

Structure and dynamics of a benthic trophic web in a Mediterranean seasonal stream

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ABSTRACT

In this work we present the results of a study conducted on the benthic macroinvertebrate community of a Southern Spain seasonal stream over a year. We constructed the food web focusing on the benthic fauna and we studied the ecology and dynamics of the community in terms of trophic resources. The benthic trophic web was composed by 35 taxa; these were not all present at the same time, but were incorporating and disappearing throughout the study period. Connectance between trophospecies varied from 0.24 to 0.59. The functional feeding group (FFG) composition of the community turned out to be fairly constant with time with a predominance of scrapers and collector-gatherers. Furthermore, data obtained from the Bray-Curtis measure and the niche overlap study, evidence the stability of the stream from a trophic point of view. Rather widespread is omnivory that plays an important role in the survival of some families. We compared the results of the trophic web study with those of other temporary streams of the same region of Southern Spain.

Key words: Benthic macroinvertebrates, functional feeding groups, trophic web, temporary water, Southern Spain.

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INTRODUCTION

In Mediterranean regions, characterised by rainy winters and arid summers, streams are generally influenced by a sequence of regular and often extreme flooding and drying periods (Gasith and Resh, 1999). The water regime is closely related to the rainfalls, and can therefore have a great variability, both seasonal and annual. Mediterranean streams can be divided into temporary, which lack water for at least part of the year, and permanent, which have water all year round. Among the former, the most widespread in Mediterranean regions are the intermittent and the seasonal streams. Intermittent streams alternate wet and dry periods, but at lower frequency than seasonal streams and with an unpredictable pattern, whose flow may persist for months or years. Seasonal streams alternate wet and dry periods every year, in accordance with the season (Williams, 2006). They usually fill during the wet season of the year, and dry out in a predictable way on an annual basis. The flow lasts for several months, long enough for macroscopic animals and plants to complete the aquatic stages of their life cycle (Williams, 2006). This trend greatly affects the biota that lives in these streams in terms of their abundance, distribution and life history. Many of these organisms have adopted a number of strategies to cope with drought periods, either resistance or re-

silience (Lake, 2011): some may suffer diapauses as larvae or eggs, others aestivate in damp or dry sediment, grow rapidly, disperse actively to other water bodies, *etc.* (Williams, 2006; Robson *et al.*, 2011).

During summer, the presence of isolated pools causes the concentration of a large number of individuals in a small space. This involves that prey are more easily subject to predation, and that individuals of various families probably have to compete for limited resources. This competition entails an expenditure of energy than in normal situations would be used for growth, development and/or production of eggs; as a consequence, this leads to an inevitable reduction in fitness. Furthermore, because of the reduced availability of food resources, macroinvertebrates tend to be more generalists, ingesting food that does not always correspond to their optimum from the nutritional point of view (Mihuc, 1997). In addition, in this type of streams, it is important to consider the hyporheic zone, an active ecotone between the surface stream and ground water. Exchanges of water, nutrients and organic matter occur in response to variations in discharge and bed topography and porosity and, during the drought period, some organisms take refuge in this area to survive to the adverse period (Boulton *et al.*, 1998).

Food web studies are generally aggregates of known feeding relationships that may overestimate the impor-

tance of rare interactions (Warren, 1989; Closs and Lake, 1994). Therefore, accurate understanding of the trophic base of stream food webs requires knowledge of both spatial and temporal variations in feeding relationships (Dekar *et al.*, 2009). Food webs of temporary water communities are poorly studied and lack in quantitative validation (Williams, 2006). In these ecosystems food chains are relatively short and are normally detritus-based, and omnivory appears to be commonplace. Omnivory, defined broadly as the ability to feed on more than one trophic level, according to classical food web theory destabilises ecological communities (Pimm and Lawton, 1978). Nevertheless, more recent conceptual syntheses suggest that omnivory must be a strong stabilising factor in food webs (McCann *et al.*, 1998). However, the role of omnivory strongly depends on the particular food web and level of aggregation. Both aquatic and terrestrial food webs can have either a larger or lower number of omnivory modules. Thus, a close inspection of species composition may be necessary to explain this variability in the frequency of omnivory (Bascompte and Melian, 2005).

In food webs of temporary water, connectance seems to decrease in more variable environments, while species interaction strength is believed to increase (Williams, 2006). Moreover, trophic complexity is a function of temporal heterogeneity and the number of trophic levels in a community seems dependent on the rate and predictability of primary and secondary production, which is likely influenced by habitat stability and predictability (Williams, 2006). Few studies have been carried out about lotic trophic webs that consider temporal changes (Closs and Lake, 1994; Dekar *et al.*, 2009), and particularly scarce are those conducted in Mediterranean streams: only few researches have focused on them (Álvarez and Pardo, 2009; Sánchez-Carmona *et al.*, 2012; López-Rodríguez *et al.*, 2012).

The aim of this work is to describe the food web of the benthic macroinvertebrate community in a seasonal stream from a Mediterranean-climate region of Southern Spain and to investigate the ecology and dynamics of its community in terms of trophic resources.

