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Inter-annual patterns in macroinvertebrate communities of wilderness streams in Idaho, U.S.A.

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Abstract

This study examined the inter-annual variation in macroinvertebrate assemblages in six wilderness streams in central Idaho over a 6-year period (1990–1995). Benthic macroinvertebrates and associated environmental correlates were sampled during baseflow each summer. Little environmental change, as assessed using coefficients of variation (CVs) for substrate size and embeddedness, width, depth and periphyton standing crops, occurred in the streams over the period of study. There was also little temporal change in macroinvertebrate assemblages based on the relative abundance of the 10 most abundant taxa, all shredder taxa and all plecopteran taxa. CVs for individual taxa were substantially greater than those of most community measures, with rare taxa contributing 30–50% of the variation for any one stream. Frequency distributions for taxa CVs excluding rare taxa were more normally distributed. Differences in assemblage structure among streams were attributed to stream size (shift in shredder assemblages) and temperature (shift in plecopteran taxa). These data indicate a long-term (multi-year) persistence in the macroinvertebrate composition of these pristine streams, thus supporting the premise that such streams are excellent references for use in long-term biomonitoring programs.

Introduction

Knowledge of the long-term persistence of lotic macroinvertebrate assemblages has major implications in the management and restoration of streams and rivers (Elliott, 1990). For example, most bioassessment programs of stream ecosystems rely on so-called reference systems. Yet there is much debate as to how resource managers should define the reference condition (e.g. Reynoldson et al., 1997) and most assume, on strong theoretical grounds, the long-term persistence of communities in these reference systems (basically, a space for time substitution). Because any long-term multiple-year bioassessment program relies on a reference system for comparison and to make judgements on system change (good or bad), the inter-annual persistence of benthic assemblages (composition and abundances) in the reference stream is a paramount assumption. Presently, the reference condition generally is based on the best available condition (Reynoldson et al., 1997; Robinson & Minshall, 1998), as most freshwater systems have been and continue to be degraded to some degree (Benke, 1990; Allan & Flecker, 1993).

Our literature search revealed less than a dozen long-term studies of lotic macroinvertebrate assemblages (e.g. McElravy et al., 1989). However, the majority of these have indicated that macroinvertebrate assemblages of relatively pristine streams are persistent over multiple years (Ward, 1975; Weatherly & Ormerod, 1990; Richards & Minshall, 1992; Johnson et al., 1994, but see Townsend et al., 1987) when adjusted for seasonal differences in life histories. For example, Johnson et al. (1994) found that Doe Run in Kentucky had a remarkably similar macroinvertebrate

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assemblage in 1990 compared with that in 1960. A few such studies have shown some variation in macroinvertebrate composition among years, but attributed these differences to changes in flow due to climatic differences (wet vs dry years)(McElravy et al., 1989; Boulton et al., 1992; Minshall et al., *in press*) or differences in environmental variability among streams (Townsend et al., 1987; Statzner & Resh, 1993).

In the present study, we compared the macroinvertebrate composition in six pristine wilderness streams over a 6 year period (1990–1995). Although some of the streams also were surveyed in years outside this period for purposes of a different study, we focused on this 6-year time period to achieve comparable climatic data for all six streams. Streams were sampled in summer under baseflow conditions to minimize structural differences attributed to life history (Richards & Minshall, 1992; Robinson et al., 1993). The six streams differed in size and aspect, thus additional a posteriori analyses focused on shredder and plecopteran assemblages among streams. For example, shredder populations were expected to shift with changes in stream size (Vannote et al., 1980) and differences in plecopteran populations should be evident due to differences in temperature regime, e.g. due to stream size or aspect (Vannote & Sweeney, 1980).

Six tributaries of Big Creek in the Frank Church River-of-No-Return Wilderness in central Idaho, U.S.A. were used for analysis (Figure 1). In the United States, the term wilderness identifies legally-designated areas that are roadless, devoid of permanent human inhabitants, generally pristine and representative of pre-settlement conditions. This particular wilderness comprises over 950 000 hectares of roadless mountainous terrain (Finklin, 1988) and provided a set of streams relatively unaffected by anthropogenic influences (see Minshall & Robinson, 1998). The Middle Fork Salmon River is the primary catchment in the wilderness, of which Big Creek is a major tributary. Primary human activities in the Big Creek catchment include backpacking, horsepacking, fishing, and hunting.

Methods

Study area

The climate of the area is semi-arid, with annual precipitation ranging from ca 450 mm in valleys to ca 880 mm at higher elevations (Minshall et al., in press). Much of the precipitation accumulates as snowfall during winter, thus peak discharge is associated with spring snowmelt. Within the study period (1990–1995), the years 1990 through 1992 were during a drought period in Idaho, while 1993 was considered a wet year with a major runoff event in summer in the Big Creek catchment. Primary vegetation on forested side-slopes is Ponderosa pine (*Pinus ponderosa* Laws) or Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco.) and aspen (*Populus tremuloides* Michx.). Sagebrush (*Artemisia*)-grass communities are predominant on south-facing slopes. However, bare soil/rock are common features in this region (ca. 20–30% of the surface area), being especially dominant on south-facing slopes. Primary riparian woody-vegetation consists of water birch (*Betula*), alder (*Alnus*), willow (*Salix*), and dogwood (*Cornus*).

