Chapter 5

SPATIAL AND TEMPORAL HETEROGENEITY, MACROINVERTEBRATE RICHNESS AND SPECIES TRAITS IN A TEMPORARY MEDITERRANEAN RIVER SYSTEM: relationships with the River Habitat Template.

INTRODUCTION

Natural ecosystems are highly heterogeneous in space and time (Kolasa & Rollo, 1991; Stewart *et al.*, 2000). The heterogeneity concept has implicit the relationship between spatial and temporal variation in environmental constrains and the responses by organisms to them (Milne, 1991). Numerous studies are focused on looking for the biological implications of these constrains in terms of processes and mechanisms (Palmer *et al.* 1995, 1997; Townsend *et al.*, 1997). However, ecologists have generally consider temporal and spatial heterogeneity separately (see Shachak & Brand, 1991), and in that sense, Resh & Rosenberg (1989) incise in the need to analyze together both heterogeneities in aquatic processes, as they occur in nature at the same time.

Several factors are responsible to provide spatial and temporal heterogeneity in nature. Abiotic factors alone or induced by organisms (Picket *et al.*, 2000) have been reported as the main causes to them. Human and natural disturbances are also important sources of heterogeneity in ecosystems, because they alter the structure of environment and the

distribution of organisms (Whiter & Harrod, 1997), although sometimes, human disturbance induces environmental homogeneity (Wiens, 2000). Different agents generate disturbance in ecosystems (see Wiens, 2000) determining the structure of aquatic communities (Resh *et al.*, 1988; Fisher & Grimm, 1991; Poff, 1992; Townsend *et al.*, 1997; Lake, 2000). In mediterranean areas, the climate itself is considered a natural predictable disturbance, altering the discharge regimes along and between years (McElravy *et al.*, 1989; Gasith & Resh, 1999). Floods and droughts are frequent in mediterranean ecosystems in different seasons (Molina *et al.*, 1994) displaying a high temporal heterogeneity. Both have been considered as the more important natural disturbances and their contribution to the stream patchiness induce a relevant spatial heterogeneity destroying and generating habitats (Lake, 2000). Although not all events causing heterogeneity are predictable (Pickett *et al.*, 2000), seasonal or annual heterogeneity in discharge in mediterranean rivers seems to be (Gasith & Resh, 1999), and evolutionary pressures have developed plant and animal communities highly adapted to it (di Castri, 1981; Stamou, 1998).

Temporary systems are well known for their variability in structure and invertebrate composition (Wiggins *et al.*, 1980; Williams, 1987), and they are present almost everywhere in the world (see Williams, 1987; Williams, 1996). Depending on the degree of temporality, rivers and streams can be classified as: permanent (flowing waters), intermittent (isolated pools) and ephemeral (dried stream beds) (see glossary at the end of this Chapter). These conditions can differ interannually (Feminella, 1996), and therefore interfere in the community composition of the following year. In mediterranean rivers this phenomena is very important, and it has been strongly associated with climatic features (McElravy *et al.*, 1989; Gasith & Resh, 1999). Moreover, the classification of mediterranean rivers in permanent, intermittent and ephemeral includes a temporal axis because the annual change of climatic conditions may imply a permanent condition from autumn to spring and permanent, intermittent or ephemeral reaches in summer in the same river (Gasith & Resh, 1999). The relationship between habitat and permanence have been poorly studied, although several studies incise in the change of habitat along time as the river is drying up (Boulton & Lake, 1992a; Williams, 1996) with riffles more affected than pools (Boulton & Lake, 1990; Stanley *et al.*, 1997). This habitat reduction during a dry season can be more or less important depending on the river characteristics (Lake, 2000), but in all cases macroinvertebrate community can be affected. On the other hand, flow patterns have also been considered heterogeneous in space and time (Poff & Ward, 1990; Palmer & Poff, 1997; Poff *et al.*, 1997). The attempts to quantify permanence in temporary systems have related macroinvertebrate community and structure to flow patterns (Feminella, 1996). The responses of macroinvertebrate communities to

permanence have been studied by several authors, reporting slightly differences in faunal composition between permanent and intermittent sites with a high overlap of assemblages (Boulton & Suter, 1986; Delucchi, 1988; Delucchi & Peckarsky, 1989; Boulton & Lake, 1992a; Feminella, 1996; Williams, 1996; del Rosario & Resh, 2000). Different levels of responses have been analyzed but most of them are focused on taxonomical richness and composition. Williams (1991, 1996) emphasize the need to perform studies looking at the different species traits in temporary streams to know the adaptation of macroinvertebrate to these fluctuating and constrained environments.

The effects of spatial and temporal heterogeneity on organism's responses create patterns that are scale-dependent (Menge & Olson, 1990; Allen & Hoekstra, 1991; Poff, 1992; Holt, 1993), as different evolutionary forces act at each scale (Levin, 1992). In stream ecology, spatial heterogeneity has been referred to basins, rivers, reach, macrohabitat or microhabitat; and the temporal one to day, season, year and multiyear approaches (for examples see Resh & Rosenberg, 1989). Habitat studies have been numerous in ecology (see McCoy & Bell, 1991), and in stream ecology its static (composition) or dynamic (flow) properties and their relation with organisms have been presented in numerous studies (e.g., Poff & Ward, 1989; Palmer *et al.*, 1995; 1996; Biggs *et al.*, 1998).

The Habitat Template Theory (Southwood, 1977, 1988) has been underlying to understand the effect of the habitat heterogeneity on the macroinvertebrate responses and adaptations. This approach is based on the idea that habitat is a frame where the evolution occurs giving characteristic life history strategies to organisms and providing a community organization at different scales of perception (Townsend & Hildrew, 1994). In the contrary hypothesis, historic and phylogenetic features would constrain specific traits, independently of habitat (Gould & Lewontin, 1979). The relationship between habitat and their matched species traits has been studied in aquatic ecosystems with more emphasis in the last decade (Resh *et al.*, 1994; Townsend & Hildrew, 1994; Persat *et al.*, 1994; Poff & Allan, 1995; Statzner *et al.*, 1997; Townsend *et al.*, 1997; Poff, 1997; Statzner *et al.*, 2001), and recent studies shown that even in distant regions, species traits converge in the same habitat (Lamoroux *et al.*, 2002). The application of the Habitat Templet Theory to aquatic ecosystems was promoted by Townsend & Hildrew (1994) in the River Habitat Templet, where different traits were established in a two-dimensional space (spatial and temporal heterogeneities). Traditionally these two dimensions have been associated with disturbance (Hildrew & Townsend, 1987; Poff & Ward, 1990), and stable environments seem to favour specialist species, whereas in unstable conditions generalist strategies are common (Southwood *et al.*, 1974; Southwood, 1988; Poff

& Allan, 1995). The level of favourableness for organisms in a habitat is variable along time and space, showing different heterogeneous patterns (Southwood, 1977). Consequently, a quantification of the habitat including spatial and temporal aspects is crucial to understand the relations of organisms with environment and the effect of heterogeneity.

Predictions made by the River Habitat Templet have been tested by several authors, and some different results have been found at different scales (Persat *et al.*, 1994; Usseglio-Polatera, 1994; Resh *et al.*, 1994), indicating that not all species traits for all species match with the same habitat because trade-offs among traits. To avoid that, several authors have suggested testing habitat-traits theories using groups of organisms with similar species traits (Statzner *et al.*, 1997). In that sense, Usseglio-Polatera (2000) grouped different macroinvertebrate taxa in groups and subgroups of organisms sharing the same category of ecological and biological traits. We have used the traits from these groups or subgroups to check for the relationship of the habitat templet and traits in a mediterranean and temporary river system.

Thereby, the aims of this study are: (1) to quantify the spatial heterogeneity in habitat composition at reach scale in a Mediterranean river network; (2) to examine how this spatial heterogeneity affects on the temporal heterogeneity in a seasonal scale; (3) to study the influence of the spatial and temporal changes on the macroinvertebrate assemblage and its species traits; and (4) to study changes between wet and dry season ocurring in these sites affected by spatial and temporal heterogeneity.

STUDY AREA

The study was carried out in the Mediterranean streams and brooks in the Sant Llorenç Natural Park area (Catalonia, NE Spain) (Figure 1). This area offers a unique opportunity to understand the change produced in the macroinvertebrate community structure between the dry and wet period in absence of heavy man disturbances, something difficult to find in areas colonized by man since 2000 years ago. In a previous paper data about water quality, macroinvertebrate feeding strategies and community structure was presented (Rieradevall *et al.*, in press).

Sant Llorenç del Munt Natural Park has been protected for 30 years. It is located north of the Barcelona metropolitan area (NE Spain) and extends on a surface area of 9630 Ha. The mountain ranges in which the park is located have a typical Mediterranean climate, with irregular and intense rains mostly falling winter but with some spring and autumn precipitation, while summer is normally a very dry period (see Figure 2). The park has a dominant karstic geology with highly permeable substrates and, therefore, surface flow in streams may cease in hours or days after the rains. However, some permanent streams exist, mostly linked to the presence of springs discharging from the karstic aquifer. Evergreen oak trees or white pines cover the park, except in the steepest areas or in places with rock outcrops. The protected studied area is situated between altitudes ranging from 280 to 1100 m and 20% of the studied reaches extended far beyond the limits of the park. The park is a quite popular area for hiking with several small tourist resorts and the number of visitants registered by the park service is close to 80,000 annually. The sampled streams belong to two main catchments that discharge to the Mediterranean Sea, the Besòs and Llobregat rivers, whose main channel and tributaries are well known from several previous studies (Prat *et al.*, 1999; 2000; 2001).