METHODS

The study was conducted in Despeñaperros stream (Sierra Morena, Jaén, Spain, 560 m asl), a Mediterranean seasonal stream with, therefore, a typical Mediterranean typology. Particularly, it belongs to the ecotype of low mountain siliceous Mediterranean streams of the Spanish Hydrological Planning Instruction. Rainfalls largely influence the flow regime of these aquatic environments, as the water flow is very shallow because geological materials are highly waterproof (mainly schist). Consequently, the water regime is relatively predictable and affected by the rains, which start in autumn. Thus, the duration of the hydroperiod depends on the amount of rainfall and the ex-

tent thereof. Moreover, the low permeability of the schist favours these rivers which suffer severe flood events when rainfall is intense. Finally, another feature of these rivers is the presence of pools in the dry season, more or less permanent, which act as reservoirs in which aquatic organisms can find refuges.

In the study period, stream width during the sampling period varied from 2.95 to 5.35 m, and depth ranged from 0.04 to 0.31 m. The substrate was composed of approximately 85% block and stones, 10% gravels and 5% sands and silt. There were some branches and trunks on the riverbed. During spring and summer there were abundant Ranunculaceae and *Nasturtium* spp. Mosses were absent at the sampling site. Riparian vegetation was abundant and mainly consisted of *Nerium oleander*, *Fraxinus* spp., *Berberis* spp., Poaceae, Umbelliferae and Compositae. Samples were collected mid monthly from November 2006, when the stream carried water, to May 2007, and biweekly in June, just before the summer drought. No pools were detected during the dry period. It was not possible to sample in mid April due to a flood caused by heavy rain. Therefore, the April sample was taken at the end of the month. Hence, a total of nine samplings was carried out over the study period. During the whole study period, a data logger placed in the riverbed (HOBO Water Temp Pro, 0.01°C accuracy) recorded the temperature hourly and temperature data were averaged for each day to produce mean daily temperatures. Before the arrival of the water, the datalogger was exposed to the atmosphere and this caused a large fluctuation of the recorded temperatures (Fig. 1). These fluctuations declined as water entered the stream enabling the beginning of the wet period to be established as 23rd to 25th October. At every sampling, physical parameters such as dissolved oxygen, conductivity, pH and discharge, were recorded *in situ* by means of an oxy-meter, a conductivity-meter, a pH-meter and a flow-meter, respectively. One-liter samples of water on each sampling date were also collected and chilled to approximately 4°C. Thereafter, each sample was transported to the laboratory for additional physicochemical analysis (Tab. 1). Analyses took place within 24 h from the sample collection.

Specimens were collected with a Surber sampler (0.09 m² area and 250 µm mesh size). In order to include the different microhabitats for having a proper representation of the community, six replicates (considering the different microhabitats) on each sampling date were carried out. Macroinvertebrates were preserved in 4% formalin and brought to the laboratory, where they were sieved with a 150 µm mesh size sieve to remove excess formalin and fine detritus. Animals were sorted by sample date and identified to family level (except for Ostracoda and Nematomorpha). Gut contents of individuals of all collected taxa were studied using the transparency methodology by

Bello and Cabrera (1999), already used in other studies dealing with aquatic insect feeding (Fenoglio *et al.*, 2009; López-Rodríguez *et al.*, 2009b). On each date, a maximum of 30 individuals of each taxon were studied, when available. These individuals were introduced in a vial with Hertwigs' liquid and heated in an oven at 65°C for approximately 24 h (a longer time in case of animals with a bigger size or heavily sclerotised cuticles and, therefore, harder to make transparent). Afterwards, individuals were placed on a slide with a cover on and examined under the microscope at 40 and 400× magnification. The percentage of the absolute gut content, as the total area occupied by the content in the whole digestive tract, and the relative gut content, as the area occupied for each component within the total gut content, were estimated. Data from the gut content analyses were used to construct the food web diagram. First, we grouped the taxa that showed the same feeding relations in trophospecies, and in order to ease this grouping and the graphical representation we divided each trophic resource in four percentage ranges: 0-25, 25-50, 50-75 and 75-100%. For those taxa for which we were not able to obtain data through the transparency method (Rhyacophilidae, Planorbidae, Ceratopogonidae, Hydrobiidae), either because they had no gut contents or because the hard structures prevented complete transparency, we sought information concerning their diet in the literature (Tachet *et al.*, 2010). To study the trophic web, several characteristics were calculated following Stevens (2009): nodes (trophospecies), as a set of organisms that share similar feeding relations; links, or feeding relations, as the connection between nodes, both direct (actual) and indirect (potential, not confirmed relations); connectance, as the proportion of possible links realised, both direct and indirect; top trophospecies, as those nodes that are fed upon by nothing; intermediate trophospecies, as those that feed on other species but are also fed upon by others; basal trophospecies, as those that feed on no other species; and top, intermediate and basal taxa, as the number of taxa included in top, intermediate and basal nodes, respectively. We used the gut content study also to assign each taxon to its functional feeding group (FFG) (*i.e.* scrapers, collector-gatherers, shredders, collector-filterers and predators; Merritt and Cummins, 1996).

To study the niche overlap (in terms of trophic resources) among the taxa that coexisted at the same time (*i.e.* present in the same month), the Horn's index (Horn, 1966), ranging from 0 (no overlap) to 1 (total niche overlap), was used. To calculate this index, counts of individuals of each taxon that fed upon a given trophic resource on each date were used. This is one of the best measures to minimise the bias due to low sample size (Krebs, 1999), as it occurs sometimes for some taxa found in the present investigation. To analyse dissimilarities between the communities of different dates, both in terms of densities of

each taxon and of FFGs, the Bray-Curtis measure was employed. In this test, rare taxa add little to the value of the coefficient and so abundant taxa weight more (Krebs, 1999). Two macroinvertebrate families, Gerridae and Notonectidae, even if present in the stream, were excluded since the study focused on the benthic fauna. For data analysis we used STATISTICA (StatSoft, 2005) and R (R Core Team, 2012).

