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Inter-annual changes in the benthic community structure of riffles and pools in reaches of contrasting gradient

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Abstract

The inter-annual variation in the structure of the benthic community of riffles and pools was evaluated in contrasting geomorphic settings. The community structure of riffles and pools was a function of habitat, reach gradient, and discharge and was taxon specific. In years of below average peak discharge, riffles had higher taxon richness than pools (66 *versus* 47) but richness was similar between habitats during a year of average discharge (56 *versus* 54). The percentage composition of oligochaetes and elmid beetles was more variable inter-annually in pools and low gradient reaches than in high gradient reaches. Differences in the percentage of collector-gatherers and scrapers in riffles and pools appeared related to inter-annual differences in discharge regimes. Two components of the annual discharge regime appear to differentially affect the composition of the benthic community in the snowmelt dominated stream studied: the magnitude of the annual peak discharge and the duration and timing of the period of extended high flow.

Introduction

Two of the physical habitats most apparent in low- to mid-order streams are riffles and pools. Gordon et al. (1992) define riffles as shallower, higher velocity regions containing coarser bed materials and having more rectangular cross-sectional profiles, and pools as deeper, lower velocity regions containing finer bed materials and having more asymmetric cross-sectional profiles. Merritt & Cummins (1996) use erosional (riffles) and depositional (pools) as primary habitat classifiers of benthic invertebrates. From an environmental monitoring standpoint, Kerans et al. (1992) recommend sampling both habitat types in biomonitoring studies, and some programs have incorporated sampling both erosional and depositional habitats in their protocols (Cuffney et al., 1993).

Despite the apparent usefulness of these habitat classifications in lotic ecology and their application in biomonitoring, few studies have examined how common measures of benthic community composition used in biomonitoring differ between riffles and pools, or how these measures may differ inter-annually in contrasting geomorphological settings.

Although numerous studies have identified the invertebrate fauna of riffles and pools, they have been done at a variety of spatial and temporal scales and at differing levels of taxonomic resolution. Logan & Brooker (1983) reviewed studies from North America and the United Kingdom and reported consistent differences in the fauna of riffles and pools. They noted, however, that all the studies had been done in upland streams; consequently, they could not generalize the studies they reviewed to lowland streams.

Subsequent to their review, McCulloch (1986) studied two lowland, low gradient streams in east Texas and found faunal patterns that differed from those reported by Logan & Brooker (1983) in upland streams. Differences in faunal composition found between the two studies could be attributed to spatial factors operating at two different scales: first, the location along the stream profile from upland to lowland areas and/or second, the reach-level geomorphological setting (i.e. high-gradient, large-substratum upland streams *versus* low-gradient, small-substratum lowland streams).

Additionally, differences in the faunal composition of riffles and pools may change temporally, and the temporally induced change may interact with the geomorphological setting in which the riffles and pools are located. Studies that have extended beyond an annual cycle frequently show that previous season flow conditions affect community composition (McElravy et al., 1989; Brown & Brussock, 1991). Riffles and pools located in reaches of contrasting gradients may be expected to respond differently to inter-annual variation in stream discharge (Leopold et al., 1964; Resh et al., 1988; Brown & Brussock, 1991; Gordon et al., 1992).

The purpose of this study was to determine whether (1) common measures of community composition of riffles and pools differed in contrasting gradients, (2) the community composition of these two habitats changed inter-annually, and (3) whether an interaction between geomorphological setting and annual flow regime influenced benthic composition. To test these relationships, riffles and pools were studied over 3 consecutive years in a single, minimally disturbed, geomorphologically complex stream segment that contained both high and low gradient reaches.

The study was confined to a single segment (Frissel et al., 1986) to control for a number of large-scale factors known to influence species distributions. These include longitudinal position along the stream profile (Vannote et al., 1980; Statzner & Higler, 1986), altitude (Ormerod et al., 1994; Carter et al., 1996) and hydrologic regime (McElravey et al., 1989; Brown & Brussock, 1991). Equally important, by limiting this study to a single isolated segment, a common species pool existed that could potentially colonize the different habitat types. This aided in reducing the known influence of longitudinal change on community composition among habitats and reaches (Statzner & Higler, 1986).

Site description

The Merced River in Yosemite Valley, Yosemite National Park, is located at an altitude of approximately 1220 m on the western side of the Sierra Nevada Mountains in eastern California, U.S.A. (Fig. 1). The valley vegetation is dominated by forest with interspersed grassy meadows. Dominant trees include yellow pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), incense cedar (*Libocedrus decurrens*) and oaks (predominantly *Quercus kelloggi*). The stream banks are sparsely wooded in black cottonwood (*Populus trichocarpa*) and willows (*Salix* spp.) in lower gradient reaches and alder (*Alnus* sp.) and maple (*Acer* sp.) in higher gradient reaches. Over 50% of the precipitation occurs during January, February and March in the form of snowfall. Peak discharge typically occurs during the months of April, May or June; by early autumn, river discharge is at an annual minimum. This portion of the Merced River is oligotrophic, with NO_3–NO_2 less than 0.05 mg l^{-1} and total phosphorus generally less than 0.01 mg l^{-1}.

The 15 km segment of the Merced River studied is 6th order and has an elevation drop of 30 m. As in many glacial valleys, high gradient reaches occur at both ends of the low gradient valley (Fig. 1). Wetted width during low flow ranged from approximately 15 to 35 m among the site locations. Substratum within the riffles ranged from boulder and cobble in areas of high gradient to gravel and coarse sand in areas of lower gradient. Substratum within the pools ranged from cobble and sand in high gradient areas to silt overlaying sand and gravel in low gradient areas.

Methods

Biological samples

Eight reaches were sampled over 3 consecutive years (1992–1994) (Fig. 1). Four reaches were high gradient (mean percentage slope = 1.49, ± 1.450 SD) and four were low gradient (mean = 0.07, ± 0.034 SD). Within each reach two types of habitat were sampled; riffle and pool. The principal sampling period was during low flow near the beginning of October each year. In each habitat, five 0.09 m^2 kicknet collections were made using a net mesh size of 209 μm. The five collections per habitat per reach were composited to form a sample unit that represented the habitat. Sampling proceeded from downstream to upstream and from near the edge (but excluding the margin) to the center of the habitat.

Because the principal sampling only occurred during autumn, additional collections were made at all eight sites in spring, and near monthly at three sites during 1993 to increase the taxonomic resolution of the study. These additional collections were made instream for late instars and aerially for adults. Adults were collected with aerial nets during daylight and black-light traps at night.

