

Benthic macroinvertebrate assemblages and macrohabitat connectivity in Mediterranean-climate streams of northern California

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Abstract. Drought leads to a loss of longitudinal and lateral hydrologic connectivity, which causes direct or indirect changes in stream ecosystem properties. Changes in macrohabitat availability from a riffle–pool sequence to isolated pools are among the most conspicuous consequences of connectivity loss. Macroinvertebrate assemblages were compared among 3 distinct stream macrohabitats (riffles [R], pools connected to riffles [Pc], disconnected pools [Pd]) of 19 Mediterranean-climate sites in northern California to examine the influence of loss of habitat resulting from drought disturbance. At the time of sampling, 10 sites were perennial and included R and Pc macrohabitats, whereas 9 sites were intermittent and included only Pd macrohabitats. Taxa richness was more variable in Pd, and taxa richness was significantly lower in Pd than in Pc but not R. These results suggested a decline in richness between Pc and Pd that might be associated with loss of connectivity. Lower Ephemeroptera, Plecoptera, and Trichoptera (EPT) richness relative to Odonata, Coleoptera, and Heteroptera (OCH) richness was observed for Pd than R and Pc macrohabitats. Family composition was more similar between R and Pc than between R or Pc and Pd macrohabitats. This similarity may be associated with greater connectivity between R and Pc macrohabitats. Correspondence analysis indicated that macroinvertebrate composition changed along a gradient from R to Pc and Pd that was related to a perennial–intermittent gradient across sites. High variability among macroinvertebrate assemblages in Pd could have been related to variability in the duration of intermittency. In cluster analysis, macroinvertebrate assemblages were grouped by macrohabitat first and then by site, suggesting that the macrohabitat filter had a greater influence on macroinvertebrate assemblages than did local site characteristics. Few taxa were found exclusively in Pc, and this macrohabitat shared numerous taxa with R and Pd, indicating that Pc may act as a bridge between R and Pd during drought. Drought is regarded as a ramp disturbance, but our results suggest that the response of macroinvertebrate assemblages to the loss of hydrological connectivity among macrohabitats is gradual, at least in Mediterranean-climate streams where drying is gradual. However, the changes may be more dramatic in arid and semiarid streams or in Mediterranean-climate streams if drying is rapid.

Key words: macrohabitats, riffles, pools, connectivity, drought, intermittent streams, macroinvertebrates, Mediterranean-climate streams.

Environmental factors affecting organisms in stream ecosystems can be thought of as hierarchically organized (Frissell et al. 1986, Church 1996). Factors operating at each level of the hierarchy act as

mechanistic filters that influence the presence and abundance of biota across a range of scales (Poff 1997). Spatial and temporal heterogeneity of habitat (the “habitat templet”) are 2 important components in the organization of stream biotic communities (Southwood 1977, 1988, Townsend and Hildrew 1994). Of the static (substrate) and dynamic (flow) features included in the habitat-templet approach, mean velocity and complex hydraulic characteristics best explain the distribution of benthic macroinvertebrates (Statzner et al. 1988), and riffles and pools are the most obvious

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macrohabitat features that can be distinguished in a stream reach (Frissell et al. 1986).

Stream ecologists traditionally have addressed how differences in physical factors between riffles and connected pools affect macroinvertebrates (Logan and Brooker 1983, Cooper et al. 1986, Brown and Brussock 1991, Boulton and Lake 1992, Angradi 1996, Ribera and Vogler 2000, Carter and Fend 2001), periphyton (Keithan and Lowe 1985, Rosenfeld and Hudson 1997, Whitledge and Rabeni 2000), and fish (Young 2001, Inoue and Nunokawa 2002). The physical differences between riffle and pool macrohabitats (e.g., velocity, particle size, depth) are apparent, but macrohabitat-related differences in macroinvertebrate composition are not always clear. For example, some studies have reported similar numbers of taxa in riffles and pools (Egglishaw and Mackay 1967, Armitage et al. 1974, Logan and Brooker 1983), whereas others have reported that riffles are richer (Brown and Brussock 1991, Carter and Fend 2001) or poorer (McCulloch 1986, Boulton and Lake 1992) in taxa than pools. Some studies have reported that macroinvertebrate taxonomic composition differs between riffles and pools (i.e., composition is unique in each macrohabitat; Scullion et al. 1982, McCulloch 1986), but significant overlap also has been reported, suggesting that macroinvertebrate taxonomic composition in these macrohabitats is not as discrete as often is presumed (Rabeni et al. 2002). Moreover, few of the above studies were done in intermittent streams (Brown and Brussock 1991, Boulton and Lake 1992). Thus, the disconnected pool has been largely neglected as a separate benthic macrohabitat from the connected riffle–pool sequence.

In streams, hydrologic connectivity refers to longitudinal (upstream–downstream), lateral (riparian–river channel), and vertical (surface water–groundwater) transfers of water (Ward et al. 1999, Lake 2003). Droughts and floods are major disturbances affecting connectivity, with droughts decreasing connectivity and floods restoring it. The riffle portions of riffle–pool sequences are gradually lost as drought progresses, and the remaining pools often become disconnected. Such pools may persist until the following wet season, when floods restore riffle–pool sequences (Boulton and Lake 1992, Williams 1996, Gasith and Resh 1999, Lake 2000, 2003, Boulton 2003). Decreases in hydrologic connectivity may cause changes in existing benthic macrohabitats while also creating new macrohabitats, e.g., riffles (R), pools connected to riffles (Pc), and isolated or disconnected pools (Pd). Change in macrohabitat patchiness over time is associated with variability in natural annual discharge and can be considerable, depending on stream size, substrate

conditions, and other features (Lake 2000, Bonada 2003). Thus, streams may simultaneously have R, Pc, and Pd macrohabitats that may persist for days or months, depending on annual climate, geomorphology, or substrate (Bonada 2003).

