

# Life history, production and coexistence of two leptophlebiid mayflies in three sites along a Northern Spain stream

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With 3 figures and 4 tables

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**Abstract:** The life history and temporal dynamics in density, biomass, growth rate and secondary production of *Habrophlebia lauta* and *Habroleptoides confusa* were compared in 3 sites along the Agüera stream in northern Spain. Both species had univoltine winter life histories. *Hb. lauta* showed greater abundance and production at downstream sites, while *Hd. confusa* did at the headwater site. The life history and temporal dynamics in population parameters differed between both species. As a result, temporal overlaps of abundance and, especially, production of these two mayflies were very low, which suggests that irrespective of their abundance, interspecific competition between *Hb. lauta* and *Hd. confusa* was unimportant along this stream system.

**Key words:** streams, life histories, secondary production, competition, Ephemeroptera.

## Introduction

Resource partitioning among species of the same guild has been linked to reducing competitive interactions (e.g. SWEENEY & VANNOTE 1981, TEAGUE et al. 1985, but see ALLAN 1995). Several studies have assessed the temporal overlap in the size, density and biomass of several aquatic invertebrates (e.g. LILLEHAMMER 1985, ELLIOTT 1987, GALLARDO-MAYENCO et al. 1998, SMITH et al. 2000), but studies that include analyses of secondary production are scarce (GEORGIAN & WALLACE 1983, RADER & WARD 1987 a, 1989 a, BENKE & JACOBI 1994). Nevertheless, secondary production provides a greater insight

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into the question of resource partitioning than the size, density or biomass because it is a better measure of resource use (BENKE 1993).

In this study, we investigated the life history and the population dynamics of *Habrophlebia lauta* (EATON) and *Habroleptoides confusa* (SARTORI & JACOB), (Ephemeroptera: Leptophlebiidae) at 3 sites along the Agüera stream (northern Spain). Our aim was to compare the production dynamics of these 2 leptophlebiids to assess the intensity of competition between them.

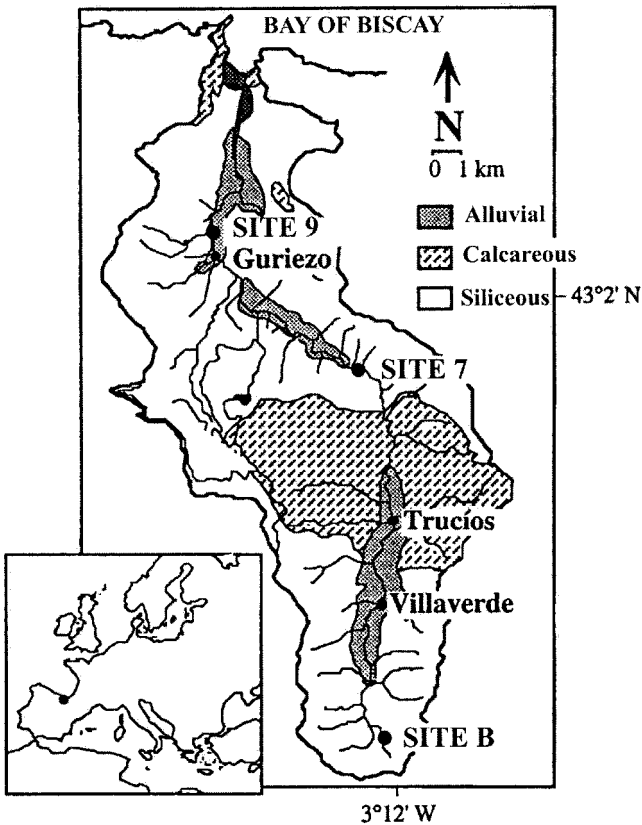
## Study sites

The Agüera is a small stream (30 km long) that flows through the Basque Country and Cantabria (northern Spain). The climate in the basin is temperate oceanic, with annual rainfall of 1330 mm in 1993 (the study year) and mean monthly temperatures that ranged from 8.6 °C in February to 20.2 °C in August. The vegetation consists mainly of pine (*Pinus radiata* D. DON) and eucalyptus (*Eucalyptus globulus* LABILL.) plantations, heathlands, meadows and small forests of *Quercus* spp. The human population is low (about 3000 inhabitants) and devoted principally to forestry and ranching.

