

Macroinvertebrate communities along a third-order Iberian stream

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The macroinvertebrate community was studied in 3 reaches along a north-Iberian stream that differ in the amount and nature of food resources. Regardless of shading and water quality, both invertebrate density and biomass were higher at the 2 downstream sites than at the headwater site. The taxonomic composition and functional organization of the faunal assemblages showed clear differences among sites: shredders and gatherers dominated the headwater site, and scrapers or gatherers, depending on the degree of shading and organic pollution, dominated the downstream sites. Macroinvertebrates responded roughly to inter-site differences in food resources, but poor relationships between temporal dynamics of shredder or scraper abundance and that of their food were found. Likewise, no clear effect of floods on invertebrate density and biomass was observed.

Keywords : streams, macroinvertebrate communities, food resources, shredders, scrapers.

Introduction

Many studies have tried to elucidate the main factors influencing macroinvertebrate community composition and abundance in streams (e.g. Hart 1992, Dudgeon 1994, Giller & Twomey 1993, Maridet et al. 1998, Tierney et al. 1998, Pardo 2000, Doisy & Rabeni 2001). Considerable attention has been paid to food resources (e.g. Hawkins & Sedell 1981, Cowan & Oswood 1984, Boulton & Lake 1992, Friberg 1997, Wallace et al. 1997) because invertebrate community structure is thought to be tightly linked to the nature and availability of these resources (Vannote et al. 1980). Additionally, environmental disturbances may exert a great influence on the macroinvertebrate communities (e.g. Resh et al. 1988, Townsend 1989, Townsend & Hildrew 1994). Variations in stream flow are seen as a major disturbance in these systems (e.g. Poff & Ward 1989, Yount & Niemi 1990, Robinson & Minshall 1998). The influence of floods on biotic communities seems to be related with their intensity, frequency and predictability (e.g. Minshall 1988, Resh et al. 1988).

In 1990, Basaguren et al. (1996) examined the macroinvertebrate assemblages of a heterotrophic and an autotrophic reach of the Agüera stream (northern Spain). The differences in fauna between both sites were explained as a result of inter-site differences in food and flow refugia availability. Furthermore, the results of that previous work suggested that the temporal patterns of macroinvertebrate communities were determined by both food and flow regime. In this paper we extend our analysis of macroinvertebrate communities to 3 reaches of the Agüera catchment: 2 shaded (first-order, and third-order) reaches, and an open third-order reach. Our main hypothesis was that inter-site differences in community features such as species composition and functional organization would reflect spatial differences in food availability. Moreover, we expected that floods would influence the temporal patterns of macroinvertebrate communities by decreasing total numbers of invertebrates, while increasing density of some opportunistic taxa.

Methods and materials

Study site

The Agüera is a third-order stream that drains a small basin (144 km²) located between Cantabria and

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the Basque Country (northern Spain). The catchment geology is dominated by siliceous materials, but calcareous outcrops are found in the central and lower part of the catchment. The climate is temperate oceanic, without severe drought in summer. During the study year (1993) the rainfall was 1330 mm, and mean monthly air temperatures ranged from 8.6° C (February) to 20.2° C (August). The catchment vegetation is mainly pine (*Pinus radiata* D. Don) and eucalyptus (*Eucalyptus globulus* Labill.) plantations, meadows, heathlands and small forests of *Quercus* spp. and *Fagus sylvatica* L. The population density is low (about 20 inhabitants/km²), and the human activities upstream of our study sites are forestry and ranching.

The 3 study reaches were distributed along the longitudinal axis of the stream system, and were named here 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 first-order tributary of the Agüera stream. The reach is surrounded by a forest of *Quercus robur* L., *Castanea sativa* Miller and *Alnus glutinosa* (L.) Gaertner among other species. Water shows low conductivity at this site (Table 1). Site 7 (43° 12' 37" N; 3° 15' 46" W) is a third-order reach located among eucalyptus plantations. The banks are covered by some narrow patches of *A. glutinosa* and *Platanus hispanica* Miller ex Münch and *E. globulus* stands. This site is located downstream a broad calcareous zo-

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 stocks (CPOM) were measured in terms of ash free dry mass.