Mediterranean-climate streams are characterized by sequential floods and droughts that are seasonally predictable but show variable intensity (McElravy et al. 1989, Molina et al. 1994, Gasith and Resh 1999). Seasonal drought is viewed as a *ramp* disturbance (i.e., the strength of the disturbance increases steadily over time; Lake 2000, 2003), but ecological responses to drought may be *stepped* (i.e., responses occurring as irregular steps as disturbance increases), rather than ramped. Steps are especially common when changes caused by drought cross critical thresholds, such as isolation of the wetted bed from littoral vegetation, loss of flow, or loss of surface and hyporheic water (Boulton 2003). However, responses to critical thresholds may vary with the intensity and timing of drought and may depend on local habitat characteristics. Thus, more empirical information is needed before ecological responses to drought disturbance can be characterized.

We examined assemblages of benthic macroinvertebrates at the macrohabitat (i.e., R, Pc, and Pd) scale at sites in Mediterranean-climate streams that ranged along a gradient from perennial to intermittent. Habitat is a key filter for macroinvertebrate assemblages (Poff 1997), so we hypothesized that assemblages would differ among macrohabitats and that taxonomic composition would be more similar within the same macrohabitat type at different sites than among different macrohabitats at a single site. We also hypothesized that reduced connectivity during drying would produce gradual, rather than rapid, changes in assemblages at the macrohabitat scale. We predicted that changes in assemblages would occur along a gradient from R through Pc to Pd, with Pc serving as a *bridge* macrohabitat between connected and disconnected conditions. Last, we predicted that assemblages would be most dissimilar between Pd and Pc/R macrohabitats and that Pc and R assemblages would be most similar because of their high connectivity.

Methods

Study area

Macroinvertebrates were quantified from 19 sites along 18 streams in the Mediterranean-climate area of northern California during spring 2002. At the time of sampling, 9 sites were from 8 intermittent streams containing only Pd macrohabitats, whereas the other 10 sites were from 10 perennial streams containing R and Pc macrohabitats. Sites were distributed in the

inland mountains of the Sierra Nevada and the coastal ranges north and south of San Francisco, California.

Sites in the Sierra Nevada were fast-flowing reaches in forested basins with medium slopes and substrates composed mainly of boulders and cobbles. Instream autotrophic biomass consisted mostly of diatom mats, encrusting green algae and cyanobacteria, and some macrophytes. Riparian vegetation was mostly *Alnus*, *Salix*, and *Populus*, with some *Pinus lambertiana*, and *Pseudotsuga menziesii* intruding from the upland coniferous forest.

Sites in the northern coastal ranges had steep channels containing coarse substrate, except for the San Geronimo River site, where gravels, sand, and bedrock predominated. Filamentous green algae, diatoms, and some macrophytes occurred at some sites. Riparian vegetation was mostly *Quercus lobata*, *Alnus*, *Corylus cornuta*, *Sequoia sempervirens*, and *Umbellularia californica*.

Sites in the southern coastal ranges, had narrow, steep channels with substrates and instream vegetation similar to the northern coastal sites. Riparian vegetation was mostly *Quercus lobata*, *Platanus racemosa*, *Juglans hindsii*, *Populus*, *Salix*, *Alnus*, *Corylus cornuta*, and *Umbellularia californica*.

Sampling

Sites were sampled following the GUADALMED Project methods (Jáimez-Cuéllar et al. 2002) used in Mediterranean-climate regions of Spain. At each site, streamwater pH, temperature, dissolved O₂ (DO), conductivity, and discharge were measured. Macroalgae and macrophytes were identified visually in the field, and the number of taxa recorded. Macroalgal taxa were divided into those with filamentous and those with encrusted growth forms. Habitat diversity was quantified using the fluvial habitat index (IHF; Pardo et al. 2002, www.guadalmed.org) developed for Mediterranean-climate streams. IHF includes 7 metrics and scores vary from 0 to 100; high values indicate high habitat diversity.

Macroinvertebrates were sampled from R, Pc, and Pd macrohabitats using a 250-μm-mesh kicknet. Samples were examined sequentially in the field, and additional samples were taken until 2 successive samples from each macrohabitat yielded no additional macroinvertebrate families. Samples were preserved in 70% ethanol, sorted to family in the laboratory, and counted. Taxa were quantified by rank abundance because of the semiquantitative nature of the samples. Rank abundances were: 1 = 1 to 3 individuals/sample, 2 = 4 to 10 individuals/sample, 3 = 11 to 100 individuals/sample, and 4 = >100 individuals/sample.

Data analysis

Analysis of variance (ANOVA) or Kruskal-Wallis tests were used to compare physical and chemical variables, macroalgal and macrophyte richness, and geomorphologic characteristics of the IHF (IHF 1–7) between perennial (R and Pc) and intermittent sites (Pd). Total taxa richness and Ephemeroptera, Plecoptera, and Trichoptera (EPT) richness relative to EPT + Odonata, Coleoptera, and Heteroptera (OCH) richness (EPT/[EPT+OCH]) were analyzed among macrohabitats (R, Pc, and Pd). Data were checked for normality and homogeneity of variances using Kolmogorov-Smirnov and Levene's tests, respectively, and transformed when appropriate. STATISTICA (1999, StatSoft, Tulsa, Oklahoma) was used for all analyses.