The three study sites were located along the longitudinal axis of the stream system and were named here as in previous papers (e.g. POZO et al. 1997, GONZÁLEZ et al. 2000). Site B (43° 12' 37" N; 3° 15' 46" W) was located on a first-order tributary of the Agüera stream (Fig. 1). The riparian forest was dominated by *Q. robur* L., *Castanea sativa* MILLER and *Alnus glutinosa* (L.) GAERTNER. The underlying geology, and the absence of human settlements in the basin led to low mineralization and low nutrient content of the water at site B (Table 1). Site 7 (43° 19' 33" N; 3° 17' 29" W) was a third-order stream (Fig. 1) in a zone dominated by eucalyptus plantations. A narrow discontinuous strip of *A. glutinosa* and *Platanus hispanica* MILLER ex MÜNCH still persisted on the river banks. In spite of urban sewage from villages located upstream, self-puri-

**Table 1.** Main characteristics of the study sites. Those parameters with annual ranges in parentheses are means of spot measures taken monthly during 1993. Periphyton biomass and coarse particulate organic matter (CPOM) were measured in terms of ash free dry mass.

	Site B	Site 7	Site 9
Stream order	1	3	3
Elevation (m)	350	80	15
Drainage area (ha)	184	6906	11535
Channel width (m)	4	10	14
Temperature (°C)	11 (6.3–16.6)	13.2 (7.7–20.3)	13.1 (6.3–19.5)
pH	6.9 (6.3–7.4)	8.2 (7.4–9.1)	7.4 (6.8–8.0)
Conductivity (µS/cm)	108 (96–121)	227 (192–289)	193 (140–262)
Oxygen (mg/l)	10.8 (8.8–12.8)	11.5 (9.8–14.0)	10.4 (8.4–12.3)
Oxygen saturation (%)	100 (92–113)	108 (100–124)	96 (82–112)
Periphyton (g/m <sup>2</sup> )	7.9 (3.5–15.4)	23.4 (2.4–90.1)	15.5 (5.5–36.9)
CPOM (g/m <sup>2</sup> )	62.4 (20.5–195.2)	13.1 (5.7–37.5)	19.5 (9.8–55)



**Fig. 1.** The Agüera stream basin, The main geological features, the main villages and the study reaches are indicated.

fication processes kept nutrient concentrations relatively low at this site (ELÓSEGUI et al. 1995). At site 9 ( $43^{\circ} 20' 20''$  N;  $3^{\circ} 20' 20''$  W) the stream flowed through croplands and meadows, but was surrounded by a well-conserved riparian forest where *Q. robur*, *P. hispanica*, *A. glutinosa*, *Fraxinus excelsior* L., and *Laurus nobilis* L. were the most common trees. This third-order site was located immediately downstream from Guriezo (Fig. 1), the foremost village in the basin, and was enriched in phosphate, nitrate and nitrite (ELÓSEGUI & POZO 1994). More details about the main characteristics of these study sites are shown in Table 1.

## Materials and methods

Benthic sampling was conducted monthly from January to December 1993. At each site, 5 randomly selected replicates were collected in riffle/run areas with a Surber sampler (area  $0.09 \text{ m}^2$ , mesh size  $250 \mu\text{m}$ ) and fixed in 5% formalin. All the samples were taken in areas that were 30 m long. In the laboratory, invertebrates were removed

from sediment and debris, identified and counted using a binocular microscope. Those leptophlebiids that were severely damaged and, therefore, could not be identified to species (which accounted for less than 1% of the total caught) were assigned to *Hb. lauta* or *Hd. confusa* in accordance with their relative abundance at each site. Head-capsule widths were measured using an ocular micrometer at 20×.

