Chapter 4

EFFECTS OF THREE DIFFERENT MACROHABITATS ON THE MACROINVERTEBRATE ASSEMBLAGE IN MEDITERRANEAN STREAMS.

INTRODUCTION

Stream ecosystems are organized in a hierarchical framework at different scales of observation (Frissell *et al.*, 1986; Church, 1996). Each level of organization constrains presence and abundance of biota in a different way, because different mechanistic filters operate (Poff, 1997). Habitat has been considered as one important factor in the regulation and organization of biota (Southwood, 1977; 1988; Townsend & Hildrew, 1994), and its spatial and temporal heterogeneity have been associated to different organisms' structure and responses (Southwood, 1977; Townsend and Hildrew, 1994). However, from the static (substrate) and dynamic (flow) features included in the habitat concept, the hydraulic environment has been considered as the main factor explaining distribution of aquatic invertebrates (Statzner *et al.*, 1988). Consequently, at reach scale, riffles and pools have been identified as the major macrohabitats present in flowing rivers and affecting to organisms (Carter & Fend, 2001).

Traditionally, stream ecologists have been interested in how physical factors controlling riffles and adjacent pools can affect the biota. Consequently, numerous studies have been carried out with macroinvertebrates (Logan & Brooker, 1983; Brown & Brussock, 1991; Boulton &

Lake, 1992; Cooper *et al.*, 1986; Angradi, 1996; Ribera & Vogler, 2000; Carter & Fend, 2001), periphyton (Keithan & Lowe, 1985; Rosenfeld & Hudson, 1997; Whitledge & Rabeni, 2000) and fishes (Young, 2001; Inoue & Nunokawa, 2002). Overall, differences between riffles and pools have been associated to abiotic and biological aspects (Brown & Brussock, 1991). Although agreements have been observed in the physical differences between riffles and pools (different velocity, particle size, depth, chemistry...), divergences in macroinvertebrate structure and composition of biota are not always totally correlated with the environmental factors measured. Similar number of taxa between riffles and pools have been reported by several authors (Egglishaw & Mackay, 1967; Armitage *et al.*, 1974; Harrel, 1969; Logan & Brooker, 1983), whereas in other cases riffles are richer (Brown & Brussock, 1991; Carter & Fend, 2001) or poorer than pools (McCulloch, 1986; Boulton & Lake, 1992). Differences in richness between both habitats have been associated to habitat stability (McCulloch, 1986; Boulton & Lake, 1992), annual peak discharge and reach gradient (Carter & Fend, 2001), although other factors as different sampling methodologies and the taxonomical level used could be important (Logan & Brooker, 1983). The uniqueness of each macrohabitat in terms of macroinvertebrates have been noticed by several authors (e.g., Scullion *et al.*, 1982; McCulloch, 1986), although a significant overlap in composition is also found because in practice both habitats are not as discrete as can be presumed (see Rabeni *et al.*, 2002). However, few of these studies have been done in intermittent rivers (Brown & Brussock, 1991; Boulton & Lake, 1992), and thereby the isolated pool as a macrohabitat different to the riffle-pool sequence has been widely neglected in most of the studies.

In mediterranean regions, rivers are characterized by a high annual and interannual discharge variation that might imply floods and droughts (Molina *et al.*, 1994; McElravy *et al.*, 1989; Gasith & Resh, 1999). Consequently, rivers and streams are affected by seasonal natural disturbances in discharge that eliminate and generate different habitats (Lake, 2000). When a drought period is coming, riffle-pool sequences change to a dominance of series of isolated pools before they dry up (Boulton & Lake, 1992; Williams, 1996; Gasith & Resh, 1999; Lake, 2000). Thereby, three macrohabitats can be identified: riffles, pools connected to riffles and isolated or disconnected pools. This change of river patchiness along time is associated to the natural discharge variability and can be more or less important depending on the river characteristics (Lake, 2000; Bonada *et al.*, Chapter 5). Consequently, rivers subjected to mediterranean climate can have at the same time riffles, adjacent and isolated pools, and this situation may remain for days or months depending of many factors (e.g., annual climate or substrate), indicating the strong relationship between spatial and temporal heterogeneity (Bonada *et al.*, Chapter 5).

Hence, the aims of our study is (1) to relate macroinvertebrate community structure and taxa richness to three different macrohabitats (riffles, connected pools and isolated pools) in a mediterranean area and (2) to know if pools adjacent to riffles act as an intermediate habitat between riffles and isolated pools in terms of macroinvertebrate assemblage.

METHODOLOGY

Sampling sites

Macroinvertebrate samples were collected from 19 reference sampling sites in the mediterranean area of northern California during spring 2002. A total of 9 sites (from 8 different rivers) were intermittent during the sampling period with disconnected pools remaining, whereas the rest (10 sites from 10 different rivers) had some flowing water with pools connected to the riffles and are located in headwaters and midstream reaches (see Bonada *et al.*, Chapter 3).

Sites were distributed in the inland mountains of Sierra Nevada, and the coastal ranges north and south of San Francisco (Figure 1). Localities in the Sierra Nevada are reaches with fast flowing waters, in forested basins, medium slopes and substrates composed by boulders and cobbles. The riparian vegetation is dominated by *Alnus* sp., *Salix* sp., *Populus* sp. with some *Pinus lambertiana* and *Pseudotsuga menziesii* from the adjacent coniferous forest. In northern coastal ranges, rivers have high slopes with coarse substrate except in San Geronimo river where gravels, sand and bedrock are important. Riparian vegetation is dominated by *Quercus lobata, Alnus* sp.*, Corylus cornuta, Sequoia sempervirens* and *Umbellularia californica.* Through the south and near the coast, sampled rivers are short, small and steep. Substrates are similar to the ones in the northern coasts. The riparian vegetation is composed by *Quercus lobata, Platanus racemosa, Juglans hindsii, Populus* sp.*, Salix sp., Alnus* sp.*, Corylus cornuta* and *Umbellularia californica.*

