

## Macroinvertebrate community structure in an intermittent and a permanent Mediterranean streams (NE Spain).

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### ABSTRACT

Benthic invertebrate communities of two undisturbed Mediterranean streams were compared with respect to seasonal variation in richness, density, biomass, size and functional feeding groups. Seasonal variability of temperature and discharge differed among these streams and constituted a source of disturbance to the community. La Solana stream is characterised by a summer dry period, floods in winter and spring and a high range of water temperature, whereas Riera Major is a permanent stream and floods are uncommon throughout the year. Richness and biomass were lower in La Solana than in Riera Major. Larvae of *Hydropsyche* gr. *pellucidula* and *Ecdyonurus insignis* Eaton from La Solana were smaller than from Riera Major. Cluster analysis revealed a different seasonal distribution of the biomass of different functional feeding groups that suggests variations in their food-web structure. Autumn communities of the two streams were the most distinctive due to a high total biomass in La Solana and a high shredder biomass in Riera Major. Marked seasonality appeared to be important determinant of invertebrate community structure.

**Keywords:** Functional feeding groups, community structure, floods, drying.

### RESUMEN

*En este estudio se compararon las comunidades de dos ríos mediterráneos no alterados con referencia a la riqueza de especies, densidad, biomasa, tamaños y grupos tróficos funcionales. La variabilidad estacional de la temperatura y del caudal son diferentes entre estos dos ríos y constituyen la fuente de alteración de la comunidad. La Solana se caracteriza por presentar veranos secos, crecidas en invierno y primavera y un amplio rango de fluctuaciones de la temperatura, mientras que la Riera Major es un río con caudal permanente y las crecidas son poco frecuentes a lo largo del año. La riqueza de especies y la biomasa fueron más bajas en La Solana que en la Riera Major. Las larvas de *Hydropsyche* gr. *pellucidula* y *Ecdyonurus insignis* Eaton de La Solana fueron más pequeños que las de la Riera Major. Un análisis de agrupamiento ha revelado una distribución estacional diferente de la biomasa y de los distintos grupos tróficos funcionales, lo que sugiere variaciones en la estructura de la red trófica. Las mayores diferencias entre los ríos se observaron en las comunidades de otoño debido a la alta biomasa total de La Solana y a la elevada biomasa de trituradores en la Riera Major. La marcada estacionalidad parece ser un factor determinante de la estructura de la comunidad de macroinvertebrados.*

**Palabras clave:** Grupos tróficos funcionales, estructura de la comunidad, inundaciones, sequías.

### INTRODUCTION

Streams in Mediterranean region are subjected to sequential seasonal events of flooding and drying over an annual cycle. Disturbance regimes are an important element to select for life-history features (Resh *et al.* 1988) that favour resistance to be removed by floods and for survival during droughts. Gasith & Resh (1999) propose that a seasonal sequence of biotic and abiotic regulation of assemblage response across the flooding-

drying period. Although environmental (abiotic) factors dominate during floods, they are reduced when the discharge decreases, which is also a time when biotic control becomes important. As the dry season progresses, environmental conditions become extreme and may again regulate stream populations and community structure. In that way, density, species composition, biomass and diversity could differ between seasonal assemblages in Mediterranean streams, reflecting temporal changes in resource availability and

habitat conditions related to intensity and frequency of seasonal disturbance.

The structure of intermittent stream communities changes markedly in response to variation in the physico-chemical regime (Boulton & Lake 1992). Closs & Lake (1994) observed an increase in the number of species and a change in functional feeding groups as the period of constant streamflow lengthened, whereas Legier & Talin (1973) and Miller & Golladay (1996) observed similar number of taxa in permanent and temporary streams. The inherent variability of intermittent streams provides an opportunity to examine the effect of seasonal variation on aspects of the function and structure of the invertebrate community. Little is known about these aspects in streams of the Mediterranean basin.