MATERIAL AND METHODS

Data collection

A total of 78 localities were visited in February (wet season) and August 1996 (dry period) and in each site the condition of the stream was recorded as permanent (>1 l/s), intermittent (only pools) or ephemeral (dry), according to Dietrich & Anderson (2000). However, because of the high ephemeral nature of the network, only 25 sites, that were permanent in winter, were sampled (Figure 1 a-b). In each site, the discharge was measured in winter and summer time using a flow meter and the section of the river channel. The structure of the habitat was recorded in wintertime estimating the percentage of gravel, cobbles or bedrock and the percentage of pools versus riffles in a 50 m reach.

Temperature, pH, conductivity and dissolved oxygen (mg/l and % of saturation) were measured "in situ" for each locality using portable equipment. Also, one liter of water was collected, kept cool and analyzed in the laboratory for calcium, potassium, chloride, sulphates, ammonia, nitrite, nitrate, phosphorus and suspended solids.

All available habitats were sampled for the macroinvertebrates using a circular net of 250 μm of mesh size, with "kicking" method with a similar time-effort in each sampling site. The

samples were preserved with formalin and sorted and identified at family level. When it was possible, genus/species were obtained. For each taxon the relative abundance is used in data analysis.
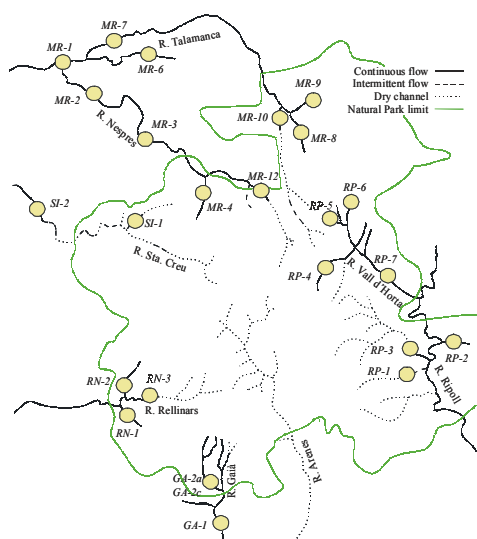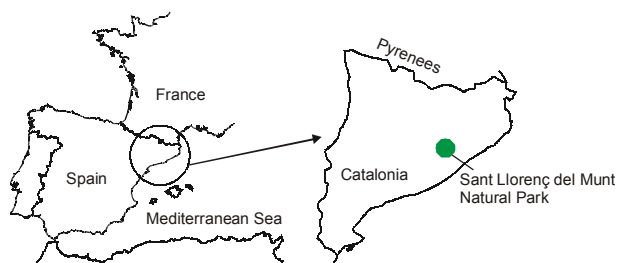

Figure 1a. Sampling area and sites with the channel status in the wet season (February 1996). Red circles indicates dried beds.
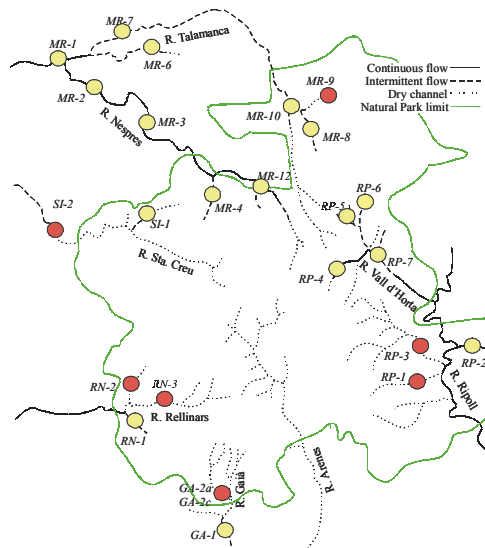
Figure 1b. Sampling area and sites with the channel status in the dry season (August1996). The black spots indicate the dry sites.
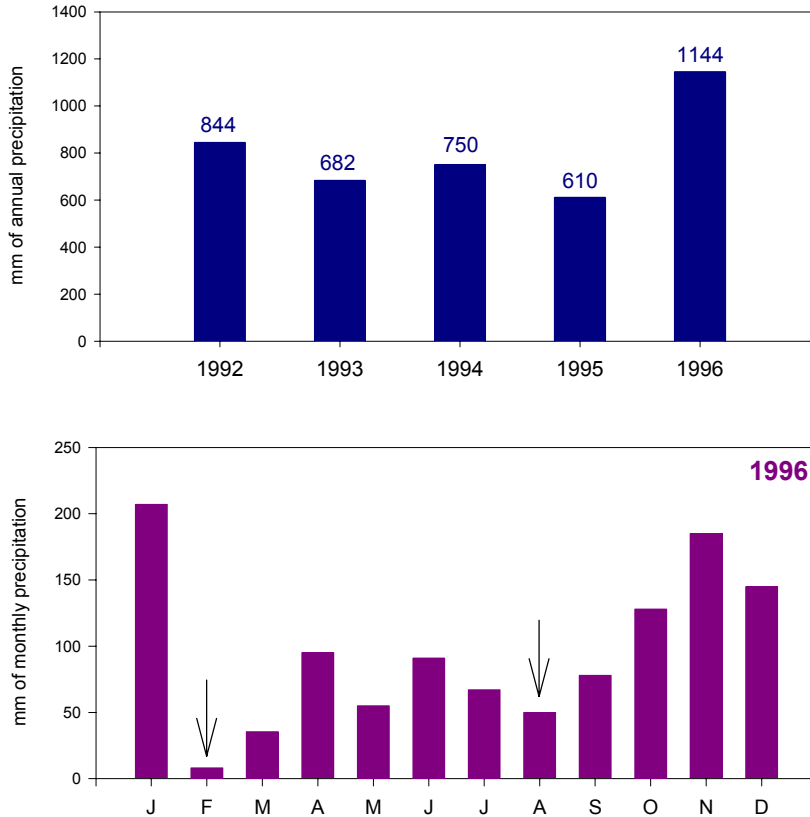
Figure 2. a. Annual precipitation between 1992 and 1996 recorded in the Park (Coll d'Estenalles area). Data from the "Servei de Parc Naturals de la Diputació de Barcelona".
b. Monthly precipitation along 1996. Arrows indicate sampling seasons.

The study was carried out in a very wet year after several ones with medium annual rainfall (Figure 2a). Most of the rain in 1996 was recorded in January and autumn months, whereas spring time presented a medium to low levels of rainfall. Consequently, samples from wet (February) and dry (August) seasons were collected after a high and low precipitation period, respectively (Figure b).

Data analysis

Seasonal changes in macroinvertebrate assemblages

Seasonal changes were measured comparing winter (February) and summer (August) sampling periods using a Canonical Correspondence Analysis (CCA) with CANOCO program (ter Braak, 1998). All the physicochemical variables measured were standardized and log-transformed previously to the analysis. CCA analysis is a multivariate ordination technique based on eigenvalues, where the variation in community composition is explained by several ordination axes, linear combinations of environmental variables (Legendre & Legendre, 1998). The family was used to this analysis, as not all taxa were identified at genus or species level.

Heterogeneity, physical factors and temporality

The spatial heterogeneity has been analyzed measuring the physical structure using three factors: a) the percentage of conglomerate bedrock versus cobbles and gravel, b) the amount of flow in each site in winter and summer and c) the percentage of riffles and pools at the time of sampling (Annex 1).

To relate habitat (as substrate composition, velocity and flow) with temporality, we formulated the hypothesis that the stream should be less temporary in each of these circumstances: 1. Over large conglomerate bedrock (no infiltration) versus areas were gravel or cobbles dominate, 2. When large pools are more important than riffles (more water accumulated), 3. When a high flow is present in winter and 4. When permanent flow exists in summer. To quantify the spatial and seasonal heterogeneity according to these factors we estimated for each sampling point a reach permanence score (RPS), in a similar way as Feminella (1996) did in a temporary stream.

RPS calculation was done as follows (Annex 2). First, we ranked the 25 localities according to the importance of four attributes separately: (1) its percentage of bedrock; (2) the percentage of pools; (3) its relative winter flow (in respect to the maximum discharge in this period); and (4) its relative summer flow (in respect to the maximum summer discharge). As we had 25 stations, for each parameter, the first station with the highest percentage of this parameter will receive a maximum score of 25, the next 24... and lower values successively until the last station that will receive score of 1 for this parameter. For each parameter all percentages were grouped in classes (i.e., 0.1-9%, 10-19%...), and for flow . When several localities had the same percentage of one of the parameters the mean rank score of its ranks scores will be

given to each of them. For example, if three stations have 90% of hard substrata and their rank is between number 24 and 22, a score of 23 was given to each of the three stations.

After the rank of sites, the four scores were added for each station and the final RPS was obtained which may vary between 100 and 4 (Table 1). In the first case, the score implies that the sampling point was arranged in the first position and is supposed to be the more permanent (mostly pools, over hard substrata and maximum flow recorded both in winter and summer). On the other hand, the last value (4) will signify that the sampling point was the last in all partial ranking (only riffles, over gravel or cobbles and with no flow or the smallest flow in both occasions), and therefore should be the more ephemeral.