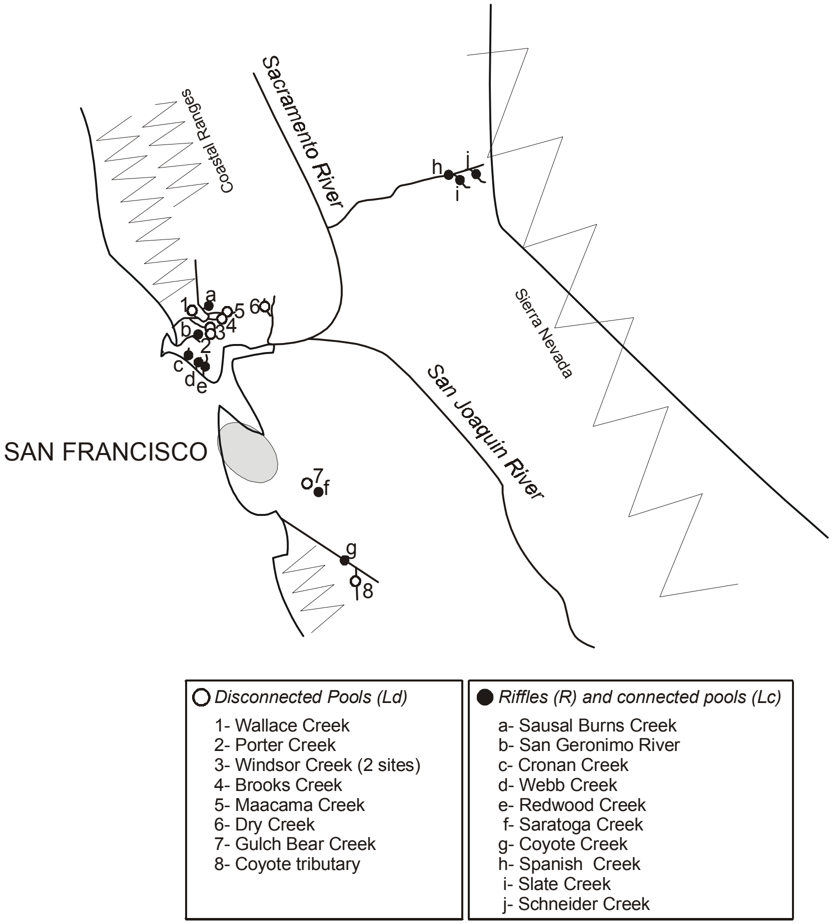


Figure 1. Sampling area.

Sampling procedure

Localities were sampled according to the GUADALMED Project methodology (Bonada *et al.*, Chapter 1; Jáimez-Cuéllar, in press). In each site, pH, temperature, oxygen, conductivity and discharge was recorded. The diversity of habitat was assessed according to the index of habitat (IHF) proposed in Pardo *et al.* (in press). This index varies between 0 and 100 (higher the value, higher is the diversity of habitats present) and evaluates the presence of different substrates, embededness, velocity regimes, instream vegetation and litter cover. Macroinvertebrates samples were collected with a kick net of 250 μm mesh size from riffles (R) and lentic (Lc) habitats in flowing reaches or from disconnected pools (Ld) in intermittent streams. Samples were firstly examined in the field, and successive samples in both habitats are taken until no more families were found by the observer. Several invertebrates seen in the field but not collected in the sample were also recorded, as the large Heteroptera and Coleoptera. All macroinvertebrate samples were preserved in alcohol 70%, sorted in the lab and identified at family level. Because of the semiquantitative nature of samples, a rank of abundances was recorded for each taxon: 1 from 1-3 individuals, 2 from 4-10, 3 from 11-100 and 4 for more than 100 individuals.

Data analysis

Differences between the three habitats have been analyzed using the number of taxa and the index EPT/(EPT+OCH) (EPT=Ephemeroptera, Plecoptera and Trichoptera and OCH=Odonata, Coleoptera and Heteroptera). Because not all data had a normal distribution and homogeneity of variances, a non-parametric Kruskal-Wallis by ranks tests was used to test significant differences between habitats. The same analysis was used to check for differences between flowing and intermittent reaches in physical and chemical parameters. Samples collected from the same habitat in different sites were used as replicates. STATISTICA Program (StatSoft, 1999) was used to carry out these analyses.

In order to check differences between macroinvertebrate compositions between habitats, a MRPP (Multi-response Permutation Procedures) was computed with PCORD Program (McCune & Mefford, 1999). This method is a nonparametric method for testing multivariate differences among pre-defined groups (R, Lc and Ld habitats), providing the statistic A and a p-value obtained by permutation (999 runs) as a result. Because its non-parametric condition this method is more appropriated than MANOVA in comparisons of data matrixes that involve species relative abundances including many zero values. To examine the meaning of the differences observed between sampled habitats, a Correspondence Analysis (CA) was performed to study the patterns of habitat distribution and the macroinvertebrates associated. This ordination technique is a multivariate approach that allows relating objects (sites) and descriptors (taxa) in a low-dimensional space. The measure used is the χ^2, appropriated for semiquantitative data. This method have been considered to produce better results than Principal Coordinate Analysis (PCA) with biological data, because matrices usually have numerous null values and χ^2 distance exclude double-zeros (Legendre & Legendre, 1998). Once the relationships between habitats and macroinvertebrates taxa were identified, a Bray-Curtis cluster was performed using a flexible method (β=-0.25) in order to check if macroinvertebrate communities were more similar between habitats that between adjacent riffle-pool sequences. Finally, to examine the most representative taxa in each habitat the

IndVal method (Dufrêne & Legendre, 1997) was applied. This procedure, independent of the CA results, examine characteristic taxa from a predefined group of objects (R, Lc and Ld) according to the presence and relative abundance of each taxa in each group independently of the others. Each taxa has associated an indicator value (IV-value) and a p-value obtained by Monte Carlo permutations (9999 runs). Only taxa with a high IV-value (over than 25) have been retained to understand patterns of macroinvertebrate distribution among habitats (Dufrêne & Legendre, 1997).

RESULTS

Physical, chemical and geomorphologic properties

Flowing water sites were characterized by a significant higher IHF, oxygen concentration and % of saturation than disconnected pools sites (Table 1). Conductivity, Temperature and pH had similar values between all samples. Discharge was highly variable between flowing water sites from 3.23 l/s to over than 6000 l/s. Obviously, because of the exclusive lentic conditions of disconnected pools, significant differences were found comparing discharge between flowing and intermittent reaches.