The dry mass of each individual was estimated from its head width using size-mass regressions constructed for these species at the study sites (GONZÁLEZ et al. 2002). Secondary production was calculated by the instantaneous growth method (RICKER 1964) or the size-frequency method (HYNES & COLEMAN 1968, HAMILTON 1969, BENKE 1979). The first method was preferred because it allows measurement of production between sampling intervals (WATERS 1977, BENKE 1984, 1993). The size-frequency method was only used for *Hd. confusa* at site B because the asynchrony of its life history at this site (see below) precluded the use of the instantaneous growth method (RADER & WARD 1987b, BENKE 1993). The biomass turnover rates were calculated as the ratio between annual production and mean annual biomass (P/B, WATERS 1969).

Negative instantaneous growth rates found during the recruitment period were recorded as zero. Growth was calculated from the previous positive growth rate when negative values were observed during the emergence period (GONZÁLEZ et al. 2000). Those interval productions that were estimated from such inferred growth rates were not included in computations of the proportional similarity (see below).

Data on density, individual mass and population biomass were log-transformed before performing two-way (time × site) ANOVAs to improve normality and homoscedasticity (ZAR 1996). Tukey Honestly Significant Difference tests (hereafter, Tukey test) were used for post-hoc comparisons when ANOVA detected significant differences (ZAR 1996).

For production calculations by the instantaneous growth method, we used the mean individual mass of all the animals taken at the same study site and sampling date. Nevertheless, the spatial and temporal differences in density, mean individual mass, and biomass mean values were tested comparing the mean values calculated for each sample.

The overlap in temporal distribution of density, biomass and production between both mayflies (interspecific overlap) was calculated with the proportional similarity index (WHITTAKER 1975):

$$PS_{ab} = \sum_{i=1}^n \min(P_{ai}, P_{bi})$$

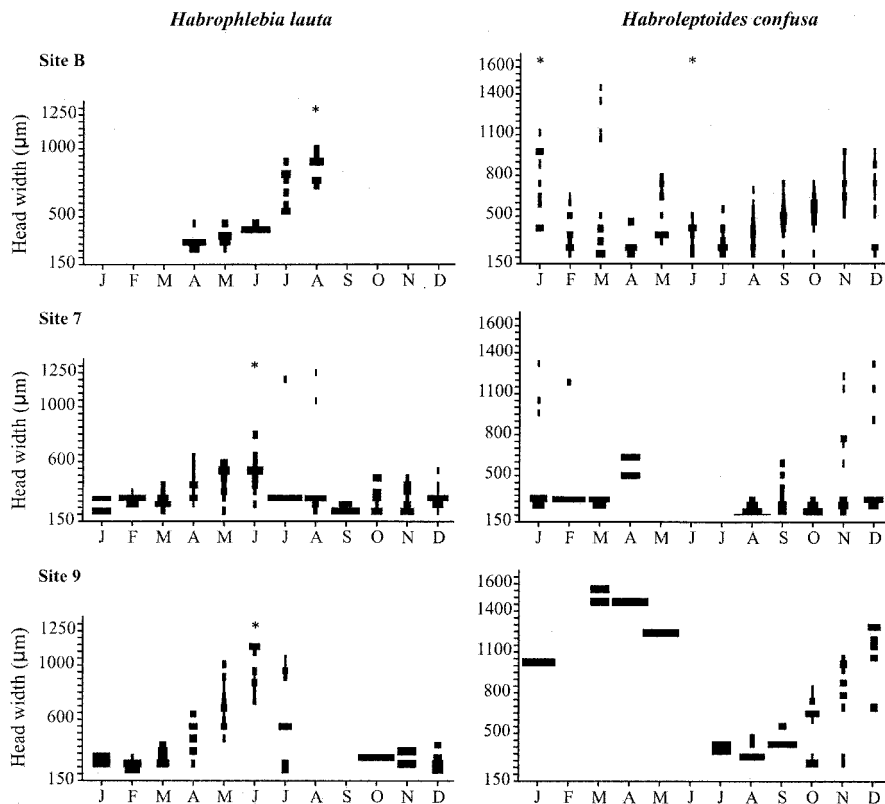
where  $PS_{ab}$  is the proportional similarity between species “a” and “b” in density, biomass or production,  $n$  is the number of time intervals,  $P_{ai}$  is the fraction of the density, biomass or production of species “a” that occurs during the time interval  $i$ , and  $P_{bi}$  is the fraction of the density, biomass or production of species “b” that occurs during the time interval  $i$ . PS values may range from 0 (no overlap) to 1 (total overlap).

