



---

## Life History and Production of *Epeorus torrentium* Eaton (Ephemeroptera: Heptageniidae) in a North Iberian Stream

---

Jose M. González, Ana Basaguren and Jesús Pozo

Department of Plant Biology and Ecology, University of the Basque Country, Bilbao, Spain

---

### Abstract

The life history and secondary production of *E. torrentium* were investigated at three sites along a small Spanish stream. This species had an univoltine winter life history with recruitment from June to November. It showed asynchronous development, which is consistent with the unpredictable environment where they dwell. *E. torrentium* showed higher density, biomass and production at the headwater site than at the downstream sites, but the annual production/biomass ratios followed the opposite spatial trend. Thus, the spatial pattern of production of this species was more related to shifts in population biomass than to changes in growth rates.

**Keywords:** Stream, mayfly, Heptageniidae, *Epeorus*, life history, secondary production.

### Introduction

Knowledge of the life histories of freshwater invertebrates is often used to link species traits to ecosystem processes. For example, it has been proposed that the temporal dynamics of certain invertebrates take advantage of periods with maximum food availability (e.g., Georgian & Wallace, 1983; Cummins et al., 1989) or avoid harsh habitat conditions (e.g., Cobb et al., 1991; Brewin et al., 2000). Habitat Templet theory suggests that life history traits such as voltinism, growth rates, generation times, and synchrony of development are related with the spatial and temporal heterogeneity of the environment (Southwood, 1977, 1988; Townsend & Hildrew, 1994). These traits are population attributes and may show intraspecific changes as a response to shifts in environment conditions (e.g., Rader & Ward, 1989; Sanchez & Hendricks, 1997; Robinson & Minshall, 1998).

Secondary production is a composite of population parameters including biomass, individual growth rate, mortality, and life history length. Thus, this measure of a population's participation in the fluxes of energy (Benke, 1993) may change in response to environmental conditions that have effects on the above parameters. Today, there are numerous studies of the production of stream insects (Huryn & Wallace, 2000), but there is no information about production dynamics of *Epeorus torrentium*. General models have shown that water temperature and individual mass explain most of the variability of secondary production in rivers and streams (Morin & Bourassa, 1992; Benke, 1993). Nevertheless, because an array of other factors can help to explain such variability (see Benke, 1993 and Huryn & Wallace, 2000 for a review), these general models lack the appropriate accuracy (Benke, 1993).

The life history and production of *Epeorus torrentium* Eaton (Ephemeroptera: Heptageniidae) were studied at three reaches along a small stream in northern Spain. Little information is available on the population dynamics of this species, mainly because its smallest nymphs are often difficult to identify (Alba-Tecedor, 1990). The life strategies of this heptageniid are discussed in relation to previous investigations of the biology of four other mayflies in the same stream system (González et al., 2000, 2001, unpublished data).

## Materials and Methods

### Study area

The study was conducted in the Agüera stream basin, a small catchment (144 km<sup>2</sup>) between the Basque Country and Cantabria, northern Spain. The area is mainly covered by pine (*Pinus radiata* D. Don) and eucalyptus (*Eucalyptus globulus* Labill.) plantations, meadows, heathlands, and *Quercus* spp. forests. The climate is temperate oceanic. Most of the basin is composed of siliceous materials, but there are calcareous outcrops in its central part and near the stream mouth. Human population densities are low, and the main activities in the basin are forestry and ranching.

The three study sites were placed along the stream gradient. They are designated as in previous papers (e.g. Elósegui & Pozo, 1998; González et al., 2000). Site B (43° 12' 37"N; 3° 15' 46"W) is located in a small first-order tributary of the Agüera stream. Water mineralization and pH are low at this site (Table 1). The banks are covered by an oak forest dominated by *Quercus robur* L., *Alnus glutinosa* (L.) Gaertner and *Castanea sativa* Miller. Site 7 (43° 12' 37"N; 3° 15' 46"W) is a third-order reach of the Agüera stream located downstream of a broad calcareous area. As a consequence, water shows higher conductivity and pH than found at the previous site (Table 1). The riparian vegetation is *E. globulus*, *A. glutinosa* and *Platanus hispanica* Miller ex Münch. Site 9 (43° 20' 20"N; 3° 20' 20"W) is a third-order reach immediately downstream of the main village in the basin. Urban pollution increases nutrient concentrations of water at this site (Elósegui & Pozo, 1994). Although the reach is mainly devoted to agriculture, the river banks are covered by a diverse riparian forest with *Q. robur*, *P. hispanica*, *A. glutinosa* and *Fraxinus excelsior* L. as the main species. During the study period, the coarse particulate organic matter was highest at site B, intermediate at site 9, and lowest at site 7 (González & Pozo, 1996). The epilithon biomass was higher at sites 7 and 9 than at site B (Lopez de Luzuriaga, 1995).