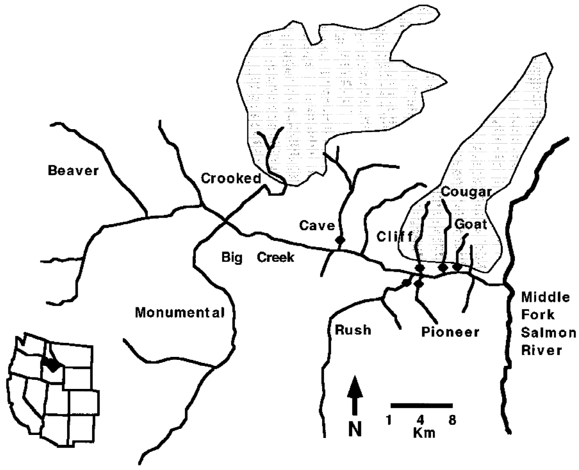

Figure 1. Map of study area and locations of research sites in the Big Creek drainage in central Idaho. Shaded areas experienced wildfire in 1988.

The six streams ranged from 2nd to 5th order in size (6–223 links) (Strahler, 1957) and had average summer discharges from 0.03 to 1.52 m^3/s (Table 1). Three of the study streams (Figure 1) experienced wildfire over parts of their catchments in summer 1988 (2 years prior to the present analysis; see Figure 1). However, little apparent impact resulted from the wildfire due to the southern aspect of the streams and placement of study sites outside of the burned area for these particular streams (Minshall et al., unpublished data). Elevations at the study sites ranged from ca. 1100 to 1200 m. Chemically, the streams reflected catchment geology (Table 1). For example, conductivity ranged from 52 μS/cm at Cave Creek to 142 at Goat Creek, with hardness and alkalinity show-

Table 1. Location, years sampled, and general site characteristics for study streams. Discharge and chemical measures averaged over the particular years of study. Temperature refers to average maximum temperature in summer.

Stream	Coordinates	Sample Year	Order	Link	Slope (%)	Elevation (m)	Discharge (m^3/s)	Temperature (°C)	Alkalinity (mg CaCO3/L)	Hardness (mg CaCO3/L)	Specific Conductance (μS/cm @ 20C)	pH
Goat	114′ 48″; 45′ 07″	1990–95	2	6	18	1125	0.03	12	60	78	142	8.1
Cliff	114′ 51″; 45′ 07″	1990–95	2	10	13	1196	0.17	13	42	54	80	7.9
Cougar	114′ 51″; 45′ 07″	1990–95	3	14	12	1095	0.11	12	46	63	106	8.0
Pioneer	114′ 51″; 45′ 06″	1990–95[a]	3	18	3	1165	0.13	11	43	71	109	7.9
Cave	114′ 57″; 45′ 08″	1990–95[a]	3	41	6	1220	0.20	15	27	39	52	7.9
Rush	114′ 51″; 45′ 07″	1991–95	5	223	1	1171	1.52	16	38	53	93	8.2

[a] No samples collected in 1991 and 1992 for Cave Creek, or 1992 for Pioneer Creek.

ing comparable differences among streams. Baseflow pH was relatively high, averaging 7.9–8.2. Summer water temperatures ranged from highs of 15–16 °C in Rush and Cave Creeks to ca 11 °C in Pioneer Creek. Minshall & Robinson (1998) provide an extensive environmental assessment for a large number of streams in this geographic region.

Field and laboratory procedures

Streams were sampled once each year in late July during summer baseflow from 1990 to 1995 (6 year period), except where noted in Table 1. The first two authors were involved in sample collection and processing throughout the course of the study thus minimizing potential variability in field measurements due to changes in personnel. Variables measured each year included major physical, chemical and biological components of the stream ecosystem. Chemical measures were specific conductance, pH, alkalinity and hardness. Temperature was recorded each sampling visit for all streams and Hobo temperature loggers (Onset Computer Corp.) were used in 1995 in Rush, Cliff and Pioneer Creeks. The streams were characterized physically using measures of discharge, channel width, substrate size (a-axis) and embeddedness, and water depth. Width was measured at five transects along each stream with each transect 50 m apart. Substrate size, embeddedness and water depth were recorded at 100 locations within each stream. These sample locations were about 1 m equidistant, beginning at the first downstream transect and moving upstream, with relative distance (in 10% increments) from the stream bank derived from a random numbers table. The physical data collected for each stream were summarized as means and coefficients of variation (CV=sd/mean*100%) (Zar, 1984). Coefficients of variation were calculated from the means generated each year and provided an indication of the temporal change in habitat conditions for each stream over the study period.

Five benthic samples (Surber net, 0.11 m^2, 250 μm mesh) were collected once each year from riffle/run habitats located near each ‘width’ transect and preserved in the field with 4% formalin (Platts et al., 1983). In the laboratory, macroinvertebrates were hand-picked from each sample using a dissecting microscope at 10×. Invertebrates were identified to at least genus (except for the Chironomidae, Hydracarina and Oligochaeta), counted and dried at 60 °C for biomass estimates. The elmid taxon *Heterlimnius* also included specimens of *Cleptelmis*. Macroinvertebrate data for each stream were summarized as means and CVs (as above) for density, biomass, taxon richness and Simpsons’ dominance index (Barbour et al., 1987). In addition, CVs were calculated using abundance data for each taxon (after Grossman et al., 1990); these were summarized as frequency distributions using all taxa and with the exclusion of rare taxa. The inclusion or exclusion of rare taxa in system monitoring and assessment has important implications for resource managers (Grossman et al., 1990; Cao et al., 1998). Rare taxa were defined as being in low abundance and present in only 1 year of sampling; these taxa typically had CVs greater than 220%. Frequency distributions were tested for normality using the Chi-square goodness of fit test with expected values determined by the *Z* statistic (Zar, 1984). Furthermore, the mean relative abundances and CVs were summarized for the 10 most abundant taxa across all streams. Lastly, assemblage stability was assessed using Kendall’s W excluding rare taxa (Grossman et al., 1982; Grossman et al., 1990). As for the physical measures, the CVs indicated the degree of temporal variation expressed by these community parameters in the study period (Grossman et al., 1990).