The Multi-Response Permutation Procedure (MRPP) computed with PC-ORD (version 4.20, MJM Software, Gleneden Beach, Oregon) was used to identify among-macrohabitat differences in macroinvertebrate composition. MRPP is a multivariate test for differences among predefined groups, and provides the statistic A and a p-value by permutation. MRPP is nonparametric, so it is more appropriate than multiple analysis of variance for comparing relative abundances of species in data matrices containing many 0 counts. Correspondence Analysis (CA) was done with CANOCO (version 4, Centre for Biometry, Wageningen, The Netherlands) to describe among-macrohabitat differences in macroinvertebrate assemblages. CA uses χ^2 distance and is recommended over other ordination methods (e.g., Principal Components Analysis) when using rank abundances or when the data have numerous 0 values (Legendre and Legendre 1998).

Cluster analysis based on Bray-Curtis similarity was done using a flexible method ($\beta = -0.25$) to assess similarity in macroinvertebrate assemblages among R, Pc, and Pd macrohabitats, and to ascertain if assemblages were more similar within the same macrohabitat at different sites than among different macrohabitats at a single site. Cluster analysis allows more detailed assessment of pairwise distances among macroinvertebrate assemblages in macrohabitats at different sites than ordination techniques, which include the whole association matrix (Legendre and Legendre 1998).

The Indicator Value (IndVal; Dufrêne and Legendre 1997) method was used to determine the most representative macroinvertebrate taxa in each macrohabitat. IndVal identifies characteristic taxa from a predefined group (i.e., R, Pc, and Pd) based on the relative frequency of occurrence of a taxon in samples of one group and the mean relative abundance of that taxon in samples of one group compared with all groups. An indicator value (IV) and a p-value obtained

by Monte Carlo permutations (9999 permutations) were associated with each taxon. Only taxa with an IV >25 (i.e., species present in >50% of the samples from one group and with a relative abundance in that group of >50%; Dufrêne and Legendre 1997) were retained.

Results

Environmental factors

Perennial sites (R and Pc macrohabitats) were characterized by significantly higher % DO saturation than intermittent (Pd macrohabitat) sites (Table 1). Streamwater pH, temperature, and conductivity were similar among sites. Discharge was highly variable in perennial sites, ranging from 3.2 to >6000 L/s. Taxa richness of filamentous and encrusted algae and macrophytes did not differ between perennial and intermittent sites (Table 1).

IHF scores were significantly higher in perennial than intermittent sites (Table 1). Riffle embeddedness and pool sedimentation (IHF-1) differed significantly between perennial and intermittent sites (Table 1). Riffle frequency (IHF-2) and velocity/depth regime (IHF-4) also differed between perennial and intermittent sites because riffles were absent from intermittent sites. No other habitat characteristics differed between perennial and intermittent sites (Table 1).

Macroinvertebrate taxa richness and EPT/(EPT+OCH) ratio

Macroinvertebrate taxa richness was more variable in Pd than in R or Pc (Fig. 1A). Taxa richness was higher in Pc than Pd ($F = 4.27, p = 0.02$; Fig. 1A). The EPT/(EPT+OCH) ratio differed significantly among macrohabitats ($H = 22.24, p < 0.001$); the EPT/(EPT+OCH) ratio was highest in R and lowest in Pd (Fig. 1B).

Macroinvertebrate composition

Macroinvertebrate composition differed significantly between R and Pd (MRPP, $A = 0.2714, p < 0.001$), R and Pc ($A = 0.1182, p < 0.001$), and Pc and Pd ($A = 0.1022, p < 0.001$). The first 2 CA axes explained 28.4% of total variability among assemblages in the 3 macrohabitats. Assemblages were ordered from R to Pc and Pd along Axis 1 (Fig. 2A). Assemblages in Pd were separated along Axis 2, indicating high variability of macroinvertebrate composition among sites of this macrohabitat. Pd assemblages near the top of Axis 2 had high abundances of Chaoboridae, Lymnaeidae, and Hydraenidae (Appendix, Fig. 2B). Pc assemblages were largely intermediate between R and Pd. Some Pc assemblages were similar to Pd assemblages, sharing Corixidae, Naucoridae, and Hydrophilidae, whereas other Pc assemblages were more similar to R assemb-

TABLE 1. Mean (± 1 SD) values for environmental variables in perennial (riffle [R] and connected pool [Pc] macrohabitats) and intermittent (disconnected pool [Pd] macrohabitat) sites. Taxa richness values for filamentous and encrusted macroalgae and macrophytes were based on taxonomic identifications that were made visually in the field. The total value of the Fluvial Habitat Index (IHF) and the individual values of each habitat variable are presented: IHF-1 = riffle embeddedness (for perennial sites) or sedimentation in pools (for intermittent sites), IHF-2 = riffle frequency, IHF-3 = substrate composition, IHF-4 = velocity/depth regime, IHF-5 = shading of stream bed, IHF-6 = elements of heterogeneity (including litter deposition), and IHF-7 = aquatic vegetation cover.

Variable	Perennial	Intermittent	ANOVA		Kruskal-Wallis test	
			F	p	H	p
pH	7.6 (0.18)	7.7 (0.19)			21.30	0.14
Dissolved O ₂ (% saturation)	92.2 (18.53)	49.6 (24.39)	18.62	<0.01		
Temperature (°C)	16.7 (2.98)	18.3 (3.03)	1.42	0.25		
Conductivity (µS/cm)	260.2 (181.99)	364.4 (159.42)	17.45	0.20		
Discharge (L/s)	1343.8 (2003.14)	0.0 (0.00)			15.08	<0.01
Filamentous algae richness	0.7 (0.67)	0.6 (0.53)			0.17	0.68
Encrusted algae richness	1.1 (1.20)	1.0 (0.50)			0.01	0.79
Macrophyte richness	1.0 (1.15)	0.8 (0.83)			0.09	0.76
IHF	69.0 (5.06)	51.7 (7.14)	379.21	<0.01		
IHF-1	10.0 (0.00)	5.0 (3.54)			11.17	<0.01
IHF-2	8.6 (2.50)	2.0 (0.00)			13.32	<0.01
IHF-3	15.1 (2.42)	16.7 (2.35)			1.18	0.28
IHF-4	6.2 (0.63)	4.4 (0.88)			11.40	<0.01
IHF-5	8.8 (2.57)	7.3 (2.18)			2.28	0.13
IHF-6	7.8 (2.39)	7.3 (1.73)			0.53	0.46
IHF-7	12.5 (4.25)	8.9 (4.17)	34.84	0.08		