Table 1. RPS Score and summer status of the channel for each site. The sites are divided into three groups (Permanent, Intermittent and Ephemeral) according to the k-means results. Only pools is referred to sites with disconnected pools in summer or with pools connected by ≤1l/s.

	FINAL SCORE (A+B+C+D)	Summer status	CATEGORY
MR2	84	Flow >1 l/s	PERMANENT
MR6	80	Only Pools	
RP2	77	Flow >1 l/s	
MR7	72.5	Flow >1 l/s	
RP7	69.5	Flow >1 l/s	
MR3	68.5	Flow >1 l/s	
MR12	66	Flow >1 l/s	
MR1	64.5	Only Pools	INTERMITTENT
MR8	64	Only Pools	
RN1	62	Flow >1 l/s	
RP4	61.5	Only Pools	
MR4	59	Only Pools	
GA1	57.5	Flow >1 l/s	
SI1	56.5	Only Pools	
RP6	52.5	Only Pools	
MR10	46.5	Only Pools	
RP5	40.5	Only Pools	
RN2	38.5	Dry	
GA2c	34.5	Dry	EPHEMERAL
SI2	31	Dry	
GA2a	31	Dry	
RN3	29.5	Dry	
MR9	16.5	Dry	
RP3	16.5	Dry	
RP1	16.5	Dry	

Macroinvertebrates and temporality

This ranking will give us the gradient of the stations according to its permanence (or ephemerally) measured by physical factors (the RPS value). To separate this gradient in three groups of sites according to their condition (permanent, intermittent or ephemeral) minimizing the error, a k-means clustering using 3 groups was performed with SPSS statistical package (SPSS, 1999). For each group of sites obtained, the error of classification (e.g., number of intermittent sites grouped in the permanent group) was calculated. The k-means method is a cluster technique where objects are separated in a pre-established number of groups, looking for higher similarities inside each groups and differences among groups (Legendre & Legendre, 1998).

Differences of macroinvertebrate richness between temporality conditions and richness were assessed using a Kruskal-Wallis non-parametric ANOVA test, as the richness values differed from normality. The STATISTICA Program was used to perform the analysis (Stat Soft, 1999).

The "4th Corner Method" (Legendre *et al.*, 1997) was used to check for differences in biological traits between temporality conditions. This statistical program uses a biological matrix (taxa *vs.* sites), a behavioral matrix (taxa *vs.* traits) and an environmental matrix (sites *vs.* environment or habitat) to create a new one that relates the different kind of habitats with the different traits. In our case, the biological matrix was February and August matrix transformed to presence/absence because requirements of the program; the environmental matrix was the pertinence of each locality to the three groups increasing in permanency, ephemerally and intermittency, according to the k-means groups; and the behavioral matrix was the value of the biological traits for each taxa. Correlations between traits and habitats were computed in the program. Two hypotheses are tested by program in these conditions:

H_0: All habitats are suitable for all individual species.
H_1: Individual species find optimal conditions in the sites where they are found.

The traits studied were classified into biological and ecological according to Usseglio-Polatera *et al.* (2000). For our study only the biological ones (more related to behavior) have been used. Information of biological traits of some taxa is not available in the paper of Usseglio-Polatera *et al.* (2000) and these were excluded from the analysis (e.g., Hydracarina, *Aquarius najas*). The biological traits used involve life cycle aspects (maximum size, life cycle duration, potential number of reproduction cycles per year, aquatic stages), resistance or resilience (dispersal, substrate relation, resistance form), physiology and morphology (respiration,

locomotion) and feeding and reproduction behavior (reproduction, food and feeding habits). Their categories are listed in Annex 3, according to the ones in the Usseglio-Polatera's paper based in a "fuzzy coding" procedure from 0 (no affinity) to *n* (high affinity). In total 63 categories have been used and they have been associated with the groups from RPS score in the same rank proposed by Usseglio-Polatera *et al.* (2000). To perform the traits matrix, each taxa was checked for the group or subgroup in the Usseglio-Polatera's list (Annex 4), and for each taxa and trait categories were selected according to the frequency of distribution. To simplify the data analysis and to avoid trade-offs, the category with a maximum affinity was selected for each group or subgroup (Annex 5).

The result of the program is a matrix of r-values and p-values associated for each biological trait used and each habitat. The r-value indicates a correlation between the habitat (permanent-intermittent-ephemeral) and the modality of the species trait (1-2-3-4-..., depending on the trait). Thus, a positive and significant r-value for one habitat and trait would indicate that the habitat has a modality of the trait corresponding to a high number, meanwhile a negative value would show the presence of a low modality of the trait (according to the Annex 3).

RESULTS

Seasonal changes and its effects on macroinvertebrates
Because of climate and geology of the sampled area, several streams dry up in summer every year, with or without pools remaining in them. While in very dry years flow may cease in all the streams, in wet years part of them maintain permanent flow. The year 1996 was a relatively wet year (Figure 2). The flow condition of the drainage network of Sant Llorenç Natural Park for both periods of time can be seen in Figures 1a (winter) and 1b (summer). Three situations observed during each sampling period are illustrated in each figure: 1) Flowing water (from 1 to 600 l/s)-(continuous line), 2) River courses with pools but without surface flow (dashed lines) and 3) Dry watercourses (dotted line). That is, permanent, intermittent and ephemeral streams. In winter, 63% of the total length network had a continuous flow, while in summer only a 26%. The rest of river length was intermittent (only pools) or ephemeral (dry). The main streams with permanent flow in summer were outside or in the limit of the park area, downstream of permanent springs with a karstic origin. Although 1996 was a wet year, 8 of the 25 sites sampled in February were totally dried up in summer.

As a change in the flow condition between the wet and the dry period was noticed, the influence of this seasonal heterogeneity on the macroinvertebrate community was studied using a CCA analysis with all the data. The results are presented in Figures 3 and 4. Chloride, sulphates, conductivity, ammonia, phosphate, nitrate and nitrite were very similar between all the sites, as the streams sampled are not affected by human influence. Thus, the results of the CCA indicated that these chemical parameters were not significantly important to explain the variability of the macroinvertebrate data and they were not considered in the analysis. On the other hand, temperature, calcium, potassium, oxygen, flow and pH were significantly different and were retained as parameters with significant changes between stations or in time. The two first axes of the CCA explained 68% of the total variability of the data.

This analysis shows the importance of annual seasonal change in the matching of the communities. The first axis explains 43% of the variance and is related to high temperatures and low oxygen and flow in the right side. Samples taken in August (high temperature and low flow) are grouped together in the positive area of the first axis and clearly separated from those of February (Figure 3). All taxa exclusive from winter are in the left part of Figure 4, as Nemouridae, Philopotamidae, Leuctridae, Athericidae, Chloroperlidae or Glossosomatide, and they can be considered as lotic taxa associated with low temperature and high flow. On the other hand, those present only in summer are lentic taxa, related to a higher temperature and no flow and are situated on the right, as most of the Coleoptera, Heteroptera and Odonata. Taxa as Baetidae, Chironomidae or Oligochaeta were located in the middle of the graph, and as they were present in both sampling periods, can be called as the core species suggested in Boulton & Lake (1992b).