This study was conducted in two second order streams of the Mediterranean region in north-eastern Spain, La Solana and Riera Major. Although both watersheds are close together, mean annual precipitation and the annual precipitation regime are slightly different, altering the flow regime and water temperature of the two streams. In La Solana flow ceases in late summer but can increase by 1-2 orders of magnitude as a result of intense rain in spring. Riera Major is a permanent stream and floods are uncommon throughout the year. The objective of this study was to describe, over an annual cycle, the structure of invertebrate community of two undisturbed Mediterranean streams with different discharge regime. The primary focus was comparing seasonal differences in structural parameters (density, biomass, individual size, richness and functional feeding groups) in this two streams, considering that stream with higher variability will present more important changes in community structure in response to flow regime.

## METHODS

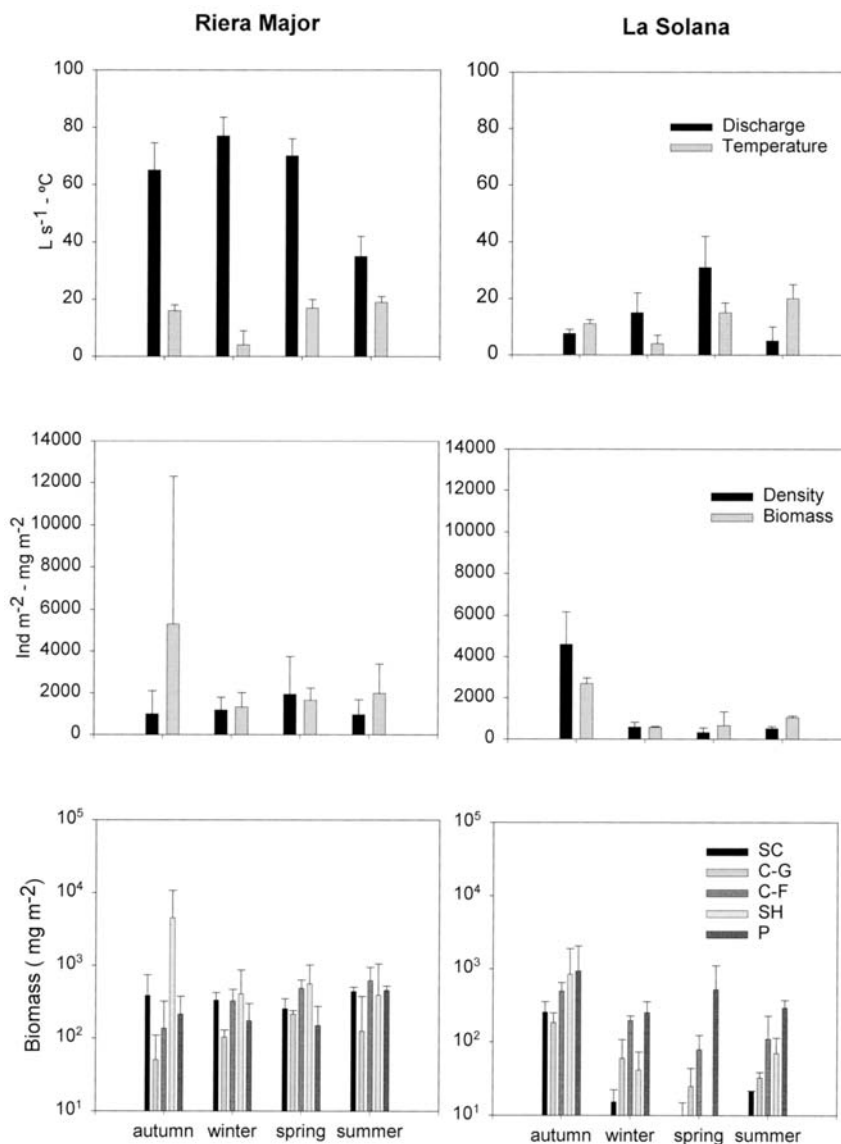
### Site description

Two second order pristine streams, tributaries of the Ter river in the NE of Spain were studied:

Riera Major (41°56'N, 2°25'E) and La Solana (42°8'N, 2°14'E) streams. Watershed size and altitude are similar (15.5 km<sup>2</sup> and 960-460 m a.s.l. Riera Major and 16.1 km<sup>2</sup> and 980-500 m a.s.l. La Solana). Mean annual precipitation is lower in La Solana (837 mm, data from 1987-1994 period) than in Riera Major (1016 mm). Precipitation is more seasonal in La Solana with a dry period from July to September and peaks in early winter and spring. The local climate of each watershed is reflected in the particular flow regime and water temperature of the two streams. Annual coefficients of variation for discharge and temperature in La Solana are twice those measured in Riera Major. In La Solana summer baseflow is <6 L s<sup>-1</sup>, and flow often ceases in late summer. Peaks are observed in spring with maximum values over 40 L s<sup>-1</sup>. Discharge in Riera Major is higher with a minimum values in summer around 30 L s<sup>-1</sup> (Figure 1).

Riera Major drains a siliceous watershed dominated by igneous rocks. Stones, boulders, and sand are the dominant components of the streambed. The riparian vegetation consists mainly of alders (*Alnus glutinosa* (L.) Gaertn.) covering (in terms of shade) most of the stream channel. Mean discharge varied from 24 to 85 L s<sup>-1</sup>. At the study reach, stream width averaged 3.7 m and depth was 30 cm. Mean monthly water temperatures ranged from 3.2 to 18.9°C. Concentration of soluble reactive phosphorus was in average 19.2±2.9 µg L<sup>-1</sup>. Maximum values were recorded in summer (73.2 µg L<sup>-1</sup>), and minimum in winter (5.5 µg L<sup>-1</sup>). The epilithic community (Guasch and Sabater, 1998) is dominated in summer by a rhodophycean alga, *Hildenbrandia rivularis* Liebm. During autumn and early spring this alga is partially covered by diatoms. During late spring and summer a filamentous green alga (*Cladophora glomerata* (L.) Kütz.) appears in places with higher water velocity.

La Solana drains a sedimentary calcareous watershed (calcite and dolomite). Riparian vegetation is made up of deciduous trees from the adjacent forest (*Fagus sylvatica* L., *Acer* spp.) and some riparian tree species (*Coryllus avellana* L., *Salix* spp.). At the site studied the streambed



**Figure 1.** Seasonal variation of discharge, water temperature, mean total density and biomass and biomass contributions of functional feeding groups, in La Solana and in Riera Major during the study period. Bars are the standard deviation. SC, scrapers; C-G, collector-gatherers; C-F, collector-filterers; SH, shredders; P, predators. *Variabilidad estacional en el caudal, temperatura del agua, densidad y biomasa media y distribución de biomasas por grupos funcionales, en La Solana y la Riera Major durante el período estudiado. La barras indican la desviación estándar. SC, ramoneadores; C-G, recolectores; C-F, filtradores; SH, trituradores; P, depredadores.*

was dominated by accumulations of sand, limestone, boulders and stones. Mean width was 5 m and average depth 10 cm. This stream is subjected to extreme fluctuations in water flow, velocity, and water temperature. During the period of study, water temperature ranged from 0.7 to 25° C. The stream was dry from July to September

and water was occasionally frozen during the winter. Soluble reactive phosphate (SRP) concentration was very low ( $8.0 \pm 0.9 \mu\text{g L}^{-1}$ ) and did not vary among seasons. The epilithic community is characterised by thick encrusting mats of filamentous cyanobacteria which are dominant in winter, and coexist with filamentous green algae

in summer and early autumn. Diatoms are noticeable during spring and autumn (Guasch & Sabater, 1998).