The same equation was used to calculate proportional similarity between sites for each species’ density, biomass and production (intraspecific overlap).

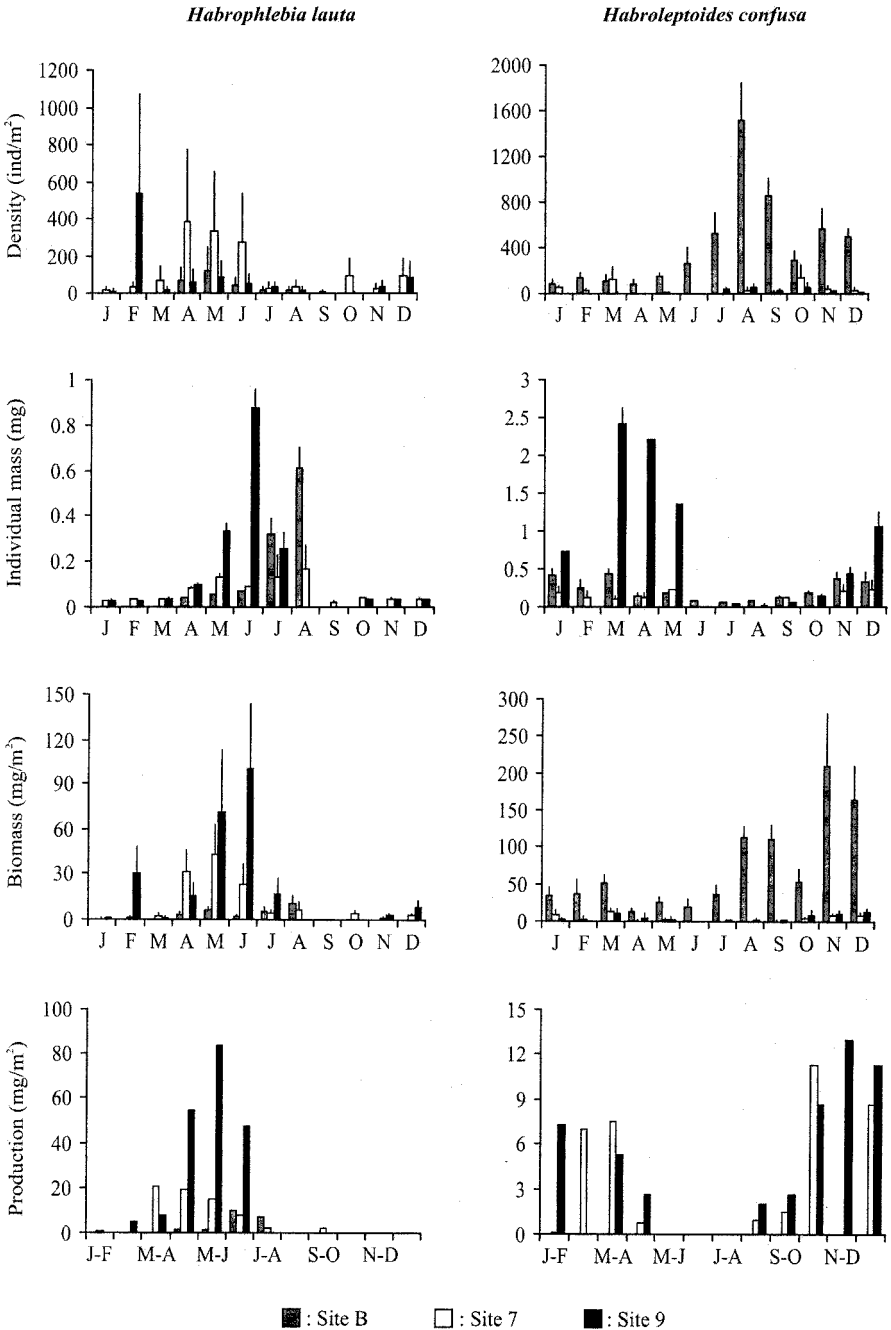
## Results

Besides *Hb. lauta* and *Hd. confusa*, the leptophlebiid fauna of the Agüera stream also includes *Thraulius bellus* EATON. Nevertheless, the latter species was very scarce (28 specimens total), and consequently, it was not studied.

*Hb. lauta* was univoltine at all the study sites (Fig. 2). It overwintered in the nymphal stage at sites 7 and 9, which indicates that it had an univoltine winter life history (sensu CLIFFORD 1982). At site B, this mayfly was recorded only from April to August, but, as the species was scarce at this site (Fig. 3), the small-sized individuals may have gone unnoticed during winter. Moreover, the head widths of the first specimens found ( $\geq 300 \mu\text{m}$ ; Fig. 2) suggested that they may have hatched before April. The first mature nymphs (those showing black wind pads) and adults of *Hb. lauta* were recorded in June at sites 7 and



**Fig. 2.** Size-frequency distribution of *Hb. lauta* (left) and *Hd. confusa* (right) at the study sites. Note vertical scale changes for each species. The asterisks indicate the sampling dates when mature nymphs were found.



**Fig. 3.** Density, individual mass, biomass and secondary production of *Hb. lauta* and *Hd. confusa*. Vertical lines indicate standard error. Note vertical scale changes in each case.