Table 1. Values of physical and chemical measured parameters. Kruskal-Wallis test between RLc and Ld are presented. ** indicates a significant differences at 0.05.

	River and site	IHF	pH	Oxygen-ppm	Oxygen-%	Temperature	Conductivity	Discharge (l/s)
R and Lc	Coyote	78	7.5	10.46	110.3	18.1	558	103.3
	Spanish	73	7.8	8.96	97.1	19.2	99	6270.95
	Cronan	81	7.4	9.96	99.7	15.4	118	454.4
	Lagunitas	83	7.8	10.6	104.6	14.6	182	1821.15
	Webb	78	7.6	10.0	96.3	13.5	340	40.95
	Saratoga	76	7.7	10.1	99.0	14.3	438	489.22
	Slate	74	7.8	8.1	89.9	20.4	108	3187.7
	Schneider	86	7.4	8.71	88.4	16.0	80	946.2
	Redwood	79	7.4	9.79	94.2	13.5	180	120.75
	Sausal Burns	62	7.8	3.85	42.8	21.7	499	3.23
Only Ld	Coyote-tributary	41	7.3	2.93	30.1	15.9	654	0
	Bear Gulch	50	7.5	6.41	67.8	17.0	578	0
	Dry	49	7.8	8.23	91.5	21.8	392	0
	Windsor site 1	50	7.9	1.47	15.5	16.6	328	0
	Windsor site 2	51	7.8	3.71	37.9	16.6	176	0
	Porter	49	7.8	2.39	24.0	15.1	262	0
	Brooks	58	7.8	5.23	59.2	22.7	331	0
	Wallace	64	7.8	6.18	62.8	16.8	208	0
	Maacama	58	7.8	5.04	57.9	22.3	351	0
Kruskal-Wallis test (χ2)		15.39	1.17	9.01	9.01	0.45	0.45	15.39
p-value		0.0001**	0.2788	0.0027**	0.0027**	0.4977	0.4977	0.0001**

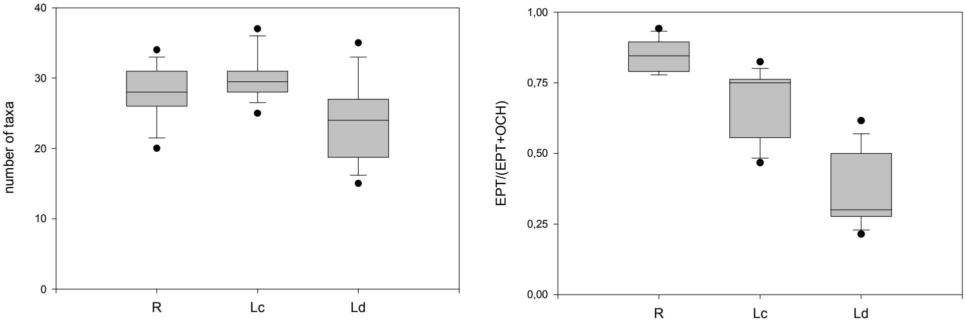


Figure 2. Box-Plots of number of taxa and EPT/(EPT+OCH) in R, Lc and Ld separately.

Changes in richness between habitats

Number of taxa is not significantly lower in Ld compared with R and Lc habitats independently (χ^2=4.34, p=0.1137) whereas significant differences are found in the EPT/(EPT+OCH) value (χ^2=20.50, p=0.000). Number of taxa presented a higher standard deviation between sampling sites in isolated pools than in riffles and connected pools (Figure 2). A decreasing number of Ephemeroptera, Plecoptera and Trichoptera taxa is observed from riffles to disconnected pools (Figure 2). Riffle samples have high values of EPT and few OCH taxa are present, whereas in connected pools a slightly higher OCH taxa or a fewer EPT were present. In disconnected pools, a high presence of OCH and few EPT taxa are noticed even though comparing with connected pools samples.

Changes in macroinvertebrate assemblages between habitats

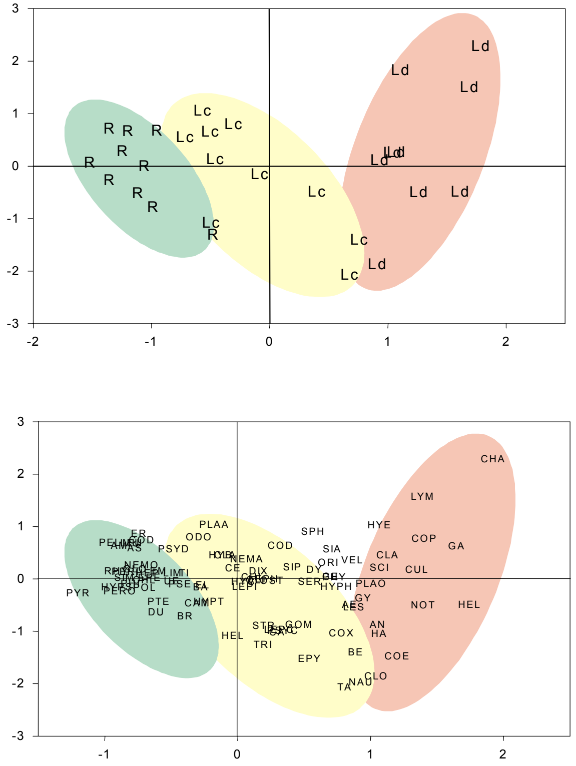
According to the MRPP results, macroinvertebrate assemblages are significantly different between all habitats (Table 2). A change of community structure from riffles to connected and disconnected pools is noticed in the first axis of the CA results (Figure 3) indicating that macroinvertebrates respond well to the differences present between habitats. The three habitats appear distinctively spread in the analysis with a clear gradient from riffles to disconnected pools. The first two axes explain together 28% of the sites variability. A longer dispersion of Ld sites in the second axis would indicate the high variability of macroinvertebrate composition found between samples from this habitat. Samples located in the top of the second axis have a distinct macroinvertebrate composition with high abundance of Chaoboridae, Lymnaeidae and Hydraenidae, whereas intermittent sites distributed through the bottom have a similar composition than some connected pools samples, sharing several Odonata (e.g. Lestidae, Calopterygidae or Coenagrionidae) and Heteroptera (e.g. Naucoridae, Corixidae and Belostomatidae). Lc samples appear to have a community between riffles and disconnected pools samples. Some Lc sites are more similar to disconnected pools with some taxa in common (e.g., Corixidae, Naucoridae, Hydrophilidae), whereas other are closer to riffles sharing taxa as Helicopsychidae, Odontoceridae or Hydroptilidae.