	Site B	Site 7	Site 9
Elevation (m)	350	80	15
Drainage area (Ha)	184	6906	11535
Channel width (m)	4	10	14
Channel slope (%)	9	0.8	0.4
Bedrock (%)	19	8	0
Boulders (%)	4	12	1
Cobbles (%)	19	33	22
Pebbles (%)	20	24	44
Gravel (%)	17	21	26
Sand (%)	7	1	6
Temperature (°C)	11 (6.3-16.6)	13.19 (7.7-20.3)	13.05 (6.3-19.5)
pH	6.9 (6.3-7.4)	8.21 (7.4-9.1)	7.40 (6.8-8.0)
Conductivity (µS/cm)	107.9 (96-121)	226.8 (192-289)	193.0 (140-262)
Oxygen (mg/l)	10.8 (8.8-12.8)	11.50 (9.8-14.0)	10.35 (8.4-12.3)
Oxygen saturation (%)	100 (92-113)	107.83 (100-124)	96.42 (82-112)
Epilithon (g/m ²)	7.9 (3.5-15.4)	23.4 (2.4-90.1)	15.5 (5.5-36.9)
CPOM (g/m ²)	62.4 (20.5-195.2)	13.1 (5.7-37.5)	19.5 (9.8-55)

ne which increases pH and conductivity of water (Table 1). Site 9 (43° 20' 20" N; 3° 20' 20" W) is a third-order reach immediately downstream Guriezo, the largest village in the basin. Its banks are covered by a well-developed riparian forest with *Q. robur*, *P. hispanica*, *A. glutinosa* and *Fraxinus excelsior* L. as the main species. Urban sewage from Guriezo increases dissolved phosphate, nitrate and nitrite concentrations of water at this site (Elósegui & Pozo 1994).

The food resources for the stream biota differed among sites (Table 1). During the study year, the levels of coarse particulate organic matter (CPOM) were highest at site B, intermediate at site 9, and lowest at site 7 (see also González & Pozo 1996); epilithon biomass was higher at sites 7 and 9 than at site B (see Lopez de Luzuriaga 1995). In 1990, Elósegui & Pozo (1998) found higher epilithon biomass at site 7 than at site 9; nevertheless, due to high temporal variability, such difference was not observed in 1993.

Sampling and data analysis

The sampling was carried out once a month during 1993. Five random replicates were taken at each site using a Surber net (area 0.09 m², mesh size 250 µm), and immediately fixed in 5 % formaldehyde. At the laboratory, the invertebrates were sorted under a binocular microscope at 10x, preserved in 70 % ethanol, identified, and counted.

The fauna was assigned to 6 functional feeding groups following several sources, mainly Merritt & Cummins (1996), and the work of Riaño (1998) on the diet of Plecoptera, Ephemeroptera and Trichoptera in the Agüera stream. The groups used were collector-filterers ("filterers"), collector-gatherers ("gatherers"), collector-gatherer-scrappers ("gatherer-scrappers"), predators, scrapers and shredders. To determine dry mass, the invertebrates were placed in preweighed aluminium foils according to their functional group, oven-dried at 60° C for 48 hours, cooled in a dessicator, and weighed again (precision 0.01 mg) in a Sartorius MC2109 balance. Preservation of samples may cause changes in the mass of macroinvertebrates (e.g. Howmiller 1972, Leuven et al. 1985, González 2000). Nevertheless, because the samples remained stored for up to 6 years, such bias should not affect the results of the comparisons among sites and dates.