**Table 2.** Summary of the temporal comparisons performed. Results of the two-way ANOVAs (time×site) are shown at left, and results of the Tukey tests among dates, at right. Values increase from right to left; those linked by the same line show no significant differences. N. S.: no significant differences.

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*Habrophlebia lauta*

Density

Time:  $p < 0.0001$  Site B May Aug Jun Apr Jul Jan Feb Mar Sep Oct Nov Dec

Site:  $p < 0.0001$  Site 7 N. S.

Interaction:  $p < 0.005$  Site 9 Feb May Apr Jun Dec Nov Mar Jul Jan Oct Aug Sep

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Mean individual mass

Time:  $p < 0.0001$  Site B Aug Jul Jun May Apr

Site:  $p < 0.0001$  Site 7 May Jun Apr Jul Aug Oct Dec Feb Nov Mar Jan Sep

Interaction:  $p < 0.0001$  Site 9 Jun May Jul Apr Mar Oct Nov Jan Dec Feb

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Biomass

Time:  $p < 0.0001$  Site B Aug May Jul Apr Jun Jan Feb Mar Sep Oct Nov Dec

Site:  $p < 0.0001$  Site 7 May Apr Jun Dec Aug Oct Jul Mar Feb Nov Jan Sep

Interaction:  $p < 0.001$  Site 9 May Jun Feb Apr Dec Jul Nov Mar Jan Oct Aug Sep

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*Habroleptoides confusa*

Density

Time:  $p < 0.0001$  Site B Aug Sep Dec Nov Jul Oct May Feb Mar Apr Jun Jun

Site:  $p < 0.0001$  Site 7 N. S.

