Hydrobiologia **452:** 209–215, 2001.

Life history and production of *Caenis luctuosa* (Burmeister) (Ephemeroptera, Caenidae) in two nearby reaches along a small stream

J. M. González[1,*], A. Basaguren[1] & J. Pozo[1]
[1]*Department of Plant Biology and Ecology, University of the Basque Country, P.O. Box 644, 48080 Bilbao, Spain*
[*]*Corresponding address: Department of Zoology, University of Coimbra, 3004-517 Coimbra, Portugal*
E-mail: xosemgv@yahoo.es

Received 17 July 2000; in revised form 26 February 2001; accepted 6 March 2001

Key words: rivers, life histories, secondary production, mayflies, *Caenis luctuosa*

Abstract

Population dynamics and production of *C. luctuosa* were compared in two reaches of the Agüera stream (northern Spain). This species showed univoltine winter life history in both sites. However, the start of the recruitment period, and the cohort production interval differed in 1 month between reaches. Secondary production of *C. luctuosa* ranged from 76 mg m^{-2} $year^{-1}$ (upper site) to 93 mg m^{-2} $year^{-1}$ (lower site). Although annual production seemed to be mainly influenced by the biomass found at each site, changes in life history may have also been important. The need to have accurate information about life history of the analysed species at the study sites when assessing secondary production is highlighted.

Introduction

Recently, the literature about life history and production of freshwater invertebrates has grown considerably. The development of the River Habitat Templet (Townsend & Hildrew 1994) has promoted a new interest on life history traits such as voltinism (e.g., Richards et al., 1997; Usseglio-Polatera et al., 2000) or length (Statzner et al., 1997) and timing (e.g., Tachet et al., 1994; Usseglio-Polatera & Tachet, 1994) of the reproductive period. Most studies on these traits consist of data collected in one site during 1 year (e.g., Majecki et al., 1997; Riaño et al., 1997). Nevertheless, some authors report spatial changes in life histories of freshwater invertebrates and try to relate these changes to differences in the physical habitat (e.g., Sanchez & Hendricks, 1997; Robinson & Minshall, 1998).

Knowledge of secondary production dynamics of stream invertebrates also has shown remarkable progress. Production is a composite of population parameters such as biomass, individual growth rate, survivorship, and development time that provide a measure of population function in the community (for a review, see Benke, 1993). Beyond quantification of energy flow, secondary production can be used to link population dynamics with other processes in the ecosystem. We find in the literature an array of papers that try to relate secondary production of some populations and communities with water chemistry (e.g., Eggert & Burton, 1994; Griffith et al., 1994), temperature (e.g., Rodgers, 1982; Morin & Bourassa, 1992), habitat stability (e.g., Robinson et al., 1992; Dudgeon, 1999), food resources (e.g., Behmer & Hawkins, 1986; Wallace et al., 1997), position in the river continuum (e.g., Wohl et al., 1995; Grubaugh et al., 1997), land use (e.g., Grubaugh & Wallace, 1995; Sanchez & Hendricks, 1997), or other human impacts (e.g., Rader & Ward, 1989; Whiles & Wallace, 1995).

Our aims in this work are (1) to describe life history and secondary production of the mayfly *Caenis luctuosa* (Burmeister, 1839) in two nearby sites along a third-order stream, and (2) to assess the consequences of changes in life history on the secondary production of this species.

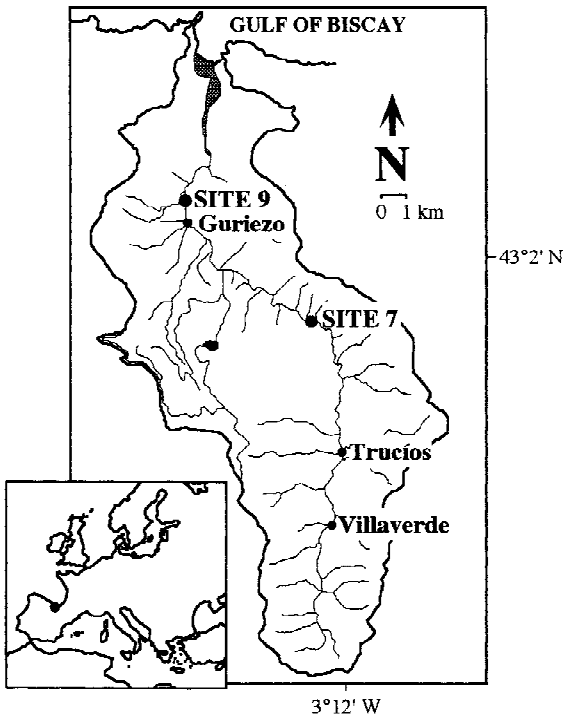

Figure 1. The Agüera stream basin. The study sites and the main human settlements are indicated.