RESULTS

Physicochemical characteristics of the stream varied largely throughout the year. As regards the temperature, maximum values were recorded at the beginning and at the end of the sampling period (19.3 and 18°C, respectively), while minimum temperatures (6°C) were recorded in January (Fig. 1, Tab. 1). During this time, the stream accumulated a total of 2962 day-degrees. Discharge changed significantly during the sampling period with a first peak in February and a second peak, although lower, between April and May. A drastic decrease was registered in January and then in June, just before the drought. The pH and oxygen values remained more or less constant during the whole period. The latter, however, decreased drastically in June. Conductivity was maximal at the beginning and at the end of the wet period, while it stayed constant for the remaining period.

The macroinvertebrate community (including the neustonic Gerridae and Notonectidae) in Despeñaperros stream was composed by 37 taxa (Tab. 2). The most abundant families were Simuliidae (with 7637.03 ind. m⁻²), Chironomidae, Lumbriculidae, Ancyliidae, and Perlodidae (1662.96 to 5733.34 ind. m⁻²). The remaining taxa had mid to relatively low density. The number of taxa during the whole period remained almost constant, with a minimum of 14 taxa at the end of June and a maximum value of 21 in February. During the year new taxa incorporated to the community, while other disappeared. Families such as Elmidae, Dugesidae, Chironomidae, Simuliidae, Tabanidae, Perlodidae and Lumbriculidae were present almost during the whole year. As regards the FFG composition of the community, it turned out to be more or less constant with time (Fig. 2). Scrapers, which feed mainly on diatoms, and collector-gatherers feeding mainly on detritus, were proportionally the most abundant throughout the sampling period, while shredders and collector-filterers were very scarce at anytime (Tab. 2). Apart from a density peak in June, predators were not very abundant proportionally, compared with the other groups. The niche overlap among taxa was relatively high. More than 85% of the taxa had a value of the Horn index higher than 0.5 (Supplementary Tabs. 1 and 2).

In general, communities found in each sampling are very similar among dates, both in terms of composition and FFGs, except for the last sampling date, just before the

drought period (Fig. 2). Comparing the Bray-Curtis measures calculated with densities of each taxon and with densities of FFGs, values are much lower in the case of FFGs (Tab. 3). The potential food web was quite complex (Fig. 3, Tab. 4). Food resources at the base of the trophic web were diatoms, detritus, fungi, pollen, coarse particulate organic matter (CPOM), and Cyanoprokariota. There were 26 basal taxa and 9 intermediate taxa, among which one family, Rhyacophilidae, was considered strictly predator, while the other 8 families incorporated in their diet also detritus, diatoms, fungi and pollen. No top taxa were present among macroinvertebrates, as vertebrates present in the stream [*Motacilla cinerea* (Tunstall, 1771), *Mauremys lep-rosa* (Schweigger, 1812), *Natrix maura* (Linnaeus, 1758), *Pelophylax perezi* (Seoane, 1885) and *Squalius pyrenaicus* (Günther, 1868)] could predate on all of them.

Despite having divided the trophic resources in four percent ranges to facilitate grouping and graphical representation (as explained above), the number of trophospecies and that of taxa were almost always very similar.

This means that a single taxon often represented one trophospecies. Directed connectance among trophospecies varied from 0.24 to 0.59, while undirected connectance ranged from 0.49 and 2.42.

DISCUSSION

As mentioned in the Methods section, Despeñaperros stream belongs to the ecotype of low mountain siliceous Mediterranean streams, which are characterised by strong seasonality. Thus, physicochemical conditions of the Despeñaperros stream in our study area are quite variable throughout the wet period (Fig. 1). Flow variations are fairly high, ranging from months with almost no flow and a few interconnected pools present in the stream to others when we could not even sample (and neither measure flow) due to a flood. In this sense it must be pointed out that, although in Fig. 1 the peak of flow appears in February, the maximum flow took place in mid April, with values very much higher than those recorded in February,