Table 2. Results of the MRPP analysis comparing macroinvertebrate community between R, Lc and Ld habitats.

	A	**p-value**
R and Ld	0,2713	0,0000114
Lc and Ld	0,1022	0,00004943
R and Lc	0,1182	0,00000614

In the cluster analysis of Figure 4, disconnected pools sites are segregated apart from riffles (R) and connected pools (Lc) habitats, which in turn, were clustered separately in all cases except for Coyote (gR) and Schneider (jLc) creeks where higher similarities between R and Lc are present. Riffles in Coyote Creek are more similar to connected pools habitat than to the rest of lotic samples. In contrast, connected pools habitat from Schneider Creek has a more riffle-community, and is grouped with the rest of Lc samples (Figure 4).

Riffles have 26 taxa with a high indicator value (IV-value) (Table 3). A high number of EPT taxa is characteristic from riffles. Stoneflies as Perlidae, Peltoperlidae and Perlodidae are restricted to R, and Nemouridae and Chloroperlidae are also present (with a high IV-value but non-significant) in connected pools. Several lotic caddisflies appear abundant and exclusive in riffles as Hydropsychidae, Rhyacophilidae, Glossosomatidae, Hydroptilidae, Brachycentridae and Uenoidae, whereas Limnephilidae is present in both habitats riffles and connected pools, but more significant in the last ones. Dipterans as Simuliidae, Tipulidae, Psychodidae and the non-insect taxa Hydracarina and Dugesiidae are indicator of riffles and absent in pools. Because of a gradient in the macroinvertebrate community is present between R and Ld through Lc (Figure 3), connected pools share taxa with riffles and disconnected pools and only 40.9% of indicator taxa are exclusive from this habitat.



Taxa's codes							
AE	Aeshnidae	DIX	Dixidae	HYPT	Hydroptilidae	PLAA	Planariidae
AM	Amelitidae	DU	Dugesiidae	LEPI	Lepidostomatidae	PLAO	Planorbidae
AN	Ancylidae	DY	Dytiscidae	LEPC	Leptoceridae	POL	Polycentropodidae
AS	Asellidae	EL	Elmidae	LEPH	Leptophlebiidae	PSE	Psephenidae
BA	Baetidae	EM	Empididae	LES	Lestidae	PSYD	Psychodidae
BE	Belostomatidae	EPE	Ephemerellidae	LEU	Leuctridae	PSYC	Psychomyiidae
BR	Brachycentridae	EPY	Ephydridae	LIM	Limnephilidae	PTE	Pteronarcyiidae
CA	Caenidae	ER	Erpobdellidae	LYM	Lymnaeidae	PYR	Pyralidae
CLA	Calamoceratidae	GA	Gammaridae	MU	Muscidae	RHY	Rhyacophilidae
CLO	Calopterygidae	GE	Gerridae	NAU	Naucoridae	SCI	Sciomyzidae
CAM	Cambaridae	GLO	Glossosomatidae	NEMA	Nematoda	SER	Sericostomatidae
CE	Ceratopogonidae	GOM	Gomphidae	NEMO	Nemouridae	SIA	Sialidae
CHA	Chaoboridae	GY	Gyrinidae	NOT	Notonectidae	SIM	Simuliidae
CHI	Chironomidae	HA	Haliplidae	ODO	Odontoceridae	SIP	Siphlonuridae
CHL	Chloroperlidae	HEL	Helicopsychidae	OLI	Oligochaeta	SPH	Sphaeridae
CLA	Cladocera	HEL	Helophoridae	ORI	Oribatidae	STR	Stratiomyidae
COE	Coenagrionidae	HEP	Heptageniidae	OST	Ostracoda	TA	Tabanidae
COP	Copepoda	HYC	Hydracarina	PEL	Peltoperlidae	TI	Tipulidae
COD	Cordulegasteridae	HYE	Hydraenidae	PERI	Perlidae	TRI	Tricorythidae
COX	Corixidae	HYB	Hydrobiidae	PERO	Perlodidae	UE	Uenoidae
COD	Corydalidae	HYPH	Hydrophilidae	PHI	Philopotamidae	VEL	Veliidae
CUL	Culicidae	HYPS	Hydropsychidae	PHY	Physidae		

	X1	**X2**	**X3**	**X4**
Eigenvalues	0.405	0.183	0.158	0.132
Cumulative % variance	19.6	28.4	36.0	42.4

Figure 3. CA graph of sites and taxa using R, Lc and Ld habitats. Eigenvalues, percentage of explained variability and taxa's codes are shown in the bottom.

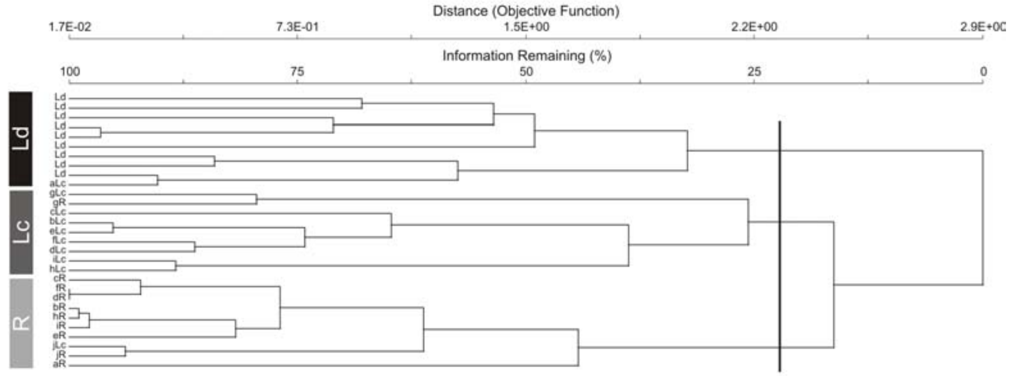


Figure 4. Bray-Curtis cluster with all data. R=riffles, Lc=connected pools; Ld=disconnected pools. Letters before R and Lc samples indicate the site and river plotted in Figure 1.

