Comparison of Benthic Macroinvertebrate Assemblages in Small Streams along a Gradient of Flow Permanence

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Abstract. Benthic invertebrates were quantified in 6 small upland streams in Alabama for 2 y to examine the degree to which variation in assemblage structure was related to the hydrologic permanence of riffle habitats. Streams differed along a gradient of flow permanence: 2 were normally intermittent (i.e., riffles ceased flowing in normal rainfall years) in summer, 1 was rarely intermittent (i.e., normally perennial), and 3 streams were occasionally intermittent (i.e., riffles ceased flowing during dry years). Despite large differences in flow permanence among streams, invertebrate assemblages differed only slightly. Presence–absence data revealed that 75% of the species (171 total taxa, predominantly aquatic insects) were ubiquitous across the 6 streams or displayed no pattern with respect to permanence; 7% of the total species were found exclusively in the normally intermittent streams. Although somewhat variable, many of the community richness and diversity measures were positively correlated with stream permanence. Year-to-year differences in assemblages within single streams appeared as great as differences between streams of contrasting permanence within a given year. Faunal similarity among streams was higher in 1995, a year with normal summer rainfall that followed a wet year (1994), than in 1994, a wet year that followed a dry year. Between-year differences in density and richness were lowest in spring and winter and greatest in summer, the season when communities were directly exposed to drying of riffles in intermittent streams. Several populations of common invertebrates during summer displayed non-random distributions along the permanence gradient. These data in general support the hypotheses that 1) benthic invertebrate assemblages show predictable, albeit subtle, relationships with stream permanence, and 2) antecedent hydrologic conditions associated with riffle permanence, perhaps because of their effects on survival and recruitment of subsequent generations, can influence the structure of benthic assemblages in streams.

Key words: invertebrates, streams, hydrology, aquatic insects, temporary habitats, community, riffles, lotic, permanence, disturbance, Alabama.

It is well known that temporary aquatic systems often harbor benthic communities that differ from those of nearby permanent systems (Wiggins et al. 1980, Williams 1996). The basis for this disparity apparently is related to system-specific differences in the physico-chemical environment (Williams 1987), proximity to sources of colonists (Boulton 1989), and the tendency for some benthic species to be intolerant of, or more rarely adapted to, temporary habitats. For example, commonly cited reasons why fewer benthic species occur in temporary versus permanent systems involve reduced colonization or survival by species typical of permanent habitats as temporary habitats dry (e.g., Wiggins et al. 1980, Wright et al. 1984, Lake et al. 1986, Bottorff and Knight 1988, Delucchi 1988). Alternatively, the evolutionary tendency for some species to become adapted to temporary habitats has been explained in terms of the selective advantages of occupying habitats with an abundance of high-quality detrital foods (Bärlocher et al. 1978, Wiggins et al. 1980) but without significant competitors or predators (Peckarsky 1983, Williams 1996, but see Larimore et al. 1959, Boulton and Suter 1986, Holomuzki and Stevenson 1992).

Intermittent streams are temporary systems with seasonal groundwater connections that cease flowing or become dry during part of the year (Gordon et al. 1992). Although these ecosystems and their faunas have been well studied in arid regions (e.g., temperate southwestern North America: Gray 1981, Fisher et al. 1982, Hill and Gardner 1987; southern Australia: Lake et al. 1986, Boulton and Lake 1992a, 1992b), they are also common in mesic regions where precipitation is seasonal and groundwater fluctuations are high (e.g., Clifford 1966, Williams and Hynes 1976, Wright et al. 1984, Bottorff and Knight 1988, Matthews 1988). Thus, physiological constraints of intermittence on aquatic organisms and their influence on the structure and function of benthic communities can apply

to systems across a wide range of climatological regimes (Boulton and Suter 1986, Lake et al. 1986).

A common way to study benthic invertebrate assemblages of perennial and intermittent streams has been to consider each stream a distinct hydrologic system and compare assemblages between systems using both univariate (e.g., Stehr and Branson 1938, Clifford 1966) or multivariate approaches (e.g., Delucchi 1988). However, because individual streams represent points on gradients in hydrologic and other physical features (Vannote et al. 1980, Minshall et al. 1985, Poff and Allan 1995) whose conditions may differ spatially and temporally, such a discrete classification scheme precludes potentially important variation in the magnitude of stream intermittence, which may vary from year to year depending on precipitation. For example, streams that are normally intermittent may, in wet years, flow continuously whereas perennial streams may become intermittent during dry or drought years. Both of these anomalous situations can have significant residual effects on benthic communities the following year (Boulton and Lake 1992b). In this sense, failure to take into account recent climatological history as well as a stream's frequency of intermittence over the long term may, in short-term studies (i.e., ≤1 y data), produce significant unaccountable variation in the data when communities are compared (Boulton and Lake 1992a).