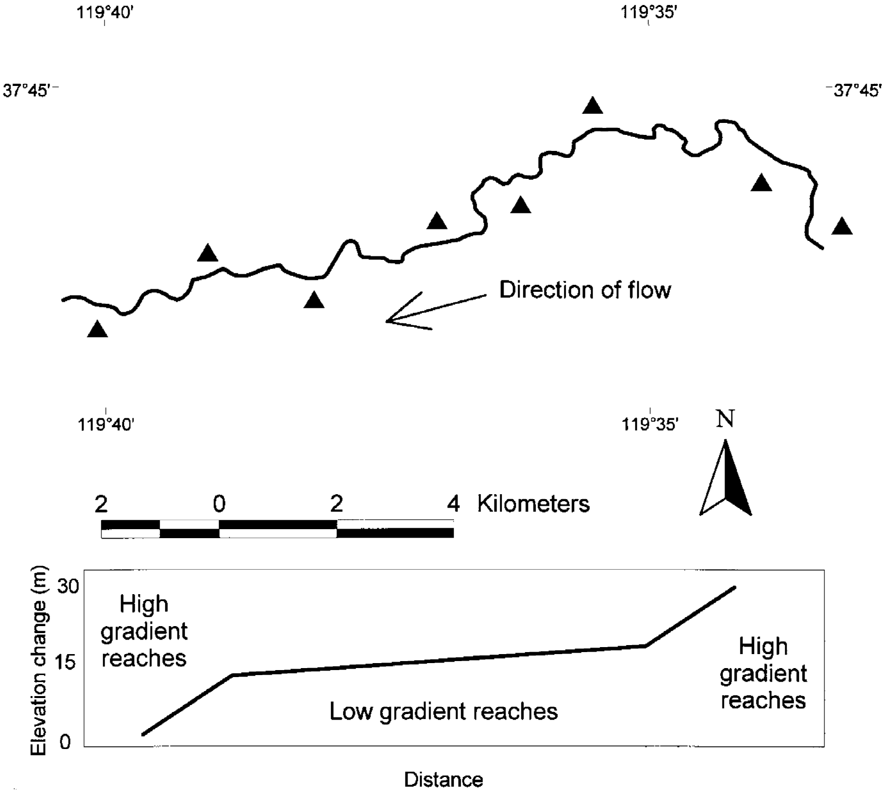

Figure 1. Map of the Merced River in Yosemite Valley. Sampling locations are depicted as triangles. Below is shown a diagram delineating reaches of high and low gradient.

Samples were preserved in the field in 10% buffered formalin. In the laboratory, each sample was rinsed using a 100 μm sieve and transferred to 80% ethanol. Each sample was then picked of large invertebrates for 15 min and cleaned of large debris. The remaining portion of the sample was subsampled using an Imhoff cone (Wrona et al., 1982). The subsampling method was tested for its ability to produce a random subsample (Wrona et al., 1982) and proved reliable for common taxa (88% of tested taxa had $0.83<\chi^2_{0.05(5)}<12.83$, representing $p > 0.05$). All invertebrates were removed from the subsample using 8× magnification and identified to the lowest practicable taxonomic level, normally species or morphospecies in all but a few taxa such as Nematoda, Crustacea and very early life-history stages.

Physical measurements

For each of the five collections per sample, two to three mean velocity (at 0.6 water depth) and depth measurements were recorded. Substratum particle size was visually estimated using an underwater viewing box at the location of each collection. The viewing box covered an area of approximately 0.09 m^2. Substratum size was categorized as percentage boulder (>256 mm), cobble (>64 mm), pebble (>32 mm), gravel (>2 mm) and sand. Average daily discharge and annual peak discharge were obtained from the U.S. Geological Survey.

Numerical methods

Eighteen measures of benthic community composition commonly used in biomonitoring were analyzed with 3-way fixed effects ANOVAs (Table 1). These measures encompassed total taxon richness, the richness of major taxonomic groups, the proportional abundance of major taxonomic groups, and the proportional abundance of functional feeding groups. The first factor of each ANOVA was habitat and had two levels, riffle *versus* pool. The second factor, gradient, had two levels, high *versus* low gradient. The third factor, year, had three levels and was treated as a repeated measure (Cooper & Barmuta, 1993). All percentage data were

Table 1. Definition of community measures

Abbreviation	Definition
S_TAX	Total number of taxa
S_MAY	Number of Ephemeroptera taxa
S_STO	Number of Plecoptera taxa
S_CAD	Number of Trichoptera taxa
S_CHI	Number of Chironomidae taxa
S_OLI	Number of Oligochaeta taxa
S_COL	Number of Coleoptera taxa
%_MAY	Percentage composition of Ephemeroptera
%_STO	Percentage composition of Plecoptera
%_CAD	Percentage composition of Trichoptera
%_CHI	Percentage composition of Chironomidae
%_OLI	Percentage composition of Oligochaeta
%_COL	Percentage composition of Coleoptera
%_PRE	Percentage composition of predators
%_CG	Percentage composition of collector-gatherers
%_FIL	Percentage composition of filterers
%_SCR	Percentage composition of scrapers
%_SHR	Percentage composition of shredders

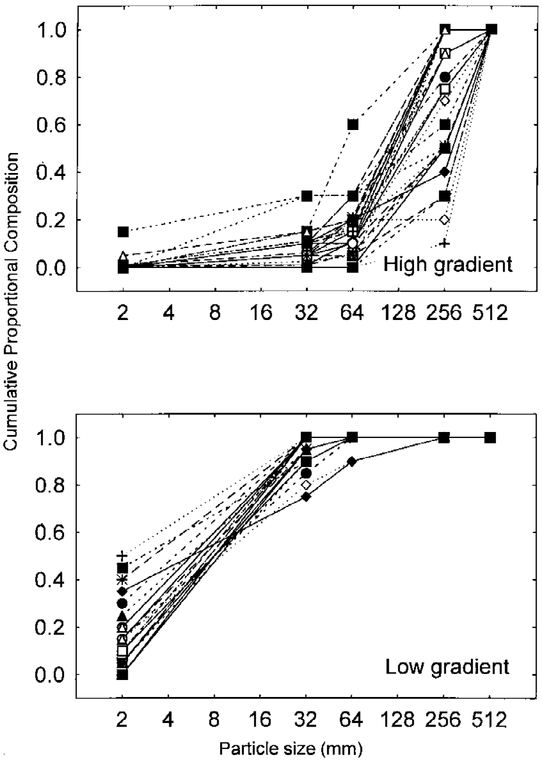

Figure 2. Cumulative proportional particle size composition of riffle samples from high and low gradient reaches.

arcsine transformed, which in all cases made those data more approximately normal.

Alpha was adjusted for the eighteen comparisons to $\alpha = 0.00284$ to maintain an experiment-wise error rate of approximately $\alpha = 0.05$. This adjustment provided a very conservative estimate of significance in the ANOVAs (Winer et al., 1991). Because of the complexity of the ANOVA design, means graphs (i.e. without error bars) are used in conjunction with the F-values and probabilities for data interpretation (Winer et al., 1991).