Community composition was examined with a detrended correspondence analysis (DCA) (Hill & Gauch 1980) using the computer program CANOCO (ter Braak 1992). DCA ordination was carried out on 35 taxa within which the 20 dominant taxa in each study site were included. The information lost was negli-

gible, since the variance explained using these main species was only 1.8 % lower than that explained when the whole community was analysed.

Before subsequent statistical analysis, data on invertebrate abundance (expressed in terms of density and biomass) were log-transformed to improve normality and homoscedasticity (Zar 1996). Two-way analysis of variance (ANOVA: time x site) was used to test differences in mean monthly values among sites. When ANOVA found significant differences ($p < 0.05$), Tukey test was performed for post-hoc comparisons. Relationships between invertebrate abundance and food (CPOM stocks or epilithon biomass; data from González & Pozo 1996 and Lopez de Luzuriaga 1995) were analysed using simple linear correlation analyses (Zar 1996).

Results

95 taxa were recorded from the 3 study sites. Richness was lowest at the headwater reach (65 taxa), intermediate at reach 7 (71), and highest at reach 9 (79). Macroinvertebrate community structure also showed clear differences among the 3 study sites. The most abundant taxa at site B were Chironomidae, *Baetis*, *Rhithrogena*, and *Echinogammarus tarragonensis* Pinkster (Fig. 1). The latter species only appeared at this site, being replaced by *E. berilloni* (Catta) in the lower study sites. At reach 7, the predominant taxa were Chironomidae, *Potamopyrgus antipodarum* (Gray), *Baetis* and *Esolus parallelepipedus* (Müller). *Potamopyrgus antipodarum* and *E. parallelepipedus* were rare species at site B (mean annual density < 30 ind/m²). Finally, at site 9, Chironomidae and Oligochaeta constituted the main part of the community.

The results from the ordination analysis (Fig. 2) also reflected the great differences among the macroinvertebrate communities found at the 3 study sites. The first axis of the DCA accounted for 29.6 % of the total variance. Samples taken at site B showed relatively low scores on axis-1, and did not overlap with those from sites 7 and 9. Densities of *Rhithrogena*, *Siphonoperla torrentium* Pictet, *Polycelis* and *Nemoura* were negatively correlated with axis-1, which indicate that they were most abundant at site B. By contrast, other taxonomic groups, as *P. antipodarum*, *Lepidostoma hirtum* Fabricius, *E. parallelepipedus*, and Hydracarina were placed at the right side of the plot.

The second axis accounted for 10.7 % of the total variance. It separated the composition of samples taken at site 9 (highest scores) from those taken at sites 7 and

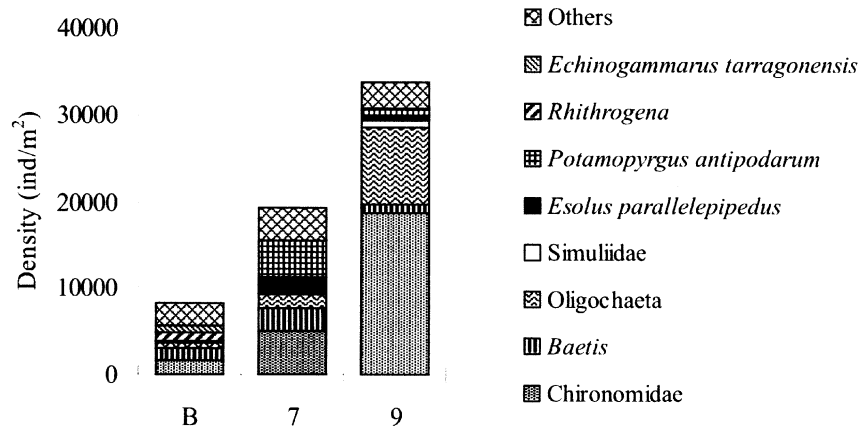


Fig. 1. Mean annual density of the main taxa found at the study sites.