Study area

The Agüera stream drains a small catchment (144 km^2) located between the Basque Country and Cantabria, northern Spain (Fig. 1). The climate in the zone is temperate oceanic, with mean monthly temperature ranging between 8.6°C (February) and 20.2°C (August) during 1993. The main land uses are pine (*Pinus radiata* D. Don) and eucalyptus (*Eucalyptus globulus* Labill.) plantations, meadows and heathlands. Autochthonous forests, dominated by *Quercus robur* L., *Q. ilex* L. and *Fagus sylvatica* L., still cover small areas in the basin. Human population is low (about 3000 inhabitants), and the only factory in the catchment is beside the stream estuary.

The two study sites are located in third order reaches (Fig. 1) that are numbered here as in previous papers (e.g., Elósegui & Pozo, 1998; González et al., 2000). At site 7 (43° 19′ 33″ N; 3° 17′ 29″ W), the stream flows through an area covered by eucalyptus plantations. Minor remnants of riparian vegetation persist, mainly discontinuous narrow strips of *Alnus glutinosa* (L.) Gaertner and *Platanus hispanica* Miller ex Münch. Due to self-purification in the reaches downstream Trucíos, water quality is good at this site

Table 1. Main characteristics of study sites. Those parameters with annual ranges in parentheses were measured monthly during 1993

	Site 7	Site 9
Elevation (m)	80	15
Drainage area (ha)	6906	11535
Channel width (m)	10	14
Channel slope (%)	0.8	0.4
Temperature (°C)	13.2 (7.7–20.3)	13.1 (6.3–19.5)
pH	8.2 (7.4–9.1)	7.4 (6.8–8)
Conductivity (μS cm^{-1})	226.8 (192–289)	193 (140–262)
Oxygen (mg/l)	11.5 (9.8–14)	10.4 (8.4–12.3)
Oxygen saturation (%)	107.8 (100–124)	96.4 (82–112)
Periphyton (g m^{-2})	23.4 (2.4–90.1)	15.5 (5.5–36.9)
CPOM (g m^{-2})	13.1 (8.7–37.5)	19.5 (9.8–55)

(Elósegui et al., 1995). Site 9 (43° 20′ 20″ N; 3° 20′ 20″ W) is located 8.5 km downstream of site 7. It drains a zone where croplands and meadows predominate. However, the channel is surrounded by a well-developed riparian forest composed, among others, by *Q. robur* L., *P. hispanica*, *A. glutinosa*, *Fraxinus excelsior* L. and *Laurus nobilis* L. Untreated sewage from Guriezo, the foremost village in the catchment, results in phosphate, nitrate and nitrite concentrations 4, 6 and 3 times higher than those found in reach 7 (Elósegui & Pozo, 1994). In 1990, epilithic biomass and chlorophyll-a concentration were higher at site 7 than at site 9 (Elósegui & Pozo, 1998). Such spatial differences were observed again in 1993 (Table 1) but, because of the high temporal variability of these parameters, they were not significant ($P>0.05$, two-way analysis of variance). More information on the study sites is shown in Table 1.

Materials and methods

Quantitative benthic samples were collected monthly from January to December 1993. At each site, five random replicates were taken using a Surber net (area 0.09 m^2, mesh size 250 μm), and preserved in the field in 5% formaldehyde. As depositional habitats were only a minor fraction of the river bed, no attempts were done to sample them. In the laboratory, invertebrates were sorted, identified and counted under a binocular microscope. Head width of each specimen was measured to the nearest 50 μm using a micrometer.

Individual dry weights of *C. luctuosa* were estimated from a head width–weight regression model

constructed using nymphs from the study sites. Live, non-damaged specimens were brought to the laboratory, measured to the nearest 50 μm, and transferred to preweighed aluminium foils. Then, they were dried at 60°C for 48 h, cooled during 1 h in a dessicator, and weighed to the nearest 0.01 mg.