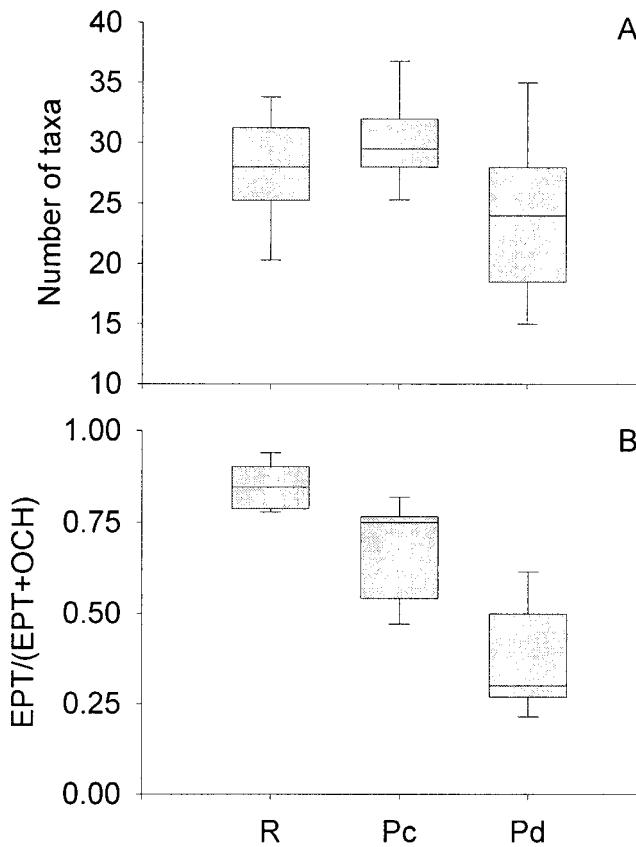


FIG. 1. Box-and-whisker plots showing the number of macroinvertebrate taxa (A) and ratio of Ephemeroptera, Plecoptera, and Trichoptera (EPT) to EPT + Odonata, Coleoptera, and Heteroptera (OCH) family richness [EPT/(EPT+OCH)] (B) in riffle (R), connected pool (Pc), and disconnected pool (Pd) macrohabitats. Plots show medians (horizontal bars), 25th and 75th percentiles (boxes), and 10th and 90th percentiles (whiskers extending from boxes).

lages, sharing Helicopsychidae, Odontoceridae, and Hydroptilidae (Fig. 2B).

Bray–Curtis cluster analysis showed a high degree of separation among assemblages in the 3 macrohabitats (Fig. 3). The 1st split separated assemblages in Pd from those in R and Pc, and the 2nd split separated assemblages in R and Pc further. Within macrohabitat types, assemblages in R were most similar to each other, whereas assemblages in Pd were the most dissimilar, consistent with the CA results (Fig. 3). However, a few sites were exceptional. The assemblages in R in Coyote Creek (gR in Fig. 3) were more similar to assemblages in Pc than to other assemblages in R, whereas the assemblage in Pc in Schneider Creek (jPc in Fig. 3) grouped more closely with assemblages in R than with other assemblages in Pc. Last, the assemblage in Pc in Sausal Burns Creek (aPc in Fig. 3) was more similar to assemblages in Pd than to assemblages in R or Pc.

Of the taxa that occurred in R, only 4.6% were exclusive to the R macrohabitat. Seventeen families (mostly EPT taxa) had an IV value significantly >25 (characteristic taxa) in R (Table 2). The stoneflies Chloroperlidae, Perlidae, Nemouridae, and Peltoperlidae were characteristic of R. Nemouridae and Chloroperlidae also had IVs >25 in Pc, but these IV values were nonsignificant (Table 2). The caddisflies Hydropsychidae, Rhyacophilidae, Polycentropodidae, Philopotamidae, and Glossosomatidae, and the mayflies Heptageniidae and Ephemerellidae were characteristic of R; Limnephilidae occurred in R and Pc, but was characteristic of Pc (Table 2). The triclad family Dugesiidae and the dipteran families Simuliidae, Tipulidae, and Empididae were characteristic of R, but Empididae had a nonsignificant IV value in Pc (Table 2).

Pc shared many taxa with R and Pd. Only 3.8% of taxa were exclusive to Pc macrohabitat, and only 6 families (Ceratopogonidae, Leptophlebiidae, Limnephilidae, Lepidostomatidae, Calamoceratidae, and Gomphidae) were characteristic of Pc (Table 2). Leptophlebiidae also had a high, but nonsignificant, IV value in Pd. Several taxa in Pc had IV values >25, but were characteristic of R or Pd. For example, Elmidae, Baetidae, Nemouridae, Ephemerellidae, Chloroperlidae, and Heptageniidae all had relatively high IV values in Pc, but were characteristic of R. Gerridae, Dytiscidae, and Sialidae had high IV values in Pc, but were characteristic of Pd.