Interaction:  $< 0.05$  Site 9 Aug Nov Oct Dec Sep Jul Mar Apr Jan May Feb Jun

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Mean individual mass

Time:  $p < 0.0001$  Site B Nov Jan Oct Dec May Sep Mar Feb Apr Aug Jul Jan

Site:  $p < 0.0001$  Site 7 May Apr Nov Dec Jan Feb Sep Mar Oct Aug

Interaction:  $p < 0.0001$  Site 9 Mar Apr May Dec Jan Nov Oct Sep Jul Aug

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Biomass

Time:  $p < 0.0001$  Site B Nov Dec Aug Sep Mar Oct May Jul Jan Feb Apr Jun

Site:  $p < 0.0001$  Site 7 N. S.

Interaction: N. S. Site 9 N. S.

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9, two months earlier than at site B. The last large nymphs were found in August (sites B and 7) and in July (site 9).

*Hd. confusa* also exhibited a univoltine winter life history at the 3 sites. This species showed a very asynchronous life cycle at site B, where the smal-

lest nymphs (head width 150–200  $\mu\text{m}$ ) were observed during 11 months, and mature nymphs, in January and June. No mature nymphs or adults of this species were recorded at sites 7 and 9.

Comparisons of density and mean individual mass of the 2 studied leptophlebiids showed that there were significant time by site interactions. Thus, it must be noted that the inter-site differences of these parameters detected by the ANOVAs must be viewed only as overall patterns because they are not applicable to all the sampling dates. The same was true for comparisons of *Hb. lauta* biomass.

Overall, the density of *Hb. lauta* was similar at sites 7 and 9 ( $p > 0.05$ , Tukey test), but it was lower at site B ( $p < 0.001$ , Tukey test). The density of *Hd. confusa* showed the opposite spatial pattern, with highest values at site B ( $p < 0.001$ , Tukey test), and no differences in density between sites 7 and 9 ( $p > 0.05$ , Tukey test). Maximum densities of *Hb. lauta* at site 9 were observed between February and June (Fig. 3, Table 2) and minimum ones from August to October. The highest densities of *Hd. confusa* at sites B and 9 were found between July and December (Fig. 3, Table 2). This species showed no temporal changes in density at site 7 (Table 2).

The mean individual mass of *Hb. lauta* did not differ between sites B and 7 ( $p > 0.05$ , Tukey test), but was highest at site 9. At site B, it clearly increased from April to August (Fig. 3, Table 2). At sites 7 and 9, mean mass of *Hb. lauta* showed no change from September to March, but increased sharply from March to May (site 7) or June (site 9) (Fig. 3, Table 2). The lowest mean individual mass of *Hd. confusa* was found at site 7 ( $p < 0.001$ , Tukey test). Because high values attained at site 9 from March to May (Fig. 3) were caused by 4 large specimens, the mean mass of this species showed no difference between sites B and 9 ( $p > 0.05$ , Tukey test). Its temporal patterns differed from those of *Hb. lauta*. At site B, the mean mass of *Hd. confusa* began to increase in August, reaching its highest values in November (Fig. 3, Table 2). At sites 7 and 9, the highest mean mass of this species was attained in May (site 7) or March–April (site 9).

The population biomass of *Hb. lauta* did not differ between sites 7 and 9 ( $p > 0.05$ , Tukey test), but lower values were observed at site B ( $p < 0.05$ , Tukey test). The highest values of biomass for this species occurred in April–June (site 7), May–June (site 9), and May–August (site B) (Fig. 3, Table 2). As occurred with density, *Hd. confusa* showed an opposite spatial pattern in population biomass: higher values at site B ( $p < 0.001$ , Tukey test) than at sites 7 and 9, and no significant differences between these 2 sites ( $p > 0.05$ , Tukey test). The highest biomass for this species at site B was found during the second part of the year (Fig. 3, Table 2). No clear temporal trends in biomass were observed at sites 7 and 9 (Fig. 3).



**Table 3.** Secondary production (P, mg m<sup>-2</sup> year<sup>-1</sup>) and biomass turnover rates (P/B, year<sup>-1</sup>) of *Hb. lauta* and *Hd. confusa* at the study sites.