The second axis, with 24.56% of the variance explained is related with the effects of water velocity and algae activity on the physicochemical characteristics and the community composition. In high flow conditions and low temperature, oxygen concentration and pH increased, while calcium carbonate precipitates. The riffle species from the lower part of Figure 4 are more related to these conditions than pool species (families on the upper part of Figure 4). The family Sphaeriidae is located in the upper part of the graph, and seems to be related with the calcium concentration that can be important for maintaining the shell.
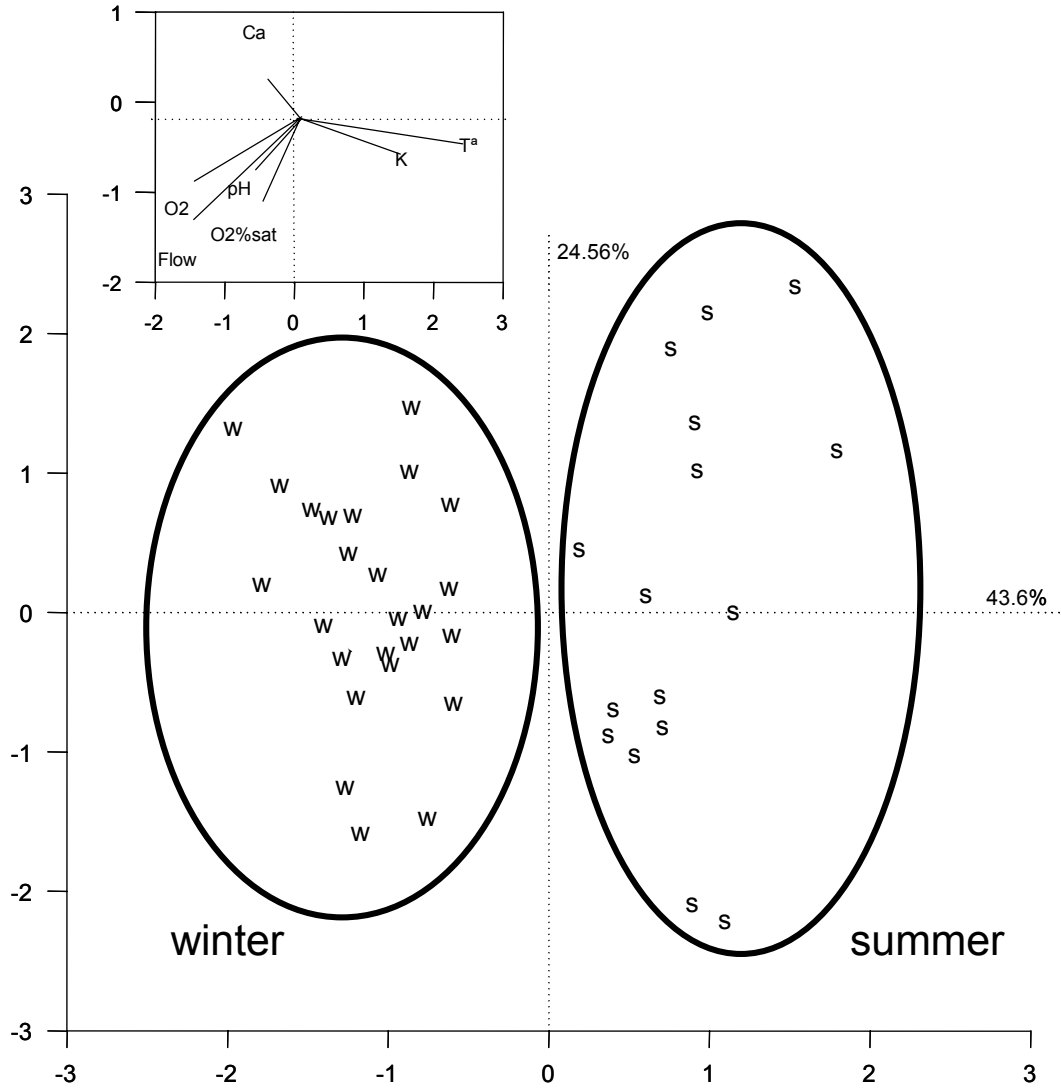
Figure 3. Results of the CCA analysis using February and August samples.
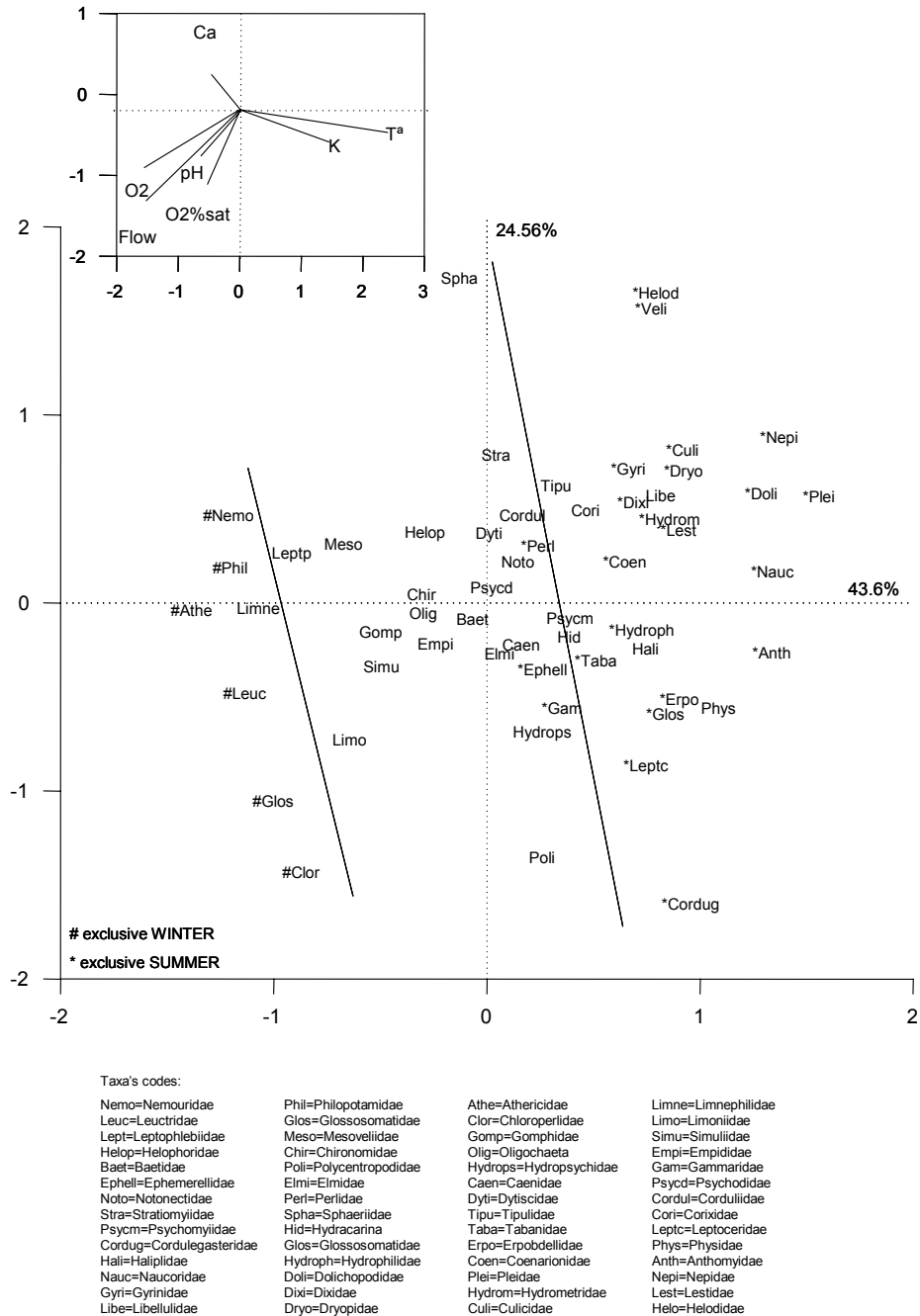
Figure 4. Results of the CCA analysis. The families are plotted. The lines separate the families only present in winter (#cold taxa) from the ones in summer (*lentic taxa) and the core species (always present).

Taxa's codes:

Nemo=Nemouridae	Phil=Philopotamidae	Athe=Athericidae	Limne=Limnephilidae
Leuc=Leuctridae	Glos=Glossosomatidae	Clor=Chloroperlidae	Limo=Limoniidae
Lept=Leptophlebiidae	Meso=Mesoveliidae	Gomp=Gomphidae	Simu=Simuliidae
Helop=Helophoridae	Chir=Chironomidae	Olig=Oligochaeta	Empi=Empididae
Baet=Baetidae	Poli=Polycentropodidae	Hydrops=Hydropsychidae	Gam=Gammaridae
Ephell=Ephemerellidae	Elmi=Elmidae	Caen=Caenidae	Psycd=Psychodidae
Noto=Notonectidae	Perl=Perlidae	Dyti=Dytiscidae	Cordul=Corduliidae
Stra=Stratiomyiidae	Spha=Sphaeriidae	Tipu=Tipulidae	Cori=Corixidae
Psycm=Psychomyiidae	Hid=Hydracarina	Taba=Tabanidae	Leptc=Leptoceridae
Cordug=Cordulegasteridae	Glos=Glossosomatidae	Erpo=Erpobdellidae	Phys=Physidae
Hali=Haliplidae	Hydroph=Hydrophilidae	Coen=Coenarionidae	Anth=Anthomyidae
Nauc=Naucoridae	Doli=Dolichopodidae	Plei=Pleidae	Nepi=Nepidae
Gyri=Gyrinidae	Dixi=Dixidae	Hydrom=Hydrometridae	Lest=Lestidae
Libe=Libellulidae	Dryo=Dryopidae	Culi=Culicidae	Helo=Helodidae

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Spatial Heterogeneity and its relationship with temporal heterogeneity

Using the ranking method described above (RPS score), the sampling stations were arranged from the most permanent to the more ephemeral from the data provided in Annex 1. The rank ordination of the stations for each attribute is indicated in Annex 2 (percentage of hard habitat, percentage of pools and the relative flow in winter and the summer). The final RPS score (the sum of the four values for each sampling site) is in Table 1 with RPS scores ranging from 16.5 to 84. This is the physical gradient defined by this index, going from the more permanent station (MR2) to the more ephemeral one (RP1).

In Table 1 together with the physical gradient according to the RPS score, the observed condition of each site in the field (with flow higher than 1 l/s in summer, only pools in summer or dry) is presented. According to these results and in order to make easier further analysis and interpretations, the gradient has been separated in three categories or groups by the k-means clustering (permanent, intermittent and ephemeral). According to the analysis the first 7 sites are classified as permanent (with an error of bad classification of 14%); the next 11 as intermittent (with an error of 27%); and the last 7 sites as ephemeral (with an error of 0%).