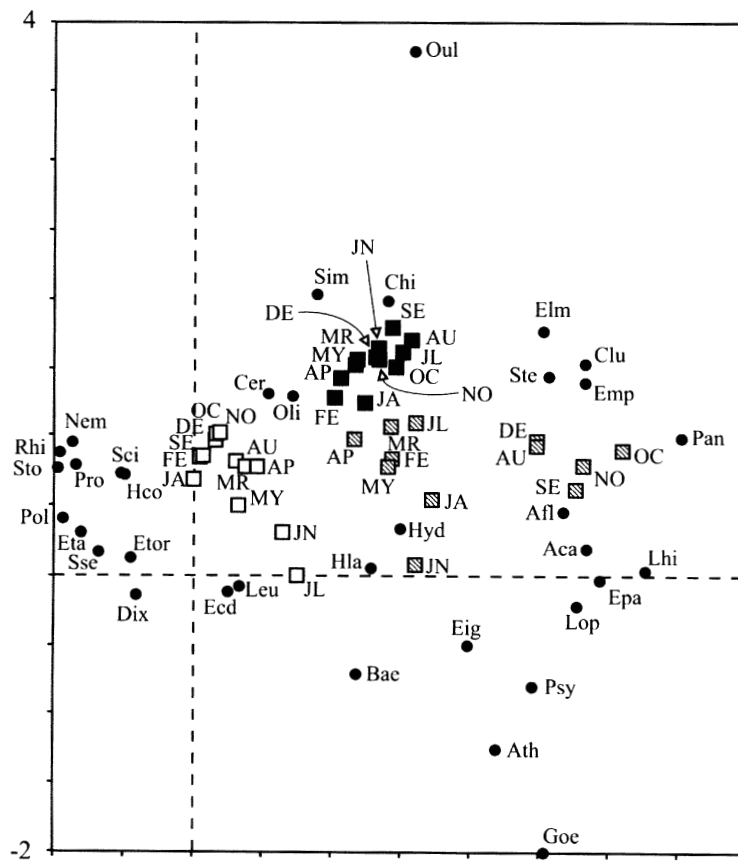


Fig.2. DCA ordination diagram of species (circles) and samples (squares). Species are labelled with the abbreviations shown in Appendix 1. Samples from site B are depicted in white, those from sites 7 are striped, and those from site 9 are black. Abbreviations for month when samples were taken are also indicated.

B. Abundant taxa that may account for this separation are Goeridae and *Atherix*, which showed very negative scores on the axis-2, and *Oulimnius* and Simuliidae, which had high scores. Chironomids were situated in the upper half of the biplot, near the samples from reach 9, denoting that although they were proportionally abundant at all sites, they attained highest densities at that reach. The third axis accounted for only 3.3 % of the total variance and was not further considered in this analysis.

The variability of scores on both axes was lower in samples from site 9 than in those from sites B and 7. Samples from reach 7 formed two discrete groups: those taken between August and December (placed at the right side of the biplot) and those taken from January to July (at the left side).

In addition to these differences in taxonomical composition, there were clear changes in the functional organization of the macroinvertebrate community. In terms of density, gatherers constituted the bulk of the fauna found at site 9 (Fig. 3). At site 7, gatherers, gatherer-scrappers and scrapers were the most abundant groups, whereas at site B, the main groups were gatherers and shredders. The importance of gatherers lessens if we study the community organization using biomass instead of density (Fig. 3). Gatherers constituted the main part of the invertebrate biomass at site 9, scrapers dominated at reach 7, and shredders at site B.

The abundance of each functional group showed very clear differences among sites ($p < 0.0005$ for the site in the two-way ANOVAs excepting the case of predator biomass, which had $p < 0.001$ for that factor).

Shredder density and biomass were highest at site B (Table 2), whereas the greatest values for gatherer-scrappers, predators and scrapers were found at site 7, and those for filterers and gatherers were recorded at site 9. Spatial patterns in density were similar to those in biomass except in the case of shredders and total macroinvertebrates. Macroinvertebrate density and biomass were significantly higher at sites 9 and 7 than at site B.