	<i>Hb. lauta</i>		<i>Hd. confusa</i>	
	P	P/B	P	P/B
Site B	19.5	8.7	412.6	5.7
Site 7	111.9	11.3	37.7	4.6
Site 9	198.5	9.6	37.6	4.6

**Table 4.** Proportional similarity indexes (PS) of density, biomass and production.

		Density	Biomass	Production
Interspecific PS				
Site B		0.22	0.24	–
Site 7		0.3	0.25	0.05
Site 9		0.18	0.20	0
Intraspecific PS				
<i>Hb. lauta</i>	Site B vs site 7	0.7	0.6	0.56
	Site B vs site 9	0.31	0.66	0.13
	Site 7 vs site 9	0.44	0.72	0.39
<i>Hd. confusa</i>	Site B vs site 7	0.42	0.49	–
	Site B vs site 9	0.72	0.43	–
	Site 7 vs site 9	0.56	0.63	0.6

Because of the asynchronous life history of *Hd. confusa* at site B impeded an accurate calculation of nymphal growth rates, the production of this population was estimated by the size-frequency method. In this case, a conservative cohort production interval of 12 months, the highest possible for univoltine species, was taken. Thus, the production and P/B values given for *Hd. confusa* at site B should be understood as minimum estimates, since the cohort production interval for this population could be shorter than one year (Fig. 2).

The annual production of *Hb. lauta* was highest at site 9, intermediate at site 7, and lowest at site B (Table 3). By contrast, production of *Hd. confusa* was higher at site B than at sites 7 and 9. Biomass turnover rates ranged from 8.7 year<sup>-1</sup> (site B) to 11.3 year<sup>-1</sup> (site 7) for *Hb. lauta*, and from 4.6 year<sup>-1</sup> (sites 7 and 9) to 5.7 year<sup>-1</sup> (site B) for *Hd. confusa* (Table 3). *Hb. lauta* concentrated its production from March to July, whereas most production of *Hd. confusa* was observed from August to December (site 9) or March (site 7) (Fig. 3).

Interspecific and intraspecific overlap in density, biomass and production are shown in Table 4. For all variables, intraspecific PS values were consistently higher than interspecific PS values, indicating that temporal dynamics showed greater differences between species than among sites. Interspecific overlap of density was similar to that of biomass, but both were considerably higher than interspecific overlap in production.

## Discussion

*Hb. lauta* and *Hd. confusa* exhibited univoltine winter life histories in all study sites. The same conclusion was reported in 11 of 12 papers about these two species (reviewed by CLIFFORD 1982). The size-frequency histograms and the timing of mature nymphs suggest that the flight period of *Hd. confusa* began earlier than that of *Hb. lauta*. Moreover, whereas the size of *Hd. confusa* nymphs increased during winter, *Hb. lauta* nymphs did not start growing until spring. Therefore, although both species coexisted during most of the year, they had life histories with very different phenologies. The patterns of growth and emergence displayed by these two leptophlebiids in the Agüera stream agree with those observed by THIBAUT (1971) in a nearby stream in South-western France.

It has been reported that other mayflies show changes in their life histories along the Agüera stream (GONZÁLEZ et al. 2000, 2001). Some inter-site differences were also observed in the phenology of *Hb. lauta* and *Hd. confusa*; these shifts consisted of longer presence and recruitment period of *Hb. lauta* at sites 7 and 9 than at site B, whereas presence and recruitment of *Hd. confusa* followed the opposite spatial trend. Such differences among sites may have emerged by chance, because the periods of presence and recruitment of *Hb. lauta* and *Hd. confusa* were shorter at the sites where they were less common. Therefore, our data do not support the existence of spatial changes in the life history of these two leptophlebiids.