Secondary production was determined by the size-frequency method (Hynes & Coleman, 1968) with the modifications by Hamilton (1969) and Benke (1979). The cohort production interval (CPI) was estimated as the time from the first hatchings to the first emergences.

Before performing statistical analyses, data on density, head width, individual weight, and biomass were log-transformed to eliminate heteroscedasticity (Zar, 1996). Spatial and temporal comparisons were made using two-way (time × site) analysis of variance (ANOVA) procedures; Tukey test was used for post-hoc comparisons among times (Zar, 1996).

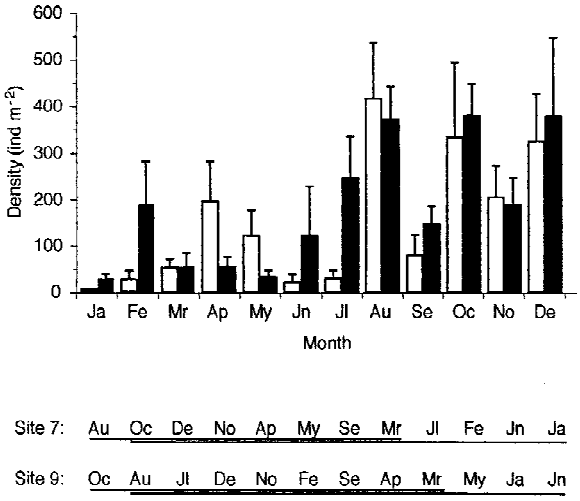

Figure 2. Density of *C. luctuosa* (mean +SE) at site 7 (white) and 9 (black) during the study period. The results of the temporal comparisons performed are showed in the bottom. Values increase from right to left; those linked by the same line do not show significant differences.

Results

The best correlation between size and weight was achieved using exponential equations that did not differ between sites ($P>0.05$, t-test). Thus, all morphometric data were pooled and one equation was calculated for both reaches:

$$DW = 0.00539\, e^{0.005HW}$$
$$n = 58, \quad r^2 = 0.842 \quad P < 0.0005,$$

where DW is dry weight (mg) and HW is head width (μm).

Density of *C. luctuosa* did not show spatial differences ($P>0.05$ for the site factor in ANOVA). Nevertheless, its temporal patterns differed between sites (Fig. 2). Maximum density at site 7 was recorded in August, and it was higher than those densities recorded in January, February, June and July. At site 9, maximum density was found in October; it only differed from those found in January, May and June.

C. luctuosa exhibited univoltine winter life histories (sensu Clifford 1982) in both sites (Fig. 3). At site 7, the first small nymphs were found in August, one month later than at site 9. High ranges of individual sizes were recorded during most of the year, indicating asynchronous life histories. At reach 7, recruitment period lasted from August to December (Fig. 3). At reach 9, it started in July and seemed to end in February, when the last small nymphs were found and a small peak in population density was recorded.

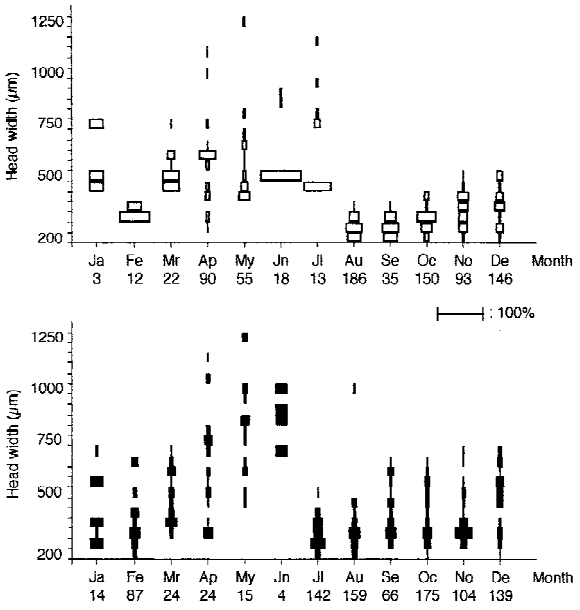

Figure 3. Size-frequency distribution of *C. luctuosa* at sites 7 (white) and 9 (black). The number of nymphs recorded in each sampling date appears in the horizontal axis.