Spatial and Temporal heterogeneity and macroinvertebrates

Figure 5 shows the number of winter families and summer families along the RPS gradient. The limit between permanent, intermittent and ephemeral stations are showed in the figure. There is a clear gap between the ephemeral and the other stations, with an increase of summer taxa in intermittent and permanent stations in summer and winter seasons. The maximum number of families has been found in a site that in summer has high percentage of pools and with flow between them (RP7). In permanent and intermittent sites, the number of families found in winter was higher than in summer. Summer season present a lower number of taxa although they enhance an increase of the total richness, with addition of an average of 8 new taxa. Although a change in richness is observed along the gradient, the Kruskal-Wallis non-parametric ANOVAs indicate that only in the ephemeral sites have significant lower values ($p < 0.03$ for total, winter and summer). No-differences were found comparing permanent and intermittent richness, in summer ($p = 0.473$), winter ($p = 0.205$) or both periods ($p = 0.628$).
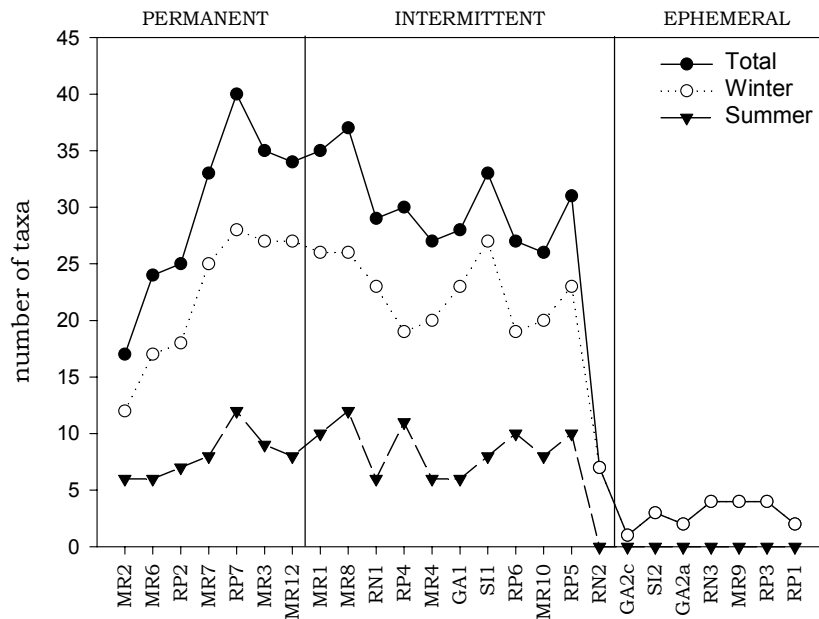
Figure 5. Variation of the number of taxa (total, winter exclusive and summer) along the RPS gradient from permanent to ephemeral reaches.

When EPT and OCH values are compared in separately in the wet and dry period (Figure 6), no differences between permanent and intermittent sites can be distinguish. Besides, ephemeral sites present a very low number of EPT and OCH fauna in winter respect intermittent and permanent conditions. Accordingly to the observed in Figure 3 and 4, differences from wet and dry period in the macroinvertebrates are based in a change from EPT dominant to OCH dominant.
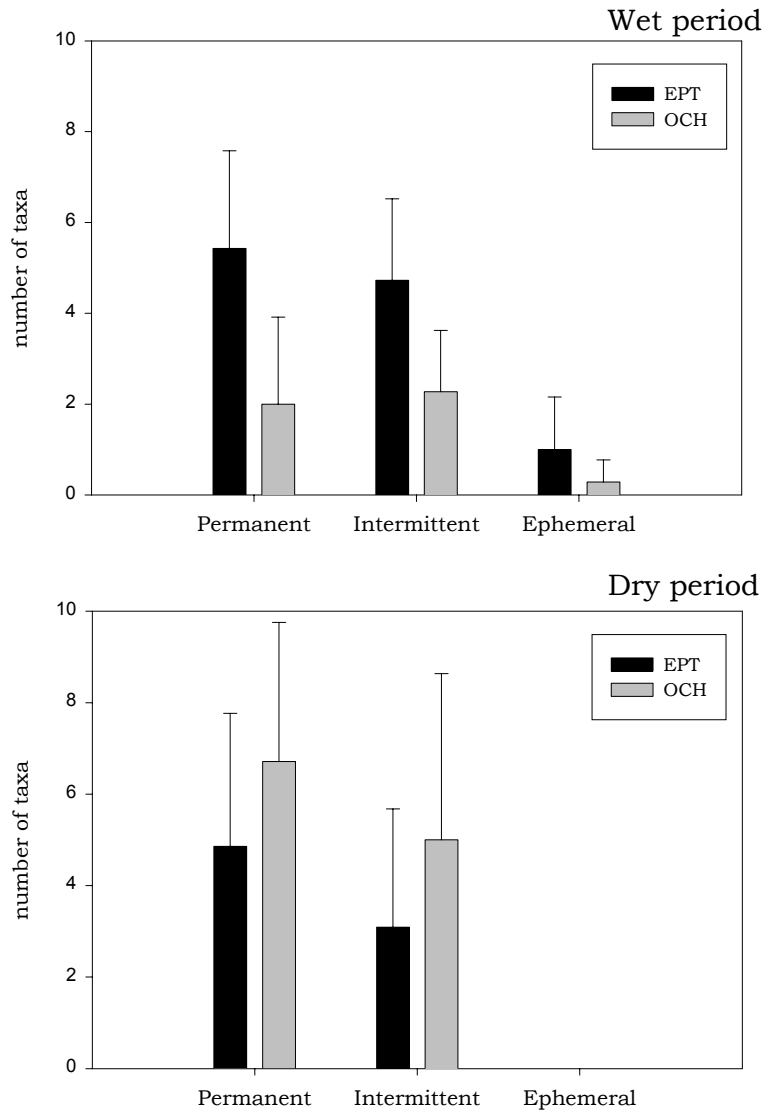
Figure 6. Mean and standard deviation of the EPT and OCH values for permanent, intermittent and ephemeral reaches in the wet and dry period.

Results from the 4th Corner Method show several significant patterns in between biological traits from permanent, intermittent and ephemeral streams (Table 2). A mix of behavior features seems to be present in permanent sites (as no significant traits are shown), while some specific ones are exclusive from intermittent and ephemeral situations, independently. However, "Maximal size", "Reproduction", "Resistance forms" and "Feeding habits" are not significant in any category, in contrast to "Life cycle duration", "Potential number of reproductions per year", "Aquatic stages", "Dispersal", "Respiration", "Locomotion and substrate relation" and "Food". In intermittent sites "Life cycle duration" is significantly over than 1 year with several reproductions per year, and its community is dominated by flying, swimmer or surface swimmer adults with aerial respiration and an active and by air dispersion. In contrast, ephemeral sites are dominated by larvae that breath by gills or tegument and are attached on the substrate. Their dispersion is by water and has short life cycle duration (lower than one year) and few reproductions per year. Food appears significant in ephemeral sites, with larvae feeding in fine sediment or detritus.

Table 2. Results of the 4th Corner Program, for each biological trait tested and flow category. The most significant traits are indicated with * (p<0.05) or ** (p<0.01).

	PERMANENT		INTERMITTENT		EPHEMERAL	
	r	p-value	r	p-value	r	p-value
Maximal size	0.036	0.192	-0.043	0.147	0.017	0.335
Life cycle duration	-0.01	0.389	0.066	**0.043***	-0.123	**0.0008****
Nº reproductions / year	-0.022	0.288	0.053	**0.094***	-0.069	**0.046***
Aquatic stages	-0.011	0.274	0.072	**0.0024****	-0.113	**0.001****
Reproduction	0.004	0.49	-0.004	0.442	-0.0001	0.509
Dispersal	-0.028	0.218	0.085	**0.011***	-0.128	**0.0005****
Resistance form	0	1	0	1	0	1
Respiration	-0.036	0.156	0.082	**0.015***	-0.103	**0.0045****
Locomotion and substrate relation	0.002	0.496	-0.054	**0.087***	0.1157	**0.001****
Food	0.018	0.317	0.032	0.188	-0.113	**0.001****
Feeding habits	0.004	0.466	0.004	0.441	-0.021	0.294

DISCUSSION

Classification of heterogeneous environment is the key to understand organisms' patterns and responses (McIntosh, 1985). Heterogeneity itself provides the presence of environmental gradients spatially continuous or discontinuous (Keddy, 1991). The spatial heterogeneity in our mediterranean system has been directly ranked in a gradient of sites to test 4 different hypotheses. The gradient of sites obtained by habitat categorization, provide a gradient of temporality (permanent, intermittent and ephemeral sites). Spatial and temporal heterogeneities can have implications on macroinvertebrates independently but the interaction between them can determine some patterns and processes (Keddy, 1991). Relationships between both heterogeneities are not easy to study because of their complexity and several methodological constraints (Kolasa & Rollo, 1991). Consequently, few studies analyze both heterogeneities (Resh & Rosenberg, 1989; Watling & Press, 2000; Wiens, 2000), and even less report the interaction between them, although Wiens (2000) suggested that variation in time often creates patterns in spatial heterogeneity. In that sense, using a simple quantitative index, we are showing how temporal heterogeneity (i.e., if the river will be permanent, intermittent or ephemeral in summer) is affected by spatial heterogeneity (i.e., the composition of habitat in terms of substrate and flow).

This easy method to quantify the spatial heterogeneity and its relationship with temporal changes should be carefully applied in other areas in the world, as rivers characteristics and climatic features are different. For example, although the hypothesis related to habitat characteristics (riffles vs. pools and gravels and cobbles vs. bedrock) can be applied in other climates, the % of winter and summer flow hypothesis can differ. In mediterranean rivers, base flow is strongly related with precipitation, evapotranspiration and ground water level (Vidal-Abarca, 1990; Camarassa & Segura, 2001). Thereby, in mediterranean climate low discharge in winter is more likely to imply temporality in summer than high discharge, than in other areas where summer flow is significant.