### Data collection and analysis

In 1993 five samples per month were collected using a Surber sampler (0.09 m<sup>2</sup>, mesh size 250 µm). The samples were preserved in the field with 5% formalin and returned to the laboratory, where invertebrates were sorted, identified, counted and measured for head width (precision 50 µm).

The individual mass of the nymphs was calculated from size-mass regressions constructed for *E. torrentium* at the study sites (González et al., in press). Secondary production was estimated by the size-

Table 1. Main characteristics of 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 weight.

|  | 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 (6.3–19.5)   |
| pH                                     | 6.9 (6.3–7.4)     | 8.2 (7.4–9.1)   | 7.4 (6.8–8.0)   |
| Conductivity ( $\mu\text{S cm}^{-2}$ ) | 108 (96–121)      | 227 (192–289)   | 193 (140–262)   |
| Oxygen ( $\text{mg l}^{-1}$ )          | 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 ( $\text{g m}^{-2}$ )       | 7.9 (3.5–15.4)    | 23.4 (2.4–90.1) | 15.5 (5.5–36.9) |
| CPOM ( $\text{g m}^{-2}$ )             | 62.4 (20.5–195.2) | 13.1 (5.7–37.5) | 19.5 (9.8–55)   |

frequency method (Hynes & Coleman, 1968; Hamilton, 1969) and the instantaneous growth method (Ricker, 1946). The former method requires knowledge of the cohort production interval (i.e. the time taken to complete larval development, CPI) (Benke, 1979, 1984). Nevertheless, because neither nymphs ready to emerge nor adults were found during the sampling period, a conservative CPI of 12 months was assumed, the maximum value for univoltine populations. For production calculations using the instantaneous growth method, the negative growth rates found during the recruitment period were recorded as zero, and those found during the emergence period were recalculated from the daily growth rate observed at the previous time interval (González et al., 2000). The biomass turnover rates were calculated as production / mean annual biomass ratios ( $P/B$  ratios, Waters, 1969).

Data on density, individual weight and biomass were log-transformed to improve normality and homoscedasticity (Zar, 1996). These population parameters were compared among sites and dates using two-way ANOVA. Tukey Honestly Significant Difference tests (hereafter, Tukey test) were used for post-hoc comparisons when ANOVAs detected significant differences ( $p < 0.05$ ) (Zar, 1996).

## Results

The highest population density of *E. torrentium* was observed at site B ( $p < 0.001$ , Tukey test, Fig. 1), but no differences were found between sites 7 and 9 ( $p > 0.05$ , Tukey test). The time  $\times$  site interaction was significant, which indicates that such a pattern of density did not occur all year. Maximum densities were observed from June to January (Fig. 1, Table 2). The nymphs found in this period accounted for 95% of the *E. torrentium* sampled during the year.

This species had an univoltine winter life cycle (sensu Clifford, 1982) at the three study sites (Fig. 2). Smallest nymphs were observed from June to November at sites B and 7, and from July to September at site 9. Large nymphs were observed in December and February which suggested that individual growth did not stop during winter. At all study sites, the growth was hard to follow from January to May, a period with very low density of *E. torrentium* nymphs (Fig. 1).



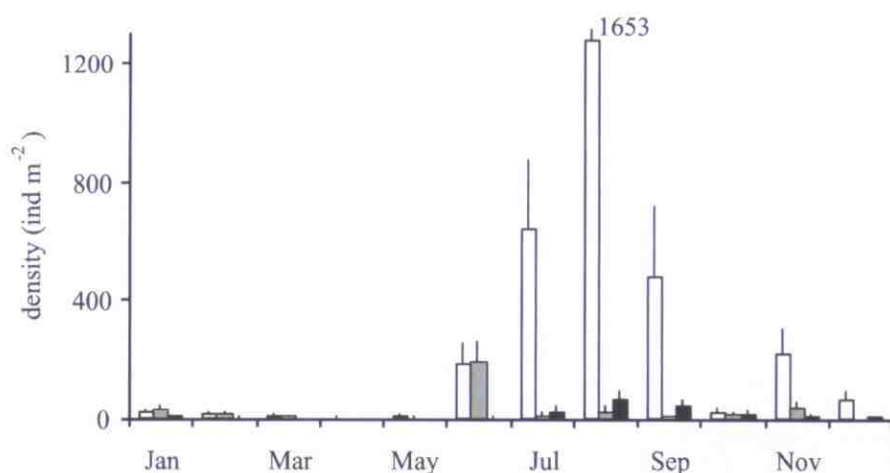


Figure 1. Density of *E. torrentium* at Sites B (white), 7 (grey) and 9 (black) during the study period. Vertical lines indicate the standard error.