Although nymphs started to grow immediately in both reaches, their greatest size remained around 750 μm during winter. Growth resumed in March, and maximum head widths were achieved in May (Fig. 3). At both sites, the first mature nymphs (individuals with black wing pads that are ready to emerge) were

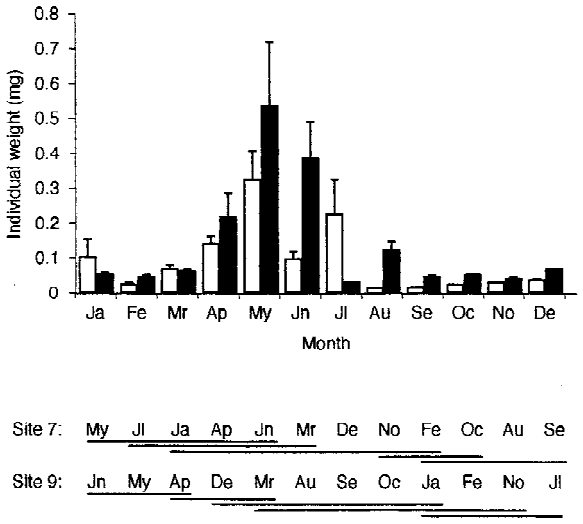

Figure 4. Individual weight of *C. luctuosa* (mean +SE) at site 7 (white) and 9 (black) during the study period. The results of the temporal comparisons performed are showed in the bottom. Values increase from right to left; those linked by the same line do not show significant differences.

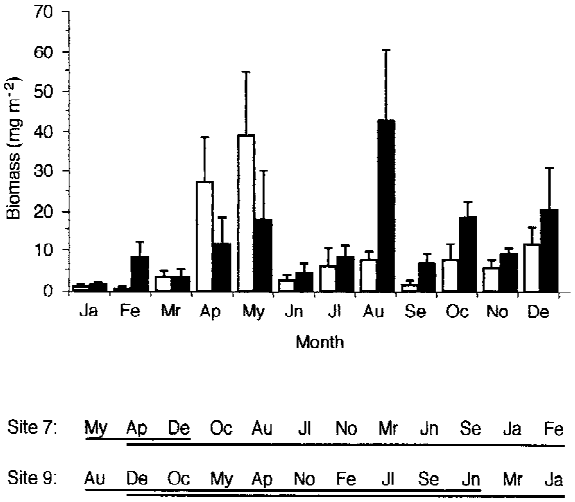

Figure 5. Biomass of *C. luctuosa* (mean +SE) at site 7 (white) and 9 (black) during the study period. The results of the temporal comparisons performed are showed in the bottom. Values increase from right to left; those linked by the same line do not show significant differences.

found in April. Thus, the CPI of *C. luctuosa* was 9 months at site 7 (August–April), and 10 months at site 9 (July–April). At the start of the emergence period, mean size and mean weight of nymphs did not show spatial differences (in both cases, $P>0.05$, *t*-test). In reach 7, emergence finished in July, when the last high sized nymphs were recorded. In reach 9, the main flight period concluded in June; nevertheless, some big specimens were recorded in August.

The mean weight of nymphs was greater at site 9 than at site 7 ($P<0.0005$ for the site factor in ANOVA, Fig. 4). However, this difference resulted from the spatial change in the phenology of *C. luctuosa*. When the mean weights of similar aged nymphs were compared (July at reach 7 with August at reach 9, August at reach 7 with September at reach 9, and so on) the differences were not significant ($P>0.05$ for the site factor in ANOVA). The greatest mean weights were found during the emergence period (Fig. 2). At both sites, weights did not increase between December and March (Fig. 4).

Biomass of *C. luctuosa* was greater at site 9 than at site 7 ($P<0.05$ for the site factor in ANOVA, Fig. 5), even when similar aged specimens were compared ($P<0.05$ for the site factor in ANOVA). This difference resulted from the high biomass recorded in August at reach 9. If we exclude this date from the comparisons no spatial differences were found ($P>0.05$ for the site factor in ANOVA). At site 7, maximum biomass was observed in May and differed from values recorded during the rest of the year excepting April and December (Fig. 5). At site 9, temporal differences in biomass were smaller. Its maximum value (August) only differed from those found in January and March. Mean annual biomass (B) was 9.5 mg m^{-2} in reach 7 and 13.1 mg m^{-2} in reach 9.