In most cases, no correlations were found between density or biomass of invertebrates and CPOM stocks or epilithon biomass. Nevertheless, a positive relationship between CPOM levels and invertebrate biomass was observed at reach 7 ($p < 0.05$, $r^2 = 0.352$). Density and biomass of shredders or grazers also showed no correlation with abundance of their food resources.

The invertebrate density increased from January to June-August, and decreased afterwards (Fig. 4). At sites 7 and 9, the invertebrate biomass followed a pattern similar to that of density, which indicates that the temporal changes in the mean individual mass of animals were small. At site B, the invertebrate biomass did not show the same temporal differences as density, and peaked in September and November.

In general, no clear relationships between variations in flow and density or biomass of macroinvertebrates were observed (Fig. 4). The flood in March, the highest that occurred during the study period, could be associated with decreases in macroinvertebrate density, but only at site 9 ($p < 0.05$). Nevertheless, in the ordination diagram (Fig. 2), samples from March and February were close, indicating that the flood did not cause major changes in community composition. Mo-

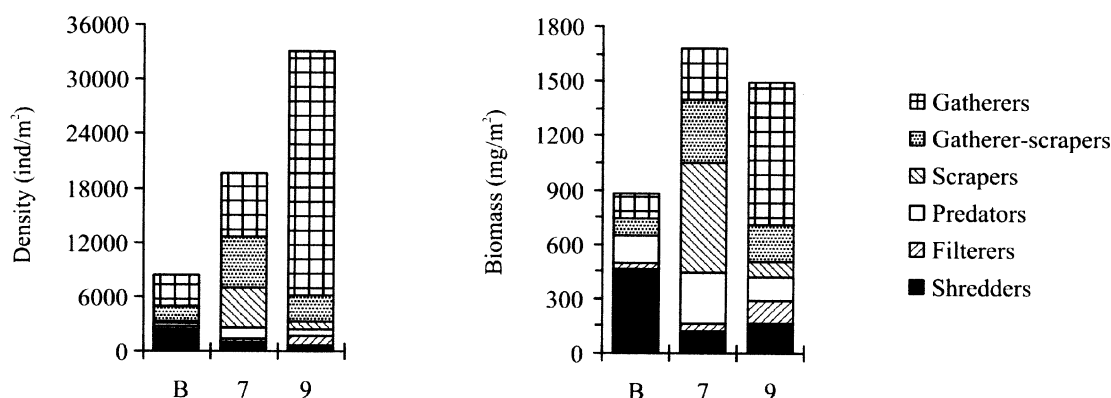


Fig. 3. Functional group composition in terms of mean annual density (left) and mean annual biomass (right) at the study sites.

Table 2. Results of the Tukey tests comparing the macroinvertebrate density and biomass found at the 3 study sites. Those values linked by the same line do not show significant differences.

	Density	Biomass
Filterers	9 > <u>B</u> 7	9 > 7 <u>B</u>
Gatherers	9 > 7 > B	9 > 7 > B
Gatherers-scrappers	7 > 9 > B	7 > 9 > B
Predators	7 > <u>B</u> 9	7 > <u>B</u> 9
Scrapers	7 > 9 > B	7 > 9 > B
Shredders	<u>B</u> > 7 > 9	<u>B</u> > 7 9
Total macroinvertebrates	9 > 7 > B	7 9 > B