Trophic relationships were assigned to each taxon based on the first choice for the taxon (or closest taxon for which there was information) as listed in Merritt & Cummins (1996) or Pennak (1989).

Results

Physical

Riffles ranged from high gradient boulder-cobble to low gradient sand-gravel (Fig. 2). Pools ranged from lateral scour pools containing mixed sediments formed by large boulders and other bank structures in high gradient reaches, to large, fine-grained corner pools at meander bends in low gradient reaches.

The Merced River hydrograph varies greatly both annually and inter-annually. Daily average discharge during the study period ranged from 0.113 $m^3 s^{-1}$ to 77.305 $m^3 s^{-1}$ (Fig. 3). The first year of sampling (1992) represented the last year of a 6-year drought. The mean of the annual peak discharges of the previous 6 years was 48.1 $m^3 s^{-1} \pm 11.60$ (± standard deviation), approximately one-half the mean annual peak discharge of 85.8 $m^3 s^{-1} \pm 49.72$ of the preceding 77 years (Fig. 4). Even though there was an extended drought, the Merced River never became intermittent. The peak spring discharges prior to the autumn sampling in 1992, 1993 and 1994 were 42.2 $m^3 s^{-1}$, 88.9 $m^3 s^{-1}$, and 53.0 $m^3 s^{-1}$, respectively. Even though the average flow year of 1993 had an annual peak discharge approximately twice the low flow years, it was only slightly higher than the 77 year mean.

During 1992 and 1994, the Merced River approached base flow by mid to late August; however, during the average flow year of 1993 the period of

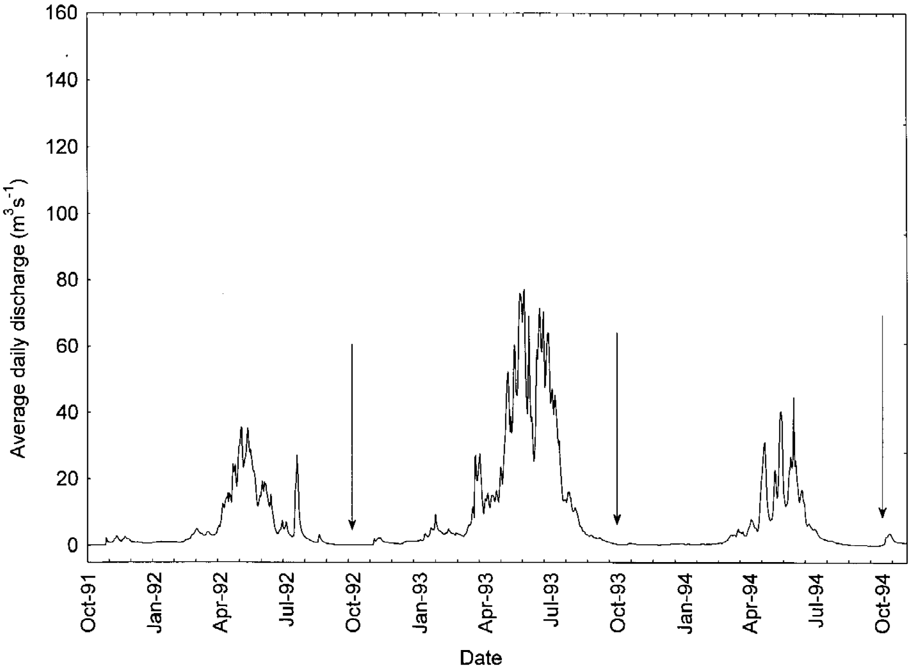

Figure 3. Average daily discharge during the period of study. Arrows indicate the dates of invertebrate collections.

high discharge extended later into the summer (Fig. 3). Mid-August discharge was still much higher (4.106 m^3 s^{-1}) than in the two low flow years.

There was inter-annual variability in discharge at the time of sampling. In 1992, discharge was 0.215 m^3 s^{-1}. In 1993, discharge was 0.357 m^3 s^{-1}, slightly higher than in 1992. However, in 1994 a storm occurred just prior to sampling and discharge rose from base level to 2.775 m^3 s^{-1}. The increased discharge represented an increase in depth of approximately 10–15 cm in riffle habitats.

No significant differences in velocity at the time of sampling were detected among years in the high gradient riffles (means for 1992–1994: 0.56, 0.70, 0.85 ms^{-1}) and pools (0.06, 0.15, 0.21 ms^{-1}). However, low gradient riffles had significantly higher velocities (0.48, 0.50, 0.69 ms^{-1}) during 1994 and low gradient pools had significantly lower velocities (0.20, 0.02, 0.12 ms^{-1}) in 1993.

Taxonomic richness

Total sampled richness of both habitats across all 3 years was 259. Total richness over the three years was similar between riffles and pools (211 taxa *versus* 204 taxa, respectively). In high gradient reaches, riffle richness (158) was similar to pool richness (166); however, in low gradient reaches, riffle richness (166) was slightly greater than pool richness (144).

Mean taxon richness was generally greater in riffles than in pools (Fig. 5). However, mean richness varied among years and there was a habitat × year interaction (Table 2). Taxon richness was much higher in riffles than in pools in 1992 and only slightly (but significantly) higher in 1994 (Fig. 5). These 2 years represented the two low peak flow years. However, there was no detectable difference between the habitats in 1993, the average peak flow year. Gradient appeared to have no effect on mean richness either between habitats or among years.

Richness of major taxonomic groups was principally a function of taxon, habitat, and gradient. A year effect was only detected in chironomid richness. Mayfly and caddisfly richness were higher in riffles than pools in both high and low gradient reaches. Both measures also were higher in high gradient versus low gradient reaches. Stonefly richness was much higher in riffles than in pools but unlike S_MAY and S_CAD no effect of gradient was observed. There was no year main effect or significant interactions on the richness of mayflies, stoneflies, or caddisflies.