Comparisons between wet and dry seasons

Changes of macroinvertebrate assemblages among seasons have been reported by several authors (Boulton & Lake, 1992b; Boulton & Lake, 1992a; Graça *et al.*, 1989). Boulton & Lake (1992b) also suggest a change of species related to the change in habitat structure. In our case, winter exclusive species as some Plecoptera (Nemouridae, Leuctridae, Chloroperlidae) or Trichoptera (Philopotamidae) are related to riffle conditions in wintertime and are called "main

flow species". They disappear with a decreasing of flow through spring and summer. These taxa are substituted by lentic species, mostly OCH species (Odonata, Coleoptera and Heteroptera) able to survive in pools or dominant lentic habitats. An overlap of macroinvertebrates between winter and summer season is also present, with several families present in both seasons and most of sites, as Chironomidae, Oligochaeta, Caenidae, Baetidae, called core species by Boulton & Lake (1992b). Core species have an even distribution in space and time, what could be related with their broad niche (Vandermeer, 1972), and in fact, these taxa have been recorded in almost all lotic stream studies. On the other hand, main flow species and tolerant lentic ones are restricted to specific habitats because, and as a consequence the show a narrower distribution.

Macroinvertebrate comparisons between permanent, intermittent and ephemeral sites

Several authors with contrasting results have compared richness in permanent and temporary sites. In part, the disparity of results is because of the different concept of temporary sites in different papers, as some consider them as sites that dry up completely in summer, whereas others refer to rivers that have isolated pools in dry period. We have considered that temporary sites included both, and we have separated them in intermittent and ephemeral localities (see Glossary at the end of this Chapter). For instance, Wrigth *et al.* (1984) or del Rosario & Resh (2000) found lower richness in temporary than permanent sites, whereas Legier & Talin (1973), Boulton & Suter (1986) and Miller & Golladay (1996) and report similar richness. Dieterich & Anderson (2000) found a 20% higher richness in the pools of two temporary Oregon streams than in a permanent stream, and a lower diversity in ephemeral sites. In our studied rivers, intermittent and permanent sites have similar taxonomical richness, but higher than ephemeral sites. The colonization of a new habitat implies a high development and abundance of some highly resilient species (Dell *et al.*, 1986; Townsend & Hildrew, 1994), and therefore a low diversity should be expected in ephemeral sites. In contrast, in the permanent and intermittent reaches, where water remains during a long period of time, we have found an increase of diversity. In that way, the dry season length have been recognized as one important factor to determine diversity in these streams, postulating that the longer the dry season is, lower is the diversity (Williams & Hynes, 1976; Abell, 1984; Williams, 1996). On the other hand, the high interannual variability in precipitation and stream discharges in mediterranean rivers (McElravy *et al.*, 1989) may imply an interannual variability in the conditions of temporality of one site (del Rosario & Resh, 2000). The low taxonomical richness in our ephemeral sites suggest a ephemeral condition the year before the study, and the high difference in richness from permanent sites, would suggest a slow recovery from the last dry

period (5-6 months ago), which is in agreement with other authors (Boulton & Lake, 1992b; but see Pires *et al.*, 2000).

Feminella (1996) studying the relationships between a gradient of permanence and macroinvertebrate assemblages, found a high correlation between EPT and an increase of permanence, what also is consistent with our results, although its importance are relative to the season analyzed (Figure 6). A higher EPT/OCH ratio in winter respect summer for all three flow categories can be related with the difference of habitat in both seasons with larger riffles in winter and more pools in summer (Williams, 1996). However, in the dry season, although several riffles are still present in permanent sites, they have a high OCH values, what could be related to a major presence of pools in summer because the habitat constriction or to life cycles of riffle families.

It has been proposed that a specific habitat can imply the presence of several macroinvertebrates with some characteristic traits adapted to the habitat that is "The habitat template theory" (Southwood, 1977, 1988). In that sense, in our study, the absence of significant traits in permanent sites could be related to high habitat variability, with riffles and pools segregated but always present, while in intermittent sites pools are dominant in at least in one season, and in ephemerals riffles are dominant. Moreover, as the disturbance is one of the agents generating spatial and temporal heterogeneity (Whiter & Harrod, 1997) the structure of the community and the evolution of the species strategies are affected. Intermittent and ephemeral streams are subjected to different types of disturbance that imply different responses of biological traits: the change of habitat into pools in summer in intermittent sites and the lack of flow in ephemeral sites in the dry season. In that sense, Wiens (2000) suggest that the evolution of behavior traits are often to be interpreted in the context of spatial heterogeneity, although the combined effects of temporal and spatial variability drive some adaptative traits. In our case, the relationship between spatial and temporal heterogeneity generates the presence of traits enclosing both heterogeneities. Aquatic stages, respiration, locomotion, food and feeding habits could be related to spatial heterogeneity, as their properties change between intermittent and ephemeral sites because the presence of pools and bedrock in intermittent and gravels/cobbles and riffles in ephemeral sites. On the other hand, maximal size, life cycle duration, potential number of reproductions per year, dispersal and resistance forms would be more related to the presence of temporal heterogeneity and affecting differently in intermittent and ephemeral sites.

As Townsend and Hildrew (1994) predicted, more disturbed sites had habitat generalist's individuals, with small size, high adult mobility and some life cycles outside the stream. In our ephemeral sites some of these traits appear as significant, as these localities are highly disturbed by a short duration of flow. Disturbance in river ecosystem have been defined in terms of intensity and frequency (Resh *et al.*, 1988), and the response of the system also depends on the degree of stability (Wishart, 1998). Ephemeral sites, because the presence of gravels and cobbles and low flow could be related with some sandbed rivers located in arid and semiarid lands with low taxonomical richness and highly resilient organisms (Wishart, 1998), exhibiting traits from r-species (Williams, 1996) as Baetidae, Caenidae, Culicidae, Chironomidae that present continuous life cycles (Gray, 1981; Gray & Fisher, 1981; Molles, 1985). Smaller individuals have been found in ephemeral sites at the beginning of the wet season (Williams, 1987, 1996) although in our case, maximal size not appears as significant, and that can be related with the sampling month far away from the colonization season. On the other hand, our results suggest that in ephemeral sites, the main way to colonization is made by drift from or flying adults laying eggs, without significant resistant forms, what is related to the high heterogeneity of the streams samples at basin scale (Figure 1 a-b). Thus, some ephemeral reaches can be connect to permanent o intermittent ones during wet period, providing organisms that disclose the role of core species in permanent and intermittent sites as refugia (Lake, 2000), and facilitating some of those core resilient species in front of resistant ones. Consequently, that would explain why resistance does not appear as significant. In fact, in mediterranean ecosystems, a predominance of resilient forms over resistance ones prevails (Fox & Fox, 1986). According to all of that, ephemeral sites would not have a unique and characteristic community (Delucchi & Peckarsky, 1989) as it derives from core species in permanent and intermittent sites with short life cycles and a fast growth.

In intermittent sites the presence of isolated pools is strongly related to the biological traits present. Temporary pools communities are composed by life history adapted taxa and random taxa that colonize and become extinct (Schneider & Frost, 1996). Predators (mainly Odonata and Heteroptera) are important taxa in pools exhibiting long life cycles (Schneider & Frost, 1996; Williams, 1996) and several reproductions per year, although their abundance can be affected by habitat duration (Bradshaw & Holzapfel, 1983; Dodson, 1987). Consequently, biotic interactions have to be stronger in these intermittent sites compared with ephemeral and permanent ones, because of the reduction of habitat in the first one (Gasith & Resh, 1999; Lake, 2000). Change of habitat structure in intermittent sites as isolated pools also enhance the presence of aerial breathers, because of the impoverished water quality in pools and lack of flow to renovate (Williams, 1996). As the isolated pools enhance the abundance of OCH

organisms respect EPT, traits found are those belonged to them. In that sense, Usseglio-Polatera (1994) in a study in the Upper Rhône River found that Coleoptera traits are characteristic and different from the Ephemeroptera and Plecoptera with Trichoptera and Odonata displaying intermediate categories.

Relationships with the River Habitat Template

Although none organism is as specific from r or K (Pianka, 1970), the gradient of permanence found from ephemeral to permanent sites can suggest a spectrum of r to K strategies (*sensu* McArthur & Wilson, 1967). Ephemeral sites seem to exhibit r-biological traits, whereas intermittent sites present traits from K-species because the abundance of Coleoptera (Usseglio-Polatera, 1994). Similary, Poff & Allan (1995) associated stable hydrological ecosystems to specialist fish species and fluctuating ones with more generalist organisms. Furthermore, Biggs *et al.* (1998) looking at periphyton community related a habitat matrix defined by disturbance and resource supply to the taxa, identifying taxa with characteristic traits in each case. Thus, traits typical from communities subjected to a high disturbance were small in size, low in biomass, with strong attachment to the surface, high growth rates... what would agree with our results in macroinvertebrates in ephemeral sites. In undisturbed or more stable sites, community was segregated according to the resource supply. Physical structure in our study has been classified as flow and structural characteristics (see Figure 7) and both providing permanent, intermittent or ephemeral reaches. Permanent sites can be present in a diverse substrates conditions (e.g., a mix of bedrock, pools, cobbles, gravels, riffles) but aways should present a high winter and summer flow. Besides, intermittent and ephemeral reaches only can exist if a low flow is present in both seasons. The three situations manifest a different level of spatial heterogeneity. Thus, ephemeral sites because the low flow in winter and the dry bed in summer present a very low spatial heterogeneity compare with intermittent sites with pools in summer. Finally, permanent sites exhibit the maximum spatial heterogeneity, as they in both seasons pools and riffles over a variety of substrates are present (Figure 7). Moreover, permanent sites may act as a refugee of riffles taxa coming from ephemeral and intermittent sites. Similarly to this spatial heterogeneity increasing from ephemeral to permanent reaches, a temporal heterogeneity is observed too in the contrary direction. Permanent habitats are temporally more stable than intermittent and ephemeral ones. Consequently, because permanent, intermittent and ephemeral reaches present different spatial and temporal heterogeneity, the "River Habitat Template" (Townsend and Hildrew, 1994) can be applied to our results. In Figure 8, the application of the "River Habitat Template" to our results is presented. Low temporal and high spatial heterogeneities correspond to permanent sites with

a mix of riffles/pool/core with few changes between wet and dry period. Besides that, intermittent sites present a higher temporal heterogeneity what affects to the community loosing riffles species in summer and sheltering species with K-traits. Finally, in ephemeral sites, the high temporal and low spatial heterogeneity imply a lower number of taxa with riffle and core species dominant, and characteristic r-species traits. Comparisons between Figure 8 and the predictions of traits in the "River Habitat Template" (see Figure 4) in Townsend & Hildrew, 1994) indicate that a high congruity with our results is present.