Table 2. Summary of the temporal comparisons performed. Results of the two-way ANOVAs (site x time) are shown at left, and results of the Tukey tests, at right. Values increase from right to left; those linked by the same line do not show significant differences.

#### Density

site:  $p < 0.0001$

Site B: Jul Aug Sep Nov Jun Dec Jan Oct Feb Mar May Apr

time:  $p < 0.0001$

Site 7: Jun Jan Nov Aug Oct Sep Jul Feb Mar May Apr Dec

interaction:  $p < 0.0001$

Site 9: Aug Sep Jul Oct Jan Nov Dec Jun Feb Mar Apr May

#### Individual weight

site:  $p < 0.0001$

Site B: May Mar Jan Apr Feb Dec Oct Nov Sep Aug Jul Jun

time:  $p < 0.0001$

Site 7: Feb Mar May Jan Nov Oct Aug Jun Jul Sep

interaction:  $p < 0.0001$

Site 9: Feb Jun Jan Nov Oct Dec Aug Sep Jul

#### Biomass

site:  $p < 0.0001$

Site B: Nov Dec Aug Sep Jul Jan May Feb Mar Oct Jun Apr

time:  $p < 0.0001$

Site 7: Jan Jun Feb Mar Nov Oct May Aug Jul Sep Apr Dec

interaction: N.S.

Site 9: Aug Jan Sep Feb Oct Nov Jun Jul Dec Mar Apr May

N.S.: no significant differences.

Mean individual mass was higher at site 9 than at sites B and 7 ( $p < 0.01$ , Tukey test, Fig. 3). However, since the time x site interaction was again significant (Table 2) such differences were time-dependent. The nymphs found from June to December showed the lowest mean mass (Fig. 3). At sites 7 and 9, the mean individual mass