Year was the only significant main effect on the richness of chironomids (S_CHI), however there also was a habitat × year interaction. The richness of chiro-

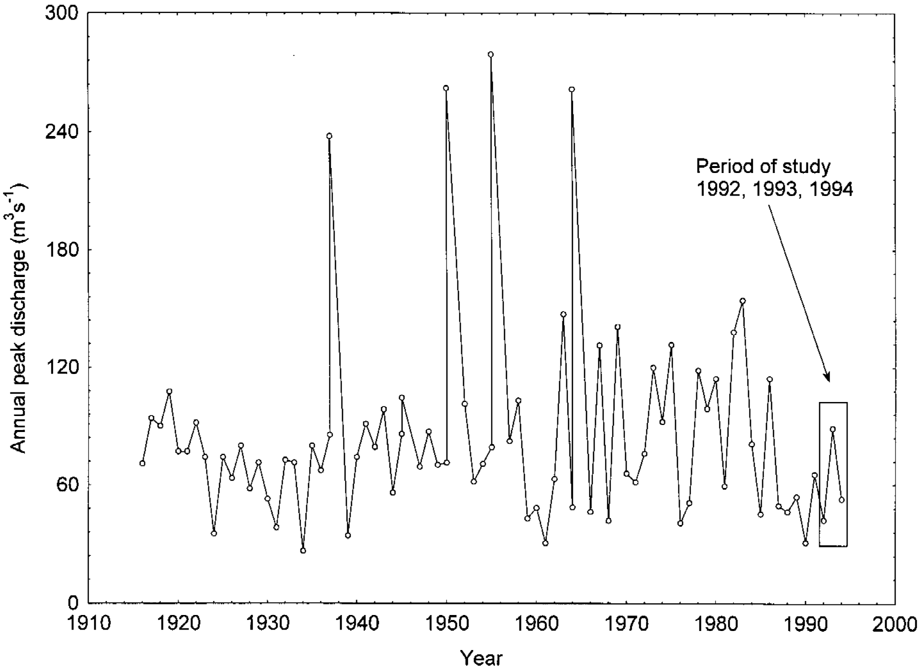

Figure 4. Annual peak discharge of the Merced River in the study segment since the early 1900s. Rectangle outlines period of study.

nomids increased from 1992 through 1994 in pools, but remained the same among the 3 years in riffles. The richness of chironomids was higher in riffles than in pools in 1992 but lower in riffles than in pools in 1993 and 1994.

Oligochaete richness (S_OLI) was affected only by gradient, with more species in low gradient than in high gradient reaches. There was a weak year effect with 1993, the average flow year, having lower richness than 1992 or 1994, particularly in low gradient riffles.

There were no effects of habitat, gradient, year or any interactions of the three main effects on the richness of Coleoptera.

Percentage taxonomic composition

Percentage composition was influenced by the year main effect more often than the main effects of habitat or gradient (Table 2).

No significant difference was detected in the percentage of mayflies between riffles and pools or between high and low gradient reaches, and %_MAY was stable among years in riffles and pools in high gradient reaches (Fig. 6). However, there was a significant year main effect and a gradient × year interaction resulting from %_MAY increasing from approximately 10% in 1992 to 40% in 1993 and declining to 10% in 1994 in low gradient reaches. The variance associated with this inter-annual change in %_MAY probably contributed to the non-significant difference between high and low gradient reaches (Fig. 6).

There were significant habitat and year main effects on the percentage of stoneflies. Riffles had higher %_STO than pools and 1993 (average flow) had a much higher %_STO than 1992 and 1994. Similar to %_MAY, %_STO appeared substantially higher in 1993 than 1992 or 1994 in low gradient reaches.

In contrast to %_STO, the percentage of caddisflies only showed a gradient main effect with higher percentages in high gradient areas *versus* low gradient areas (Fig. 6, Table 2).

Percentage chironomids showed only a year main effect with %_CHI increasing from 1992 through 1994.

Percentage oligochaetes displayed a year main effect as well as a gradient × year interaction. Percentage oligochaetes was highest in 1992. In high gradient reaches %_OLI was approximately the same among years, but in low gradient reaches there was a substantial reduction between 1992 and 1993 and only a slight increase in 1994.

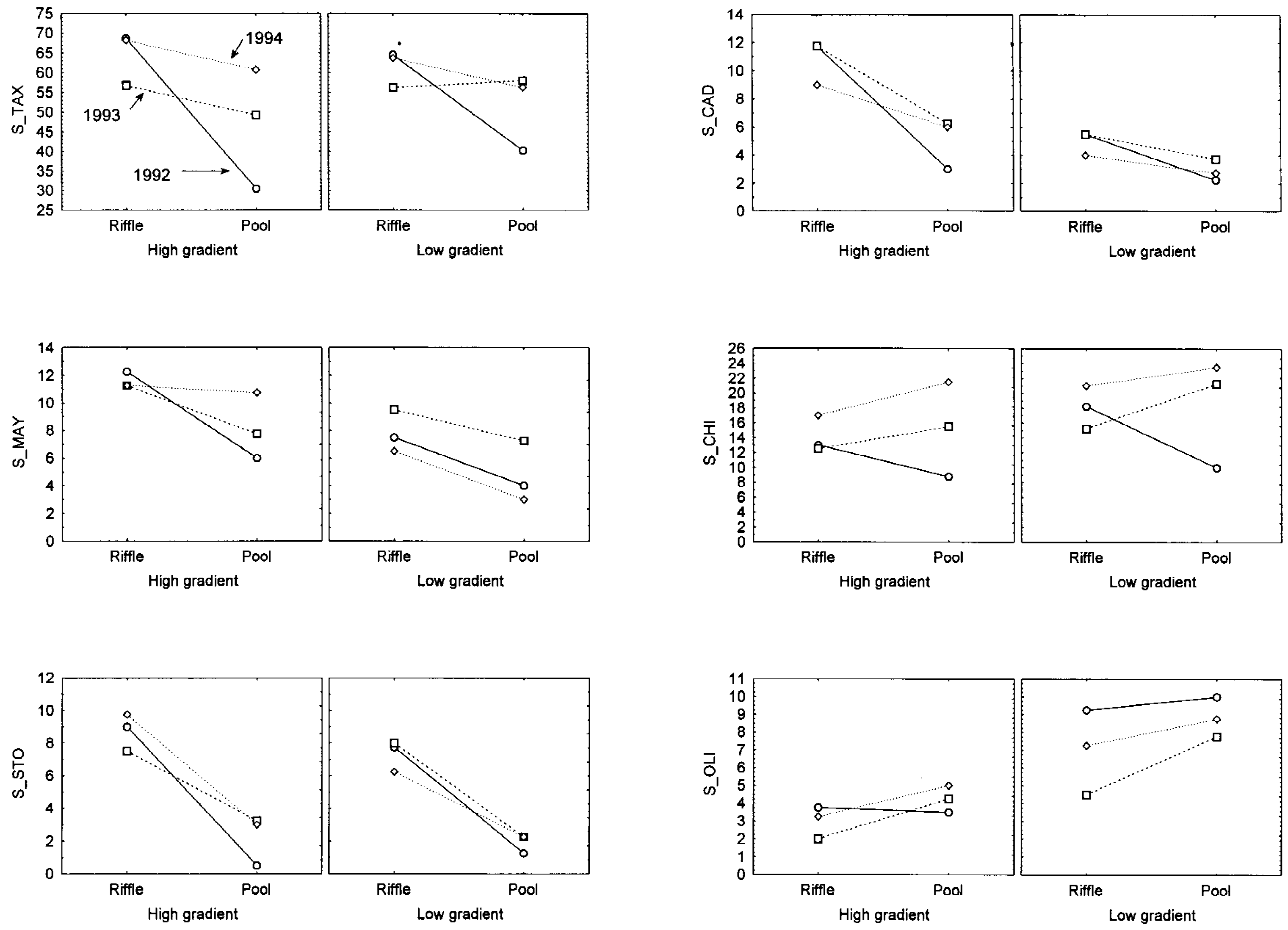

Figure 5. Means graphs of richness values. Note: abscissa is variable and no error bars are depicted. Circles with solid line equals 1992, squares with dashed line equals 1993, and diamonds with dotted line equals 1994. Refer to Table 2 for significant differences.