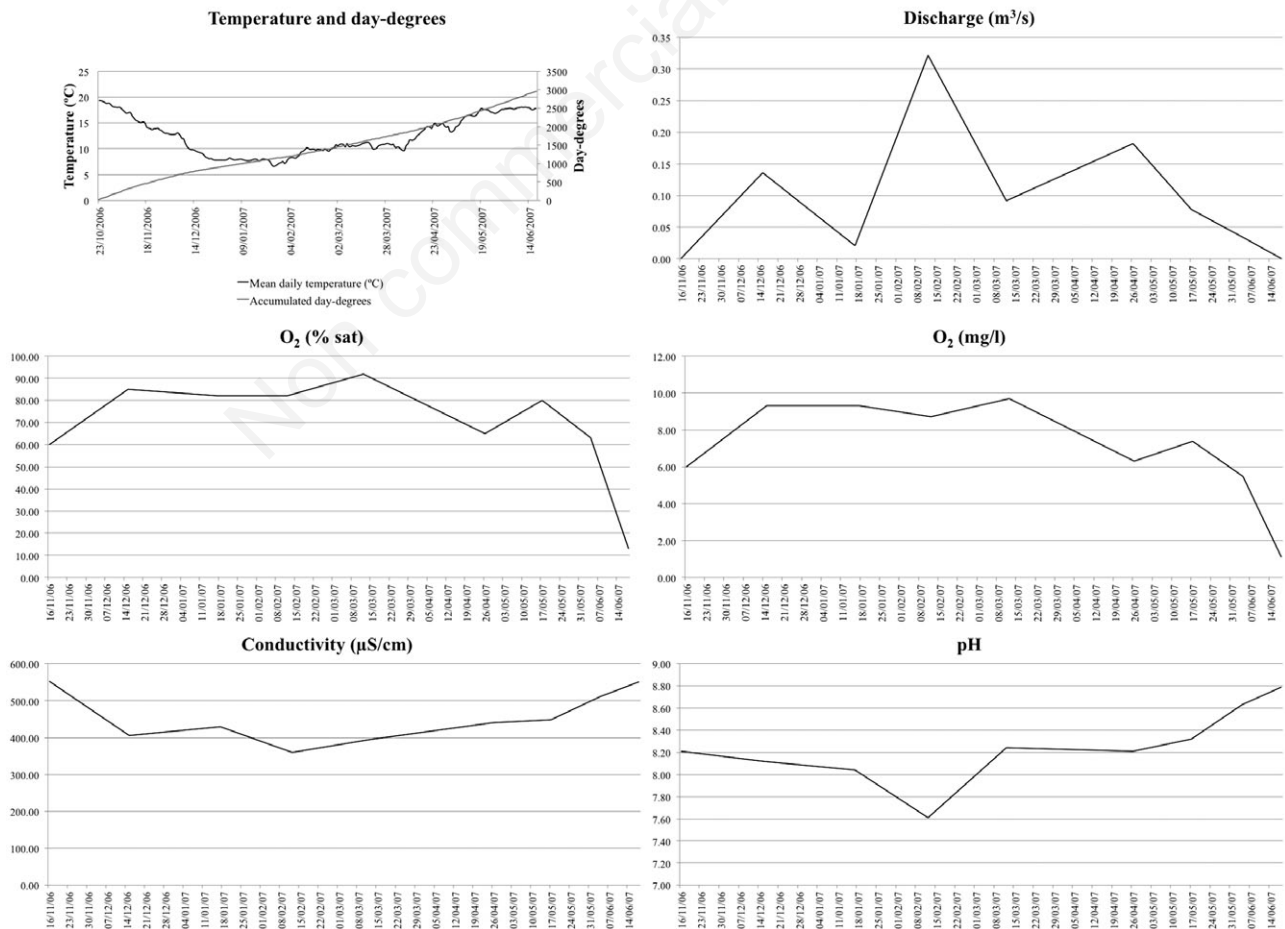


Fig. 1. Variation of the main physicochemical parameters throughout the study period in Despeñaperros stream.

Tab. 1. Physicochemical parameters of Despeñaperros stream.

Physicochemical parameters	No.	Mean	SD	Minimum	Maximum
pH	9	8.24	0.34	7.61	8.79
Ammonium (mg L ⁻¹)	9	0.65	1.84	0.00	5.55
Phosphates (mg L ⁻¹)	9	0.01	0.01	0.00	0.03
Nitrates (mg L ⁻¹)	9	0.03	0.04	0.00	0.11
Nitrites (mg L ⁻¹)	9	0.04	0.05	0.00	0.13
Sulfates (mg L ⁻¹)	9	22.55	7.26	10.14	33.24
Chlorides (mg L ⁻¹)	9	49.10	8.70	36.40	68.25
Alkalinity (meq l ⁻¹)	9	39.85	7.86	24.64	50.02
SS (mg L ⁻¹)	9	4.02	4.17	0.60	12.60
Ca (mg L ⁻¹)	9	65.96	12.80	50.40	88.00
Mg (mg L ⁻¹)	9	29.70	7.77	20.90	40.34
Hardness (mg CaCO ₃ L ⁻¹)	9	286.94	54.13	213.87	379.77
Turbidity (NTU)	9	1.33	0.87	0.40	3.20
O ₂ (% sat)	9	69.11	23.75	13.00	92.00
O ₂ (mg L ⁻¹)	9	7.03	2.73	1.10	9.70
Temperature (°C)	5908	12.54	3.86	5.90	25.87
Conductivity (µS cm ⁻¹)	9	454.89	69.43	359.00	553.00
Discharge (m ³ s ⁻¹)	9	0.10	0.11	0.00	0.32

SD, standard deviation; SS, suspended solids; Ca, calcium; Mg, magnesium; NTU, nephelometric turbidity unit; O₂, oxygen.

Tab. 2. Density and functional feeding groups of the macroinvertebrate taxa present in Despeñaperros stream.

Taxa	Density (ind. m ⁻²)	FFG
Ancylidae	1918.51	Sc
Anthomyiidae	7.41	Sc
Athericidae	7.41	Sc+P*
Capniidae	925.93	Sc+C-G
Ceratopogonidae	18.52	P*+C-G*+Sc*
Chironomidae	5733.34	Sc+P
Dolichopodidae	3.70	C-G
Dugesidae	503.70	Sc+P*
Dytiscidae larvae	55.55	Sc+P*
Elmidae adult	101.86	C-G+Sc
Elmidae larvae	442.58	Sc+C-G
Ephemereididae	555.56	C-G+Sc
Gammaridae	3.70	C-G
Gerridae	22.22	P*
Glossiphoniidae	101.86	Sc+C-G+P*
Glossosomatidae	3.70	Sc
Halipididae larvae	24.07	Sc
Hydraenidae	27.77	Sc
Hydrobiidae	1.85	C-G*+Sh*
Hydropsychidae	66.66	Sc+P+C-F*
Leuctridae	370.37	C-G+Sc
Libellulidae	3.70	Sc+P*
Limnephilidae	9.26	C-G+Sc
Limoniidae	222.22	C-G+Sc
Lumbriculidae	2037.03	Sc+C-G
Nematomorpha	1.85	C-G
Notonectidae	9.26	P*
Ostracoda	24.07	Sc+C-G
Perlodidae	1662.96	Sc+C-G+P
Planorbidae	7.41	Sc*+Sh*
Psychomyiidae	5.56	Sc+C-G
Rhyacophilidae	1.85	P*
Sciirtidae larvae	9.26	C-G
Simuliidae	7637.03	C-F
Tabanidae	185.17	Sc+C-G+P*
Taeniopterygidae	377.78	Sc+C-G
Tipulidae	37.04	Sc+C-G+Sh*

