms of size-frequency distribution (percentage of each size class). These histograms were used to identify different cohorts and estimate their approximate life spans.

Independently, life spans were estimated using the method outlined in Marchant & Yule (1996) that...
relates larval life spans (or cohort production interval, CPI) to the ratio between cohort production (CP) and annual production (P): CPI = (365CP)/(P/B)B. The ratio P/B used in the previous formula was obtained from Benke’s (1993) equation: log P/B = 0.716 + 0.03T − 0.382 log Wm, where T is mean annual water temperature (°C) and Wm is maximum individual dry weight (mg). Mean annual water temperature at the study site was 19°C; maximum individual dry weights were assumed to equal the mean dry weights of the largest size class, thus including the small variations due to sexual dimorphism (female mature nymphs larger than males).

Body length and dry mass of each size class, and other parameters used to estimate production are shown in Table 1. When very few nymphs were present at a sampling date, samples from consecutive weeks were combined. This was especially the case for L. eximius, which was only analyzed on a monthly basis, except in July 1994 when the large number of nymphs permitted a 15-day discrimination.

### Secondary production

Annual production was approximated by the size-frequency method (Benke 1984). CPI of each species was deduced from the graphs of relative frequency of size classes. CPI was used to correct the size-frequency calculation of the annual production (multiplying it by 365/CPI) since all the studied species were multivoltine (Benke 1984). Nymphal dry weight (DW) was obtained from published regressions using body length (BL) measures of taxa in the same family and with a similar body shape (review in Johnston & Cunjak 1999). For T. consortis, the curve ln DW = −9.95 + 4.84 ln BL, proposed by Miserendino (2001) for Meridialaris was used. For L. eximius, the equation DW = 0.00921BL 3.22 (McCullough et al. 1979) developed for Tricorythodes minutus was used. Additionally, the general regression curve proposed for Ephemeroptera by Smock (1980), ln DW = −3.96 + 2.46 ln BL, was used to further estimate DW of T. consortis and L. eximius.

### Results

Dry and wet seasons did not coincide exactly with historic records, mainly because the study period was drier than normal (Figure 1). The first dry period spanned from June to September 1994, the first wet period from October 1994 to May 1995. The second dry season extended from June to mid-November 1995, followed by a wet period that lasted until the end of the study in April 1996 (Figure 1).

### Life cycles

A total of 1516 nymphs of T. consortis and 407 nymphs of L. eximius were measured. Both species showed asynchronous and continuous multivoltine life cycles. Small to large nymphs were present in the majority of the sampling dates (Figures 2(a), 3(a)). Mature nymphs and emergent adults of both species were present throughout the entire year (arrows in Figures 2b, 3b).
Figure 2. *Thraulodes consortis.* (a) Box-plot of body length in the different sampling dates; (b) size-class histogram, width of bars represents the relative frequency of each class in the respective sampling date, arrows indicate the presence of adults or ready to moult nymphs, dotted lines indicate different cohorts (total development time for each cohort is also marked, in weeks).
Figure 3. *Leptohyphes eximius*. (a) Box-plot of body length in the different sampling dates; (b) size-class histogram. Width of bars represents the relative frequency of each class in the respective sampling date, arrows indicate the presence of adults or ready to moult nymphs, dotted lines indicate different cohorts (total development time for each cohort is also marked, as number of weeks).

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Thraulodes consortis life span (obtained directly from the size-class graph, Figure 2(b)) reached a mean of 124 days (n = 12, range 98–140 days), and presented five or six cohorts in a year (dotted lines in Figure 2(b)). For the same data, Marchant & Yule’s method obtained a life span of 133 days (using DW–BL regressions for Meridialaris) or 156 days (using Smock’s general regression for Ephemeroptera).

Leptohyphes eximius was not represented in the samples by large nymphs (size classes 5–6) during a three-month period (last months of 1994); this pattern coincided with a previous large adult emergence (August 1994). Mean life spans approximated from the size-class graph (Figure 3(b)) were 74 days (n = 9, range 63–91 days), presenting six or seven cohorts per year. The low abundances of this species did not allow a detailed temporal analysis, and samples had to be analyzed on a monthly instead of a weekly basis as in the previous species. This shortcoming resulted in a lower resolution of the cohorts from the size-class histograms that made their estimation directly from the graphs difficult (Figure 3(b)). Nevertheless, the estimation obtained independently, using the method of Marchant & Yule, was exactly the same (74 days, using the general DW–BL regression for Ephemeroptera). The life span calculated using regressions for Tricorythodes minutus Traver (with more robust bodies) did not coincide with the two previous calculations, obtaining a larval development time of 116 days.

Secondary production
The mean annual production (Table 2, means of the two years) of T. consortis was 1.515 or 3.170 g DW/m² year depending on the regression used to estimate weight from body length. Mean annual biomass reached 0.13 or 0.26 g/m² using the same regressions. The high frequency of this species in the samples permitted a detailed temporal analysis (mostly weekly or biweekly) analysis of variation in density (N) and biomass (B) in relation to precipitation. Density and biomass declined abruptly after heavy storms but recovered quickly (Figure 4). The effect of rainfall was generally more evident on biomass than on density (compare N and B curves in Figure 4), suggesting that larger nymphs were impacted. Daily production (Table 3) in the wet seasons (mean of the two study periods 0.00274 g/m²) was doubled in the dry periods (mean 0.00539 g/m²). Nevertheless, mean N and B of these same periods did not vary significantly (Table 3).