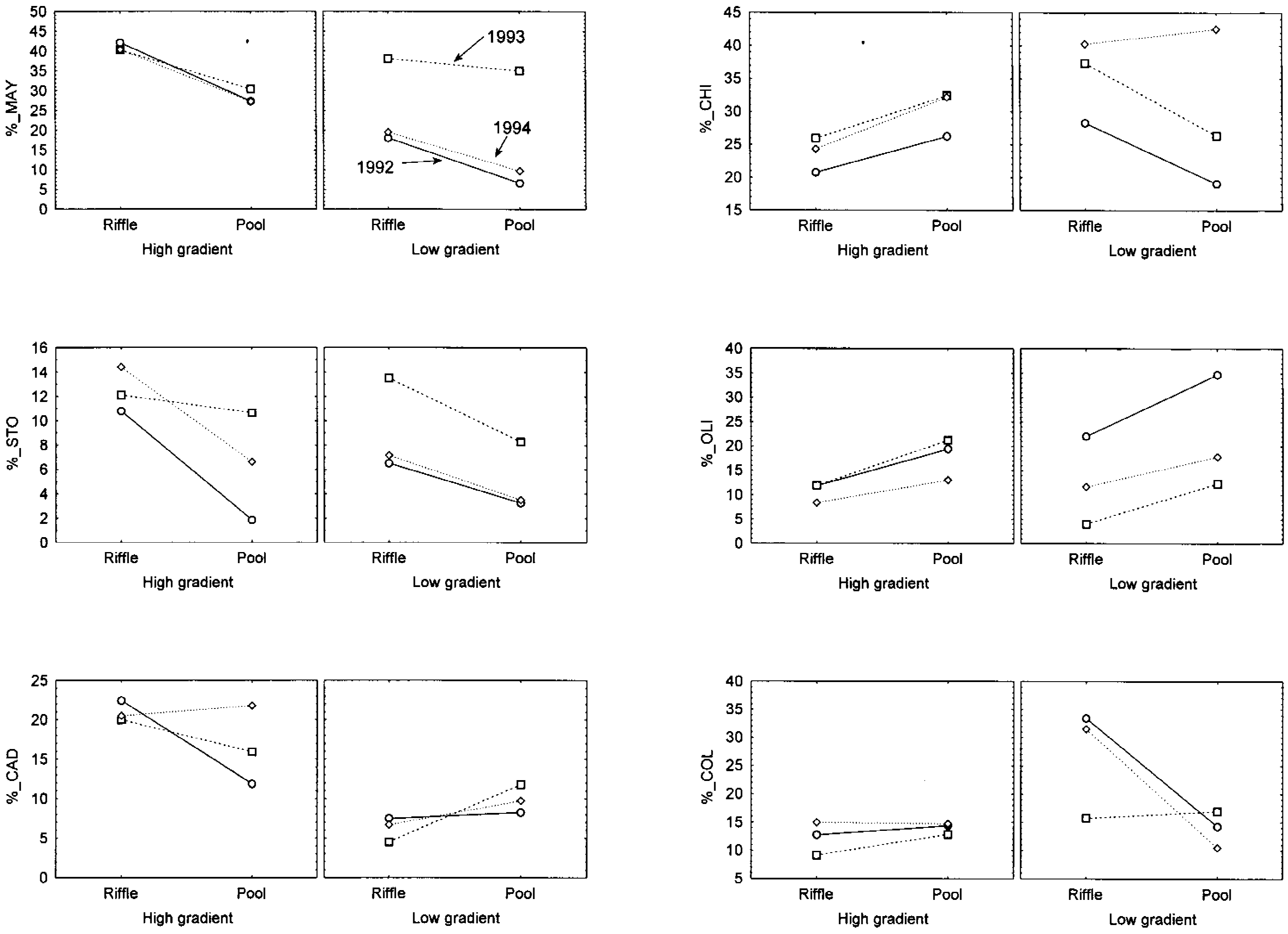

Figure 6. Means graphs of percentage composition of higher taxa. Note: abscissa is variable and no error bars are depicted. Circles with solid line equals 1992, squares with dashed line equals 1993, and diamonds with dotted line equals 1994. Refer to Table 2 for significant differences.