### Biological characteristics

A 30 metre stretch in each stream was sampled monthly between October 1992 and October 1993. La Solana stream was not sampled between July and September because it was dry. Individual stones were used as the sampling units and ten individual stones were randomly collected at each site using a net (mesh size 250  $\mu\text{m}$ ). Twenty stones were measured by wrapping them in aluminium foil and their area was estimated through a multiple regression involving the foil weight and linear measurements of the three main dimensions of the stone ( $r=0.991$ ,  $n=20$ ,  $p<0.001$ ). Therefore, we only measured the linear dimensions to obtain the surface area of the stones at each sampling time. Invertebrates were identified to species or genus level, except for Diptera (family), Acari, and Oligochaeta. Assignment of taxa to functional feeding groups followed the classification of Cummins & Merritt (1996). Each macroinvertebrate taxa was weighed to calculate biomass as dry weight (60° C until constant weight). At each site, final instar larvae of *Hydropsyche gr. pellucidula* and *Ecdyonurus insignis* (Eaton) were measured and weighed separately to provide an estimation of the average length and biomass of these species. Total length was measured for Ephemeroptera and head capsule width was measured for Trichoptera. Taxon richness and the Shannon-Wiener diversity index were also calculated.

### Data analysis

Length and biomass of measured species were compared between streams using a t-test. The normality of data distribution and homogeneity of variances were assessed to determine whether data transformation was required. Biomass values were  $\log(x+1)$  transformed before the analysis. Two-way analysis of variance (sampling

site and sampling time as factors) was applied to samples in order to compare biological variables between sites. Classification analyses of samples were done with UPGMA agglomerative clustering on the Euclidean distance index (Statistica for Windows, StatSoft, 1995).

## RESULTS

Forty-five and thirty-eight taxa were recorded in Riera Major and La Solana respectively. Taxon composition was dominated by Trichoptera (14 and 11 taxa in the two sites) and Diptera (9 and 7 taxa) followed in importance by Ephemeroptera, Plecoptera and Coleoptera (Table 1). Diptera was the most abundant group followed by Ephemeroptera and Trichoptera at the two sites. Density was higher in Riera Major than in La Solana except for autumn when La Solana had more individuals (Figure 1). Density increased in Riera Major from autumn to spring (from 988 to 1930  $\text{ind m}^{-2}$ ) and decreased in summer (960  $\text{ind m}^{-2}$ ). Mean autumn abundance in La Solana was 4590  $\text{ind m}^{-2}$  while density during the rest of the year was around 500  $\text{ind m}^{-2}$ .

Species richness was significantly lower (ANOVA,  $F=10.42$ ,  $p=0.009$ ) in La Solana, mainly in winter, spring and summer. Richness in Riera Major was greatest in winter due to the presence of several species that mainly appear in that season (*Rhyacophila tristis* Pictet, *Tinodes* sp. and Limoniidae) and those that persisted from autumn to the end of winter like *Perlodes intricata* Pictet. In autumn, richness decreased in Riera Major and was similar to that found in La Solana. In this stream the overlap of species between seasons was considerable, with a similar number of species in all seasons. Therefore, only a small increase in species richness was observed in spring, reflecting the absence of some insect taxa from autumn-winter period (Table 1). The Shannon-Wiener diversity index was not significantly different between the two sites.

In both streams, the highest biomass occurred in autumn (Fig. 1). Biomass increased nearly four times in autumn with respect to the average values

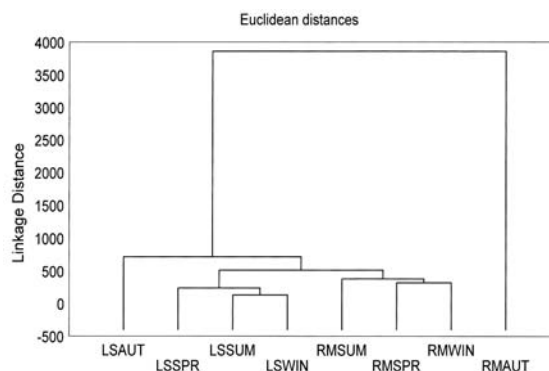
**Table 1.** Mean macroinvertebrate biomass (mg DW m<sup>-2</sup>) and diversity index in the two streams during the sampling period. Values in parentheses indicate standard deviation. X, biomass <0.1 mg m<sup>-2</sup>. *Densidad media de macroinvertebrados (mg PS m<sup>-2</sup>) e índice de diversidad en los dos ríos durante el período de muestreo. Los valores entre paréntesis indican la desviación estándar. X, biomasa <0.1 mg m<sup>-2</sup>.*