Table 3. Results of the IndVal method for R, Lc and Ld habitats. The indicator value (IV) and the p-value associated are shown.

R community

Species	IV-value	p-value
Hydropsychidae	96.4	0.0001
Simuliidae	93.2	0.0001
Rhyacophilidae	79.5	0.0001
Chloroperlidae	79.2	0.0001
Perlidae	77	0.0001
Tipulidae	77.2	0.0003
Heptageniidae	71.2	0.0012
Baetidae	64.3	0.0024
Ephemerellidae	68.6	0.003
Nemouridae	66.3	0.004
Philopotamidae	47.5	0.0045
Elmidae	64	0.0078
Empididae	62.3	0.0094
Polycentropodidae	47.5	0.0103
Dugesiidae	35.3	0.0251
Peltoperlidae	36.8	0.0311
Oligochaeta	54.4	0.2661
Hydracarina	53.6	0.3208
Glossosomatidae	44.9	0.0338
Hydroptilidae	44.8	0.1332
Psephenidae	39.3	0.1853
Brachycentridae	31.7	0.0973
Uenoidae	30.8	0.2069
Limnephilidae	28.3	0.7391
Psychodidae	26.2	0.1952
Perlodidae	25.5	0.187

Lc community

Species	IV-value	p-value
Calamoceratidae	40	0.0081
Ceratopogonidae	62.6	0.0116
Limnephilidae	56.3	0.0133
Gomphidae	36.2	0.0288
Leptophlebiidae	59.4	0.0454
Lepidostomatidae	55	0.0461
Elmidae	54.2	0.1537
Ostracoda	53.6	0.1095
Baetidae	53.6	0.1497
Gerridae	52.9	0.0833
Dytiscidae	52.5	0.1044
Empididae	43.2	0.2049
Nemouridae	39.5	0.324
Sialidae	36.2	0.2078
Ephemerellidae	34.8	0.6309
Heptageniidae	34.1	0.542
Chloroperlidae	34.1	0.6763
Nematoda	30.6	0.4342
Sericostomatidae	27.4	0.2517
Oribatidae	27	0.8311
Corduliidae	26.5	0.0842
Psephenidae	25.7	0.6808

Ld community

Species	IV-value	p-value
Copepoda	64.8	0.0001
Planorbidae	78.8	0.0002
Culicidae	71.7	0.0002
Gammaridae	55.6	0.0009
Gerridae	72.5	0.0012
Veliidae	47.5	0.0029
Physidae	69.8	0.004
Oribatidae	63.1	0.0043
Cladocera	45.4	0.0128
Lymnaeidae	33.3	0.0223
Gyrinidae	40	0.0225
Hydraenidae	40	0.025
Dystiscidae	60.1	0.0334
Sialidae	49	0.0361
Oligochaeta	52.1	0.4418
Leptophlebiidae	45.7	0.776
Dixidae	40.9	0.4475
Ostracoda	40.4	0.7215
Hydrophilidae	34.2	0.1263
Corixidae	28.9	0.3482
Haliplidae	26.2	0.1038

Some Ephemeroptera, Plecoptera and Trichoptera highly significant in riffles are also present in connected pools, as Heptageniidae, Baetidae, Ephemerellidae, Nemouridae and Chloroperlidae. The caddisfly Limnephilidae is also evenly distributed in lotic and adjacent lentic habitats, being more abundant in the last one. Although connected pools have some characteristic Coleoptera as Dytiscidae, others as Elmidae and Psephenidae are also present in riffles. Several exclusive taxa characterize connected pools, as the woody-cased caddisflies Lepidostomatidae and Calamoceratidae and two families of Odonata (Gomphidae and Corduliidae) which are typical from Lc but not from Ld. Other taxa characteristic from connected pools are also present in the disconnected ones, as Leptophlebiidae and Sialidae, found in both habitats but more significantly present in Lc than Ld. On the other hand, Gerridae and Dytiscidae are more representative from disconnected pools, although they are also present in Lc. Only Oligochaeta appear evenly distributed in riffles and disconnected pools. Although both habitats have many exclusive taxa, disconnected pools present a higher percentage of exclusivity (71.4%) than riffles (61.5%), indicating that connected pools are more similar to riffles than to disconnected pools. Heteroptera are highly significant in disconnected pools, with Gerridae, Veliidae and Corixidae as the most representative families. Gyrinidae, Haliplidae, Hydraenidae and Dytiscidae are also characteristic from Ld, jointly with three Mollusca families (Planorbidae, Physidae and Lymnaeidae). Crustaceans also are typical from this habitat, with Copepoda, Cladocera and Ostracoda as highly significant taxa.

DISCUSSION

Is the community in isolated pools impoverished?

Patterns in macroinvertebrate structure differ between riffles, adjacent pools and isolated pools but overall, no differences in richness between each independent habitat are observed. Previous studies reported similar number of taxa between riffles and adjacent pools (e.g., Scullion *et al.*, 1982; Logan & Brooker, 1983) what would agree with our results. Numerous controversies are found in the literature about the richness in riffles and pools. Boulton & Lake (1992) studying two intermittent rivers in Australia found in global a higher richness in pools than in riffles. Similarly, in a more arid area of North America, McCulloch (1986) found a higher number of taxa in pools than in riffles. On the other hand, Carter & Fend (2001) in a California river system found more taxa in riffles in low-gradient reaches but similar in high-gradient ones. Our study include a high variety of river typology in the riffle-pool samples (permanent and temporary sites in summer located in headwaters and midstream reaches) that could explain that in global, riffles and pools have a similar number of taxa. However, several problems should be present when number of taxa in riffles and pools are compared, because methodologies, sampling periods and taxonomic resolution used are different in most of studies (Logan & Brooker, 1983).

The habitat fragmentation in intermittent sites respect permanent ones does not imply a lower richness in isolated pools. Consequently, similar number of taxa would indicate that isolated pools operate as islands (*sensu* McArthur & Wilson, 1967) with organisms with high colonization and low extinction rates (Lawton, 2000). In fact, organisms found exclusively in these environments, as most of Coleoptera and Heteroptera, have been recognized to have these biological traits (Williams, 1987). However, Williams (1987) in a study of a temporary pond in Canada indicates that richness in temporary pools changes along the year, with maximum value in spring time. Consequently, the time when sampling was performed (spring) could affect the richness in isolated pools.