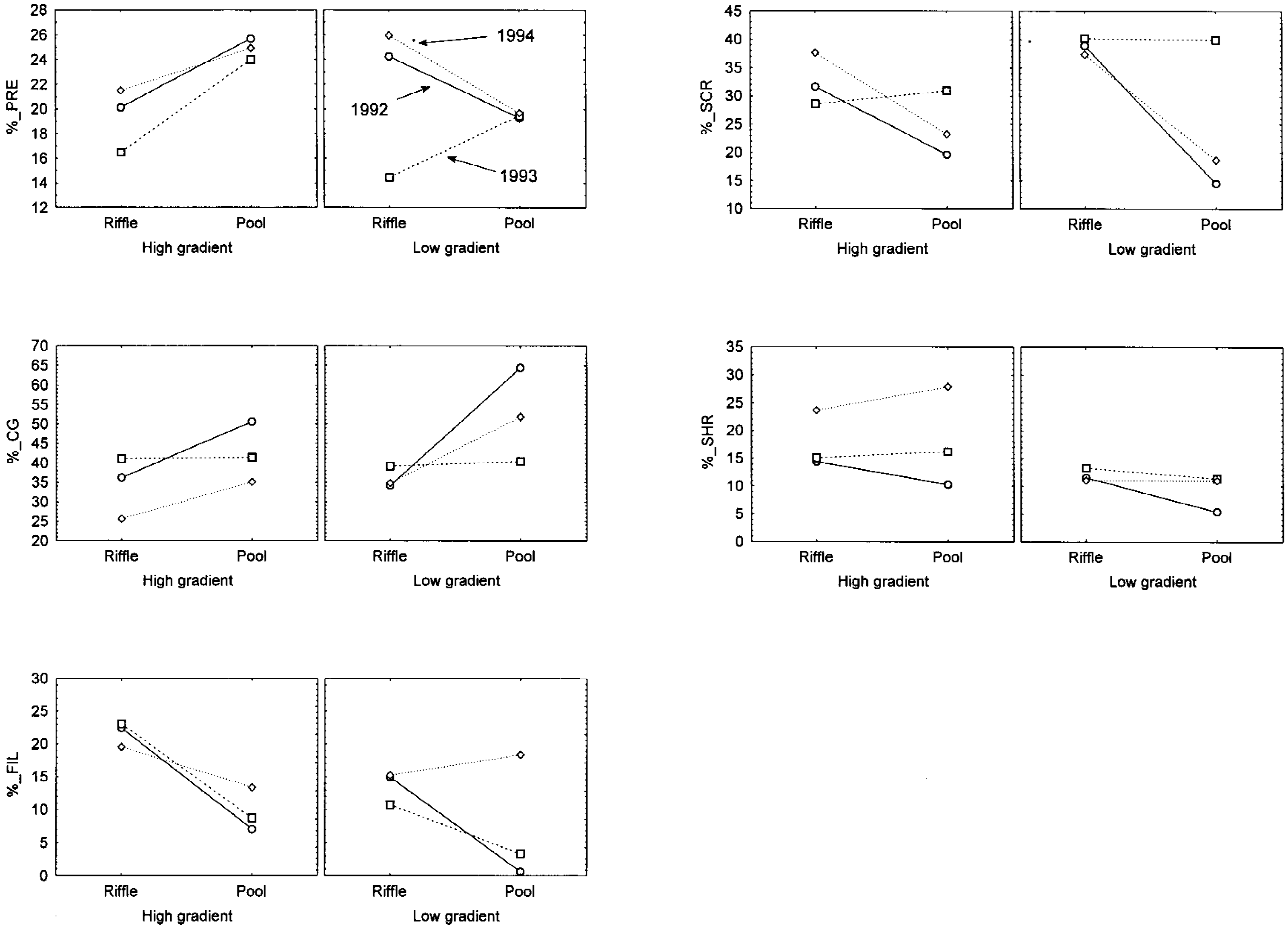

Figure 7. Means graphs of percentage composition of functional feeding groups. Note: abscissa is variable and no error bars are depicted. Circles with solid line equals 1992, squares with dashed line equals 1993, and diamonds with dotted line equals 1994. Refer to Table 2 for significant differences.

Table 2. Three-way ANOVA results. Adjusted critical α (α_{ind}=1–(1–α)$^{1/\mathrm{m}}$) with α's = 0.05, 0.01, 0.001 and m = 18. *0.00284 < $P \geq$ 0.00055, ** 0.00055 < $P \geq$ 0.00005, *** P < 0.000005.

	Habitat		Gradient		Year	
	F	*P*	*F*	*P*	*F*	*P*
S_TAX	16.39	0.00161*	0.05	0.82120	6.64	0.00507
S_MAY	15.04	0.00220*	18.28	0.00108*	1.50	0.24332
S_STO	139.11	0.00000***	3.00	0.10886	1.19	0.32051
S_CAD	34.43	0.00008**	35.91	0.00006***	3.54	0.04500
S_CHI	0.15	0.70666	5.35	0.03929	23.03	0.00000***
S_OLI	2.13	0.17000	16.52	0.00157*	4.94	0.01595
S_COL	7.12	0.02045	3.53	0.08486	6.88	0.03476
%MAY	4.17	0.06581	7.06	0.02233	11.15	0.00045
%STO	18.51	0.00156*	4.05	0.07184	12.50	0.00030**
%CAD	0.02	0.88677	17.08	0.00166*	0.38	0.68979
%CHI	0.01	0.90773	3.94	0.07048	10.63	0.00050**
%OLI	7.73	0.01792	0.94	0.35234	9.03	0.00137*
%COL	5.53	0.03664	9.17	0.01051	5.76	0.00907
%PRE	0.53	0.48055	0.46	0.51001	11.11	0.00038**
%CG	19.46	0.00085*	4.47	0.05614	4.96	0.01574
%FIL	11.00	0.00616	3.54	0.08422	3.17	0.06021
%SCR	11.90	0.00481	0.85	0.37405	4.80	0.01762
%SHR	0.33	0.57805	12.95	0.00366	8.23	0.00189*

There were no significant main effects on the percentage of Coleoptera but there was a significant habitat × year interaction. Percentage Coleoptera in pools was similar among the three years, but low gradient riffles in 1993 had substantially lower %_COL than low gradient riffles in 1992 and 1994.

Functional feeding groups

There were relatively few significant main effects or interactions on the percentage composition of functional feeding groups (Table 2).

Percentage predators had both a year main effect and a habitat × year interaction. The year main effect indicated that %_PRE was lower in 1993 (the average flow year) than in 1992 and 1994 in the low gradient riffles. Percentage predators remained similar among years in pools but was variable in riffles (Fig. 7).

There was only a habitat main effect on the percentage of collector-gatherers. Pools contained higher %_CG than riffles. Although not significant, there was a weak interaction between habitat and year indicating little difference in %_CG between riffles and pools in 1993.

The only additional significant effect was a year main effect on the percentage of shredders, with %_SHR increasing from 1992 through 1994, particularly in the high gradient reaches.

Discussion

Numerous studies have shown distinct differences in the fauna of riffles and pools. However, the variability of numerous measures of community composition that can be attributed to riffle/pool habitat structure has not been fully documented regionally or inter-annually.

Differences in the fauna between these habitats have been attributed to a number of abiotic factors such as: (1) differences in substratum size (Minshall & Minshall, 1977) and substratum heterogeneity (Percival & Whitehead, 1929); (2) the presence of organic matter (Rabeni & Minshall, 1977; Scullion et al., 1982); (3) disturbance intensity (Brown & Brussock,

Table 2. contd.

	Habitat × gradient		Habitat × year		Gradient × year		Habitat × Gradient × year	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
S_TAX	1.28	0.28027	11.85	0.00026**	1.10	0.34971	0.65	0.53203
S_MAY	0.04	0.84571	1.37	0.27359	4.16	0.02814	1.40	0.26566
S_STO	1.15	0.30471	3.75	0.03819	2.42	0.11036	2.66	0.09079
S_CAD	7.54	0.01772	6.07	0.00733	0.32	0.72693	1.40	0.26589
S_CHI	0.12	0.74682	11.87	0.00026**	0.15	0.86383	1.09	0.35097
S_OLI	0.08	0.78710	1.82	0.18360	2.76	0.08312	0.15	0.86048
S_COL	0.00	0.92289	5.44	0.01130	0.60	0.55478	1.77	0.19140
%_MAY	0.20	0.66425	0.66	0.52514	9.43	0.00110*	0.06	0.94237
%_STO	0.74	0.41005	0.89	0.42537	2.47	0.10984	2.60	0.09938
%_CAD	2.49	0.14270	1.14	0.33783	0.29	0.74864	0.57	0.57603
%_CHI	5.47	0.03750	1.41	0.26455	3.91	0.03380	0.80	0.46022
%_OLI	0.10	0.75270	0.44	0.64756	8.52	0.00182*	0.18	0.83500
%_COL	9.36	0.00990	9.87	0.00074*	1.39	0.26875	5.52	0.01059
%_PRE	2.57	0.13461	8.08	0.00207*	1.10	0.34342	2.39	0.11294
%_CG	2.15	0.16831	6.35	0.00614	2.79	0.08110	0.77	0.47578
%_FIL	1.09	0.31631	4.02	0.03127	2.01	0.15573	0.39	0.68192
%_SCR	0.97	0.34299	6.94	0.00418	2.66	0.09017	0.42	0.66444
%_SHR	0.61	0.45074	1.75	0.19459	5.34	0.01204	0.04	0.95853

1991) and disturbance frequency (McElravy et al., 1989); and (4) human impact (Kerans et al., 1992).