	Riera Major				La Solana			
	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
OLIGOCHAETA	0.8 (1.0)	0.3 (0.2)	0.7 (0.5)	X	4.7 (3.3)	0.3 (0.2)	X	X
ANNELIDA								
<i>Erpobdella</i> sp.	153 (105)	126 (115)	110 (37.3)	371 (461)	-	-	-	-
MOLLUSCA								
<i>Ancylus fluviatilis</i> Müller	4 (1.8)	0.8 (1.1)	0.4 (0.3)	1.2 (1.5)	-	-	-	-
Lymnaeidae	-	-	-	X	0.9 (1.3)	0.2 (0.3)	-	3.5 (2.8)
EPHEMEROPTERA								
<i>Epeorus sylvicola</i> Pictet	94 (24)	111 (100)	62 (61)	315 (205)	72 (94)	6.4 (9.1)	-	-
<i>Ecdyonurus insignis</i> Eaton	262 (347)	153 (133)	124 (28)	75 (101)	9.6 (4.9)	7.8 (2.5)	5.4 (6.2)	18 (3)
<i>Baetis</i> spp.	26 (32)	70 (39)	158 (188)	95 (107)	171 (133)	58 (42)	19 (6)	20 (2)
<i>Ephemerella ignita</i> Poda	-	X	0.63 (0.04)	0.27 (0.28)	10.2 (1.5)	0.7 (0.1)	3.1 (4.3)	7.1 (6.8)
<i>Ephemera</i> sp.	-	X	-	-	3.9 (2)	1.3 (0.7)	1 (0.9)	-
<i>Caenis</i> sp.	-	-	0.1 (0.2)	X	4 (4)	0.3 (0.2)	X	X
PLECOPTERA								
<i>Protonemura vandeli</i> Berthélemy	0.4 (0.5)	0.8 (0.4)	1 (1.1)	0.4 (0.2)	7 (5)	1.7 (0.9)	X	X
<i>Anphinemura triangularis</i> Ris	1.6 (2.2)	3.1 (3)	1.1 (1.6)	-	2.1 (0.9)	-	-	-
<i>Leuctra</i> sp.	0.5 (0.6)	0.6 (0.6)	2.8 (3.7)	0.9 (0.8)	37 (39)	6.5 (3.1)	2.9 (3.5)	5.5 (2)
<i>Perla marginata</i> Panzer	40 (46)	22 (23)	3.4 (5.6)	43 (42)	49 (70)	37 (52)	-	-
<i>Perlodes intricata</i> Pictet	4.6 (5.5)	2.4 (3.1)	-	0.2 (0.3)	57 (2.7)	1.3 (0.8)	1.1 (1.6)	0.2 (0.2)
ANISOPTERA								
Aeschnidae	-	-	-	-	765 (1060)	69 (97)	464 (656)	267 (87)
COLEOPTERA								
<i>Elmis</i> spp.	2.5 (1.6)	1.6 (1)	2.4 (0.9)	10 (11)	84 (62)	2.5 (0.7)	6.3 (1.4)	3.2 (1.8)
<i>Dryops</i> sp.	-	0.5 (0.5)	0.2 (0.2)	1 (1.3)	-	-	-	-
<i>Potamophilus acuminatus</i> Fabricius	2 (2.6)	0.8 (1.1)	-	0.6 (1)	-	-	-	-
<i>Dupophilus brevis</i> Mulsant & Rey	0.7 (1.1)	0.2 (0.2)	0.5 (0.7)	0.5 (0.8)	-	-	13.7 (8.9)	1 (1.4)
TRICHOPTERA								
<i>Rhyacophila dorsalis</i> Curtis	-	10.5 (8.4)	20 (22)	14 (12.5)	19.3 (8.1)	9.6 (7.2)	-	-