Several authors have not found conformity with "River Habitat Template" and traits (Resh *et al.*, 1994; Statzner *et al.*, 1997) because the trade-offs among traits and the use of different taxa. On the other hand, Persat *et al.* (1994) also found no significant relationship between some fish traits in Upper Rhône River and the "River Habitat Template" that seems a result of the scale of observation, the evolution of fishes in the area and the history of the river. In our case, the quite good congruity with our findings and the "River Habitat Template" theory confirm the utility of groups of taxa with similar traits to confirm ecological theories (Statzner *et al.*, 1997).
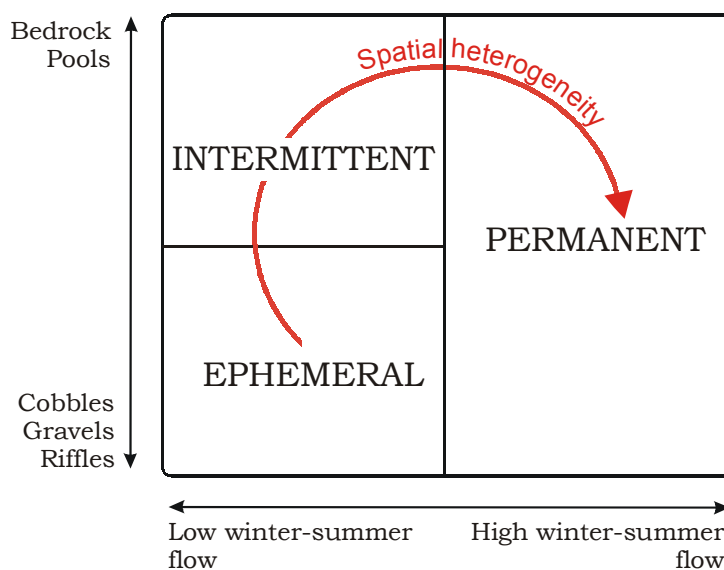

Figure 7. Categorization of habitat by flow and substrate, for permanent, intermittent and ephemeral sites. A increase of spatial heterogeneity from ephemeral to permanent sites is noticed.
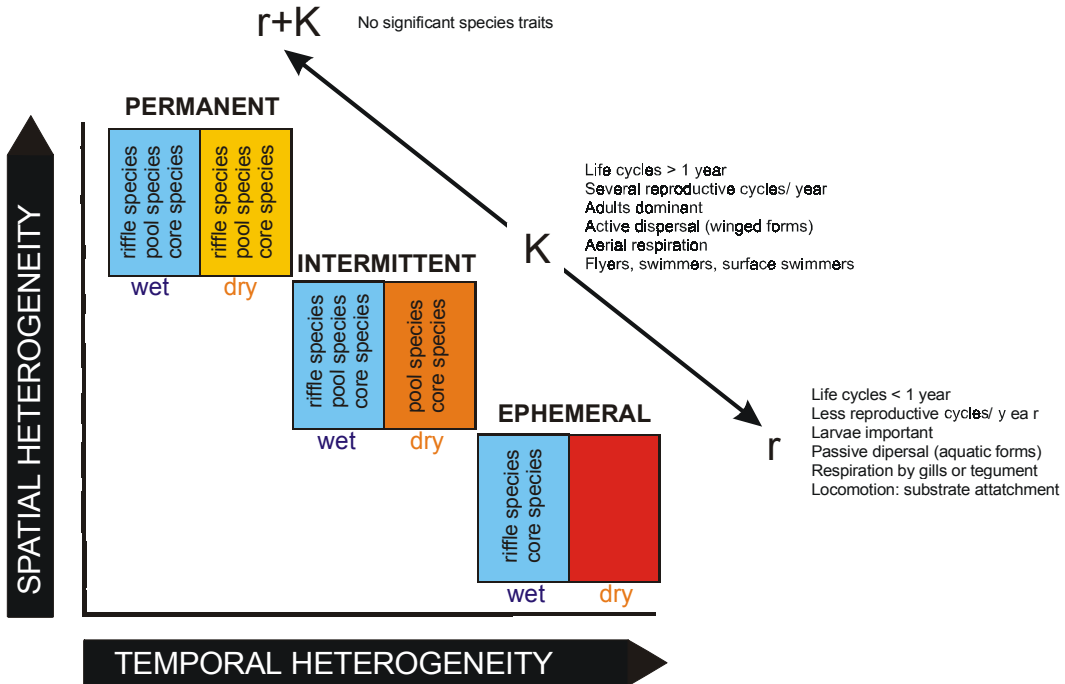
Figure 8. Application of permanent, intermittent and ephemeral conditions to the "River Habitat Template" from Townsend & Hildrew (1994).

Concluding remarks

Mediterranean streams are known for their flow fluctuations along and between years that may cause, mostly in summer, very deep changes in environmental conditions (Gasith & Resh, 1999). Although a different macroinvertebrate assemblage is observed between seasons in all sites (Figure 4), more fine information can be obtained with the categorization of sites in permanent, intermittent and ephemeral. Temporary changes in mediterranean rivers have been related to the climate (e.g. Gasith and Resh, 1999), but other factors may influence and increase or decrease its importance. In our study, either climate or geomorphology of the area sampled interferes on the temporality of rivers and macroinvertebrate responses, providing heterogeneity on responses at different scales. In mediterranean rivers, all these factors can have important consequences in designing of biomonitoring programs in these areas, and methods adapted to these areas have to be developed and tested (Bonada *et al.*, Chapter 1).

Although natural disturbance is present in mediterranean rivers and streams (McElravy *et al.*, 1989; Resh *et al.*, 1990; Gasith & Resh, 1999) and despite the high spatial and temporal heterogeneity observed, mediterranean rivers seems very stable compare with other arid and semiarid areas (Wishart, 1998), as the habitat and temporality appear as the main organizer factors of the macroinvertebrate community. This study agrees with the idea that natural disturbances are determinants to structure of aquatic ecosystems (Fisher & Grimm, 1991; Stanley & Fisher, 1992).

The presence of such variability in streams and responses enhance a high biodiversity in mediterranean rivers, and the moderate stress conditions could be responsible to it (Bond, 1983; Bonada *et al.*, Chapter 3). This enlightened the importance of preservation of small streams from headwaters (as those of Sant Llorenç Natural Park) together with the summer pools in the entire basin, as these are the biodiversity refuges for macroinvertebrates in Mediterranean basins (Vidal-Abarca *et al.*, 1996).

GLOSSARY

Permanent: Is referred to rivers and streams with flowing water either during wet and dry periods.

Intermittent: Is referred to rivers and streams that present isolated pools during dry period. These pools can dry up or not, depending on the length of the dry season.

Ephemeral: Is referred to rivers and streams that dry up completely in dry period. In general they only contain water after heavy rain periods.

Temporay: Is applied to rivers and streams that dry up or recede in isolated pools. Both, intermittent and ephemeral rivers and streams would be included in this category.

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Annex 1. Physical structure estimated in each sampling site.

Site	%Bedrock	%Pools	Winter flow (l/s)	% winter flow	Summer flow (l/s)	% summer flow
RP1	0	0	2.92	0.83	DRY	0
RP2	90	70	51.75	14.79	10.84	52.19
RP3	0	0	13.76	3.93	DRY	0
RP4	80	70	19.05	5.44	0.07	0.34
RP5	0	60	3.53	1.01	1	4.81
RP6	60	70	25.9	7.4	0	0
RP7	40	80	137.31	39.23	2.2	10.59
GA1	15	10	278.66	79.62	9.66	46.51
GA2a	15	50	0.1	0.03	DRY	0
GA2c	0	0	343	98	DRY	0
RN1	30	20	164.53	47.01	20.77	100
RN2	40	20	57.57	16.45	DRY	0
RN3	0	10	114.14	32.61	DRY	0
MR1	70	20	191	54.57	0.29	1.4
MR2	100	30	350	100	15.58	75.01
MR3	50	40	159.4	45.54	18.67	89.89
MR4	40	80	54.78	15.65	0	0
MR6	90	90	200	57.14	0	0
MR7	80	60	208.56	59.59	1	4.81
MR8	90	70	6.24	1.78	1	4.81
MR9	0	0	3.49	1	DRY	0
MR10	50	60	16.84	4.81	0	0
MR12	20	70	152.47	43.56	7.73	37.22
SI1	60	80	1	0.29	0	0
SI2	70	10	33.86	9.67	DRY	0

Annex 2. Ranking of sites according to each physical parameter.