In the present study, differences in the structure of the benthos in riffles and pools were a function of gradient, year, and the interaction of these factors. In general, the composition of the benthic community was more variable inter-annually in low gradient reaches than in high gradient reaches. The interaction of in-stream geomorphological setting (gradient and substratum size) and inter-annual differences in discharge most likely influenced the structure of the benthic community.

In years of lower discharge, riffles had significantly higher mean taxon richness than pools; however, in the average flow year no difference was detected. Scullion et al. (1982) also showed approximately equal richness in riffles and pools from the River Wye, a flashy uncontrolled stream, whereas richness was higher in riffles than in pools in a controlled, hydrologically stable stream. McElravey et al. (1989) also found that richness was sensitive to discharge regime and showed that richness was reduced in both wet years and drought years.

Gradient influenced the richness of riffles and pools among years. Although not statistically significant, in low gradient reaches during the average flow year (the year of higher discharge), mean richness was higher in pools than in riffles; an observation also made by McCulloch (1986) in low gradient sand-gravel reaches.

In general, mayfly, stonefly and caddisfly richness was higher in riffles than in pools, however these differences were influenced by the gradient of the reach. Caddisfly richness was generally low in both habitats in low gradient reaches.

Canton et al. (1984) reported that certain taxa become established during periods of drought. In the present study, oligochaete richness (and abundance) was similar between riffles and pools during the final year of a 6-year drought (the first year of the present study). However, oligochaete richness decreased during the period of average (higher) flow. Armitage et al. (1974) indicated that oligochaetes are more affected by flow disturbances than many other lotic invertebrates because they are intimately associated with the sediment and may be displaced under high flow conditions. Oligochaetes only partially recovered during the third year of the study. Lacking an aerial stage probably inhibits recolonization by oligochaetes after high flow events (Armitage et al., 1974).

Percentage composition of major taxonomic groups was affected mainly by differences among years, particularly in low gradient reaches. Only stoneflies showed a habitat effect, with uniformly higher percentages found in riffles *versus* pools. Differences among years were largely caused by variability in the abundance of *Capnia* spp.

Four of the six higher taxa evaluated had greater inter-annual variation in percentage composition in the low gradient reaches *versus* the high gradient reaches. These reaches contained sand and gravel substrata that are more easily displaced than the boulder and cobble substrata found in the high gradient reaches (Leopold et al., 1964).

In the present study, the percentage of chironomids was rather stable in the high gradient reaches and although variable in the low gradient reaches, there was no relationship to the previous season's peak discharge. McElravey et al. (1989), however, found that the percentage of chironomids was positively correlated to the previous wet season peak discharge. Kerans et al. (1992 see Table 3) also found that the proportion of chironomids was partly a function of inter-annual differences in flow.

The high variability in the percentage abundance of certain higher taxa in the low gradient reaches was partly caused by the decrease in the oligochaete, *Slavina appendiculata*, and the increase in the mayfly, *Ephemerella* cf *infrequens*. The percentage increase in *E.* cf *infrequens* was not solely a function of the loss of *S. appendiculata*, but represented a doubling in the density of *E.* cf *infrequens* during the average flow year (1993). The low percentage of mayflies in 1994 was not due to increased percentage of oligochaetes as observed in 1992 but to increased percentage of chironomids.

The analysis of functional feeding groups is a common practice in biomonitoring studies (Resh & Jackson, 1993). In this study, as well as in Angradi (1996), collector-gatherer densities were significantly higher in pools than riffles. These observations contrast with Kerans et al. (1992) who detected no difference between riffles and pools in the percentage of collector-gatherers. However, Kerans et al. (1992) used a mesh size of approximately 1 mm and most likely did not collect the numerous small collector-gathers such as naidids, chironomids, and microcrustaceans. No other feeding groups showed significant differences between habitats in the present study.

There was an interaction of habitat × year for percentage predators. Predators were lower in riffles than in pools in the high gradient reaches and during the high discharge year in the low gradient reaches. However, during the two low discharge years, predators were higher in riffles than pools in the low gradient reaches. The increase in percentage predators in the low gradient riffles during 1992 was attributed to high densities of the mite *Lebertia* and the predacious Tanypodinae, *Pentanura*. In the next low flow year, 1994, *Lebertia* again was very abundant along with the Tanypodinae, *Meropelopia* (predominately) and *Macropelopia*.

Although differences in discharge existed at the time of sampling each year, the factor most correlated to changes in structure was discharge on the annual scale. There were greater similarities in the communities between the 2 years with low peak discharge (1992 and 1994) than between the years of low discharge at the time of sampling. The composition of the benthic community also was poorly related to the mean velocity measured at the time of sampling.

McElravy et al. (1989) correlated inter-annual and seasonal changes in the benthic community to discharge and found the structure of the community differed between years of low and high spring discharge. However, their study indicated that the autumn benthic community was relatively unaffected by the previous wet season discharge regime. In contrast, differences in the structure of the autumn benthic community of the present study seemed to be some function of the previous spring or early summer discharge.

Significant differences in the annual hydrograph exist between this study and McElravy et al. (1989). The geographic regions in which both studies were conducted have a Mediterranean climate and receive most of their precipitation during winter and spring. However, in the coastal stream studied by McElravy et al. (1989), there is no storage of the precipitation in the form of a snow pack. Consequently, flow events are closely linked to precipitation events and base flow conditions develop earlier in the summer, thereby allowing the benthic community to develop during an extended period of stable flow during late spring and summer.

In contrast, large snow packs occur in the Sierra Nevada, the location of this study, and the major flow event occurs during snowmelt in the spring. The amount of snow pack and climatic conditions leading to the period of spring runoff can greatly affect (1) the magnitude of the peak discharge and (2) the temporal extent of the period of high spring runoff. These two aspects of discharge may affect the composition of the benthos differentially. High peak discharge, with its associated sediment displacement, may more strongly affect oligochaetes and other fine sediment resident fauna such as elmid beetles. Conversely, an extended period of high flow during late-spring and summer may affect species that emerge during this period.