<i>Rhyacophila tristis</i> Pictet	-	2.2 (4)	-	1.7 (3)	-	3.1 (4.4)	1.5 (2.1)	3.2 (4.6)
<i>Rhyacophila meridionalis</i> Pictet	-	-	-	-	-	-	6.5 (9.2)	-
<i>Agapetus</i> sp.	7.8 (11)	48 (43)	25 (18)	19 (23)	9 (8.5)	0.3 (0.5)	-	0.5 (0.7)
<i>Hydropsyche</i> spp.	-	-	-	-	87 (53)	90 (15)	27 (16)	15 (1.4)
<i>Hydropsyche pellucidula</i> Curtis	102 (137)	170 (82)	116 (12)	216 (34)	400 (100)	102 (28)	52 (60)	88 (112)
<i>Hydropsyche sitalai</i> Döhler	25 (35)	118 (36)	121 (34)	351 (358)	-	-	-	-
<i>Psychomyia pusilla</i> Fabr.	-	0.7 (1.1)	0.4 (0.3)	0.2 (0.2)	2.8 (0.2)	0.8 (0.9)	1.5 (1.9)	X
<i>Tinodes</i> sp.	2.4 (1.5)	X	-	-	-	-	-	-
<i>Polycentropus</i> sp.	4.4 (6.2)	2.3 (2.2)	13 (3.4)	17.1 (6)	31 (23)	8.4 (4.2)	2.7 (3.8)	17.3 (10)
<i>Halesus radiatus</i> Curtis	4372 (6077)	264 (428)	501 (649)	20 (34)	750 (353)	22 (31)	-	58 (43)
<i>Sericostoma</i> sp.	151 (173)	129 (47)	46 (20)	359 (397)	-	-	-	-
<i>Silo</i> sp.	5 (7)	11 (19)	3 (4)	23 (14)	-	-	-	-
<i>Hydroptila</i> sp.	-	-	-	X	X	-	-	-
<i>Philopotamus</i> sp.	-	5 (7.2)	11 (15.3)	16.4 (14.5)	-	1.9 (2.6)	-	1.0 (1.2)
<i>Wormaldia</i> sp.	-	-	-	X	-	-	-	-
DIPTERA								
Simuliidae	5.8 (8.3)	6.6 (5)	14.4 (13.2)	2 (3.1)	2.3 (1.3)	2 (0.4)	0.3 (0.3)	5 (5.5)
Chironomidae	17.2 (22)	28 (30)	45 (52)	11.4 (5.5)	108 (96)	8 (2)	4.3 (4.1)	11 (1.1)
Empididae	8 (11)	4.3 (3.2)	1.4 (0.7)	0.5 (0.4)	6.8 (9.6)	8 (6.7)	1.7 (0.7)	-
Athericidae	2 (0.2)	0.2 (0.4)	-	2.4 (1.5)	11.2 (13)	0.3 (0.4)	0.9 (1)	0.4 (0.3)
Ceratopogonidae	-	-	X	X	1.6 (1.3)	0.1 (0.2)	X	X
Blephariceridae	1.7 (2.4)	2.8 (1.7)	34 (48)	-	-	-	-	-
Psychodidae	-	-	X	-	-	-	X	0.2 (0.3)
Stratiomyidae	X	-	-	-	-	-	X	0.9 (1.3)
Limoniidae	2.7 (1.4)	-	-	-	-	-	-	-
Richness	25 (1.4)	30.6 (0.6)	28 (2.0)	30 (3.5)	26.5 (0.7)	24.5 (0.7)	20.5 (2.1)	23.5 (2.1)
Shannon-Wiener Diversity	3.2 (0.2)	3.3 (0.06)	3.1 (0.3)	3.1 (0.3)	2.6 (0.8)	3.1 (0.1)	3.1 (0.02)	2.8 (0.3)