Secondary production of *C. luctuosa* (P) was also great at site 9 (92.8 mg m^{-2} $year^{-1}$) than at site 7 (75.6 mg m^{-2} $year^{-1}$). However, the P/B ratio found at reach 7 (7.9 $year^{-1}$) was greater than that found at reach 9 (7.1 $year^{-1}$). No spatial differences in cohort P/B ratios were observed (5.9 $year^{-1}$ at both reaches).

Discussion

C. luctuosa exhibited univoltine winter life histories in the two reaches of the Agüera stream. Clifford (1982) states that this is the most common type of life cycle among *Caenis* species. Nevertheless, the same author indicates that almost 31% of the studied populations are bivoltine and reports that the life cycle of many *Caenis* species can be quite flexible. This is true for *Caenis luctuosa*, as it can show univoltine winter (e.g., Brittain, 1974; Alba-Tercedor, 1981), bivoltine (e.g., Landa, 1968; Mol, 1983) and non-seasonal multivoltine life histories (Perán et al., 1999) depending on location.

Table 2. Comparisons of production (P, mg m^{-2} $year^{-1}$) and biomass turnover rate (*P*/*B*, $year^{-1}$) of *Caenis* species. Multivoltine populations are indicated with asterisks

Species	*P*	*P*/*B*	Habitat (site)	Reference
C. rivulorum	30	–	Experimental stream (Dorset, UK)	Welton et al. (1982)
C. luctuosa	76	7.9	Reach 7 (Northern Spain)	This study
Caenis spp.	82	59.1	Coastal plain stream (Georgia, USA)	Benke & Jacobi (1994)
Caenis spp.	86	58.8	Coastal plain stream (Georgia, USA)	Benke & Jacobi (1994)
C. luctuosa	93	7.1	Reach 9 (Northern Spain)	This study
Caenis sp. *	206	10.1	Experimental stream (Alabama, USA)	Rodgers (1982)
Caenis sp. *	271	11.5	Experimental stream (Alabama, USA)	Rodgers (1982)
Caenis sp. *	273	11.6	Experimental stream (Alabama, USA)	Rodgers (1982)
C. amica *	400	13.0	Experimental pond (Virginia, USA)	Christman & Voshell (1992)
C. horaria *	539	10.2	Woodland pond (Geneva, Switzerland)	Oertli (1993)
C. simulans	560	4.4	Plains stream (Minnesota, USA)	MacFarlane & Waters (1982)
Caenis sp. *	676	12.7	Experimental stream (Alabama, USA)	Rodgers (1982)
C. simulans	940	4.2	Plains stream (Minnesota, USA)	MacFarlane & Waters (1982)
C. luctuosa *	8158	23.7	Semiarid stream (Murcia, Spain)	Perán (1997)

The flexibility of the life cycles of this species becomes apparent in the Agüera stream, where we found that the start of egg hatching and the CPI differed by 1 month between reaches located only a few kilometres apart. Changes between sites 7 and 9 in the phenology and CPI of the mayfly *Ephemerella ignita* (Poda) also have been reported (González et al., 2000). Moreover, other works that describe changes in the life history of aquatic insects between reaches of a given river can be found in the literature (e.g., Wise, 1980; Sanchez & Hendricks, 1997). Usually, such spatial differences are explained as consequence of differences in water temperature (e.g., Payne & Miller, 1996; Robinson & Minshall, 1998; see Sweeney, 1984, for a review). Unfortunately, we did not conduct continuous recording of water temperature at the study sites. More difficulties arise considering that *C. luctuosa* hatches later and shows shorter CPI at site 7 than at site 9, while the life history of *E. ignita* exhibited the opposite spatial difference (González et al., 2000). Thus, it was not possible to establish the cause of the delay in the start of hatchings of *C. luctuosa* at site 7.

In both reaches, the life history of *C. luctuosa* was asynchronic with extended recruitment periods. Such traits are also exhibited by *E. ignita* in these reaches (González et al., 2000), and may be related to the unpredictable flow regimes that characterizes the Agüera stream. In such situations, asynchrony may increase the probability that part of the population is in a non-vulnerable stage during disturbances (e.g., Fisher & Grimm, 1988; Corkum et al., 1997).