Two additional factors may help explain the influence of flow on benthic composition of these habitats. There were two non-significant interactions between habitat and year for collector-gatherers and scrapers. These interactions suggest that during the low flow years of 1992 and 1994 collector-gatherers had lower percentage abundance in riffles than pools, and scrapers had higher percentage abundance in riffles than pools. However, during 1993, the average flow year, no difference was detected in the percentage of these feeding groups between habitats. One explanation for the observed pattern could be that the resources each feeding group uses were distributed differently among the years. This would occur, particularly in pools, if organic matter washes out during high peak flow because of increased shear stress (Gordon et al., 1992) or does not accumulate during years when high discharge extends into the summer. The lack of particulate organic matter overlaying the substrata may allow resources for scrapers to accumulate in pools. Conversely, it would not be advantageous for collector-gatherers to remain in pools devoid of organic matter. Hawkins et al. (1982) also related the trophic structure of riffles and pools to food quality and availability but found no effect of gradient; however, their study was conducted over less than a year.

Understanding the factors affecting the distribution of benthic invertebrates in lotic systems is fundamental to basic stream ecology and the use of benthic invertebrates in impact assessment. Minshall (1988) clearly showed that our understanding of the factors responsible for invertebrate distributions is dependent on both the spatial and temporal scale of the study. Resh & Rosenberg (1989) and McElravy et al. (1989) showed the lack of temporal extent in most stream studies.

Streams and their habitats are contained within a geomorphological and hydrological template that influences their physical characteristics temporally (Frissell et al., 1986). It is clear that most studies are limited spatially or temporally; however, these limits decrease the ability to generalize the responses of benthic communities to biotic and abiotic influences.

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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: 42–63.

Armitage, P. D., A. M. Machale & D. C. Crisp, 1974. A survey of stream invertebrates in the Cow Green basin (Upper Teesdale) before inundation. Freshwat. Biol. 4: 369–398.

Brown, A. V. & P. P. Brussock, 1991. Comparison of benthic invertebrates between riffles and pools. Hydrobiologia 220: 99–108.

Canton, S. P., L. D. Cline, R. A. Short & J. V. Ward, 1984. The macroinvertebrates and fish of a Colorado stream during a period of fluctuating discharge. Freshwat. Biol. 14: 311–316.

Carter, J. L., S. V. Fend & S. S. Kennelly, 1996. The relationships among three habitat scales and stream benthic invertebrate community structure. Freshwat. Biol. 35: 109–124.

Cooper, S. D. & L. Barmuta, 1993. Field experiments in biomonitoring. In Rosenberg, D. M & V. H. Resh (eds), Freshwater Biomonitoring and Benthic Macroinvertebrates. Chapman and Hall, New York: 488 pp.

Cuffney, T. F., M. E. Gurtz & M. R. Meador, 1993. Methods for collecting benthic invertebrate samples as part of the National Water Quality Assessment Program, U.S. Geological Survey Open-File Report 93–406: 66 pp.

Frissell, C. A., W. J. Liss, C. E. Warren & M. D. Hurley, 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ. Manage. 10: 199–214.

Gordon, N. D., T. A. McMahon & B. L. Finlayson, 1992. Stream Hydrology: An Introduction for Ecologists. John Wiley & Sons, New York; 526 pp.

Hawkins, C. P., M. L. Murphy & N. H. Anderson, 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. Ecology 63: 1840–1856.

Kerans, B. L., J. R. Karr & S. A. Ahlstedt, 1992. Aquatic invertebrate assemblages: spatial and temporal differences among sampling protocols. J. n. am. Benthol. Soc. 11: 377–390.

Leopold, L. B., M. G. Wolman & J. P. Miller, 1964. Fluvial Processes in Geomorphology. W. H. Freeman and Company, San Francisco: 522 pp.

Logan, P. & M. P. Brooker, 1983. The macroinvertebrate faunas of riffles and pools. Wat. Res. 17: 263–270.

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

McElravy, E. P., G. A. Lamberti & V. H. Resh, 1989. Year-to-year variation in the aquatic macroinvertebrate fauna of a northern California stream. J. n. am. Benthol. Soc. 8: 51–63.

Merritt, R. W. & K. W. Cummins, 1996. An Introduction to the Aquatic Insects of North America. Kendall/Hunt Publishing Company, Dubuque, Iowa: 862 pp.

Minshall, G. W., 1988. Stream ecosystem theory: a global perspective. J. n. am. Benthol. Soc. 7: 263–288.

Minshall, G. W. & J. N. Minshall, 1977. Microdistribution of benthic invertebrates in a Rocky Mountain (U.S.A.) stream. Hydrobiologia 55: 231–249.

Ormerod, S. J., S. D. Rundle, S. M. Wilkson, G. P. Daly, K. M. Dale & I. Juttner, 1994. Altitudinal trends in the diatoms, bryophytes, macroinvertebrates and fish of a Nepalese river system. Freshwat. Biol. 32: 309–322.

Pennak, R. W., 1989. Fresh-water Invertebrates of the United States: Protozoa to Mollusca. John Wiley & Sons, Inc., New York: 628 pp.

Percival, E. & H. Whitehead, 1929. A quantitative study of the fauna of some types of stream-bed. J. Ecol. 17 282–314.

Rabeni, C. F. & G. W. Minshall, 1977. Factors affecting microdistribution of stream benthic insects. Oikos 29: 33–43.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace & R. Wissmar, 1988. The role of disturbance in stream ecology. J. n. am. Benthol. Soc. 7: 433–455.

Resh, V. H. & J. K. Jackson, 1993. Rapid assessment approaches to biomonitoring using benthic macroinvertebrates. In Rosenberg, D. M & V. H. Resh (eds), Freshwater Biomonitoring and Benthic Macroinvertebrates. Chapman and Hall, New York: 488 pp.

Resh, V. H. & D. M. Rosenberg, 1989. Spatial-temporal variability and the study of aquatic insects. Can. Entomol. 121: 941–963.

Scullion, J., C. A. Parish, N. Morgan & R. W. Edwards, 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.

Statzner, B. & B. Higler, 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwat. Biol. 16: 127–139.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Can. J. Fish. aquat. Sci. 37: 130–137.

Winer, B. J., D. R. Brown & K. M. Michels, 1991. Statistical Principles in Experimental Design. McGraw-Hill, Inc., New York: 1057 pp.

Wrona, F. J., J. M. Culp & R. W. Davies, 1982. Macroinvertebrate subsampling: a simplified apparatus and approach. Can. J. Fish. aquat. Sci. 39: 1051-1054.