for the rest of the year, due mainly to the trichopteran *Halesus radiatus* Curtis. In La Solana, Anisoptera (*Onychogomphus uncatus* Charpenter) was also an important group in autumn contributing to the increase of biomass. Predators showed high biomass values in La Solana over the year. Shredder biomass in this stream was also high in autumn (ca. 750 mg m<sup>-2</sup>) but decreased during the rest of the year (ca. 50 mg m<sup>-2</sup>). This group practically disappeared during the spring. Collectors dominated in autumn and winter whereas scrapers were poorly represented (between 7 and 254 mg m<sup>-2</sup>). In Riera Major shredder biomass was extremely high in autumn. The proportion of biomass attributable to scrapers varied with primary production which was higher in summer. Collectors were less abundant in autumn and increased during spring. Predators increased in summer (Fig. 1).

Although biomass was always lower in La Solana than in Riera Major, differences were not significant ( $p > 0.05$ ). However, the size and biomass of the last instar larvae of *Hydropsyche gr. pellucidula* (size,  $t = -5.9$ ,  $p < 0.001$ ; biomass,  $t = -3.2$ ,  $p < 0.01$ ) and *Ephemerella insignis* (size,  $t = -4.8$ ,  $p < 0.001$ ; biomass,  $t = -4.0$ ,  $p < 0.01$ ) were significantly lower in La Solana.

The shredder/collector ratio was 23 and 8 times higher in Riera Major and La Solana respectively. During the year the collector-filterer group was more abundant than the collector-gatherer in the two streams ( $CF/CG > 1$ ). Scrapers were not so abundant in La Solana; the ratio between scrapers and the rest of the detritivores was always lower than 0.4. The ratio between biomass of predators and the rest of the groups was



**Figure 2.** Cluster analysis of the two sites and sampling occasions using functional feeding group biomass. Euclidean distances are indicated. LS= La Solana, RM= Riera Major, AUT= Autumn, SPR= Spring, SUM= Summer, WIN= Winter. *Análisis de agrupamiento de las dos localidades y muestreos utilizando grupos tróficos funcionales. Se indican las distancias euclídeas. LS=La Solana, RM=Riera Major, AUT=otoño, SPR=primavera, SUM=verano, WIN=invierno.*

below 0.3 in Riera Major. However, this ratio in La Solana was always higher, with a maximum of 4.4 during spring (Table 2).

A cluster analysis (Fig. 2) using distribution of trophic biomass separated autumn communities from the two streams. The community during autumn was notable for high biomass of shredders which was extremely high in Riera Major. Two more distinct cluster were identified: winter-to-summer communities from the two sites. These communities were characterised by high biomass of predators in La Solana and by a more equal biomass distribution between feeding groups in Riera Major.

**Table 2.** Biomass ratios between different functional feeding groups. SH, shredders; COL, collectors; FC, collector-filterers; CG, collector-gatherers; SC, scrapers; P, predators. *Relaciones de biomasa entre grupos tróficos funcionales. SH, trituradores; COL, colectores; FC, filtradores; CG, recolectores; SC, ramoneadores; P, depredadores.*

	Riera Major				La Solana			
	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
SH/COL	24.4	0.94	0.80	0.52	1.23	0.16	0.06	0.50
CF/CG	2.70	3.13	2.30	4.95	2.70	3.25	3.20	3.41
SC/SH+COL	0.08	0.39	0.20	0.39	0.17	0.05	0.06	0.10
P/TOTAL	0.04	0.15	0.10	0.30	0.53	0.80	4.41	1.24



## DISCUSSION

Seasonal variability of temperature and discharge differed among these streams. The temperature range was greater in La Solana, with higher temperatures in spring and summer and occasional frozen periods in winter. The discharge in La Solana decreased during summer until it ceased and floods are common in winter and spring. This temporal variability observed in La Solana may constitute a source of disturbance to the community as has been described for many intermittent streams (Boulton *et al.*, 2000) and determine lower species richness and smaller individuals of some species. Similar results have also been observed in flood disturbed freshwater systems (Townsend *et al.*, 1997). On an annual basis, no significant difference in diversity ( $H'$ ) existed between these two streams, these results concurs with those reported by Miller & Golladay, 1996.