Small streams in temperate-deciduous forests of eastern North America may become intermittent in summer (e.g., Kirby et al. 1983, Delucchi 1988, Holomuzki and Stevenson 1992, Wallace et al. 1992), as rainfall declines and high evapotranspiration lowers the water table. At this time riffles may cease to flow, pools may become isolated, and rheophilic invertebrates may incur physiological stress associated with non-flowing conditions. The timing and degree of intermittency occurring in these mesic habitats vary from stream to stream and from year to year. The purpose of this study was to quantify permanence across 6 similar-sized streams that vary naturally in their degree of permanence, and to compare benthic macroinvertebrate assemblages among streams along this permanence gradient. Specifically, I tested two hypotheses: 1) benthic assemblages vary predictably in streams along a gradient of flow permanence; and 2) faunal differences among

streams in a given year vary according to antecedent climatological conditions that influence flow permanence.

Study Sites

I studied 6 small, unnamed streams (hereafter called S–1 through S–6) within the Talladega National Forest, Alabama (Shoal Creek Ranger District, 33°47′N, 85°33′W). All are tributaries of Shoal Creek and its larger tributary, Choccolocco Creek, part of the upper Coosa River System. The streams lie in close proximity (<4.7 km apart) and their watersheds have similar geomorphology (1st-order stream channels), parent geology (low-grade metamorphic rock; Lay Dam formation), and soils (moderately deep Fruithurst–Chewacla and Fruithurst–Tallapoosa-Badin complexes). All 6 streams are classified as intermittent on blue-line topographic maps of the US Geological Survey. Intermittent streams in this region normally cease flowing or become completely dry in late summer, and flows resume with increased rainfall in autumn.

Stream channels at baseflow are narrow (<1.5 m, Table 1), and stream water is well oxygenated (>7 mg/L), circumneutral (pH: 6.0–7.0), clear (turbidity < 3.0 NTU), and low in suspended materials (total solids: <35 mg/L; conductivity: <30 μS/cm^2 at 25°C; total hardness and alkalinity: <30 mg/L as $CaCO_3$; N and P: <0.2 mg/L; J. W. Feminella, unpublished data). There were some notable differences among the streams in basin area, channel gradient, annual temperature range, and mean riffle velocity, but all streams had similar elevation, mean annual temperature, riparian shading, and substrate features (Table 1). Vegetation in these mostly forested watersheds consists mainly of mixed coniferous (shortleaf, loblolly, and longleaf pines) and deciduous species (white and red oaks, and hickories). Riparian zones were largely intact and provided dense shading of the channel from April through October. Sites were selected as part of a long-term study to elucidate the effects of forest understory thinning and prescribed burning on water quality in 3 of the 6 streams (i.e., S–4 to S–6). Although 2 of these streams (i.e., S–4 and S–5) were sampled during forest thinning operations, preliminary data analyses suggest that this practice had no mea-

TABLE 1. Physical factors in the 6 study streams (S-1 through S-6), March 1994–December 1995. Basin area, elevation, and mean channel gradient were determined from USGS 7.5-min topographic maps of the US Geological Survey. Temperature was monitored continuously (Hobo-Temp© data loggers) March 1994–April 1995. Channel measurements (width, velocity, and substrate diameter [=diam.] and variation) were determined from 5 riffles per stream sampled on 6 dates (March, August, and December, 1994 and 1995).

Stream	Basin area (ha)	Elevation (m)	Gradient (m/m)	Summer shade (%)	$\bar{x}$ Annual temperature (°C)	Annual temperature range (°C)	$\bar{x}$ Channel width (m)	$\bar{x}$ Riffle velocity (m/s)	Median substrate diam. (mm)	Substrate variation (% CV)
S-1	39.4	350	0.048	91	14.9	1.3–23.0	1.39	0.33	38.4	25.0
S-2	61.4	356	0.021	87	14.5	3.2–20.6	0.66	0.15	19.2	35.4
S-3	32.3	338	0.060	89	14.2	2.1–21.0	0.86	0.22	54.4	23.5
S-4	30.8	356	0.024	95	14.7	3.5–21.0	0.74	0.21	20.8	26.6
S-5	20.9	360	0.037	98	14.6	9.0–21.0	0.60	0.19	12.0	39.6
S-6	54.3	335	0.044	94	14.6	2.3–23.1	0.61	0.20	30.4	25.8

surable effects on benthic macroinvertebrates (J. W. Feminella, unpublished data).