Principal components analysis (PCA with varimax rotation) was performed using the relative abundances of 1. the 10 most abundant taxa (these taxa comprised >75% of the assemblage in any one stream), 2. all shredder taxa (after Merritt & Cummins, 1984), and 3. all plecopteran taxa. We expected to see differences among streams for these two latter groups due to differences in stream size (temperature regime and organic matter content) and aspect (solar input and riparian differences)(sensu Vannote et al., 1980). Data were arcsin(sqrt(X)) transformed to enhance normality, eliminate the dependence of the variance on the mean and ensure that the components of the variance were additive (Elliott, 1977; Zar, 1984) prior to running PCA.

The remaining material from each benthic sample was dried at 60 °C, weighed, ashed at 550 °C, rewet, redried at 60 °C and reweighed for determination of benthic organic matter (BOM) as ash-free dry mass (AFDM). Five periphyton samples were collected from individual rocks in each stream using the method described in Robinson & Minshall (1986). Samples were immediately frozen in a liquid-nitrogen charged Taylor-Wharton 3DS Dry Shipper and returned to the laboratory. In the laboratory, samples were extracted for chlorophyll *a* in 100% methanol for 24 h and then measured using a Gilford (model 2200) spectrophotometer (Holm-Hansen & Reimann, 1978; APHA, 1989). Periphyton AFDM also was determined from these samples as described above for BOM (Lorenzen, 1966; Stockner & Armstrong, 1971). BOM and periphyton biomass data were summarized as means and CVs as described above.

Results

Habitat conditions

Average substrate diameters ranged from 12.5 cm at Goat Creek to 22.9 cm at Cliff Creek (Table 2) indicating that cobble substrata dominated most stream beds. However, a more intensive analysis later revealed that the stream bed of Cliff Creek had a greater percentage of boulders than Pioneer Creek (Davis & Minshall, 1999). Mean substrate embeddedness typically was less than 50%, with Goat Creek showing the highest (59%) and Rush Creek the lowest (30%). Average bankfull width reflected stream size, with Goat having the lowest (1.0 m) and Rush Creek the highest (11.5 m). Bankfull widths of the other streams ranged from 2.5 m to 5.2 m. Baseflow water depth also varied with stream size (11 cm in Goat Creek to 27 cm in Rush Creek). Goat Creek exhibited about four times the average amount of benthic organic matter (114 g/m^2) as the other streams (range 17–35 g/m^2). Periphyton biomass (as chlorophyll *a* and AFDM) was highest in the more open-canopied Rush and Cave Creeks (2–4 times higher) than in the other more closed-canopied streams (Table 2).

The physical measures in Table 2 displayed relatively little temporal variation among summers over the study period, as indicated by low coefficients of variation (CVs). Indeed, most CVs were less than 30% for these measures. The exception was the CV for substrate embeddedness in Cave Creek, although this value (48%) is still relatively low. In contrast, BOM and periphyton biomass showed relatively higher CVs, indicating these measures are more temporally variable than other habitat measures. Here, CVs generally were higher than 50% but less than 100%. Exceptions were periphyton AFDM in Cougar Creek (117%) and BOM in Rush Creek (22%). In general, these results suggest little temporal change in most summer habitat conditions in these streams during the period of study.

Macroinvertebrate assemblages

A total of 125 macroinvertebrate taxa were identified from the streams during the study, ranging from 66 taxa in Pioneer Creek to 86 taxa in Cougar Creek. Goat Creek, the smallest stream sampled, had the lowest average taxon richness and macroinvertebrate density; whereas Rush Creek, the largest stream sampled, had the highest values (Table 3). Cave and Rush Creeks had, on average, 2–4 times more invertebrate biomass (1334–2117 mg/m^2) than the other streams (range 511–725 mg/m^2). Simpson's index was relatively low for all streams, suggesting numbers were dominated by a few taxa. Indeed, the 20 most abundant taxa comprised >80% of the assemblage in any of the study streams, as is commonly observed for lotic systems.

Coefficients of variation for most of these community measures were low indicating little differences in these community attributes among years in the streams (Table 3). CVs for taxon richness were the lowest among these measures ranging from 8% at Cliff Creek to 22% at Cougar Creek. Simpson's index CVs also were relatively low and quite similar among streams (25–30%). Invertebrate abundances showed

Table 2. Substrate size and percent embeddedness, bankfull width, baseflow water depth, benthic organic matter (BOM) and periphyton biomass as chlorophyll *a* and AFDM for each of the study streams. Numbers calculated from all annual averages. Std=standard deviation, CV=coefficient of variation. Numbers in parantheses are measurements per year.