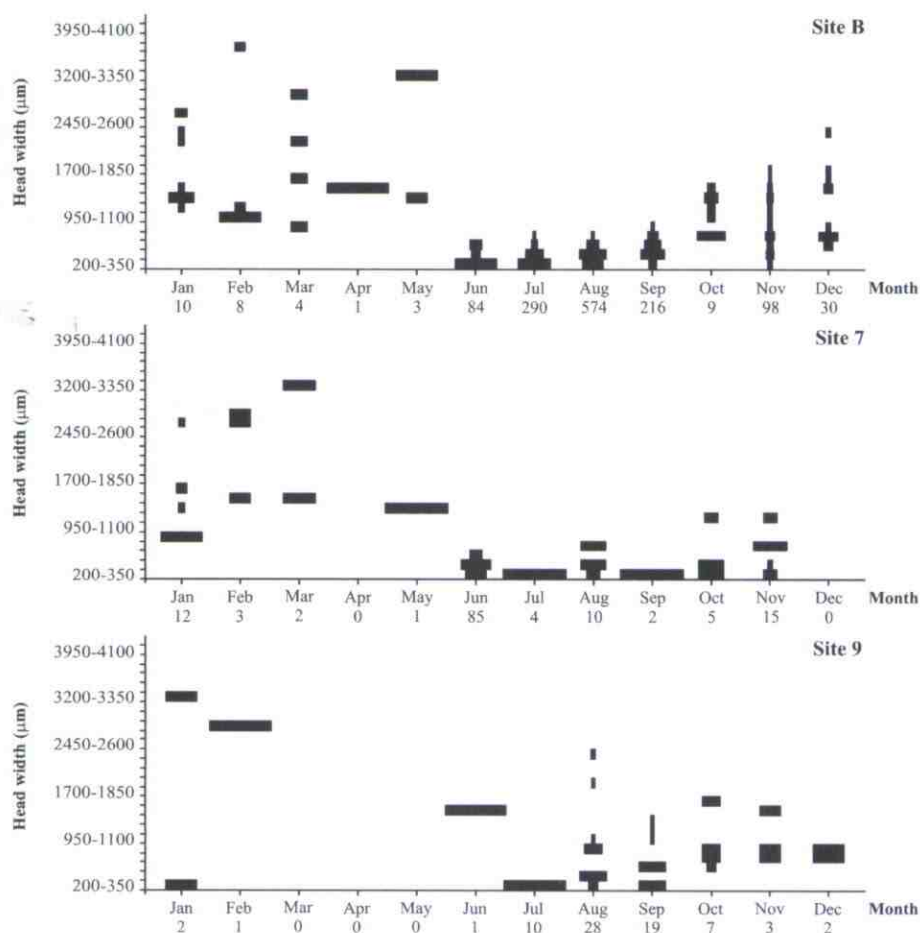


Figure 2. Size-frequency plot of *E. torrentium* from January to December 1993 at the study sites. Width of bars represents percentage of nymphs in each size class on a given sampling date. The number of nymphs recorded at each sampling date is shown on the horizontal axis.

reached its maximum in February (Table 2). The increase of individual mass was gradual at site B, where maximum values were observed in May.

As in the case of density, the population biomass of *E. torrentium* was higher at site B than at sites 7 and 9 ( $p < 0.001$ , Tukey test, Fig. 4). There was no time  $\times$  site interaction which means that the spatial differences observed were not time-dependent. At site B, the highest values were observed in November and December, but only differed significantly from those found in October and from January to June (Fig. 4, Table 2). At sites 7 and 9, the *E. torrentium* biomass did not show clear temporal patterns. Mean annual biomass was  $24 \text{ mg m}^{-2}$  at site B,  $6.6 \text{ mg m}^{-2}$  at site 7 and  $8.5 \text{ mg m}^{-2}$  at site 9.

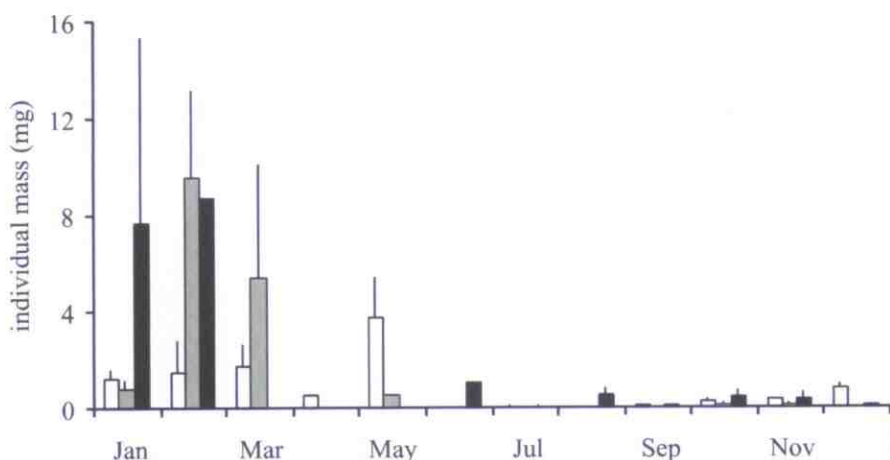


Figure 3. Mean individual mass of *E. torrentium* nymphs at Sites B (white), 7 (grey) and 9 (black) during the study period. Vertical lines indicate the standard error.

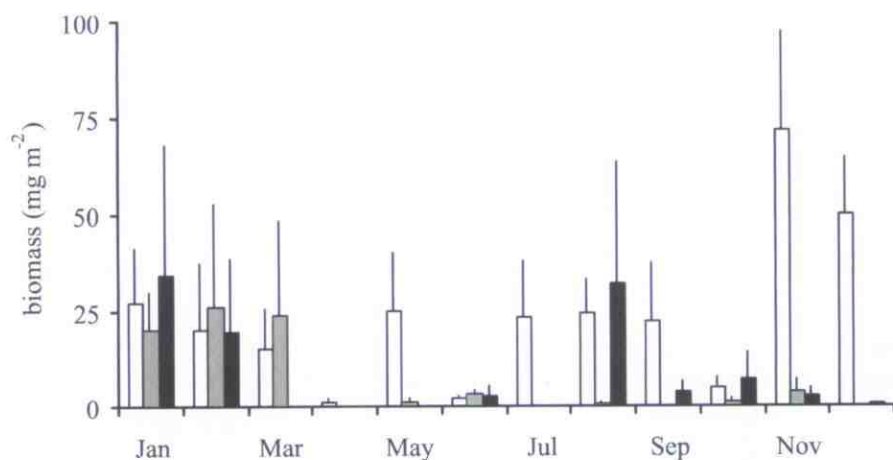


Figure 4. Biomass of *E. torrentium* nymphs at Sites B (white), 7 (grey) and 9 (black) during the study period. Vertical lines indicate the standard error.