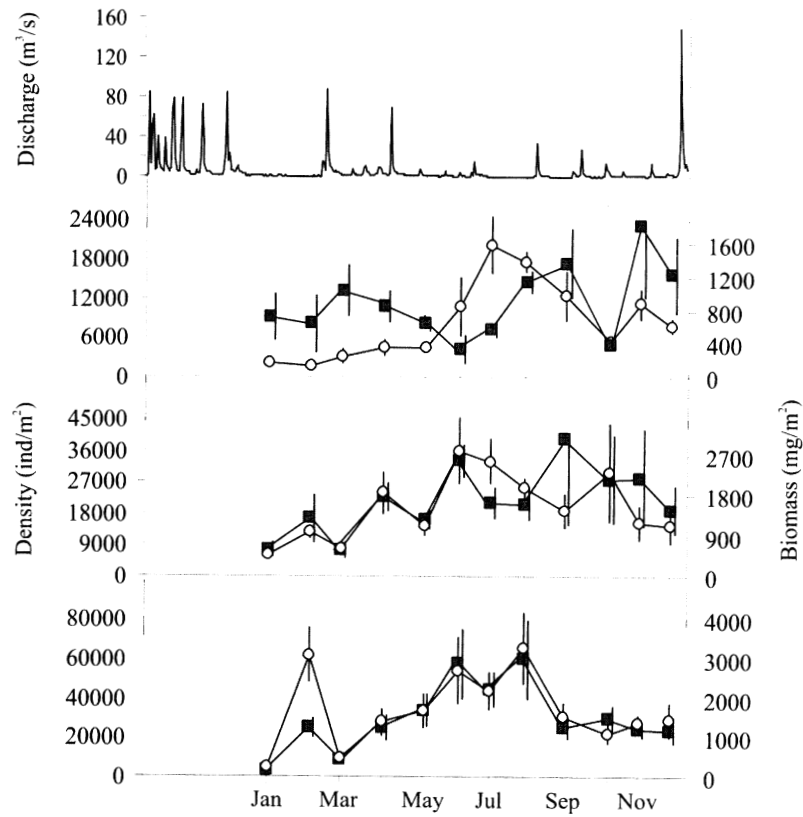


Fig. 4. Daily discharge of the Agüera stream at site 9 from October 1992 to December 1993 (top), and changes in density (circles) and biomass (squares) of invertebrates at sites B, 7, and 9. Vertical lines indicate standard errors.

reover, invertebrate biomass variations from February to March were not significant ($p > 0.05$). The floods observed during autumn 1992 also had no effect on macroinvertebrate density, as values registered in December 1993 (i.e. without previous floods) did not differ significantly from densities recorded in January 1993 (at all sites, $p > 0.05$).

Discussion

The taxonomic composition of the macroinvertebrate community differed from site to site. Basaguren & Riaño (1994) and Basaguren et al. (1991) also reported marked differences between the benthic assemblages found at a headwater and at a third-order site of the Agüera stream. The results of the ordination analysis showed that the community found at site 9 had the smallest temporal changes. At site B, greater differences between samples were observed, but no temporal patterns emerged. By contrast, samples taken at site 7 between August and December differed from those taken from January to July, which had axis-1 scores similar to those exhibited by samples from site 9. The proximate cause is that *L. hirtum* and *P. antipodarum* had their highest densities in August-December. Nevertheless, the ultimate cause remains obscure.

The River Continuum Concept hypothesis predicts that the invertebrate communities of undisturbed small streams (i.e. order ≤ 3) of temperate regions are dominated by shredders and gatherer-collectors (Vannote et al. 1980). This was the case for the forested, undisturbed, first order site B, but not for the open site 7 nor for the polluted site 9. Although an array of factors (e.g. water chemistry, substrate, temperature) differed between the study sites, the observed changes in the functional organization of the community were in accordance with the shifts in food resources. The predominance of shredders and gatherers in canopied upper reaches, such as site B, has been reported previously in other river systems (e.g. Hawkins & Sedell 1981, Friberg 1997, Maridet et al. 1998) and in the Agüera stream (Basaguren & Riaño 1994, Basaguren et al. 1996). Similarly, other authors have also pointed out that scrapers may be the dominant group in open reaches (e.g. Dudgeon 1989, Basaguren et al. 1996, Grubaugh et al. 1997). Finally, the high importance of gatherers (mainly chironomids and oligochaetes) at site 9 may be interpreted as a consequence of urban sewage inputs (e.g. Cao et al. 1997).