FFG, functional feeding group; Sc, scrapers; P, predators; C-G, collector-gatherers; Sh, shredders; C-F, collector-filterers. *Functional feeding groups deduced from the literature.

even if this parameter could not be recorded. The benthic macroinvertebrate community of the Despeñaperros stream is composed by 35 taxa, although other families of macroinvertebrates are also present in the stream, as Notonectidae and Gerridae, in the neuston. As these two families live on the surface of the water and feed mostly on prey from the outside or emerging organisms, they have been excluded from the study, which deals with the benthic fauna.

We neither consider in our food web the five taxa of vertebrates present in the stream: the grey wagtail *M. cinerea*, the Mediterranean pond turtle *M. leprosa*, the viperine snake *N. maura*, the Iberian water frog or Pérez's frog *P. perezi*, and the Iberian chub *S. pyrenaicus*. Nevertheless, all of them can interact – from a trophic point of view – with the benthic macroinvertebrate community. *Motacilla cinerea* captures aquatic insects both in larval and aerial stages, as well as terrestrial prey (Santamarina, 1993). *Mauremys leprosa* shows a wide trophic spectrum as it feeds on insects, amphibians, mollusks, crustaceans, fishes, plants, carrions, etc. (Salvador, 1997). The feeding of *N. maura* in the Iberian peninsula is based mainly on oligochaetes, insects, anurans (tadpoles and adults) and fishes (Valverde, 1967). *Pelophylax perezi* is an opportunist and generalist species with a variable diet according to place and season; during its adult stage it feeds mainly on terrestrial and flying insects (but also vertebrates), while aquatic prey are generally a low percentage of its diet (García-Paris et al., 2004). It is mainly in winter when the feeding of *P. perezi* is linked to aquatic habitats (Hernández and Seva, 1986). The *P. perezi* tadpoles are principally detritivorous and phytophagous, and occasionally they can be captured by predator macroinvertebrates, like some dragonflies (García-Paris et al., 2004). Finally,

S. pyrenaicus shows a wide trophic range and a pronounced generalist character, consuming plant and animal material (Blanco-Garrido *et al.*, 2003). According to Doadrio (2001) and Kottelat and Freyhof (2007), small aquatic arthropods are the main component of its diet. Particularly, the feeding habits of this species have been studied in the same mountain range of the present study by Blanco-Garrido *et al.* (2003), who found that Chironomidae were among the most frequently ingested prey in summer. As tadpoles, *S. pyrenaicus* fries can also be captured by predator macroinvertebrates.

In November, at the beginning of the sampling period, 17 taxa composed the community. Many of them are organisms with strategies to cope with drought and are able to stay in the stream during this period in a resting stage (either in the egg, or in the juvenile stages, or in both) (Lopez-Rodríguez *et al.*, 2009a, 2009b). In the following months, the number of taxa increases slightly until reaching a maximum of 21 taxa in January and February, after which the number begins to decrease until a minimum value of 14 taxa at the end of June. This can be explained

by the fact that, at the beginning and at the end of the wet period, (*i.e.* after and before the drought) the volume of water is very low and only a low number of taxa can face these adverse conditions. The FFG composition is fairly constant with time; scrapers are always the dominant group, followed by collector-gatherers. Shredders are scarce throughout the year, presenting their maximum proportion in April and at the beginning of June. Collector-filterers are represented by a single family, Simuliidae, and for this reason they are scarce or even absent during the whole sampling period, presenting a maximum proportion in early June. As regards predators, although the number of the taxa in each date is very low, from one (in December, March and April) up to a maximum value of seven at the beginning of June, the values of their density are always very high compared to those of the other taxa. Higher proportions are found in November, January and March, while the minimum proportion is in late June, when predators are represented by members of a single family, Chironomidae. In this date this family is represented by a high number of individuals, though only few