The production of *E. torrentium* was much higher at site B than at the downstream sites (Table 3). However, the highest annual *P/B* ratios were observed at sites 7 and 9. Thus, the spatial differences in secondary production of this species were mainly due to shifts in biomass. The two methods used to estimate the production of *E. torrentium* at site B gave similar results (Table 3), and 80% of the annual production observed at this site occurred from June to January (Fig. 5).

Table 3. Secondary production ( $P$ ,  $\text{mg m}^{-2} \text{ year}^{-1}$ ) and annual production/biomass ( $P/B$ ,  $\text{year}^{-1}$ ) of the mayflies studied at the Agüera stream. Where two values are given, the first one is the estimate obtained using the instantaneous growth method, and the second one, the estimate from the size-frequency method. When only one figure is given, it represents the result of the size-frequency method.

| Species                       | Site | $P$       | $P/B$   | Reference             |
|-------------------------------|------|-----------|---------|-----------------------|
| <i>Caenis luctuosa</i>        | 7    | 76        | 7.9     | González et al., 2001 |
|                               | 9    | 93        | 7.1     |                       |
| <i>Epeorus torrentium</i>     | B    | 190–172   | 7.9–7.2 | present study         |
|                               | 7    | 64        | 9.6     |                       |
|                               | 9    | 83        | 9.7     |                       |
| <i>Ephemerella ignita</i>     | 7    | 1156–1329 | 8.6–8.7 | González et al., 2000 |
|                               | 9    | 480–496   | 9.5–9.8 |                       |
| <i>Habroleptoides confusa</i> | B    | 413       | 5.7     | unpublished data      |
|                               | 7    | 38        | 4.6     |                       |
|                               | 9    | 38        | 4.6     |                       |
| <i>Habrophlebia lauta</i>     | B    | 20        | 8.7     | unpublished data      |
|                               | 7    | 112       | 11.3    |                       |
|                               | 9    | 199       | 9.6     |                       |

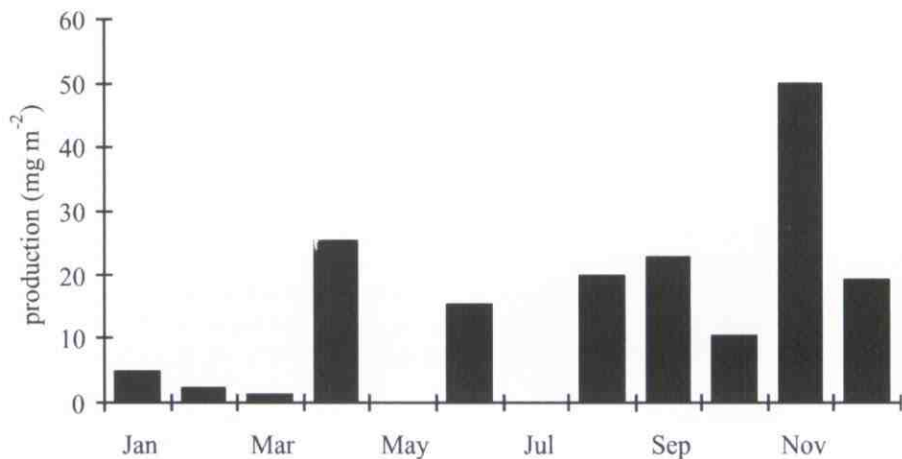


Figure 5. Temporal dynamics of secondary production of *E. torrentium* at Site B.

## Discussion

*E. torrentium* had a univoltine winter life history in the Agüera stream. Univoltinism is common among *Epeorus* spp. but in the literature, *E. torrentium* has been regarded as a bivoltine winter–summer species (Clifford, 1982). However, some degree of flexibility in its life history may exist, since Thibault (1971) described a bivoltine



winter–summer cycle for this species in a nearby stream in Southwestern France. He observed recruitment of small nymphs virtually during all the year. Most of the population had a univoltine winter life cycle, but a small fraction was bivoltine. In the present study, no evidence of a second generation was found, and the recruitment period (six months) was not as long as that reported by Thibault (1971).