The mean weight of *C. luctuosa* nymphs also showed spatial changes, with higher values at site 9 than at site 7. However, this seems to be the result of the observed shifts in the life history of this species, as no differences were found between the mean weights of similar aged specimens. Furthermore, mean nymphal weight was similar in both reaches at the start of the emergence period. This may have great importance considering that individual weight is linked to fecundity in aquatic insects (e.g., Sweeney & Vannote, 1978; Smock & Macgregor, 1988). In such case, our results suggest that the observed delay in recruitment of *C. luctuosa* at site 7 had no consequences on its reproductive success.

The density of *C. luctuosa* did not show spatial changes. Nevertheless, its biomass and secondary production were greater in reach 9 than in reach 7. It is difficult to link greater production in site 9 with the observed earlier hatching of eggs, as population density and mean individual weight were similar to those measured in site 7. On the other hand, earlier hatching in reach 9 may result in the spatial differences in *P*/*B* ratio (i.e., lower biomass turnover rate at site 9), as longer CPIs lead to smaller *P*/*B* values (Waters, 1979; Benke, 1984). However, this fact should have decreased production of *C. luctuosa* at site 9. In consequence, the spatial changes in secondary production of *C. luctuosa* may be purely attributed to the

observed differences in biomass. The same conclusion was reached in a previous paper on production dynamics of *E. ignita* in the Agüera stream (González et al., 2000).

Although the observed changes in the life cycle of *C. luctuosa* had no consequences on its annual production, we do not believe that they had no influence on the energetics of the community. Spatial changes in the temporal dynamics of biomass of this species were found (Fig. 5) and, thus, differences between sites in the phenology of production would be expected.

The secondary production of *C. luctuosa* in the Agüera stream was low relative to values obtained for *Caenis* species in previous reports (Table 2). Although our estimates were similar or higher than those reported for other univoltine populations (Welton et al., 1982; Benke & Jacobi, 1994), they were much lower than those recorded by MacFarlane & Waters (1982) for *C. simulans*, which is also univoltine. All other studied *Caenis* populations are multivoltine and show higher production values than those found in the Agüera stream.

The *P*/*B* ratios recorded in this study were also among the lowest values recorded in the literature, which agrees with the observed cessation of growth during winter. Nevertheless, such *P*/*B* values were higher than those of the populations studied by MacFarlane & Waters (1982), which attained high productions due to high biomass. All the multivoltine *Caenis* showed higher *P*/*B* values than those found in the Agüera. Finally, the cohort *P*/*B* ratios that we reported at sites 7 and 9 were inside the usual range in the literature (2–8, Benke, 1993). In fact, the low production of *C. luctuosa* found in the Agüera stream seems to be a consequence of both low mean annual biomass, and low biomass turnover rate.

In summary, we found spatial changes in the life history of *C. luctuosa* when comparing its population dynamics in two nearby reaches of one small stream. Such changes cannot be easily related with differences between sites in annual production. Nevertheless, shifts in cohort production intervals and, consequently, shifts in biomass turnover rates may be linked with these differences in life history. Furthermore, contrasting temporal patterns of secondary production might be expected at both sites. Thus, considering the flexibility in the life histories of some aquatic insects, assumptions about CPIs, and *P*/*B* ratios must be discouraged in studies of secondary production.

Acknowledgements

Financial support for data collection and analysis was provided by the research project DGICYT PB 92-0459 (Ministerio de Educación y Ciencia). Additionally, J. M. González received a Ph.D. grant from the Basque Government. We also thank E. González, J. Molinero and J. R. Díez for their help in the field work, and A. Otermin, X. Larrañaga and J. Barquín for laboratory assistance. Special thanks to P. Riaño for her aid in invertebrate identification. Suggestions made by two anonymous referees are also greatly appreciated.

References

Alba-Tercedor, J., 1981. Life cycle and ecology of mayflies from Sierra Nevada (Spain), IV. Limnetica 6: 23–34.

Behmer, D. J. & C. P. Hawkins, 1986. Effects of overhead canopy on macroinvertebrate production in a Utah stream. Freshwat. Biol. 16: 287–300.

Benke, A. C., 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. Limnol. Oceanogr. 24: 168–171.