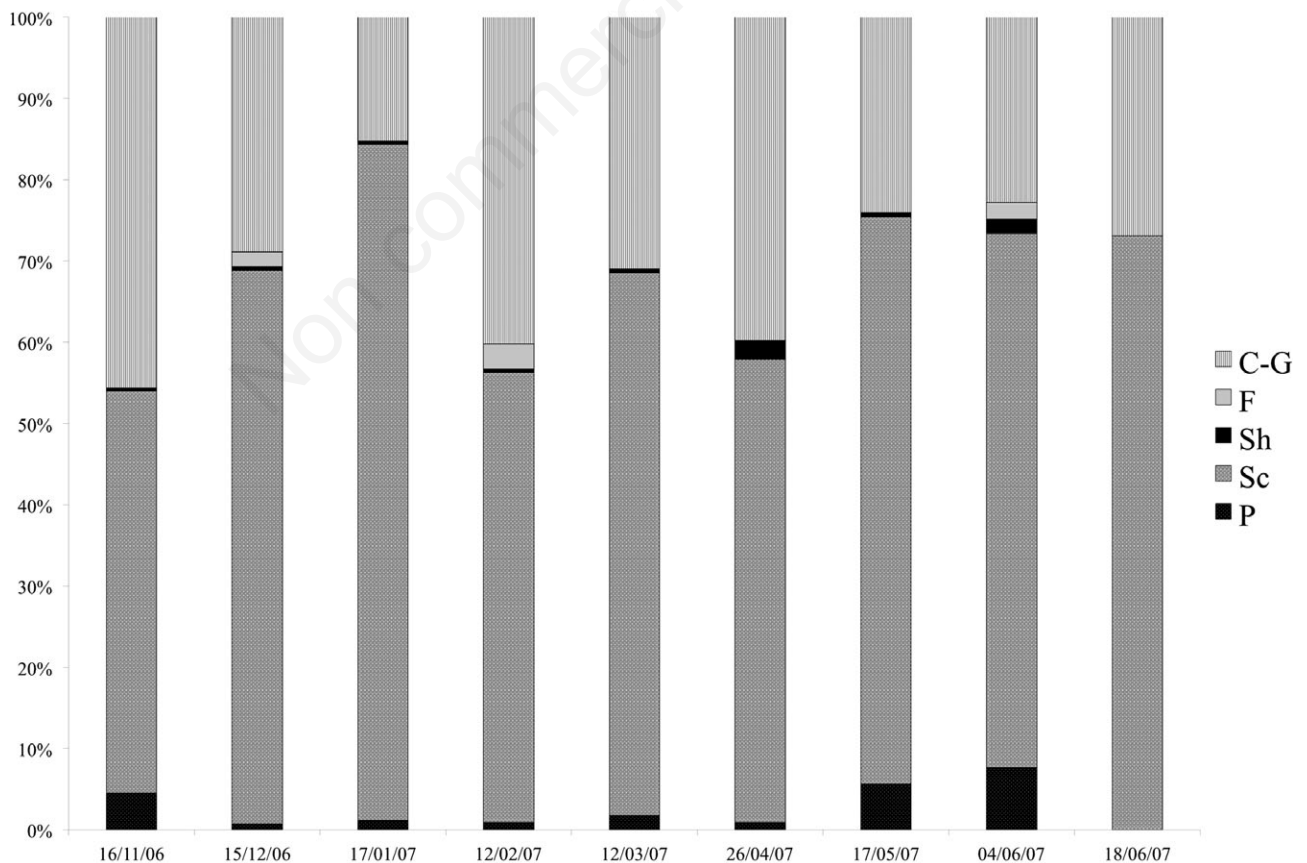


Fig. 2. Functional feeding group composition (in percentage) in each sampling date during the study period in Despeñaperros stream. C-G, collector-gatherers; F, filterer; Sh, shredders; Sc, scrapers; P, predators.

of them act as predators. It is interesting to note that blackflies (Simuliidae), typically filter-feeders, at the beginning and at the end of the wet period behave both as predators and collector-filterers unlike other months. The presence of animal remains in the gut of blackflies has been already recorded by other authors (Allan and Castillo, 2007). This trend can be explained by the fact that in a situation of water scarcity, aquatic fauna is concentrated in a small space and Simuliidae have a greater chance of ingesting small prey in suspension when filtering water. On the other hand, some blackfly species feed by scraping the substrate (Allan and Castillo, 2007), and this behaviour could also explain the presence of diatoms and invertebrates in the digestive tract of this family. Taking into account that the presence of animal remains in the gut of these organisms coincides with periods of water reduction, the ingestion due to a higher concentration of animals during water scarcity period seems to have more support.

It is also interesting to highlight the large number of Plecoptera taxa and particularly the very high density of Perlodidae in this stream, contrary to Williams' statement (2006) that in temporary waters Plecoptera and Odonata are scarcely represented, whereas other groups, such as Diptera or Ephemeroptera, are particularly well-suited. In fact, some other authors studying Mediterranean streams also found that Diptera, and particularly Chironomidae, were dominant (Sánchez-Carmona *et al.*, 2012). The high density of Perlodidae in Despeñaperros stream can be attributed both to the ability of some species of this family

to cope with dry periods and to their omnivorous diet (Sanz *et al.*, 2010; Tierno de Figueroa *et al.*, 2011). Analysing the gut contents, indeed, we found that part of the individuals feed almost exclusively on vegetable matter, while others present both plant and animal matter (López-Rodríguez *et al.*, 2009b). This omnivorous behaviour gives them surely greater flexibility and therefore more chances of survival. In this sense, conceptual syntheses suggest that omnivory must be a strong stabilising factor in food webs (McCann *et al.*, 1998). The stabilising role of omnivory has been discussed in a subsequent work (Melian and Bascompte, 2002) in which predators with high selective searching behaviour are confirmed to have less chance of survival than non-specialised generalist predators.

Comparing the FFG composition of Despeñaperros stream, predictable and seasonal, with that of an unpredictable stream from the same region such as the Arroyo de las Perdices (Sierra de Huétor, Granada, Southern Spain), we note that the latter shows a greater variability with time. In addition, in the Arroyo de las Perdices, collector-gatherers are the dominant group throughout the whole period (López-Rodríguez *et al.*, 2012). Usually, in fact, detritus is the main trophic resource in this kind of streams. At temperate latitudes, the notion that small streams are predominantly heterotrophic and dependent on allochthonous detritus is well established (Fisher and Likens, 1973; Hynes, 1975; Wallace *et al.*, 1997). Predominance of collector-gatherers was also found in two intermittent streams of Australia (Boulton and Lake, 1992), in

Tab. 3. Bray-Curtis dissimilarity index among sampling dates calculated for densities of each taxon and functional feeding groups in Despeñaperros stream.