Some authors have found correlations between the abundance of shredders and detritus (e.g. Hawkins & Sedell 1981, Cowan & Oswood 1984, Dudgeon 1989,

Stout et al. 1993, Whiles & Wallace 1995, Murphy & Giller 2000). However, others have not found such correlations (e.g. Boulton & Lake 1992, Friberg 1997, Maridet et al. 1998, Doisy & Rabeni 2001). In the Agüera stream, shredders did not follow strictly the same spatial pattern as their food: density of shredders was higher at site 7 than at site 9 in spite that the latter accumulated more CPOM than the former. Spatial changes in CPOM quality could obscure the relationship between shredders and their food (e.g. Smock & MacGregor 1988, Hawkins et al. 1982, Dudgeon & Wu 1999). At the present study, higher shredder biomass - CPOM stocks ratios were found at downstream reaches than at headwater (9.0, 8.4 and 7.3 in sites 9, 7 and B) suggesting that 1) shredders would be less limited by CPOM quantity at site B, a forested, headwater reach, than at the downstream sites, and 2) shredders were more efficient in CPOM use in downstream reaches, a fact reported previously by Basaguren et al. (1996). This suggested difference in shredder efficiency could be linked to spatial changes in detritus quality because 3 study sites with differing composition of CPOM were compared (González & Pozo 1996). Furthermore, the nutrient content of leaf litter, one of the main components of its quality (Anderson & Sedell 1979, Cummins & Klug 1979, Webster & Benfield 1986, Boulton & Boon 1991), increases with conditioning time at downstream reaches of the Agüera stream, but not at oligotrophic headwaters (Pozo 1993, Molinero et al. 1996). Nevertheless, these spatial changes in detritus quality, if they existed, could not explain the observed spatial pattern of shredder abundance. Thus, our data indicate that other factors besides CPOM quantity and quality have determined shredder abundance at each site. Among them, sewage inputs at site 9 could be important, since they might explain the almost total absence of *L. hirtum* at this reach (mean annual density 6 ind/m²), an abundant shredder at site 7 (mean annual density 184 ind/m²) with reported low tolerance to pollution (González del Tánago & García de Jalón 1984, Bargas et al. 1990).

Food limitation in shredder communities has been often pointed out in literature (e.g. Gee 1988, Richardson 1991, Dobson & Hildrew 1992, Basset & Glazier 1995). The low levels of detritus standing stocks (González & Pozo 1996), the correlation found between invertebrate biomass and CPOM stocks, and the high ratio shredder biomass / detritus mass (see above) could indicate that this is also the case with shredder guild at site 7. Nevertheless we must recognize that more evidence is needed to prove this hypothesis. More studies on the spatial distribution of shredders in re-

lation to their food (e.g. Friberg 1997, Dobson 1999) or on the response of shredders to food additions (e.g. Richardson 1991, Dobson & Hildrew 1992) could help to confirm or rule out such an explanation.

Both invertebrate density and biomass were higher at the downstream sites than at the upper site. Basaguren et al. (1996) also reported higher density at site 7 than at a headwater reach in the Agüera stream, and suggested that it could be due to lower impact of floods on invertebrate communities at downstream reaches. Nevertheless, in our case, we had no evidence of such fact, and the spatial patterns observed could have other explanations. For example, some authors have noted that open reaches, as it is the case for site 7, support higher invertebrate abundance than canopied ones (e.g. Hopkins 1976, Hawkins et al. 1982, Behmer & Hawkins 1986, Maridet et al. 1998), which is attributed to higher food quality of periphyton than leaf detritus (Anderson & Cummins 1979). On the other hand, high faunal density at site 9 could be a consequence of the organic sewage from Guriezo which allows high densities of Chironomidae and Oligochaeta (Wiederholm 1984).