A higher variation in taxonomical composition is observed in isolated pools respect riffles and adjacent pools sites. Richness and biodiversity in streams have been strongly associated to disturbance and stability (Resh *et al.*, 1988; Vinson & Hawkins, 1998). According to the third Thienemann's principle (1954) richness is related to the length in which site has remained stable. Because disconnected pools are consequence of discharge disturbance in the beginning of a drought period (Lake, 2000), as far as the isolated pool have been disconnected to riffles, more stable should be and more taxa should hold (Thienemann, 1954; Williams, 1987). However, other factors have been recognised to influence richness in isolated pools. Schneider & Frost (1996) in a experimental study in Wisconsin found that the effect of predation and competition in temporary ponds is related to the habitat duration. Consequently, it is likely that a mix of factors (duration of isolated pools from permanent sites and predation, and even pool size) contribute to the high variability of richness in intermittent sites. Moreover, this explains the variability found in our data because some pools may be recently disconnected and other were since many weeks.

Are macroinvertebrates restricted to a specific macrohabitat?

All studies comparing riffles and pool habitats found a different macroinvertebrate community in each habitat (e.g., Logan & Brooker, 1983). However, the number of exclusive taxa for each habitat is variable. Armitage *et al.* (1974) found more unique taxa in pools than in riffles, whereas Scullion *et al.* (1982) demonstrated the opposite pattern. We found a higher exclusivity number of taxa in riffles than in pools, but lower than in isolated pools. The macroinvertebrate taxa indicator from riffles and pools agree with the one found in other studies (e.g., see Rabeni & Minshall, 1977; Armitage *et al.*, 1974; Scullion *et al.*, 1982;

McCulloch, 1986; Malmqvist *et al.*, 1993) although slightly differences in some taxa are found. Overall, in our study and elsewhere, riffles hold a numerous EPT fauna (Scullion *et al.*, 1982) whereas in pools OCH taxa are significant (Scullion et la., 1982; Logan & Brooker, 1983; McCulloch, 1986). However, some beetles are found in riffles, as Elmidae (considered to have lotic habitat requirements —Tachet *et al.*, 2000), and some ephemeropterans and plecopterans inhabit adjacent pools, as Leptophlebiidae (an indicator family in pools —Armitage *et al.*, 1974).

Isolated pools present a long list of restricted fauna with few similarities with riffles. This habitat is highly associated to OCH, Crustacea and Mollusca. Most of Mollusca have been recorded to pools (Logan & Brooker, 1983), but because their biological traits (long-lived organisms and slow dispersion) they have been rarely collected in intermittent sites (Brown & Brussock, 1991), except for Physidae recorded in some temporary pools (Williams, 1987). In our study, Mollusca is highly an indicator of isolated pools. Two causes could explain these observations. Mediterranean areas are characterized by high variability in hydrology between years (McElravy *et al.*, 1989), and evidences exist that macroinvertebrates are affected by the discharge and rainfall conditions of the previous year (Feminella, 1996). Consequently, intermittent sites during sampling period might be permanent in the year before, allowing the presence and survival of several mollusks. However, whatever the temporary condition in previous years, some Mollusca taxa could survive the last dry period creating a protective layer of dried mucous (Eckblad,1973), whereas other may have some life cycles adaptations beeing able to reproduce before the pool dries up (Brown, 1982). Crustaceans as Copepoda, Cladocera and Ostracoda, are significant indicators of isolated pools in our study and elsewhere. For instance, Williams (1987) in a comparative study in temporary pools in four distant regions found a highly convergent crustacean fauna.

Significant differences have been found between all sampled habitats in macroinvertebrate structure. However, high convergences have been noticed in indicator taxa between riffles and adjacent pools. Riffles and pools at the same site are more different that all sampled riffles or pools separately. Different arguments are found in literature about this phenomenon. Our results are similar to the ones found by McCulloch (1986) in two Texas streams. Similarly, Angradi (1996) in a study of three Appalachian streams comparing several microhabitats found strongest differences between habitats than between streams. However, in a study including several data from UK Rivers and streams, Logan & Brooker (1983) found the contrary. Angradi (1996) suggest that the scale of study is important to get one or another conclusion. In that sense, in a comparative study between riffles and pools in several mediterranean areas in the world, Bonada *et al.* (Chapter 3) found that, using common taxa, differences between regions were more important than differences between habitats in SWAustralia and South Africa, what is attributed to different local and historical processes acting in both areas.

Are connected pools an intermediate habitat?

Because of discrete habitats do not have a discrete taxa (Rabeni *et al.*, 2002), different degrees of similarity can be established between macrohabitats. When a drought is coming, riffles dry up quicker than pools (Boulton & Lake, 1990; Stanley *et al.*, 1997) and thereby, significant distances in macroinvertebrate structure should be present between riffles and isolated pools. In our study, nine families are indicator taxa from riffles and adjacent pools, whereas isolated pools only share four taxa with connected pools and one with riffles. Consequently, a gradient of flow conditions from riffles to isolated pools is shown by macroinvertebrate community. The CA analysis exhibit that some connected pools samples are close to riffles whereas some isolated pools samples are similar to connected pools in macroinvertebrate structure. As we have suggested previously, the high standard deviation of richness in isolated pools samples could be a consequence of the timing that these pools have been disconnected to riffles. Macroinvertebrate structure shows that some isolated pools have similar composition than some connected pools, whereas others have more distinct taxa with lots of predators (e.g., surprisingly, Chaoboridae was very abundant in one of the samples) indicating that these isolated pools are older than the ones close to connected pools but with an intermittent condition. However, in the case that sites would be disconnected from riffles at the same time, they could hold different macroinvertebrate composition because different taxa could colonize these “islands” and different predators could regulate the food web allowing the presence of a variety of different taxa. Consequently, we suggest that the higher dissimilarity observed in macroinvertebrate assemblage from isolated pools samples could be explained by (1) different time of disconnection from the riffle, (2) different taxa that colonize the pool, (3) different prey selection by newly arrived predators. These isolated pools became controlled only by local events (Lake, 2000), whereas in flowing water sites local and longitudinal processes may influence macroinvertebrate structures in riffles and pools.