Date	16/11/06	15/12/06	17/01/07	12/02/07	12/03/07	26/04/07	17/05/07	04/06/07
Density of each taxon								
15/12/06	0.57							
17/01/07	0.62	0.33						
12/02/07	0.55	0.40	0.33					
12/03/07	0.73	0.50	0.28	0.31				
26/04/07	0.71	0.37	0.40	0.33	0.29			
17/05/07	0.61	0.65	0.69	0.58	0.72	0.61		
04/06/07	0.84	0.86	0.89	0.87	0.91	0.89	0.62	
18/06/07	0.84	0.96	0.94	0.89	0.97	0.97	0.81	0.67
Density of FFGs								
15/12/06	0.34							
17/01/07	0.46	0.16						
12/02/07	0.40	0.07	0.18					
12/03/07	0.57	0.30	0.21	0.24				
26/04/07	0.46	0.14	0.11	0.09	0.16			
17/05/07	0.24	0.35	0.42	0.41	0.53	0.41		
04/06/07	0.60	0.73	0.80	0.76	0.84	0.79	0.57	
18/06/07	0.30	0.42	0.49	0.47	0.59	0.48	0.08	0.53

FFGs, functional feeding groups.

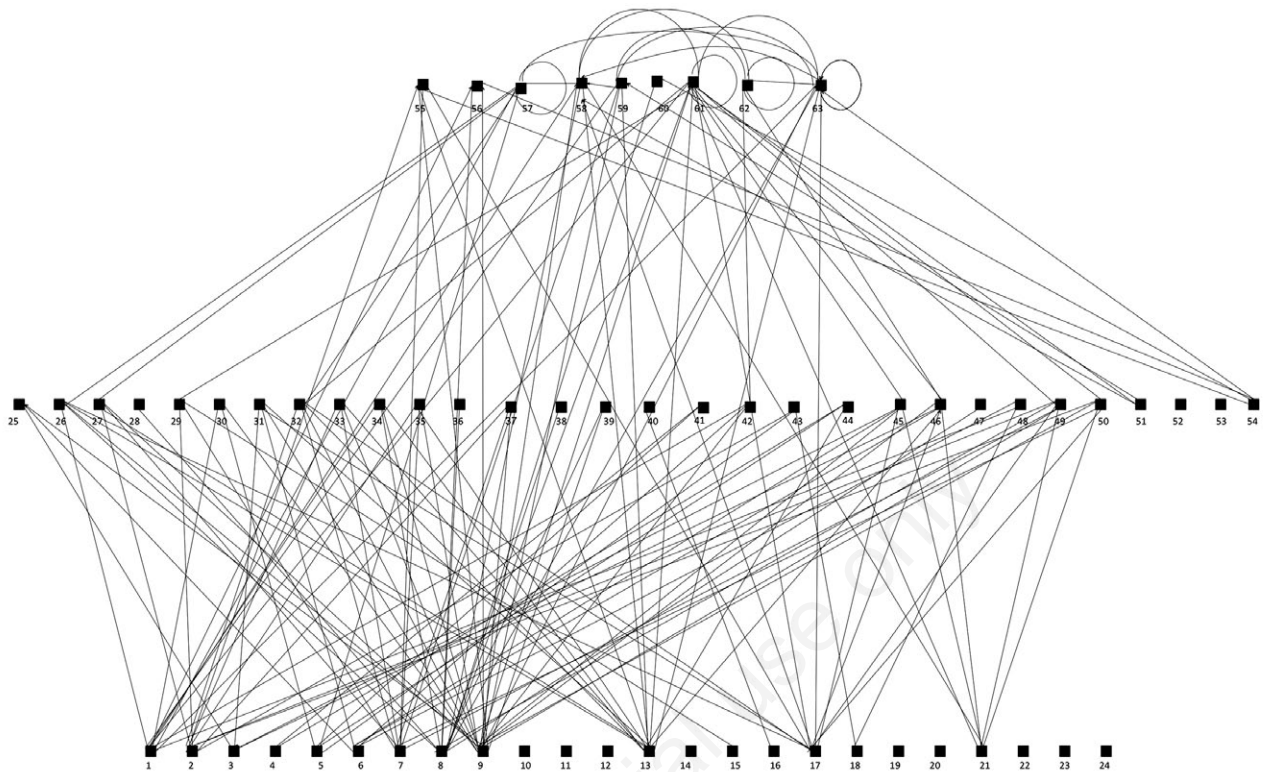


Fig. 3. Potential benthic macroinvertebrate food web in Despeñaperros stream. Lines with arrows indicate a direct link, while lines without arrows indicate an undirected link. Food items are denoted by the corresponding numbers. 1) Detritus 0-25%; 2) detritus 25-50%; 3) detritus 50-75%; 4) detritus 75-100%; 5) diatoms 0-25%; 6) diatoms 25-50%; 7) diatoms 50-75%; 8) diatoms 75-100%; 9) fungi 0-25%; 10) fungi 25-50%; 11) fungi 50-75%; 12) fungi 75-100%; 13) pollen 0-25%; 14) pollen 25-50%; 15) pollen 50-75%; 16) pollen 75-100%; 17) coarse particulate organic matter 0-25%; 18) coarse particulate organic matter 25-50%; 19) coarse particulate organic matter 50-75%; 20) coarse particulate organic matter 75-100%; 21) Cyanoprokaryota 0-25%; 22) Cyanoprokaryota 25-50%; 23) Cyanoprokaryota 50-75%; 24) Cyanoprokaryota 75-100%; 25) Elmidae adult; 26) Dugesiidae; 27) Glossiphonidae; 28) Hydraenidae; 29) Ostracoda, 30) Scirtidae larvae; 31) Limoniidae; 32) Lumbriculidae; 33) Elmidae larvae; 34) Ancyliidae; 35) Psychomyiidae; 36) Haliplidae larvae; 37) Tipulidae; 38) Athericidae; 39) Glossosomatidae; 40) Dolichopodidae; 41) Gammaridae; 42) Limnephilidae; 43) Hydrobiidae; 44) Nematomorpha; 45) Leuctridae; 46) Ephemerellidae; 47) Anthomyidae; 48) Planorbidae; 49) Taeniopterygidae; 50) Capniidae; 51) animal matter 0-25%; 52) animal matter 25-50%; 53) animal matter 50-75%; 54) animal matter 75-100%; 55) Tabanidae; 56) Dytiscidae larvae; 57) Ceratopogonidae; 58) Simuliidae; 59) Hydropsychidae; 60) Libellulidae; 61) Perlodidae; 62) Rhyacophilidae; 63) Chironomidae.

Tab. 4. Food web parameters of Despeñaperros stream. Global potential food web and actual food web for each date.

Trophic web	Nodes (trophospecies)	Link		Connectance		Top	Trophospecies Intermediate	Basal	Taxa		
		Direct	Undirect	Directed	Undirected				Top	Intermediate	Basal
Global potential	28	105	86	0.13	0.23	0	9	19	0	9	26
Actual											
16/11/06	11	42	27	0.35	0.49	0	2	9	0	2	14
15/12/06	7	29	25	0.59	1.19	0	1	6	0	1	17
17/01/07	13	41	77	0.24	0.99	0	3	10	0	3	17
12/02/07	12	44	94	0.31	1.42	0	8	3	0	3	17
12/03/07	10	35	36	0.35	0.8	0	1	9	0	1	13
26/04/07	10	30	39	0.3	0.87	0	1	9	0	1	14
17/05/07	9	26	78	0.32	2.17	0	3	6	0	3	12
04/06/07	12	38	75	0.26	1.14	0	6	6	0	7	10
18/06/07	9	23	87	0.28	2.42	0	3	6	0	3	8

six Mediterranean streams in Andalusia, Southern Spain (Sánchez-Carmona *et al.*, 2012), and in two summer-dry streams in Oregon, USA (Dieterich *et al.*, 1997).