Although other works in the Agüera stream have related the flow regime with changes in community functional organization (Riaño et al. 1993) or density (Basaguren et al. 1996), no obvious relationships between the temporal dynamics of invertebrates and that of discharge emerged in this work. This result was unexpected because the 1993-floods were more intense than those observed by Riaño et al. (1993) and Basaguren et al. (1996) in 1990. Such discordance must be interpreted with caution because, due to the rapid recovery of some stream invertebrate communities (e.g. Maier 2001), a monthly sampling may be inaccurate to observe the effects of floods on these communities, especially in streams, such as the Agüera, that experience frequent, unpredictable floods. Moreover, the influence of flow regime goes beyond temporal reductions in their abundance, since it constitutes a major component of the habitat template (Minshall 1988, Poff & Ward 1990). In this sense, it is noteworthy that the present knowledge on the Agüera invertebrates suggests that they follow asynchronous life histories with extended recruitment periods (González et al. 2000, González et al. 2001, Basaguren et al. 2002), a trait that becomes advantageous in systems exposed to frequent, unpredictable floods (e.g. Poff & Ward 1989, Rader & Ward 1989, Robinson & Minshall 1998). Thus, even if 1993-floods had not caused reduction in invertebrate abundance or community composition, we would be far from saying that they had no consequences on the invertebrate assemblages.

In summary, the results of this study indicate very different invertebrate communities from site to site, both in terms of composition and functional organization. In spite of scraper and shredder abundances did not strictly follow the spatial pattern found for CPOM stocks and epilithon biomass, the functional structure of the invertebrate assemblages may be related to the nature of the food resources present at each site. The temporal patterns of the invertebrate communities during the study year could not be related with the occurrence of floods. Nevertheless, other community traits suggest that the flood regime of this small stream exerts a great influence on the stream-dwelling invertebrate communities.

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Appendix: Abbreviations used in Fig. 2.

- Aca: Hydracarina
 Afl: *Ancylus fluviatilis* (Müller). Mollusca
 Ath: *Atherix* spp. Diptera
 Bae: *Baetis* spp. Ephemeroptera
 Cer: Ceratopogonidae. Diptera
 Clu: *Caenis luctuosa* (Burmeister). Ephemeroptera
 Chi: Chironomidae. Diptera
 Dix: Dixidae. Diptera
 Ecd: *Ecdyonurus* spp. Ephemeroptera
 Eig: *Ephemerella ignita* (Poda). Ephemeroptera
 Elm: *Elmis* spp. Coleoptera
 Emp: Empididae. Diptera
 Epa: *Esolus parallelepipedus* (Müller). Coleoptera
 Eta: *Echinogammarus tarragonensis* Pinkster. Amphipoda
 Eto: *Epeorus torrentium* Eaton. Ephemeroptera
 Goe: Goeridae. Trichoptera
 Hco: *Habroleptoides confusa* (Sartori & Jacob). Ephemeroptera
 Hla: *Habrophlebia lauta* (Eaton). Ephemeroptera
 Hyd: *Hydraena* spp. Coleoptera
 Leu: Leuctridae. Plecoptera
 Lhi: *Lepidostoma hirtum* Fabricius. Trichoptera
 Lop: *Limnius opacus* Müller. Coleoptera
 Nem: *Nemoura* spp. Plecoptera
 Oli: Oligochaeta
 Oul: *Oulimnius* spp. Coleoptera
 Pan: *Potamopyrgus antipodarum* (Gray). Mollusca
 Pol: *Polycelis* spp. Tricladia
 Pro: *Protonemura* spp. Plecoptera
 Psy: Psychomyiidae. Trichoptera
 Rhi: *Rhithrogena* spp. Ephemeroptera
 Sci: Scirtidae. Coleoptera
 Sim: Simuliidae. Diptera
 Sse: *Sericostoma selysii* Pictet. Trichoptera
 Ste: *Stenelmis* spp. Coleoptera
 Sto: *Siphonoperla torrentium* Pictet. Plecoptera