The five mayfly species that have been studied in the Agüera stream, *Caenis luctuosa* (Burmeister), *E. torrentium*, *Ephemerella ignita* (Poda), *Habroleptoides confusa* (Sartori and Jacob), and *Habrophlebia lauta* (Eaton), have univoltine winter life histories (González et al., 2000, 2001, unpublished data), which is reported as the most common life cycle among the Ephemeroptera from temperate regions (Clifford, 1982). No obvious pattern emerged by comparing the phenologies of the life history of these five species. Furthermore, those of *E. ignita* and *C. luctuosa* changed among sites (González et al., 2000, 2001). Nevertheless, recruitment periods were very long in most cases; brief only in the less abundant populations (*Habroleptoides confusa* and *E. torrentium* at site 9, González et al., unpublished data). Another trait that was common to these five mayflies was the asynchrony of their life histories. Population asynchrony may include disadvantageous traits such as lower mating success, predator swamping and gene flow among populations (Sweeney & Vannote, 1981; Robinson et al., 1992). Nevertheless, it also provides benefits in variable environments by increasing the proportion of a population being in a non-vulnerable stage during disturbances (e.g., Fisher & Grimm, 1988; Scrimgeour et al., 1988; Zwick, 1996; Corkum et al., 1997). Thus, the asynchronous life histories observed in the Agüera stream could be interpreted as a result of the frequent and unpredictable floods that macroinvertebrates experience in this system. Basaguren & Riaño (1994) have also pointed out that the flow regime of the Agüera stream exerts a great influence on the invertebrate communities, and other authors (e.g., Rader & Ward, 1989; Robinson & Minshall, 1998) have associated asynchronous life histories with changing and unpredictable flow regimes.

The density, biomass and production of *E. torrentium* were all higher at the head-water site than at the downstream sites. The same shifts in *Epeorus* density were reported by Bargas et al. (1990) in other streams of the area, and by Graça et al. (1989) in a Portuguese river. Wohl et al. (1995) also found higher biomass and production of *Epeorus* at two first-order sites than at a third-order site in an Appalachian stream. More information is needed to identify the factors (e.g. water temperature, chemistry, hydraulics, substrate, food) that caused such patterns.

Conservative assumptions about CPIs may lead to underestimates of production when the size-frequency method is used (Benke, 1993; Morin & Dumont, 1994; Salas & Dudgeon, 2001). Nevertheless, the CPI of 12 months chosen in this study appeared to be correct at site B, because it gave a production estimate similar to that obtained using the instantaneous growth method (Table 3). We had no clear indication of shorter CPIs at downstream sites, but even with CPIs of 8 months, the *E. torrentium* production would be much lower than estimated at site B.

In contrast to abundance and production, the *P/B* ratios were highest at the two downstream sites. Thus, as was the case with the other mayflies in the Agüera stream (González et al., 2000, 2001, unpublished data), the differences in *E. torrentium*



production among sites were more related to spatial changes in biomass than to shifts in these ratios (i.e., growth rates; Waters, 1969). Furthermore, no common pattern was found along the Agüera stream neither in the secondary production nor in the *P/B* ratios of the five mayflies studied (Table 3). *E. torrentium* and *H. confusa* showed their highest production at the headwater site, whereas production of *C. luctuosa*, *E. ignita* and *H. lauta* at this site was virtually zero or much lower than that found at the downstream sites.

The production and biomass turnover rates of *E. torrentium* in the Agüera stream were within the range of published values for other *Epeorus* species, from  $7 \text{ mg m}^{-2} \text{ year}^{-1}$  (*E. nr. dispar* in North Carolina, Huryn & Wallace, 1987) to  $209 \text{ mg m}^{-2} \text{ year}^{-1}$  (*E. sylvicola* in the Atlas Mountains, Morocco; Ouashine et al., 1996) for production, and from  $6.3 \text{ year}^{-1}$  (*E. sylvicola*; Ouashine et al., 1996) to  $10.8 \text{ year}^{-1}$  (*Epeorus* sp. in Hong Kong, China; Dudgeon, 1999) for *P/B* ratios. Similarly, the production and *P/B* ratio values of *E. torrentium* were well inside the range of values found in the Agüera stream for other mayfly species (Table 3).