Pd had the highest % of taxa that were exclusive (11.3%) to the Pd macrohabitat, and 14 taxa were characteristic of this macrohabitat (Table 2). Heteroptera families, especially Gerridae and Veliidae, were characteristic of Pd, as were the Coleoptera families Dytiscidae, Gyrinidae, and Hydraenidae, the Mollusc families Planorbidae, Physidae, and Lymnaeidae, and the crustacean groups Copepoda and Cladocera. Other characteristic taxa were Culicidae, Oribatidae, Gammaridae, and Sialidae. Oligochaeta was the only taxon with IV >25 in R and Pd, but Oligochaeta was not characteristic of either R or Pd.

Discussion

Uniqueness of benthic assemblages in macrohabitats

Earlier studies comparing riffle and pool macroinvertebrate faunas reported distinct assemblages in each macrohabitat (Scullion et al. 1982, Logan and Brooker 1983, McCulloch 1986). However, the number of exclusive taxa reported in these macrohabitats was variable. McCulloch (1986) found more unique taxa in pools (probably Pc) than in R, whereas Scullion et al. (1982) found the opposite pattern. We found a slightly higher number of exclusive taxa in R than in Pc, but a

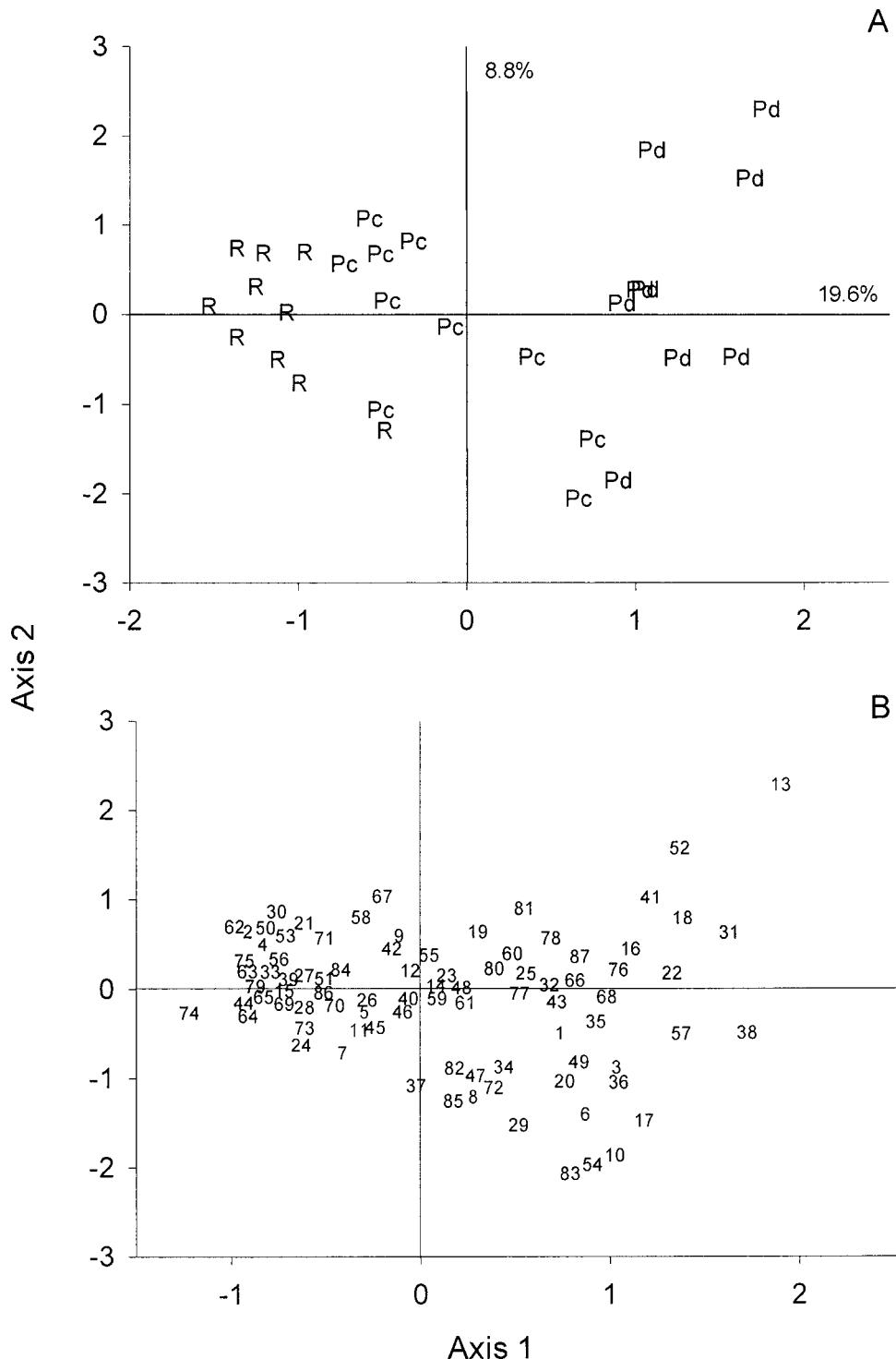


FIG. 2. Correspondence Analysis (CA) plots of sites (A) and macroinvertebrate taxa (B). The % of total variance explained by each axis is shown next to the axis. R = riffles, Pc = connected pools, Pd = disconnected pools. Codes for taxa as in Appendix.

lower number of exclusive taxa in R than in Pd. Characteristic taxa in R, Pc, and Pd were generally consistent with those of other studies (Armitage et al. 1974, Rabeni and Minshall 1977, Scullion et al. 1982, McCulloch 1986, Malmqvist et al. 1993).