Autumn was a rich period for macroinvertebrate fauna in La Solana: high density, biomass and richness were observed in this stream from October to December. In spite of the ephemeral conditions during the drought could cause a decline in species richness as was described in intermittent streams (Williams & Hynes, 1976; Dieterich & Anderson, 2000), summer drying in La Solana did not reduce the recruitment potential. Higher discharge and allochthonous inputs of organic matter favoured the high biomass of collectors and shredders. High numbers of shredders were observed in autumn but shredders almost disappeared during the rest of the year when benthic organic matter content declined (personal observation) as a consequence of discharge. Gasith & Resh (1999) expected, in mediterranean regions, an increase in abundance of the biota during an intermediate period between drying (summer) and flooding (winter-spring) sequence. With the initiation of repeated winter-spring floods, a rapid shift in macroinvertebrate assemblage was observed in La Solana according to similar reductions described in different intermittent and permanent streams (Miller & Golladay,

1996; Fisher *et al.* 1982; Molles, 1985). Riera Major in autumn was dominated by the shredder *H. radiatus* in response to the high allochthonous coarse particulate organic matter inputs. In contrast to La Solana, particulate matter is present all year round in this stream (Romani *et al.*, 1998) and allows the persistence of detritivorous feeding groups.

A slight increase of scraper biomass was observed in summer in Riera Major. Light is a limiting factor for primary production in this stream, higher biomass of periphyton and patches of *Cladophora glomerata* were only observed from June to August (Guasch & Sabater, 1998). Epilithic biofilms in La Solana reached their maximum biomass accumulation in autumn, when minimum values of discharge and high water temperature also occurred. During this period scraper biomass showed a slight increase. In winter low temperatures and low light reduce the net primary production. The dynamics of phosphorus in La Solana cannot be separated from the calcium carbonate chemistry. Because of its calcium-saturated water, phosphate is removed from the water column via coprecipitation with  $\text{CaCO}_3$  (Martí & Sabater, 1996). The low nutrient availability reduces periphyton biomass and consequently reduces food resources for macroinvertebrates. Moreover, La Solana had a significant fraction of the streambed covered by a stromatolitic crust (3-9 mm thick), which could also partially explain the low biomass of scrapers. The encrusting biofilm is an unsuitable habitat for macroinvertebrates, supporting only the first instar larvae of some Chironomidae and Ephemeroptera (Sabater *et al.* 2000).

Seasonal variation in biomass distribution among species affects food web structure from different streams (Thompson & Townsend, 1999). The present study demonstrates that although La Solana and Riera Major have a similar community composition, they showed a different seasonal distribution of the biomass of functional feeding groups that suggests variations in their food-web structure. Riera Major is characterised by a more stable, structurally com-

plex and species-rich community. Although algal productivity was low, it was enough to maintain a substantial biomass of scrapers during the year. Detritivorous biomass is also important in this stream but seasonal variability is slight. La Solana was characterised by a greater contribution of predator biomass, mainly the nymphs of the dragonfly favoured by the low flow conditions that concentrated their prey species and eliminated fish predators. Similar results have been described in other intermittent streams (Boulton & Lake, 1992 a, b; Stanley *et al.*, 1994). Moreover, the community in this stream reflects an important seasonal variation in the way in which biomass was distributed among functional feeding groups. There was a sequence characterised by distinct pre-dry period (spring-summer) with dominance of predators, and post-dry period (autumn) when biomass of all functional groups increase significantly.

Higher seasonal differences in flow and temperature regime observed in La Solana seem to determine a macroinvertebrate community characterised by low densities and biomass, and small individuals. Moreover, hydraulic conditions in this stream, indirectly affect the abundance of functional feeding groups: floods influence litter retention and consequently detritivorous abundance; dry period favours some predator strategies. Several direct and indirect factors act together, to know the separate role of each one, studies in different hydraulic years are needed.

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