Inter-site differences in density and biomass of *Hb. lauta* and *Hd. confusa* were much more evident. The former species showed highest values at sites 7 and 9, and the latter at site B. Water temperature could be one factor affecting this pattern, because it also showed clear differences among sites. The Thermal Equilibrium Hypothesis (SWEENEY & VANNOTE 1978, VANNOTE & SWEENEY 1980) predicts that each species has an optimum temperature that allows maximum reproductive success and population stability. In the Agüera stream, *Hb. lauta* showed greater abundance at the warmer sites and a concentrated growth in spring and summer whereas *Hd. confusa* was more abundant at the cooler, headwater site, and grew most rapidly in autumn-winter. Thus, we suggest that the optimum temperature of *Hb. lauta* is higher than that of *Hd. confusa*, and that this could be the reason for the different patterns in abundance and growth. However, we must recognise that we lack the bioenergetic data required to support such interspecific differences in optimum temperatures. Moreover, an array of alternative hypotheses can be invoked to explain the observed spatial segregation, because we are comparing one oligotrophic headwater with 2 third-order sites that are more nutrient enriched.

The spatial differences in secondary production can be viewed as a result of the observed shifts in biomass because production is a function of popula-

tion biomass and biomass turnover rate (i.e. individual growth rates, WATERS 1969). Annual production of *Hb. lauta* and *Hd. confusa* in the Agüera stream fell well inside the reported values for leptophlebiids, which range from  $1 \text{ mg m}^{-2} \text{ year}^{-1}$  for *Paraleptophlebia* sp. in an acidic low order stream (GRIF-FITH et al. 1994) to  $4250 \text{ mg m}^{-2} \text{ year}^{-1}$  for *P. heteronea* (MCDUNNOUGH) below a dam in the upper Colorado River (RADER & WARD 1989 b). Compared with previously reported values, *Hd. confusa* at site B can be regarded as having a high-medium production, *Hb. lauta* at sites 7 and 9 as having a medium production, and *Hb. lauta* at site B and *Hd. confusa* at sites 7 and 9 as having a low production.

The biomass turnover rates of *Hb. lauta* were much higher than those of *Hd. confusa*, but, again, were among the reported values for leptophlebiids. The values for these mayflies range from  $2.5 \text{ year}^{-1}$  for *Habrophlebia vibrans* NEEDHAM in a stream in Quebec (LAUZON & HARPER 1986) to  $15.4 \text{ year}^{-1}$  for *Choroterpes mexicanus* ALLAN below a reservoir in a Texas river (MCCLURE & STEWART 1976). In this context, biomass turnover rates of *Hb. lauta* in the Agüera stream can be regarded as high, while those of *Hd. confusa* are low-medium.

The interspecific overlap measured using production was lower than those measured using density or biomass. Since production incorporates data on growth rates, it is not a mere measure of "population presence" but also gives information on "population activity". For example, interspecific PS index found at site 9 in May was lower for production (0) than for biomass (0.05) because most individuals found on this date were large nymphs close to their emergence (Fig. 2).

The interspecific temporal overlap of density and biomass, and that of production at sites 7 and 9 were low ( $PS \leq 0.24$ ). Such low values do not seem to be fortuitous, because the PS values for intraspecific comparisons were consistently higher than those for interspecific comparisons. This temporal displacement in production dynamics suggests that competition between these two species may be very low (e.g. GEORGIAN & WALLACE 1983). The interspecific temporal overlap of production found in this study is similar to that found by GEORGIAN & WALLACE (1983) in their study of scraper insects but much lower than those reported by RADER & WARD (1987 a, 1989 a) for grazer mayflies and BENKE & JACOBI (1994) for snag-dwelling mayflies.

In summary, we found that *Hb. lauta* and *Hd. confusa* exhibited univoltine winter life histories in the Agüera stream. These mayflies showed opposite spatial trends: density, biomass and production of *Hb. lauta* were highest at the two downstream sites, whereas highest values for *Hd. confusa* were found at the headwater site. Our results indicate that the competition between these species was very low. These two leptophlebiids showed clear spatial segregation but, even in the case they had coexisted in the same site, temporal segregation in resource use would have reduced interspecific competition.

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