As in other studies (Scullion et al. 1982, Logan and Brooker 1983, McCulloch 1986), R had a predominance of EPT taxa, whereas OCH taxa were more abundant in Pc and Pd than in R. Pd macrohabitats had the lowest EPT/(EPT+OCH) ratios of the 3 macrohabitats.

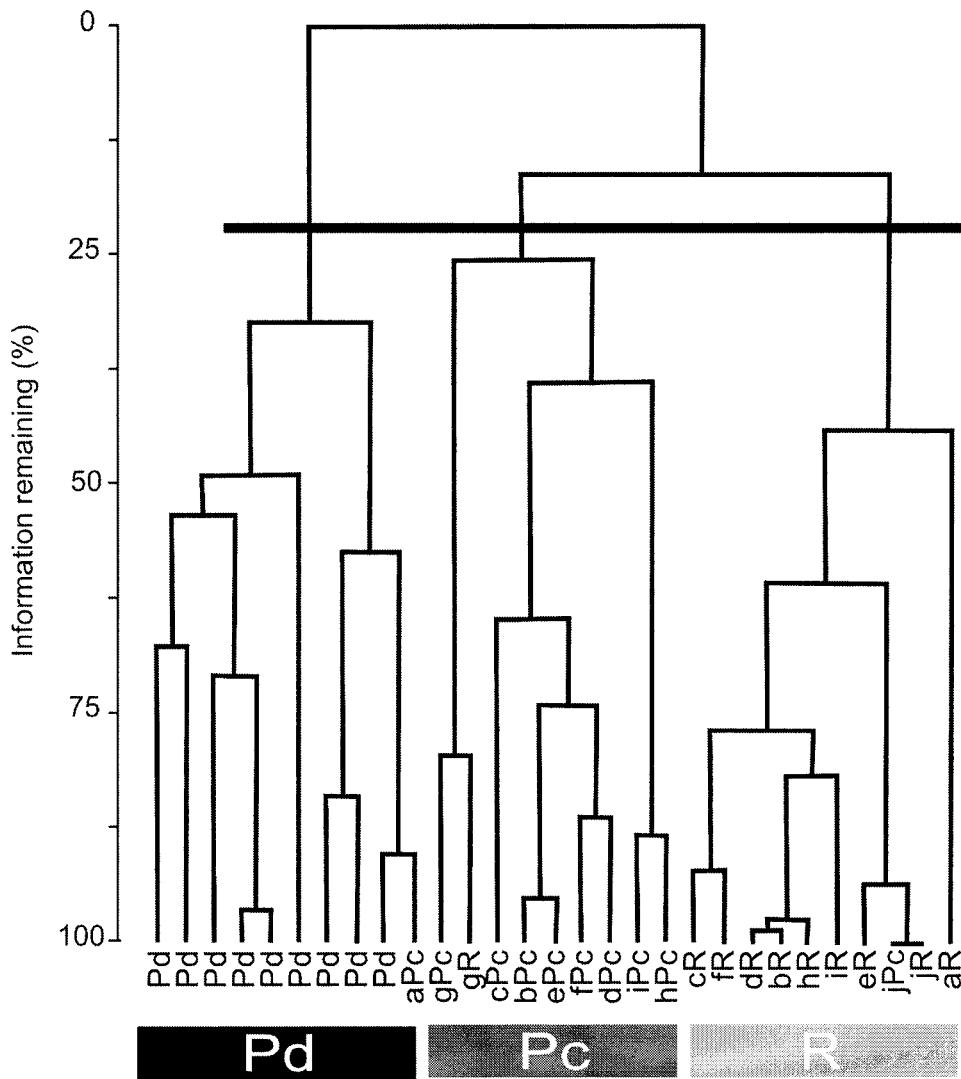


FIG. 3. Bray–Curtis dendrogram of macroinvertebrate composition. R = riffles, Pc = connected pools, Pd = disconnected pools. R and Pc assemblages with the same initial letter are from the same sampling site and river. a = Sausal Burns Creek, b = San Geronimo River, c = Cronan Creek, d = Webb Creek, e = Redwood Creek, f = Saratoga Creek, g = Coyote Creek, h = Spanish Creek, i = Slate Creek, j = Schneider Creek.

Pd could be a refuge from desiccation for some tolerant lentic (i.e., OCH) but probably not for rheophilic (i.e., EPT) macroinvertebrates (Brown and Brussock 1991). This pattern would explain the low similarity between R and Pd in our sites, and it underscores the value of using the EPT/(EPT+OCH) ratio to characterize the assemblages in each macro-habitat. Pd also had several characteristic noninsect taxa, including Crustacea and Mollusca. Except for Physidae, Mollusca are rarely recorded in intermittent sites (Williams 1987). The presence of some Mollusca in Pd could be explained by morphological (Eckblad 1973) or life-cycle (Brown 1982) adaptations, along with high variability in hydrology among years

(McElravy et al. 1989), which could yield permanence in one year and intermittence the next.

Does macrohabitat connectivity influence taxa richness?

Differences in taxa richness between riffles and pools have been associated with habitat stability (McCulloch 1986, Boulton and Lake 1992), peak annual discharge, and reach gradient (Carter and Fend 2001), but sampling method and taxonomic resolution also are important factors (Logan and Brooker 1983). The degree of habitat connectivity also may influence assemblage richness and diversity. Drought causes loss of hydrologic connectivity among stream habitats. Low connectivity is hypothesized to yield low richness

TABLE 2. Indicator Value (IV) scores and associated *p*-values obtained by Monte Carlo permutations (9999 runs) for macroinvertebrate taxa in riffle (R), connected pool (Pc), and disconnected pool (Pd) macrohabitats. Taxa in each macrohabitat are listed in order of decreasing IV, and only taxa with IV >25 are shown. Characteristic taxa for a macrohabitat type have *p* < 0.05.