Stream	Parameter	Substrate Size (cm) (100/yr)	Substrate Embeddedness (100/yr)	Bankfull Width (m) (5/yr)	Baseflow Depth (cm) (100/yr)	BOM (g/m2) (5/yr)	Chlorophyll (mg/m2) (5/yr)	Periphyton AFDM(g/m2) (5/yr)
Goat	mean	13	59	1.0	11	114	5.0	1.8
	std	3	13	0.1	1	63	2.8	1.3
	CV (%)	22	23	14	8	55	55	73
Cliff	mean	23	50	3.6	20	25	8.5	2.5
	std	3	14	1.1	2	11	7.5	2.4
	CV (%)	12	29	32	10	45	88	95
Cougar	mean	19	47	2.5	19	35	2.9	2.3
	std	4	4	0.5	2	16	2.0	2.7
	CV (%)	20	8	20	8	47	70	117
Pioneer	mean	16	34	2.8	16	18	6.4	2.0
	std	2	13	0.6	1	9	4.3	0.9
	CV (%)	13	39	23	9	50	66	47
Cave	mean	17	44	5.2	16	24	19.1	5.9
	std	2	21	0.7	2	17	18.0	4.8
	CV (%)	9	48	14	10	73	94	81
Rush	mean	18	30	11.5	27	17	20.9	5.5
	std	4	8	3.0	5	4	14.3	3.0
	CV (%)	24	27	27	19	22	68	54

the widest range in CVs among streams, ranging from 23% at Cliff Creek to 108% at Pioneer Creek. CVs for macroinvertebrate biomass were lowest at Cougar Creek (32%) and highest at Goat Creek (65%). Kendall's coefficient of concordance (W) ranged from 0.40 at Rush Creek to 0.62 at Cave Creek (Table 3) further indicating the relative stability in assemblage composition over time in these streams.

Frequency distributions of coefficients of variation for individual taxa resulted in a strongly right-skewed relationship with rare taxa determining from ca 30 to 40% of the distribution (Figure 2). These rare taxa typically had CVs greater than 220%. Frequency distributions with the exclusion of rare taxa were more normally distributed; 4 of 6 streams displayed a normal distribution (Chi-square, $p<0.05$) with the other two being quite close to normal (Figure 2). These results also can be viewed graphically by plotting cumulative frequency distributions (Figure 3). The removal of rare taxa caused the curves to be more sigmoid, indicating a normal distribution. The average CV for species, excluding rare taxa, ranged from 113% at Cave Creek to 139% at Goat Creek. Coefficients of variation for the 10 most common taxa are summarized in Table 4. CVs ranged from 17% for the Hydracarina at Cave Creek to 128% for *Epeorus longimanus* at Rush Creek and *Zapada cinctipes* at Cave Creek. In general, most CVs for these common taxa ranged from 30% to around 100%. Within this group of taxa (Table 4), CVs for individual taxa varied among streams by an average of 41%. For example, CVs for Oligochaeta ranged from 39% at Pioneer Creek to 78% at Goat Creek.

Principal components analysis was effective for illustrating compositional differences of communities among the study streams. PCA based on the ten most abundant taxa showed clear differences among streams (Figure 4) and reflected differences in stream

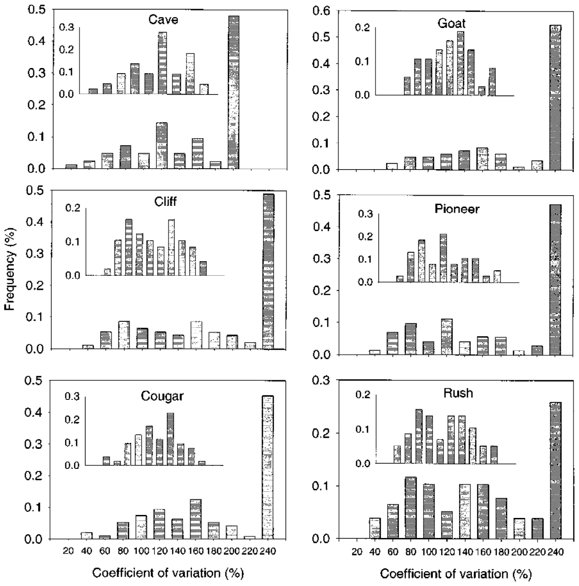

Figure 2. Frequency distribution plots for CVs from individual taxa sampled in each stream. For each stream, the large graph is with rare taxa included and the inset graph is with rare taxa excluded.

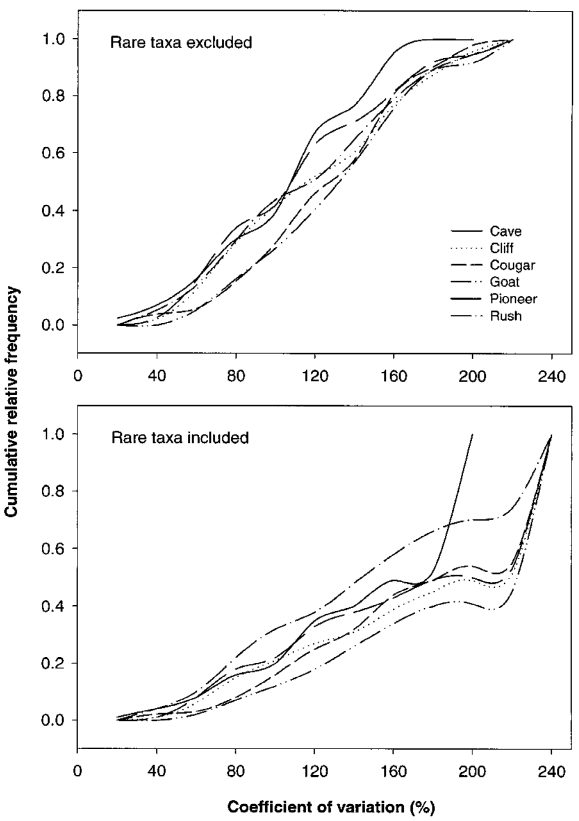

Figure 3. Cumulative relative frequency curves using taxa coefficients of variation. Lower graph are curves with rare taxa included, upper graph are curves with rare taxa excluded.