In contrast with the results reported for other temporary lotic systems of temperate climates and specifically in other temporary Mediterranean streams, in Despeñaperros stream scrapers are the dominant group. The same result has been found by Álvarez and Pardo (2009) for the Gorg Blau torrent, a spring-fed, temporary stream located in the mountainous northern area of the Mediterranean island of Majorca (Spain). This indicates that primary production is very important in the Despeñaperros stream (as shown by the great development of diatoms). Algae are more easily assimilated by animals and decompose faster than allochthonous organic matter, generating large amounts of high quality food and algal-derived detritus (Gray and Fisher, 1981; Hall *et al.*, 2001).

As the wet period advances, not many dissimilarities are detected in the communities of each date but on the last date, before the drought. Not surprisingly, differences among dates, although small, are slightly higher considering taxa separately than FFGs. This indicates that the roles that organisms have in the community are always the same, though the taxa composition varies. From a functional point of view, this would indicate a higher stability of the stream ecosystem, where different processes involved in the nutrient cycle and energy flux are always realised though by different organisms. This is also supported by the results of the niche overlap analyses. The high values of niche overlap indicate a high degree of complementarity among taxa. Thus, if due to a perturbation some taxa cannot survive and disappear from the food web, there will be others able to hold the same trophic role. In fact, redundant taxa may strengthen both resistance and resilience in drought (Lake, 2011), but species reduction or elimination may reduce the efficiency of resource utilisation and productivity depending on the identity of the species that are lost (Cardinale *et al.*, 2006).

Considering the entire food web that could potentially develop in Despeñaperros stream, if all the mentioned taxa had been present simultaneously (including also the vertebrates previously cited), this would have been much more complex than what studied here, which included 26 basal taxa, 9 intermediate taxa and 5 top taxa (vertebrates). Connectance varied from 0.24 to 0.59. These values are less variable than those reported for the Arroyo de las Perdices, a temporary intermittent stream, fluctuating between 0.20 and 0.75 (López-Rodríguez *et al.*, 2012). The values of these two streams are much higher than those reported for 6 temporary water courses located in the same region of Southern Spain, which range from 0.09 to 0.14 (Sánchez-Carmona *et al.*, 2012).

CONCLUSIONS

In conclusion, the environmental disturbances occurring in this seasonal stream have a great impact on the macroinvertebrate community, though the effects are lower than expected when considering functional groups instead of taxa. Thus, redundant taxa would maintain the stability of this ecosystem. Moreover, we detected a certain change in the trophic web with time, highlighting the importance of this kind of studies that take into account not only a single sampling date but the dynamics along the whole wet period.

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