%	% Bedrock		% Pools		% Winter flow		% Summer flow	
%	*Site*	*Rank A*	*Site*	*Rank B*	*Site*	*Rank C*	*Site*	*Rank D*
100	MR2	25			MR2	25	RN1	25
90 to 99	RP2	23	MR6	25	GA2c	24		
	MR6	23						
	MR8	23						
80 to 89	RP4	20.5	RP7	23			MR3	24
	MR7	20.5	MR4	23				
			SI1	23				
70 to 79	MR1	18.5	RP2	19	GA1	23	MR2	23
	SI2	18.5	RP4	19				
			RP6	19				
			MR8	19				
			MR12	19				
60 to 69	RP6	16.5	RP5	15				
	SI1	16.5	MR7	15				
			MR10	15				
50 to 59	MR3	14.5	GA2a	13	MR7	21	RP2	22
	MR10	14.5			MR1	21		
					MR6	21		
40 to 49	RP7	12	MR3	12	RN1	18	GA1	21
	RN2	12			MR3	18		
	MR4	12			MR12	18		
30 to 39	RN1	10	MR2	11	RP7	15.5	MR12	20
					RN3	15.5		
20 to 29	MR12	9	RN1	9				
			RN2	9				
			MR1	9				
10 to 19	GA1	7.5	GA1	6	RN2	6	RP7	19
	GA2a	7.5	RN3	6	MR4	6		
			SI2	6	RP2	6		
0.1 to 9	RP1	3.5	RP1	2.5	SI2	2.5	RP5	16
	RP3	3.5	RP3	2.5	RP6	2.5	MR8	16
	RP5	3.5	GA2c	2.5	RP4	2.5	MR7	16
	GA2c	3.5	MR9	2.5	MR10	2.5	MR1	16
	RN3	3.5			RP3	6	RP4	16
	MR9	3.5			MR8	6		
					RP5	6		
					MR9	6		
					RP1	6		
					SI1	6		
					GA2a	6		
0							SI1	11
							RP6	11
							MR6	11
							MR4	11
							MR10	11
DRY							RP3	4.5
							RP1	4.5
							RN3	4.5
							RN2	4.5
							SI2	4.5
							MR9	4.5
							GA2c	4.5
							GA2a	4.5

Annex 3. Biological traits and categories according to Usseglio-Polatera at al. (2000).

TRAITS	n°	MODALITIES
Maximal size	1	≤0.25 cm
	2	>0.25-0.5 cm
	3	>0.5-1 cm
	4	>1-2 cm
	5	>2-4 cm
	6	>4-8 cm
	7	>8 cm
Life duration	1	≤ 1 year
	2	>1 year
Potential number of reproduction cycles per year	1	<1
	2	1
	3	>1
Aquatic stages	1	egg
	2	larva
	3	pupa
	4	adult
Reproduction	1	ovoviviparity
	2	isolated eggs, free
	3	isolated eggs, cemented
	4	clutches, cemented or fixed
	5	clutches, free
	6	eggs or clutches, in vegetation (endophytic)
	7	clutches, terrestrial
	8	asexual reproduction
Dispersal	1	aquatic passive
	2	aquatic active
	3	aerial passive
	4	aerial active
Resistance forms	1	eggs, statoblasts, gemmunles
	2	cocoons
	3	cells against desiccation
	4	diapause or dormancy
	5	none
Respiration	1	tegument
	2	gill
	3	plastron
	4	spiracle (aerial)
Locomotion and substrate relation	1	flier
	2	surface swimmer
	3	swimmer
	4	crawler
	5	burrower (epibenthic)
	6	interstitial (endobenthic)
	7	temporarily attached
	8	permanently attatched
Food	1	fine sediment + microorganisms
	2	detritus <1 mm
	3	plant detritus ≥1 mm
	4	living microphytes
	5	living macrophytes
	6	dead animal ≥1 mm
	7	living microinvertebrates
	8	living macroinvertebrates
	9	vertebrates
Feeding habits	1	absorber
	2	deposit feeder
	3	shredder
	4	filter-feeder
	5	piercer (plant or animals)
	6	predator (carver/engulfer/swallower)
	7	parasite, parasitoid

Annex 4. Taxa list and biological traits group associated indicating the maximum affinity category according to Usseglio-Polatera at al. (2000).

	gr. / sgr.		gr. / sgr.		gr. / sgr.
Dugesia sp.	c1	*Gerris argentatus*	g3	*Laccobius* sp.	g1
Oligochaeta	h	*Gerris brasili*	g3	*Hydraena* sp.	g1
Erpobdella sp.	c1	*Gerris gibbifer*	g3	*Limnebius* sp.	g1
Glossiphoniidae	b1	*Gerris lacustris*	g3	*Beraea* sp.	e2
Ancylus fluviatilis	e2	*Hydrometra stagnorum*	g2	Glossosomatidae	e2
Radix sp.	e1	*Mesovelia vittigera*	g2	*Hydropsyche* sp.	e1
Lymnaea sp.	c2	*Notonecta maculata*	g2	*Hydropsyche exocellata*	e1
Physa acuta	e2	*Notonecta* sp.	g2	*Hydropsyche* sp1	e1
Gyraulus sp.	e2	*Velia caprai*	g1	*Hydropsyche* cf. *bulbifera*	e1
Pisidium sp.	b2	*Nepa cinerea*	g3	*Hydropsyche* gr. *pellucidula*	e1
Gammaridae	b1	*Naucoris maculatus*	g2	*Hydroptila* sp.	e2
Hydracarina	-	*Plea minutissima*	g2	*Mystacides* sp.	e2
Baetis sp.	e2	*Dryops* sp.	g1	*Limnephilus* sp.	f
Cloeon sp.	e1	*Agabus* sp.	g3	*Mesophylax aspersus*	f
Caenis sp.	f	*Bidessus* sp.	g2	*Odontocerum albicorne*	c2
Ephemerella sp.	f	*Graptodytes* sp.	g2	*Wormaldia* sp.	e1
Heptageniidae	f	*Dytiscus marginatus*	g3	*Polycentropus* sp.	e1
Leptophlebiidae	f	*Laccobius* sp.	g1	*Tinodes waeneri*	e2
Chloroperlidae	c2	Laccophilus sp.	g2	*Tinodes maculicornis*	e2
Leuctridae	f/c	*Meladema* sp.	g3	*Tinodes* sp.	e2
Nemoura sp.	f	*Metaporus* sp.	g2	Antomyiidae	c2
Perlodidae	c	*Stictonectes* sp.	g2	Athericidae	d2
Aeshnidae	d	*Yola* sp.	g2	Ceratopogonidae	c2
Coenagrionidae	d2	*Oulimnius* sp.	e3	Chironomidae	e/c
Cordulegasteridae	d1	*Potamophylus* sp.	e3	Culicidae	e3
Corduliidae	d1	*Riolus* sp.	e3	Dolichopodidae	g3
Gomphidae	d1	*Gyrinus* sp.	g3	Dixidae	e1
Lestidae	d2	*Haliplus* sp.	g2	Empididae	c2
Libellulidae	d/c	*Helodes* sp.	e3	Limoniidae	c
Sigara lateralis	g1	*Helophorus* sp.	g1	Psychodidae	e2
Hesperocorixa linnaei	g1	*Limnebius* sp.	g1	Simuliidae	e
Micronecta cf. *scholtzi*	e3	*Hydrochus* sp.	g1	Stratiomyidae	e3
Parasigara perdubia	g1	*Berosus* sp.	g3	Tabanidae	g3
Parasigara sp.	g1	*Helochares* sp.	g1	Tipulidae	c1
Aquarius najas	-	*Hydrous (=Hydrophilus) sp.*	g3		

Annex 5. Maximum affinity value for each trait and group/subgroup from data provided by Usseglio-Polatera.

var1= Maximal size; **var2**=Life duration; **var3**=number reproductioncycles per year; **var4**=aquatic stages; **var5**=reproduction; **var6**=dispersal; **var7**=resistance forms; **var8**=respiration; **var9**=locomotion and substrate relation; **var10**=food; **var11**=feeding habits.

gr. / sgr.	**Biological Trait**										
	var1	**var2**	**var3**	**var4**	**var5**	**var6**	**var7**	**var8**	**var9**	**var10**	**var11**
b1	5	2	2	1	1	1	5	1	4	8	3
b2	7	2	2	2	1	1	5	2	5	2	5
c	4	2	2	2	4	2	5	1	4	8	7
c1	4	2	2	1 / 2	4	2	5	1	4	8	7
c2	4	1	2	2	4	1	5	1	4	8	7
d	5	2	1	2	6	4	5	2	4	8	7
d1	5	2	1	2	2	4	5	2	4	8	7
d2	4	1	2	2	6	4	5	2	4	8	7
e	3	1	2	1	4	1	5	1	4	4	4
e1	3	1	2	1	4	1	5	1	4	4	5
e2	3	1	2	1	4	1	5	1	4	4	4
e3	2	1	2	2	4	4	5	2	4	4	4
f	4	1	2	2	4	4	5	2	4	3	3
g1	2	2	2	1	4	4	5	4	3	4	3
g2	2	2	3	2	4	4	5	4	3	8	6
g3	4	2	2	2	4	4	5	4	4	8	6