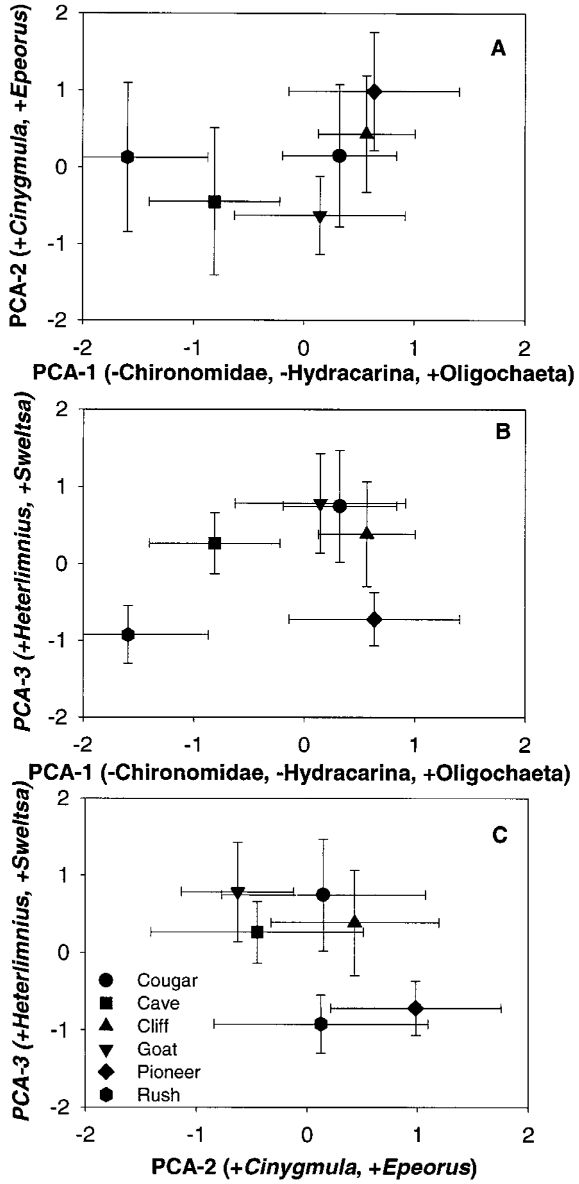

Figure 4. Results from the principal components analysis based on the ten most abundant taxa found in the study streams. Error bars represent the mean ± 1 standard deviation in factor scores (annual values) for each stream along that particular axis. The length and width of the error bars (hypothetical ellipse) provides an indication of the amount of temporal variation in each stream over the study period based on the specific taxa located along each axis. The symbol before each taxon indicate the relationship (positive or negative) of that taxon with that axis. Taxa on axes had factor loadings greater than 0.70.

Table 3. Summary of biotic measures quantified annually for each study stream; see Table 1 for exact years included for each sream. Taxon richness is based on the total number of taxa identified in each stream during each year of the study. Std = standard deviation. CV = coefficient of variation

		Goat	Cliff	Cougar	Pioneer	Cave	Rush
Numbers (no./m2)	mean	1733	4028	3048	5959	6453	9873
	std	1002	941	1244	6431	1660	6002
	CV (%)	58	23	41	108	26	61
Biomass (mg/m2)	mean	550	725	511	616	1334	2117
	std	356	376	161	319	650	725
	CV (%)	65	52	32	52	49	34
Taxon Richness	mean	31	39	40	34	42	45
	std	4	3	9	6	4	6
	CV (%)	12	8	22	18	9	14
Simpson's	mean	0.23	0.24	0.19	0.22	0.17	0.19
	std	0.06	0.06	0.05	0.07	0.05	0.05
	CV (%)	25	27	28	30	27	28
Kendall's W		0.48	0.59	0.42	0.52	0.62	0.40

size (Rush Creek) and aspect (north-facing Pioneer Creek). Here, the three axes explained 62% of the variation in community composition among streams. Axis-1 was derived from differences in the abundances of chironomids, Hydracarina and oligochaetes with Rush and Cave Creeks showing greater abundances of chironomids and Hydracarina, and fewer oligochaetes than the other streams. The heptageniids *Epeorus longimanus* and *Cinygmula mimus* were weighted heavily on axis-2, and Goat and Cave Creeks had lower abundances of these taxa than the other streams. Pioneer Creek showed the highest abundances for these mayflies. Axis-3 was based on differences in the abundances of the elmid *Heterlimnius* and the stonefly *Sweltsa*. Pioneer and Rush Creeks displayed low abundances for these taxa, whereas the other four streams showed higher abundances. These data indicate that Rush and Pioneer Creeks, and probably Cave Creek, had different assemblages than those found in the other streams. Cliff and Cougar Creeks (similar size and south-facing streams) clearly exhibited high similarity in benthic composition based on the 10 most abundant taxa. The lengths in the error bars suggest that all streams, based on the 10 most abundant taxa, exhibited similar magnitudes of temporal change in assemblage structure during the study period.