Benke, A. C., 1984. Secondary production of aquatic insects. In: Resh, V. H. & D. M. Rosenberg (eds), The Ecology of Aquatic Insects. Praeger Publishers, New York: 289–322.

Benke, A. C., 1993. Concepts and patterns of invertebrate production in running waters. Verh. int. Ver. Limnol. 25: 15–38.

Benke, A. C. & D. J. Jacobi, 1994. Production dynamics and resource utilization of snag-dwelling mayflies in a blackwater river. Ecology 73: 1219–1232.

Brittain, J. E., 1974. Studies on the lentic Ephemeroptera and Plecoptera of southern Norway. Norsk entomol. Tids. 21: 135–154.

Christman, V. D. & J. R. Voshell, 1992. Life history, growth and production of Ephemeroptera in experimental ponds. Ann. ent. Soc. Am. 85: 705–712.

Clifford, H. F., 1982. Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. Quaest. Entomol. 18: 15–90.

Corkum, L. D., J. J. H. Ciborowski & R. G. Poulin, 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.

Dudgeon, D., 1999. Patterns of variation in secondary production in a tropical stream. Arch. Hydrobiol. 144: 271–281.

Eggert, S. L. & T. M. Burton, 1994. A comparison of *Acroneuria lycorias* (Plecoptera) production and growth in northern Michigan hard- and soft-water streams. Freshwat. Biol. 32: 21–31.

Elósegui, A. & J. Pozo, 1994. Spatial versus temporal variability in the physichal and chemical characteristics of the Agüera stream (Northern Spain). Acta Oecol. 15: 543–559.

Elósegui, A. & J. Pozo, 1998. Epilithic biomass and metabolism in a north Iberian stream. Aquat. Sci. 60: 1–16.

Elósegui, A., X. Arana, A. Basaguren & J. Pozo, 1995. Self-purification processes along a medium-sized stream. Environ. Manage. 19: 931–939.

Fisher, S. & N. Grimm, 1988. Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem. Verh. int. Ver. Limnol. 23: 1183–1189.

González, J. M., A. Basaguren & J. Pozo, 2000. Life history and production of *Ephemerella ignita* (Poda) (Ephemeroptera, Ephemerellidae) in a north Iberian stream. Arch. Hydrobiol. 147: 535–545.

Griffith, M. B., S. A. Perry & W. B. Perry, 1994. Secondary production of macroinvertebrate shredders in headwater streams with different baseflow alkalinity. J. n. am. benthol. Soc. 13: 345–356.

Grubaugh, J. W. & J. B. Wallace, 1995. Functional structure and production of the benthic community in a Piedmont river: 1956–1957 and 1991–1992. Limnol. Oceanogr. 40: 490–501.

Grubaugh, J. W., J. B. Wallace & E. S. Houston, 1997. Production of benthic macroinvertebratre communities along a southern Appalachian river continuum. Freshwat. Biol. 37: 581–596.

Hamilton, A. L., 1969. On estimating annual production. Limnol. Oceanogr. 14: 771–782.

Hynes, H. B. N. & M. J. Coleman, 1968. A simple method of assessing the annual production of stream benthos. Limnol. Oceanogr. 13: 569–573.

Landa, V., 1968. Developmental cycles of Central European Ephemeroptera and their interrelations. Acta ent. bohemoslov. 65: 276–284.

MacFarlane, M. B. & T. F. Waters, 1982. Annual production by caddisflies and mayflies in a western Minnesota plains stream. Can. J. Fish. aquat. Sci. 39: 1628–1635.

Majecki, J., M. Grzybkowska & R. Reddy, 1997. Density, production and life cycle of *Brachycentrus subnubilus* Curtis (Trichoptera: Brachycentridae) in a lowland river, Central Poland. Hydrobiologia 354: 51–56.

Mol, A. W. M., 1983. *Caenis lactea* (Burmeister) in the Netherlands (Ephemeroptera: Caenidae). Entomol. berich. 43: 119–123.

Morin, A. & N. Bourassa, 1992. Modèles empiriques de la production annuelle et du rapport *P*/*B* d'invertebrés benthiques d'eau courante. Can. J. Fish. aquat. Sci. 49: 532–539.

Oertli, B., 1993. Leaf litter processing and energy flow through macroinvertebrates in a woodland pond (Switzerland). Oecologia 96: 466–477.