R			Pc			Pd		
Taxon	IV	<i>p</i>	Taxon	IV	<i>p</i>	Taxon	IV	<i>p</i>
Hydropsychidae	96.4	<0.01	Ceratopogonidae	62.6	<0.05	Planorbidae	78.8	<0.01
Simuliidae	93.2	<0.01	Leptophlebiidae	59.4	<0.05	Gerridae	72.5	<0.01
Rhyacophilidae	79.5	<0.01	Limnephilidae	56.3	<0.05	Culicidae	71.7	<0.01
Chloroperlidae	79.2	<0.01	Lepidostomatidae	55	<0.05	Physidae	69.8	<0.01
Tipulidae	77.2	<0.01	Elmidae	54.2	0.15	Copepoda	64.8	<0.01
Perlidae	77	<0.01	Baetidae	53.6	0.14	Oribatidae	63.1	<0.01
Heptageniidae	71.2	<0.01	Ostracoda	53.6	0.10	Dytiscidae	60.1	<0.05
Ephemerallidae	68.6	<0.01	Gerridae	52.9	0.08	Gammaridae	55.6	<0.01
Nemouridae	66.3	<0.01	Dytiscidae	52.5	0.10	Oligochaeta	52.1	0.44
Baetidae	64.3	<0.01	Empididae	43.2	0.20	Sialidae	49	<0.05
Elmidae	64	<0.01	Calamoceratidae	40	<0.01	Veliidae	47.5	<0.01
Empididae	62.3	<0.01	Nemouridae	39.5	0.32	Leptophlebiidae	45.7	0.77
Oligochaeta	54.4	0.26	Gomphidae	36.2	<0.05	Cladocera	45.4	<0.05
Hydracarina	53.6	0.32	Sialidae	36.2	0.20	Dixidae	40.9	0.44
Polycentropodidae	47.5	<0.05	Ephemerallidae	34.8	0.63	Ostracoda	40.4	0.72
Philopotamidae	47.5	<0.01	Chloroperlidae	34.1	0.67	Gyrinidae	40	<0.05
Glossosomatidae	44.9	<0.05	Heptageniidae	34.1	0.54	Hydraenidae	40	<0.05
Hydroptilidae	44.8	0.13	Nematoda	30.6	0.43	Hydrophilidae	34.2	0.12
Psephenidae	39.3	0.18	Sericostomatidae	27.4	0.25	Lymnaeidae	33.3	<0.05
Peltoperlidae	36.8	<0.05	Oribatidae	27	0.83	Corixidae	28.9	0.34
Dugesiidae	35.3	<0.05	Corduliidae	26.5	0.08	Haliplidae	26.2	0.10
Brachycentridae	31.7	0.09	Psephenidae	25.7	0.68			
Uenoidae	30.8	0.20						
Limnephilidae	28.3	0.73						
Psychodidae	26.2	0.19						
Perlodidae	25.5	0.18						

because exchanges of matter, energy, and organisms are constrained between patches (Ward et al. 1999). Therefore, low taxa richness should be expected in disconnected habitats. Sheldon et al. (2002) reported lower taxa richness in ephemeral and temporary lakes than semipermanent river channels in an Australian dryland river. In our study, taxa richness was lower in Pd than in Pc, presumably because of decreased hydrologic connectivity in Pd. In contrast, taxa richness was similar between R and Pc, presumably because of relatively high connectivity between R, Pc, and other parts of the whole fluvial ecosystem.

Boulton (2003) suggested that decreases in taxa richness at the stream-reach scale follow a stepped (vs ramped) pattern during drought, with faunal responses occurring as irregular steps instead of gradual changes as drying disturbance progresses. At the macrohabitat scale, one would expect R to dry first. Taxa richness should increase slightly in Pc as R dries because Pc may shelter some R taxa from desiccation before they emerge or die (i.e., concentration of individuals in Pc as drying progresses). Pc macrohabitat becomes Pd macrohabitat after cessation of flow, so Pd could have similar taxa richness to Pc

before environmental conditions become harsh and taxa richness declines because of desiccation. Thus, similarity of taxa richness between Pc and Pd should be a function of the time since cessation of flow. In our study, we did not know how long Pd macrohabitats had been disconnected from R macrohabitats, but the high variability of richness among Pd macrohabitat may have been related to the duration of hydrologic separation. The coefficient of variation (CV) of taxa richness was lower in Pc (11.5%) than in R (15.3%) or Pd (26.1%), suggesting that Pc may be the least variable macrohabitat during drought. These patterns suggest that changes in taxa richness at the macrohabitat scale follow a ramped pattern during drought; i.e., the loss of R is gradual, and Pc provides a consistent refuge before drying converts Pc to Pd.

Does connectivity influence macroinvertebrate composition?

Sheldon et al. (2002) reported that temporary lake assemblages were distinct from assemblages in more permanent sites, and we observed significant differences in macroinvertebrate assemblage structure among 3 stream macrohabitats. The greatest similarity

in taxa composition occurred between hydrologically connected R and Pc macrohabitats. Moreover, the greater variability in taxonomic composition observed in Pd (cf. R and Pc) may have been a consequence of differences in the duration of disconnection of Pd from R at different sites (Stanley et al. 1997, Lake 2003).

In temporary ponds, predator abundance may increase as the duration of inundation increases (Schneider and Frost 1996). In our study, macroinvertebrate composition of some Pd assemblages was similar to composition of Pc assemblages, whereas other Pd assemblages had a fauna distinctly different from Pc assemblages and also had a high abundance of predators (e.g., Chaoboridae). This pattern suggests that some Pd macrohabitats were disconnected from R for a longer period than other Pd macrohabitats. On the other hand, differential colonization and predation in Pd may produce distinctive macroinvertebrate assemblages even among Pd sites that have been disconnected for the same length of time.