Overall, 29 shredder taxa were identified in this study. PCA based on the shredder assemblage found in each stream reflected differences in stream size and amount of benthic organic matter. Axis-1 was derived from the abundances of the stoneflies *Sweltsa* and *Yoroperla brevis*, and the Limoniinae (*Antocha*) (Figure 5). Cave, Pioneer and Rush Creeks clearly had lower abundances of these taxa than the other streams,

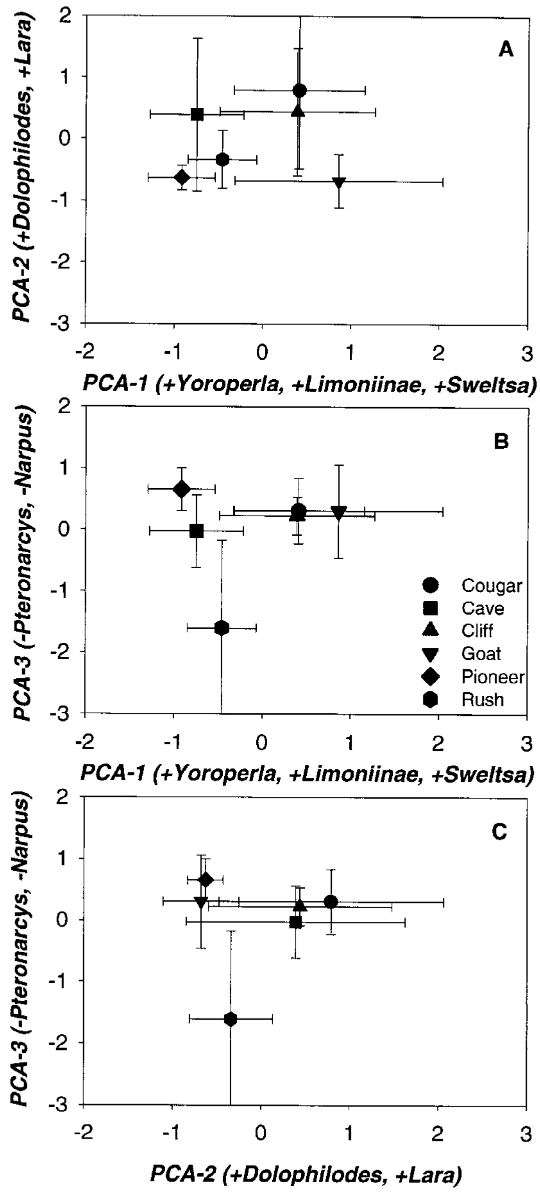

Figure 5. Results from the principal components analysis based on the relative abundances of shredders found in each stream during the study period. Error bars represent the mean ± 1 SD of factor scores (annual values) for that particular axis. The symbol before each taxon indicates the relationship (positive or negative) of that taxon with that axis. Taxa listed on the axes had factor loadings greater than 0.60.

Table 4. Mean relative abundances, standard deviations (std) and coefficients of variation (CV) for the 10 most abundant taxa for all sites and years combined. Values based on mean relative abundances from each year, with number of years included for each stream in parantheses.

Stream	Measure	Oligochaeta	Chironomidae	*Baetis bicaudatus*	*Heterlimnius*	*Zapada cinctipes*	*Cingmula*	Hydracarina	*Simulium*	*Sweltsa*	*Epeorus Longimanus*
Goat (*n*=6)	mean	0.26	0.15	0.07	0.14	0.04	0.01	0.02	0.04	0.03	0.01
	std	0.20	0.08	0.05	0.08	0.03	0.01	0.01	0.05	0.02	0.01
	CV (%)	78	56	73	54	70	98	86	110	64	117
Cliff (*n*=6)	mean	0.35	0.10	0.15	0.07	0.04	0.04	0.01	0.03	0.03	0.03
	std	0.15	0.05	0.06	0.03	0.03	0.03	0.00	0.02	0.03	0.03
	CV (%)	42	54	42	49	83	76	29	69	96	107
Cougar (*n*=6)	mean	0.27	0.12	0.17	0.14	0.07	0.04	0.02	0.02	0.02	0.01
	std	0.11	0.04	0.06	0.09	0.06	0.04	0.01	0.02	0.02	0.01
	CV (%)	43	36	37	65	96	88	65	87	106	97
Pioneer (*n*=5)	mean	0.33	0.10	0.14	0.05	0.05	0.09	0.01	0.01	NA	0.03
	std	0.13	0.06	0.08	0.02	0.03	0.07	0.01	0.01	NA	0.03
	CV (%)	39	60	55	43	65	75	96	61	NA	108
Cave (*n*=4)	mean	0.14	0.22	0.11	0.15	0.01	0.01	0.08	0.04	0.01	0.01
	std	0.10	0.14	0.06	0.05	0.01	0.01	0.01	0.04	0.01	0.01
	CV (%)	68	62	56	32	128	91	17	113	63	49
Rush (*n*=6)	mean	0.08	0.31	0.11	0.01	0.01	0.03	0.09	0.03	0.01	0.02
	std	0.06	0.17	0.07	0.00	0.01	0.04	0.03	0.03	0.01	0.03
	CV (%)	71	55	63	77	92	109	38	85	99	128

with Goat showing the greatest abundances of these taxa. Axis-2 was based on the abundances of the caddisfly *Dolophilodes* and the elmid *Lara*. They were more abundant in Cave, Cliff and Cougar Creeks, and less so in Pioneer and Goat Creeks. Axis-3 was dominated by *Narpus* and *Pteronarcys californica*. *P. californica* was most abundant in Rush Creek. This analysis revealed that shredder assemblages were different in Rush Creek, where *P. californica* dominated, and Goat Creek, where *Y. brevis* and Limoniinae were common, than in the other streams where *Dolophilodes*, *Sweltsa* and *Lara* were more common. These three axes explained 40% of the variation in shredder assemblages among the study streams. The relative lengths in the error bars suggest that Pioneer Creek showed less temporal variation in shredder assemblages than the other streams.