Evidences exist about invertebrates moving away from riffles before they start to dry up (e.g., Delucchi, 1989). Several paths have been suggested for the movement of macroinvertebrates under a drought: upstream, downstream, hyporheic zone and to the laterals in banks or non-drying pools (Williams, 1981). We found that isolated pools could be refuges for some tolerant-lentic and long-lived fauna as Mollusca, but not for flow-preference invertebrates because low convergence in indicator taxa between riffles and isolate pools has been observed. Consequently, under a drought lotic macroinvertebrates can move to the next upstream riffles (Delucchi, 1989) but as drying bed moves towards, emergence is required to survive. In that sense, Brown & Brussock (1991) comparing riffles and pools in an intermittent river in Arkansas pointed out that riffle taxa displayed a life-cycle adaptation to avoid drought instead of an active migration to pools.

In summary, our results suggest that macrohabitats act as filters to enable the presence, absence and abundance of specific taxa (Poff, 1997). A gradient of flow conditions (from R to Ld) is congruent with a gradient of macroinvertebrate assemblages, but not in number of taxa. Abiotic and biotic factors acting at local or broad scale could be the responsible of these changes in biota. Low convergences between riffles and isolated pools in dominant taxa would suggest that isolated pools are not a refugee of lotic families under a drought, although it is likely that they could hold more tolerant-lentic taxa. Consequently, river macroinvertebrates in mediterranean areas are highly flexible under environmental conditions as a result of the climate, suggesting that despite of natural disturbances (floods and droughts) a high richness is present under different river and habitat conditions.

REFERENCES

ANGRADI, T. R. (1996). Inter-habitat variation in benthic community structure, function, and organic matter storage in 3 Appalachian headwater streams. *J. N. Am. Benthol. Soc.*, 15(1): 42-63.

ARMITAGE, P. D.; MACHALE, A. M. & CRISP, D. C. (1974). A survey of stream invertebrates in the Cow Green basin (Upper Teesdale) before inundation. *Freshwat. Biol.*, 4: 369-398.

BOULTON, A. J. & LAKE, P. S. (1990). The ecology of two intermittent streams in Victoria, Australia. I. Multivariate analysis of physicochemical features. *Freshwat. Biol.*, 24: 123-141.

BOULTON, A. J. & LAKE, P. S. (1992). The ecology of two intermittent streams in Victoria, Australia. II. Comparisons of faunal composition between habitats, rivers and years. *Freshwat. Biol.*, 27: 99-121.

BROWN, K. M. (1982). Resource overlap and competition in pond snails: an experimental analysis. *Ecology*, 63(2): 412-422.

BROWN, A. V. & BRUSSOCK, P. P. (1991). Comparisons of benthic invertebrates between riffles and pools. *Hydrobiologia*, 220: 99-108.

CARTER, J. L. & FEND, S. V. (2001). Inter.-annual changes in the benthic community structure of riffles and pools in reaches of contrasting gradient. *Hydrobiologia*, 459: 187-200.

CHURCH, M. (1996). Channel morphology and typology. In: Petts, G. & Callow, P. (eds.). *River flows and channel forms*. Blackwell Science. Oxford. 185-202pp.

COOPER, S. D.; DUDLEY, T. L. & HEMPHILL, N. (1986). The biology of chaparral streams in Southern California. In: DeVries, J. (ed.). *Proceedings of the chaparral ecosystem research conference*. Report n°62. California Water Resources Center. Davis. 139-151pp.

DELUCCHI, C. M. (1989). Movement patterns of invertebrates in temporary and permanent streams. *Oecologia*, 78: 199-207.

DUFRÊNE, M. & LEGENDRE, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs,* 67:345-366.

ECKBLAD, J. W. (1973). Population studies of three aquatic gastropods in an intermittent backwater. *Hydrobiologia*, 41: 199-219.

EGGLISHAW, H. J. & MACKAY, D. W. (1967). A survey of the bottom fauna of streams in the Scottish Highlands. Pt. III. Seasonal changes in the fauna of three streams. *Hydrobiologia*, 30: 334-350.

FEMINELLA, J. W. (1996). Comparison of benthic macroinvertebrate assemblages in small streams along a gradient of flow permanence. *J. N. Am. Benthol. Soc.*, 15: 651-669.

FRISSELL, C. A.; LISS, W. J.; WARREN, C. E. & HURLEY, M. D. (1986). A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management*, 10(2): 199-214.

GASITH, A. & RESH, V. H. (1999). Streams in Mediterranean climate region: Abiotic influences and biotic responses to predictable seasonal events. *Annu. Rev. Ecol. Syst.*, 30: 51-81.

HARREL, R. C. (1969). Benthic macroinvertebrates of the Otter Creek drainage basin, northcentral Oklahma. *S. West. Nat.*, 14: 231-248.

INOUE, M. & NUNOKAWA, M. (2002). Effects of longitudinal variations in stream habitat structure on fish abundance: an analysis based on subunit-scale habitat classification. *Freshwat. Biol.*, 47: 1594-1607.

JÁIMEZ-CUÉLLAR, P.; VIVAS, S.; BONADA, N.; ROBLES, S.; MELLADO, A.; ÁLVAREZ, M.; AVILÉS, J.; CASAS, J.; ORTEGA, M.; PARDO, I.; PRAT, N.; RIERADEVALL, M.; SÁINZ-CANTERO, C.; SÁNCHEZ-ORTEGA, A.; SUÁREZ, M. L.; TORO, M.; VIDAL-ABARCA, M. R.; ZAMORA-MUÑOZ, C. & ALBA-TERCEDOR, J. (in press). Protocolo Guadalmed (PRECE). *Limnética.*

KEITHAN, E. D. & LOWE, R. L. (1985). Primary production and spatial structure of phytolithic growth in streams in the Great Smoky Mountains National Park, Tennessee. *Hydrobiologia*, 123: 59-67.

LAKE, P. S. (2000). Disturbance, patchiness, and diversity in streams. *J. N. Am. Benthol. Soc.*, 19(4): 573-592.

LAWTON, J. H. (2000). Concluding remarks: a review of some open questions. In: Hutchings, M. J.; John, E. A. & Stewart, A. J. A. (eds.). *The Ecological Consequences of Environmental Heterogeneity*. British Ecological Society. Blackwell Science. 401-424pp.