Annual production (Table 2) estimated for L. eximius was 0.32 or 0.84 g DW/m² year while mean biomass was 0.02 or 0.05 g/m² depending on the regression used (Smock 1980 or McCullough et al. 1979, respectively). The number of nymphs permitted only a monthly analysis of population parameters (except July 1994) in relation to rainfall (Figure 5). This species presented a pattern similar to T. consortis, but the negative effect of precipitation was even more pronounced. Daily production (Table 3) in the dry periods (0.00226 g/m²) was much higher than in the rainy seasons (0.0004 g/m²). In contrast to T. consortis, mean values of N and B of L. eximius showed significantly higher values in the dry periods (Table 3).

Discussion
The overall coincidence of life span estimation using two different methods (analysis of size-class histograms, and Marchant & Yule method) is remarkable, mainly because the amount of work needed to obtain a detailed size-class histogram is enormous compared with data needed for the Marchant & Yule method (mean water temperature and maximum weight of the studied species). Nevertheless, the type of regression curve used to calculate DW from BL had a large impact on life span estimation. Thus, it would be important to use regressions constructed upon the same or very closely related taxa to those under study.

Life spans obtained in other lotic environments for species of Leptohyphes and Thraulodes are very variable. Leptohyphes life spans range from the extremely

Table 2. Mean annual biomass, annual production and P/B ratio of Thraulodes consortis and Leptohyphes eximius nymphs at Las Conchas stream, Sierra de San Javier, Tucumán, Argentina, for two periods: 22 dates from May 1994 to April 1995 (1st year), and 17 dates from May 1995 to April 1996 (2nd year).

<table>
<thead>
<tr>
<th>Species</th>
<th>Biomassa (g/m²)</th>
<th>Productiona (g/m² year)</th>
<th>P/B ratio</th>
<th>Biomassb (g/m²)</th>
<th>Productionb (g/m² year)</th>
<th>P/B ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>T. consortis (1st year)</td>
<td>0.116</td>
<td>1.40</td>
<td>12.07</td>
<td>0.244</td>
<td>2.29</td>
<td>9.39</td>
</tr>
<tr>
<td>T. consortis (2nd year)</td>
<td>0.138</td>
<td>1.63</td>
<td>11.81</td>
<td>0.275</td>
<td>4.05</td>
<td>14.73</td>
</tr>
<tr>
<td>L. eximius (1st year)</td>
<td>0.022</td>
<td>0.36</td>
<td>16.36</td>
<td>0.053</td>
<td>0.93</td>
<td>17.55</td>
</tr>
<tr>
<td>L. eximius (2nd year)</td>
<td>0.019</td>
<td>0.28</td>
<td>14.74</td>
<td>0.046</td>
<td>0.74</td>
<td>16.09</td>
</tr>
</tbody>
</table>

aDry mass versus body length regressions from Miserendino (2001) for T. consortis and McCullough et al. (1979) for L. eximius.
bDry mass versus body length regressions from Smock (1980) for both taxa.
short 12 days reported for \textit{L. packeri} in a stream from Arizona (Jackson & Fisher 1986) to 115 days estimated for \textit{Leptohyphes} sp. in Venezuela (Jacobsen et al. 2008). The period of 74–77 days obtained here is more similar to the 82 days of \textit{Leptohyphes} sp. from Costa Rica (Ramírez & Pringle 1998).

The period of 124 days obtained here for \textit{T. consortis} is somewhat shorter than that known for undetermined \textit{Thraulodes} species in Costa Rica (159 days; Ramírez & Pringle 1998) and Venezuela (242 days; Jacobsen et al. 2008).

The regression curves used to obtain DW from BL also influenced greatly the annual production estimates. Ramírez & Pringle (1998) found annual production values for a species of \textit{Thraulodes} of 0.0023–0.0042 g/m² year (three orders of magnitude lower than those obtained here). Jacobsen et al. (2008) reported higher values for a \textit{Thraulodes} species from Venezuela (0.450 g/m² year), but not as high as the values obtained here. The high P obtained in this study is probably due to the higher densities present in Las Conchas stream, and to the somewhat shorter life cycles.

Annual production reported for unidentified \textit{Leptohyphes} species are also lower than our results. Ramírez & Pringle (1998) obtained 0.0022–0.0044 g/m² year in Costa Rica; but Jacobsen et al. (2008) found an annual production of 0.240 g/m² year for \textit{Leptohyphes} spp., approximating our lowest results.

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Table 3. Mean density, mean biomass, and daily production of \textit{Thraulodes consortis} and \textit{Leptohyphes eximius} nymphs at Las Conchas stream, Sierra de San Javier, Tucumán, Argentina, in the dry and wet periods 1994–1996.

<table>
<thead>
<tr>
<th>Periods</th>
<th>\textit{T. consortis}</th>
<th>\textit{L. eximius}</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Density (individuals/m²)</td>
<td>Biomass (g/m²)</td>
</tr>
<tr>
<td>Dry 1 (1994)</td>
<td>149</td>
<td>0.087</td>
</tr>
<tr>
<td>Dry 2 (1995)</td>
<td>270</td>
<td>0.227</td>
</tr>
<tr>
<td>Wet 1 (1995)</td>
<td>214</td>
<td>0.134</td>
</tr>
<tr>
<td>Wet 2 (1996)</td>
<td>111</td>
<td>0.101</td>
</tr>
</tbody>
</table>
Intense rainfall events and associated spates occur mainly during the wet season, and thus density and biomass of macroinvertebrates are commonly reported to peak in the dry season (Flecker & Feifarek 1994; Ramírez & Pringle 1998; Molineri 2008). Density and biomass of *T. consortis* and *L. eximius* decreased markedly after each storm event, and daily production in both species differs markedly between dry and wet periods. Mean values of density and biomass for the entire wet period did not reflect this pattern in *T. consortis*. This may be explained because this is one of the most common species in the stream, and its large standing stocks guarantee the rapid recuperation observed.

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