The third PCA was completed using all plecopterans (20 taxa) identified in the study streams (Figure 6). Axis-1 was based on the abundances of *Kogotus*, *Kathroperla* and *Skwala*, axis-2 on the abundances of *Zapada cinctipes*, *Alloperla* and *Isoperla*, and axis-3 on the abundances of *Nemoura* and *Visoka cataractae*. These three axes explained 39% of the variation in stonefly assemblages among the study streams. Axis-1 indicated that those three taxa were most common in Cave Creek and less common in the other streams. Axis-2 revealed that *Z. cinctipes*, *Alloperla* and *Isoperla* were more common in Pioneer and Cougar Creeks than in the other streams. Axis-3 showed that *Nemoura* and *Visoka* were most abundant in Goat Creek. The lengths of the error bars suggest that Cave and Goat Creeks exhibited the most temporal variation in plecopteran assemblage structure during the study period than the other streams.

Discussion

Our results suggest the extended (5–6 years) persistence of benthic assemblages, in terms of composition and relative abundances, in pristine streams. However, trends in reference conditions should be evaluated in long-term data that account for changes (statistical noise) due to climate (e.g. wet vs dry years, McElravy et al., 1989) or other landscape influences (Richards et al., 1996); both of which occurred in this study. For example, the impact of the major runoff event in 1993 was clearly evident in plecopteran assemblages in streams that had part of their catchments burned in

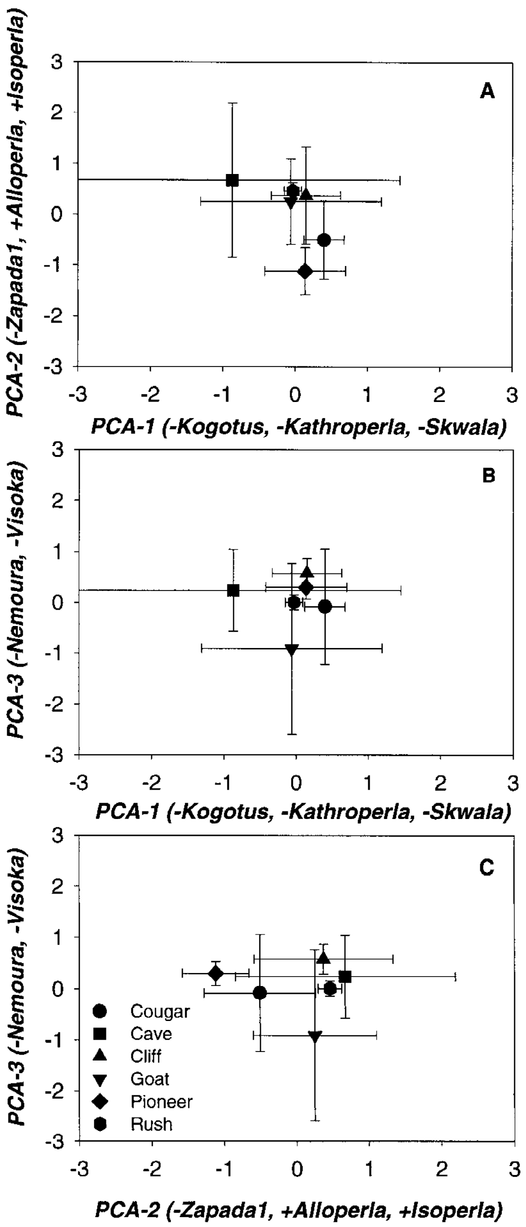

Figure 6. Results from the principal components analysis based on the relative abundances of Plecoptera (stoneflies) found in each stream during the study period. Error bars represent the mean ± 1 SD of factor scores (annual values) for that particular axis. The symbol before each taxon indicate the relationship (positive or negative) of that taxon with that axis. Taxa listed on the axes had factor loadings greater than 0.60. *Zapada*1 = *Z. cinctipes*.

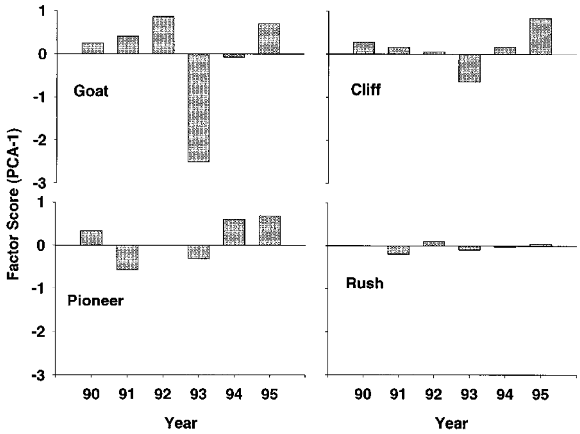

Figure 7. Bar graph illustrating individual year factor scores from axis 1 of the PCA based on the plecopteran assemblages collected in each stream. Only selected streams are shown with Goat and Cliff Creeks being south-facing and having part of their catchment burned in 1988, whereas Pioneer and Rush Creeks are north-facing with none of their catchments being burned in 1988. Note the substantial change in factor scores in Goat and Cliff Creeks in 1993 that was not evident in Pioneer and Rush Creeks. No data in 1992 for Pioneer Creek.

1988 (Figure 7, Goat and Cliff Creek) and with recovery already visible in 1994. Elliott (1990) stressed the importance of long-term studies in providing a robust statistical requirement for determining temporal change in biological systems. Specifically, the monitoring of reference systems for a period of several years or more provides important information on general changes in stream conditions due to external factors (Elliott, 1990), thus enhancing interpretation of biotic changes in 'test' streams.