In conclusion, the life history and production dynamics of *E. torrentium* are in accordance with those showed by the other mayflies studied in the Agüera stream. All species have relatively long recruitment periods that may be seen as a 'bet-hedging' strategy allowing high resilience after floods. The spatial pattern of secondary production of this species and the other studied mayflies is mainly determined by their biomass at each site, with a minor influence of shifts in biomass turnover rates.

## Acknowledgements

The research was supported by the projects PB92-0459 and PB95-0498 from the Spanish Government (Ministerio de Educación y Ciencia) and by a Ph.D. grant to J. M. González from the Basque Government (Departamento de Educación, Universidades e Investigación). We are grateful to P. Riaño for her field and laboratory assistance, and to M.A. Puig for confirming our mayfly identifications. The comments made by two anonymous referees to improve the manuscript are also greatly acknowledged.

## References

- Alba-Tercedor J (1990): Life cycle and ecology of mayflies from Sierra Nevada (Spain), IV. *Limnetica* 6: 23–34.
- Bargos T, Mesanza JM, Basaguren A, Orive E (1990): Assessing river water quality by means of multifactorial methods using macroinvertebrates. A comparative study of main water courses of Biscay. *Water Res* 24: 1–10.
- Basaguren A, Riaño P (1994): Trophic structure variability of the invertebrate communities in the Agüera stream (Northern Spain). *Verh Int Verein Limnol* 25: 1727–1732.
- Benke AC (1979): A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. *Limnol Oceanogr* 24: 168–171.

- Benke AC (1984): Secondary production of aquatic insects. In: Resh VH, Rosenberg DM, eds., *Ecology of Aquatic Insects*. New York, Praeger, pp. 289–322.
- Benke AC (1993): Concepts and patterns of invertebrate production in running waters. *Verh Int. Verein Limnol* 25: 15–38.
- Brewin PA, Buckton ST, Ormerod SJ (2000): The seasonal dynamics and persistence of stream macroinvertebrates in Nepal: do monsoon floods represent disturbance? *Freshwat Biol* 44: 581–594.
- Clifford HF (1982): Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. *Quaest Entomol* 18: 15–90.
- Cobb DG, Galloway TD, Flannagan JF (1991): Life history adaptations of mayflies to an unstable reach of Wilson Creek, Manitoba, Canada. In: Alba-Tercedor J, Sanchez-Ortega A, eds., *Overview and Strategies of Ephemeroptera and Plecoptera*. Florida, Sandhill Crane Press, pp. 465–481.
- Corkum LD, Ciborowski JH, Poulin RG (1997): Effects of emergence date and maternal size on egg development and sizes of eggs and first-instar nymphs of a semelparous aquatic insect. *Oecologia* 111: 69–75.
- Cummins KW, Wilzbach MA, Gates DM, Perry JB, Taliaferro, WB (1989): Shredders and riparian vegetation. *BioScience* 39: 24–30.
- Dudgeon D (1999): Patterns of variation in secondary production in a tropical stream. *Arch Hydrobiol* 144: 271–281.
- Elósegui A, Pozo J (1994): Spatial versus temporal variability in the physical and chemical characteristics of the Agüera stream (Northern Spain). *Acta Oecol* 15: 543–559.
- Elósegui A, Pozo J (1998): Epilithic biomass and metabolism in a north Iberian stream. *Aquat Sci* 60: 1–16.
- Fisher SG, Grimm NB (1988): Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem. *Verh Int Verein Limnol* 23: 1189–1193.
- Georgian T, Wallace JB (1983): Seasonal production dynamics in a guild of periphyton-grazing insects in a southern Appalachian stream. *Ecology* 64: 1236–1248.
- González E, Pozo J (1996): Longitudinal and temporal patterns of benthic coarse particulate organic matter in the Agüera stream (northern Spain). *Aquat Sci* 58: 355–366.
- González JM, Basaguren A, Pozo J (2000): Life history and secondary production of *Ephemerella ignita* (Poda) (Ephemeroptera, Ephemerellidae) in a north Iberian stream. *Arch Hydrobiol* 147: 535–545.
- González JM, Basaguren A, Pozo J (2001): Life history and production of *Caenis luctuosa* (Burmeister) (Ephemeroptera, Caenidae) in two nearby reaches along a small stream. *Hydrobiologia* 452: 209–215.
- González JM, Basaguren A, Pozo J (in press): Size-mass relationships of stream invertebrates in a North Spain stream. *Hydrobiologia*.
- Graça MAS, Fonseca DM, Castro ST (1989): The distribution of macroinvertebrate communities in two Portuguese rivers. *Freshwater Biol* 22: 297–308.
- Hamilton AL (1969): On estimating annual production. *Limnol Oceanogr* 14: 771–782.
- Hurn AD, Wallace JB (1987): Local geomorphology as a determinant of macrofaunal production in a mountain stream. *Ecology* 68: 1932–1942.
- Hurn AD, Wallace JB (2000): Life history and production of stream insects. *Annu Rev Entomol* 45: 83–110.