Payne, B. S. & A. C. Miller, 1996. Life history and production of filter-feeding insects on stone dikes in the lower Mississippi River. Hydrobiologia 319: 93–102.

Perán, J., J. Velasco & A. Millán, 1999. Life history and secondary production of *Caenis luctuosa* (Ephemeroptera) in a semiarid stream (Southeast Spain). Hydrobiologia 400: 187–194.

Rader, R. B. & J. V. Ward, 1989. Influence of impoundments on mayfly diets, life histories, and production. J. n. am. benthol. Soc. 8: 64–73.

Riaño, P., A. Basaguren & J. Pozo, 1997. The life history and food habits of *Siphonoperla torrentium* (Plecoptera: Chloroperlidae) in Northern Spain. In Landolt, P. & M. Sartori (eds), Ephemeroptera and Plecoptera: Biology — Ecology — Systematics, MTL, Fribourg: 60–64.

Richards, C., R. J. Haro, L. B. Johnson & G. E. Host, 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshwat. Biol. 37: 219–230.

Robinson, C. T. & G. W. Minshall, 1998. Macroinvertebrate communities, secondary production, and life history patterns in two adjacent streams in Idaho, USA. Arch. Hydrobiol. 142: 257–281.

Robinson, C. T., L. M. Reed & G. W. Minshall, 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.

Rodgers, E. B., 1982. Production of *Caenis* (Ephemeroptera: Caenidae) in elevated water temperatures. Freshwat. Invertebr. Biol. 1: 2–16.

Sanchez, M. & A. C. Hendricks, 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.

Smock, L. A. & C. A. Macgregor, 1988. Impact of the American chestnut blight on aquatic macroinvertebrates. J. n. am. benthol. Soc. 7: 212–221.

Statzner, B., K. Hoppenhaus, M. F. Arens & P. Richoux, 1997. Reproductive traits, habitat use and templet theory: a synthesis of world wide data on aquatic insects. Freshwat. Biol. 38: 109–135.

Sweeney, B. W., 1984. Factors influencing life-history patterns of aquatic insects. In Resh, V. H. & D. M. Rosenberg (eds), The Ecology of Aquatic Insects. Praeger Publishers, New York: 56–100.

Sweeney, B. W. & R. L. Vannote, 1978. Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. Science 200: 444–446.

Tachet, H., P. Usseglio-Polatera & C. Roux, 1994. Theoretical habitat templets, species traits, and species richness: Trichoptera in the Upper Rhône Rive and its floodplain. Freshwat. Biol. 31: 397–415.

Townsend, C. R. & A. G. Hildrew, 1994. Species traits in relation to a habitat templet for river systems. Freshwat. Biol. 31: 265–275.

Usseglio-Polatera, P. & H. Tachet, 1994. Theoretical habitat templets, species traits, and species richness: Plecoptera and Ephemeroptera in the Upper Rhône River and its floodplain. Freshwat. Biol. 31: 357–375.

Usseglio-Polatera, P., M. Bournaud, P. Richoux & H. Tachet, 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. Freshwat. Biol. 43: 175–205.

Wallace, J. B., S. L. Eggert, J. L. Meyer & J. R. Webster, 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277: 102–104.

Waters, T. F., 1979. Influence of benthos life history upon the estimation of secondary production. J. Fish Res. Bd Can. 36: 1425–1430.

Welton, J. S., M. Ladle & J. A. B. Bass, 1982. Growth and production of five species of Ephemeroptera larvae from an experimental recirculating stream. Freshwat. Biol. 12: 103–122.

Whiles, M. R. & J. B. Wallace, 1995. Macroinvertebrate production in a headwater stream during recovery from anthropogenic disturbance and hydrological extremes. Can. J. Fish. aquat. Sci. 52: 2402–2422.

Wise, E. J., 1980. Seasonal distribution and life histories of Ephemeroptera in a Northumbrian river. Freshwat. Biol. 10: 101–111.

Wohl, D. L., J. B. Wallace & J. L. Meyer, 1995. Benthic macroinvertebrate community structure, function and production with respect to habitat type, reach and drainage basin in the southern Appalachians (U.S.A.). Freshwat. Biol. 34: 447–464.

Zar, J. H., 1996. Biostatistical Analysis. 3rd edn. Prentice Hall, Upper Saddle River, NJ, USA, 662 pp.