Environmental variability has been invoked as a possible mechanism for observing persistence in assemblage structure in some streams but not in others (Townsend et al., 1987; Richards & Minshall, 1992). For example, Ward (1975) found little difference in assemblage composition in a stream sampled 29 years apart when instream habitat conditions were essentially the same. Similarly, Richards & Minshall (1992) found little temporal similarity for five streams impacted by wildfire that showed much physical change among years relative to five streams in unburned catchments that showed little habitat change among the years of study. Our study streams also showed little change among years in measured habitat variables and this habitat constancy was reflected in the long-term persistence of benthic assemblages. Regardless, long-term trends can provide important information on successional trajectories of streams following disturbance (e.g. Giller et al., 1991; Minshall et al., *in press*) or colonization of new streams (Milner, 1994), and such systems would be expected to show low temporal persistence (Townsend et al., 1987).

Coefficients of variation have been used in a number of studies examining spatial and temporal variation of stream biota (e.g. Robinson et al., 1994 for diatoms; Minshall & Robinson, 1998 for macroinvertebrates, Grossman et al., 1990 for fishes) and stream habitat (Robinson et al., 1994; Robinson & Minshall, 1996, 1998). Grossman et al. (1990) advocates the use of CVs over other measures such as Kendall's W (also see Palmer et al., 1997). In the present study, Kendall's W displayed medium values suggesting some degree of temporal stability in assemblage composition. CVs for community measures tended to be much lower (usually $<$50%, excluding Pioneer Creek for numbers) than those for individual taxa (mean excluding rare taxa = 127%). Taxon richness displayed the lowest values (average = 14%) among the community measures and is known to be a parameter sensitive to various kinds of disturbance. For example, systems demonstrating high CVs for this measure may be indicative of being disturbed or heterogenous. Minshall & Robinson (1998) found CVs for taxon richness to be higher among more spatially heterogeneous streams. Robinson et al. (1994) demonstrated a strong relationship between environmental heterogeneity (expressed as CVs) and structural changes in diatom assemblages of burned streams.

Coefficients of variation for individual taxa also have important implications in the long-term assessment of riverine assemblages. As mentioned, taxon CVs averaged 127% and ranged from ca. 30 to 100% for common taxa (Table 4). These values are similar to those found for fish (average 96%, Grossman et al., 1990). The frequency distributions of taxa CVs in the present study were strongly affected by inclusion of rare taxa. Cao et al. (1998) argue the importance of retaining rare taxa in stream bioassessment and monitoring as rare taxa may be more sensitive to environmental change (also see Gaston, 1994). Our data indicate that analyses at the species level are quite important for stream bioassessment; e.g. 30 – 50% of the distribution patterns were attributed to rare taxa. However, the data also suggest that excluding rare taxa also can show important patterns in assemblage characteristics that may change in disturbed systems. Any deviation from a normal distribution pattern may indicate some degree of impairment or temporal instability. For example, a frequency distribution skewed towards the left (all species show little temporal change) may indicate the predominance of a few taxa such as shown for heavily disturbed or environmentally stable systems (Connell, 1978). In contrast, a shift in the frequency curve towards the right (many species with high CVs) would be suggestive of a temporally variable system in which species frequently shift in rank abundances. This, of course, needs to be more fully tested with additional temporal data sets that include systems that are known to have been, or are, disturbed. Similar arguments can be tested using frequency curves including rare taxa. Our data suggest that rare taxa may be common contributors to assemblage structure in pristine streams, consequently the loss of rare taxa would substantially alter frequency distribution curves (see e.g. Cao et al., 1998).

Vannote et al. (1980) suggested that spatial differences among benthic assemblages in streams were a result of changes in energy inputs (allochthonous vs autochthonous inputs), stream size and differences in thermal regimes. Poff & Ward (1989) expanded these ideas to include spatial differences based on differences in flow regime (also see Minshall, 1988). Our results support these scenarios, as a strong spatial difference was observed in shredder populations as stream size increased and between similarly sized streams that differed in aspect. For example, shredder structure was substantially different between Goat Creek (the smallest study stream with a closed canopy) and Rush Creek (the largest study stream with an open canopy) and the other streams were placed intermediate (Figure 5) (e.g. Minshall & Robinson, 1998). Differences in plecopteran structure often reflect differences in temperature regimes (Ward & Stanford, 1982; Ward, 1992). For example, Cave and Rush Creeks had similar plecopteran assemblages and were the warmest streams (Rush Creek had 1510 degree days in 1995), whereas Pioneer Creek was the coldest stream (1111 degree days in 1995) and had a different plecopteran assemblage than the other streams. Pioneer Creek also has a northern aspect whereas Cave Creek, in addition to Cliff and Cougar, has a southern exposure. The similar maximum summer temperature of the smaller Cave Creek with the larger, more-open Rush Creek may be due to the southern exposure of Cave Creek (Table 1).

Our results suggest that long-term persistence of stream benthic communities should be assessed at the level of individual taxa. Biotic responses to changes in stream habitats are more individualistic and some community-level parameters actually may obscure efforts to elucidate long-term response patterns (Robinson & Minshall, 1998). For example, we found that community measures of biomass and numbers were quite variable, although taxonomic composition was seemingly persistent. This is to be expected as macroinvertebrate abundances can change quickly in response to food availability (Richards & Minshall, 1988), life history dynamics (Robinson et al., 1992), short-term fluctuations in environmental conditions (Flecker & Fiefarek, 1994; Elosegui & Pozo, 1994; Death, 1996) and season (Boulton et al., 1992; Ruse, 1995), whereas assemblage composition (presence or absence of species) may be maintained. The importance of long-term studies cannot be over-emphasized (Grossman et al., 1990) and our results further stress the importance of species level analyses in the long-term monitoring of stream ecosystems.

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