- Hynes HBN, Coleman MJ (1968): A simple method of assessing the annual production of stream benthos. *Limnol Oceanogr* 13: 569–573.
- Lopez de Luzuriaga A (1995): *Dinámica y Colonización Perifíticas en el Río Agüera*. M.S. Thesis. Bilbao, Universidad del País Vasco.
- Morin A, Bourassa N (1992): Modèles empiriques de la production annuelle et du rapport P/B d'invertébrés benthiques d'eau courante. *Can J Fish Aquat Sci* 49: 532–539.
- Morin A, Dumont P (1994): A simple model to estimate growth rate of lotic insect larvae and its value for estimating population and community production. *J N Am Benthol Soc* 13: 357–367.
- Ouashine H, Céréghino R, Lavandier P (1996): Influence of temperature and macrophytes development on the larval population dynamics of *Epeorus sylvicola* Pict (Ephemeroptera) in a torrential river of the 'Haut-Atlas de Marrakech', (Morocco). *Ann Limnol* 32: 27–31.
- Rader RB, Ward JV (1989): Influence of impoundments on mayfly diets, life histories, and production. *J N Am Benthol Soc* 8: 64–73.
- Ricker WE (1946): Production and utilization of fish populations. *Ecol Monogr* 16: 373–391.
- Robinson CT, Minshall GW (1998): Macroinvertebrate communities, secondary production, and life history patterns in two adjacent streams in Idaho, USA. *Arch Hydrobiol* 142: 257–281.
- Robinson CT, Reed LM, Minshall GW (1992): Influence of flow regime on life history, production, and genetic structure of *Baetis tricaudatus* (Ephemeroptera) and *Hesperoperla pacifica* (Plecoptera). *J N Am Benthol Soc* 11: 278–289.
- Salas M, Dudgeon D (2001): Laboratory and field studies of mayfly growth in tropical Asia. *Arch Hydrobiol* 153: 75–90.
- Sanchez M, Hendricks AC (1997): Life history and secondary production of *Cheumatopsyche* spp. in a small Appalachian stream with two different land uses on its watershed. *Hydrobiologia* 354: 127–139.
- Scrimgeour GJ, Davidson RJ, Davidson JM (1988): Recovery of benthic macroinvertebrates and epilithic communities following a large flood in an unstable, braided, New Zealand river. *N Z J Mar Freshwater Res* 22: 337–344.
- Southwood TRE (1977): Habitat, the templet for ecological strategies? *J Anim Ecol* 46: 337–365.
- Southwood TRE (1988): Tactics, strategies and templets. *Oikos* 52: 3–18.
- Sweeney BW, Vannote RL (1981): *Ephemerella* mayflies of White Clay Creek: bioenergetic and ecological relationships among six coexisting species. *Ecology* 65: 1353–1369.
- Thibault M (1971): Le développement des Ephéméroptères d'un ruisseau à truites des Pyrénées-Atlantiques, Le Lissuraga. *Ann Limnol* 7: 53–120.
- Townsend CR, Hildrew AG (1994): Species traits in relation to a habitat templet for river systems. *Freshwater Biol* 31: 265–275.
- Waters TF (1969): The turnover ratio in production ecology of freshwater invertebrates. *Am Nat* 103: 173–185.
- Wohl DL, Wallace JB, Meyer JL (1995): Benthic macroinvertebrate community structure, function and production with respect to habitat type, reach and drainage basin in the southern Appalachians (U.S.A.). *Freshwater Biol* 34: 447–464.

- Zar JH (1996): *Biostatistical analysis*, 3rd edition, Upper Saddle River, Prentice Hall, pp. 277–279.
- Zwick P (1996): Variable egg development of *Dinocras* spp. (Plecoptera, Perlidae) and the stonefly seed bank theory. *Freshwater Biol* 35: 81–100.



Copyright of Aquatic Insects is the property of Swets & Zeitlinger, BV and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.