LEGENDRE, P. & LEGENDRE, L. (1998). *Numerical Ecology*. Developments in Environmental Modelling 20. Elsevier. The Netherlands. 853pp.

LOGAN, P. & BROOKER, M. P. (1983). The macroinvertebrate faunas of riffles and pools. *Water Res.*, 17(3): 263-270.

MALMQVIST, B.; NILSSON, A. N.; BAEZ, M.; ARMITAGE, P. D. & BLACKBURN, J. (1993). Stream macroinvertebrate communities in the island of Tenerife. *Arch. Hydrobiol.*, 128(2): 209-235.

MCARTHUR, R. H. & WILSON, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press. Princeton.

MCCULLOCH, D. L. (1986). Benthic macroinvertebrate distributions in the riffle-pool communities of two east Texas streams. *Hydrobiologia*, 135: 61-70.

MCCUNE, B. & MEFFORD, M. J. (1999). *PC-ORD for Windows: Multivariate Analysis of Ecological Data v. 4.20*. MjM Software, Gleneden Beach, Oregon.

MCELRAVY, E. P.; LAMBERTI, G. A. & RESH, V. H. (1989). Year-to-year variation in the aquatic macroinvertebrate fauna of northern California stream. *J. N. Am. Benthol. Soc.*, 8(1): 51-63.

MOLINA, C.; VIDAL-ABARCA, M. R. & SUÁREZ, M. L. (1994). Floods in arid south-east Spanish areas: a historical and environmental review. In: Rossi, G. (ed.). *Coping with Floods*. Kluwer Academic Publishers. The Netherlands. 271-278pp.

PARDO, I., ÁLVAREZ, M., MORENO, J. L., VIVAS, S., BONADA, N., ALBA-TERCEDOR, J., JAIMEZ, P., MOYA, G., PRAT, N., ROBLES, N., TORO, M., VIDAL-ABARCA, M. R. (in press). El habitat de los ríos mediterráneos. Diseño de un índice de diversidad de habitat. *Limnética.*

POFF, N. L. (1997). Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J. N. Am. Benthol. Soc.*, 16(2): 391-409.

RABENI, C. F. & MINSHALL, G. W. (1977). Factors affecting microdistribution of stream benthic insects. *Oikos*, 29: 33-43.

RABENI, C. F.; DOISY, K. E. & CALAT, D. L. (2002). Testing the biological basis of a stream habitat classification using benthic invertebrates. *Ecological Applications*, 12(3): 782-796.

RESH, V. H.; BROWN, A. V.; COVICH, A. P.; GURTZ, M. E.; LI, H. W.; MINSHALL, G. W.; REICE, S. R.; SHELDON, A. L.; WALLACE, J. B. & WISSMAR, R. (1988). The role of disturbance in stream ecology. *J. N. Am. Benthol. Soc.*, 7: 433-455.

RIBERA, I. & VOGLER, A. P. (2000). Habitat types as a determinant of species range sizes: the example of lotic-lentic differences in aquatic Coleoptera. *Biol. J. Linn. Soc.*, 71: 33-52.

ROSENFELD, J. S. & HUDSON, J. J. (1997). Primary production, bacterial production and invertebrate biomass in pools and riffles in southern Ontario streams. *Arch. Hydrobiol.*, 139: 301-316.

SCHNEIDER, D. W. & FROST, T. M. (1996). Habitat duration and community structure in temporary ponds. J. *N. Am. Benthol. Soc.*, 15(1): 64-86.

SCULLION, J.; PARISH, C. A.; MORGAN, N. & EDWARDS, R. W. (1982). Comparison of benthic macroinvertebrate fauna and substratum composition in riffles and pools in the impounded River Elan and the unregulated River Wye, mid-Wales. *Freshwat. Biol.*, 12: 579-595.

STATSOFT, INC. (1999). *STATISTICA for Windows (Computer Program Manual).* Tulsa, UK.

STATZNER, B.; GORE, J. A. & RESH, V. H. (1988). Hydraulic stream ecology: observed patterns and potential applications. *J. N. Am. Benthol. Soc.*, 7(4): 307-360.

SOUTHWOOD, T. R. E. (1977). Habitat, the templet for ecological strategies?. *J. Anim. Ecol.*, 46: 337-365.

SOUTHWOOD, T. R. E. (1988). Tactics, strategies and templets. *Oikos*, 52: 3-18.

STANLEY, E. H.; FISHER, S. G. & GRIMM, N. B. (1997). Ecosystem expansion and contraction in streams. *BioScience*, 47: 427-435.

TACHET, H.; RICHOUX, P.; BOURNAUD, M. & USSEGLIO-POLATERA, P. (2000). *Invertébrés d'eau douce. Systématique, biologie, écologie.* CNRS Editions. Paris. 588pp.

THIENEMANN, A. (1954). Ein drittes biozonotishes Grundprinzip. *Arch. Hydrobiol.*, 49(3): 421-422.

TOWNSEND, C. R. & HILDREW, A. G. (1994). Species traits in relation to a habitat templet for river systems. *Freshwat. Biol.*, 31: 265-275.

VINSON, M. R. & HAWKINS, C. P. (1998). Biodiversity of stream insects: variation at local, basin and regional scales. *Annu. Rev. Entomol.*, 43: 271-293.

WHITLEDGE, G. W. & RABENI, C. F. (2000). Benthic community metabolism in three habitats in an Ozark stream. *Hydrobiologia*, 437: 165-170.

WILLIAMS, D. D. (1981). Migrations and distribution ofc stream benthos. In: Lock, M. A. & Williams, D. D. (eds.). *Perspectives in running water ecology.* Plenum Press. New York. 115-208pp.

WILLIAMS, D. D. (1987). *The Ecology of Temporary Waters.* The Blackburn Press. New Jersey. 205pp.

WILLIAMS, D. D. (1996). Environmental constraints in temporary waters and their consequences for the insect fauna. *J. N. Am. Benthol. Soc.*, 15(4): 634-650.

YOUNG, K. A. (2001). Habitat diversity and species diversity: testing the competition hypothesis with juvenile salmonids. *Oikos*, 95: 87-93.