We propose that the high variability among macroinvertebrate assemblages in Pd macrohabitat at different sites may be explained by: 1) the duration of the hydrologic disconnection of Pd from nearby R macrohabitats, 2) differential macroinvertebrate colonization, 3) differential predation by colonizing predators, and 4) other environmental factors that differ naturally among Pd macrohabitats. For example, changes in physicochemical variables, sedimentation rates, and associated changes in algal and macrophyte biomass may occur after loss of hydrologic connectivity during drought, and macroinvertebrate responses may be associated with these changes (Boulton 2003). We did not find significant differences in macrophyte and macroalgal richness, aquatic vegetation cover, litter deposition, or substrate composition between perennial and intermittent sites at the reach scale (Table 1); however, some of these factors may be important at the microhabitat scale (e.g., within a single Pd), and could explain, in part, the faunal uniqueness of a given site.

Overall, our results indicate that differences between R and Pc macrohabitats were greater than differences among perennial sites throughout the study area. Our results are consistent with those reported from 2 Texas streams (McCulloch 1986) and 3 Appalachian streams (Angradi 1996), but they differ from several UK streams (Logan and Brooker 1983) where riffles and pools at the same site were more similar to each other than they were to similar macrohabitats at different sites. Angradi (1996) proposed that the scale of observation accounts for whether one or the other conclusion is reached: at large spatial scales, high similarity is expected between assemblages in different macrohabitats within a site because other large-scale filters (e.g., basin character-

istics, zoogeography) may be more influential on faunal assemblages than local habitat characteristics. In a study comparing common taxa in riffles and pools in several Mediterranean-climate regions, Bonada (2003) reported that differences among regions were greater than differences between macrohabitats. Bonada (2003) attributed this result to differential influence of local vs regional environmental and historical processes. However, relatively small-scale studies such as ours suggest that macrohabitat type has a greater influence on macroinvertebrate assemblages than local characteristics of a site.

In summary, our data suggest that, at least for these Mediterranean-climate streams, changes in taxa richness and macroinvertebrate assemblages during drought follow a ramp model (but see Acuña 2004). Pc macrohabitat represents an intermediate condition between R/Pc and Pd macrohabitats. The rate of drying and other abiotic or biotic factors may be crucial in determining assemblage responses (Boulton 2003), and rate of drying (ramp slope) may determine whether faunal responses are stepped or ramped. Rate of drying depends on climatic conditions, channel morphology, and discharge during the wet season (Bonada 2003). Drought in Mediterranean-climate streams may have a milder effect on macroinvertebrate assemblages than drought in more arid climates where channel drying is faster, and may be similar to intermittence in temperate-deciduous streams where streambed drying may occur more slowly during drought. On the other hand, even in Mediterranean-climate streams, ramped or stepped models could apply depending on the habitat characteristics of a site. A ramped pattern could develop when site geomorphology and hydrology allow isolated pools to form gradually during drought. A stepped response could occur in situations where drying occurs suddenly (e.g., gravel substrate, very low winter flow). Natural or anthropogenic alterations of Mediterranean streams that increase aridity or modify habitat characteristics (e.g., climate change, riparian vegetation alterations, water abstraction) may alter the way assemblages respond to drought, emphasizing the vulnerability of these ecosystems.

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APPENDIX. Codes for macroinvertebrate taxa plotted in Fig. 2B.

Taxon	Code	Taxon	Code
Aeshnidae	1	Hydroptilidae	45
Amelitidae	2	Lepidostomatidae	46
Ancylidae	3	Leptoceridae	47
Asellidae	4	Leptophlebiidae	48
Baetidae	5	Lestidae	49
Belostomatidae	6	Leuctridae	50
Brachycentridae	7	Limnephilidae	51
Caenidae	8	Lymnaeidae	52
Calamoceratidae	9	Muscidae	53
Calopterygidae	10	Naucoridae	54
Cambaridae	11	Nematoda	55
Ceratopogonidae	12	Nemouridae	56
Chaoboridae	13	Notonectidae	57
Chironomidae	14	Odontoceridae	58
Chloroperlidae	15	Oligochaeta	59
Cladocera	16	Oribatidae	60
Coenagrionidae	17	Ostracoda	61
Copepoda	18	Peltoperlidae	62
Cordulegasteridae	19	Perlidae	63
Corixidae	20	Perlodidae	64
Corydalidae	21	Philopotamidae	65
Culicidae	22	Physidae	66
Dixidae	23	Planariidae	67
Dugesiidae	24	Planorbidae	68
Dytiscidae	25	Polycentropodidae	69
Elmidae	26	Psephenidae	70
Empididae	27	Psychodidae	71
Ephemerallidae	28	Psychomyiidae	72
Ephydriidae	29	Pteronarcyidae	73
Erpobdellidae	30	Pyralidae	74
Gammaridae	31	Rhyacophilidae	75
Gerridae	32	Sciomyzidae	76
Glossosomatidae	33	Sericostomatidae	77
Gomphidae	34	Sialidae	78
Gyrinidae	35	Simuliidae	79
Haliplidae	36	Siphlonuridae	80
Helicopsychidae	37	Sphaeridae	81
Helophoridae	38	Stratiomyidae	82
Heptageniidae	39	Tabanidae	83
Hydracarina	40	Tipulidae	84
Hydraenidae	41	Tricorythidae	85
Hydrobiidae	42	Uenoidae	86
Hydrophilidae	43	Veliidae	87
Hydropsychidae	44		