Methods

Quantifying stream permanence and long-term climatological variation

I derived a relative index of permanence for each of the 6 streams by ranking each stream according to the following 3 physical variables measured in channels: 1) median discharge; 2) minimum discharge at summer baseflow; and 3) mean wetted area of riffle at summer baseflow. Stream permanence was then scored by summing the separate ranks of each these variables for each stream (i.e., with the lowest and highest scores representing lowest and highest stream permanence scores, respectively). I used a combination of discharge measures and habitat variables (i.e., wetted area of riffles at baseflow), rather than a single estimate of permanence (e.g., minimum discharge alone), as a more effective means of quantifying changes in riffle habitat quality during drying that could influence benthic assemblages independently of flow variables alone. Discharge was measured with a Marsh-McBirney Flowmeter (using the cross section/incremental method, see Platts et al. 1983) every 4–6 wk at each site from March 1994 to December 1995 ($n = 25$, see also Fig. 1). Most (>85%) discharge measurements were made at least 4 d after a storm (and usually after a much longer period) to characterize low-flow conditions in riffles during each period. Riffle area was determined during March, Au-

gust, and December of each year at 5 riffles per stream by multiplying wetted riffle width (3 cross-stream transects per riffle) by its length (2 longitudinal transects per riffle), and averaging the 5 riffle area estimates in each stream.

Because the streams were not continuously gauged for discharge, nor were they close to downstream gauging stations, I had no historical records of streamflow beyond my discharge measurements. Therefore, to assign probability of stream permanence occurring in a given year (i.e., intermittence frequency), I examined earlier summer rainfall data (June through September, 1970–1995) in conjunction with personal observations of stream intermittence during the study period. Rainfall is the primary source of variation in runoff, particularly in small upland basins, because it is the ultimate source of water (Viessman et al. 1977, Gordon et al. 1992); it also has been used as a key physical factor in relating hydrologic disturbances to changes in benthic invertebrate populations (e.g., McElravy et al. 1989, Feminella and Resh 1990). I derived intermittence frequency by ranking years according to the following 3 rainfall parameters: 1) total summer rainfall; 2) lowest single summer month's rainfall; and 3) lowest rainfall during 2 consecutive summer months. An overall ranking of the years was then made by summing the separate ranks of each rainfall parameter for each year. This ranking was used to characterize long-term climatological variation and, in turn, a stream's potential for intermittency in a given year. Rainfall data were based on monthly means from a National Oceanic and Atmospher-
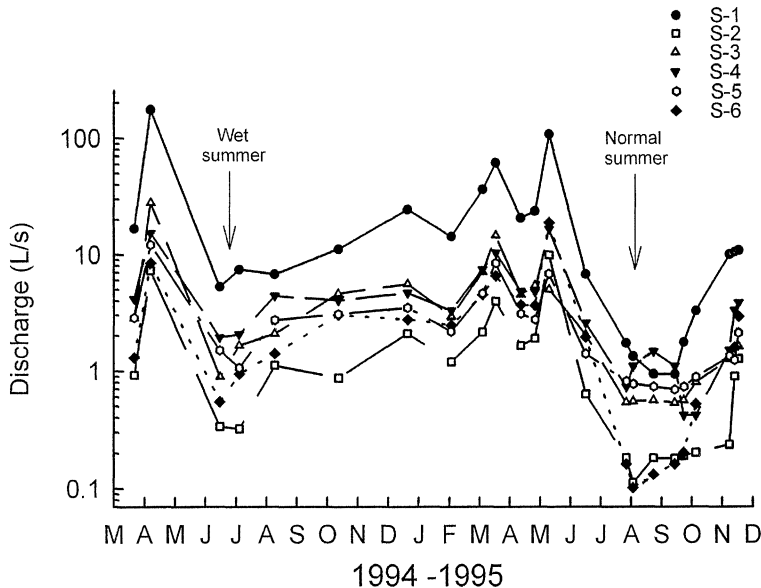
FIG. 1. Discharge of the 6 study streams (S–1 to S–6), Talladega National Forest, Alabama, March 1994–December 1995. 1994 was a wet summer in which all 6 streams flowed continuously and 1995 was a normal (i.e., drier) summer (see Fig. 2) in which 2 streams (S–2 and S–6) became intermittent. Tick marks directly above letters symbolizing month on the x-axis indicate the start of each month.

ic Administration climatological station in Anniston, Alabama, 25 km SW of the study sites. Data from this station corresponded to long-term precipitation patterns in the region, measured both 19 km SE (Heflin station: $r = 0.92$, $p < 0.001$, $n = 34$ y) and 19 km N (Jacksonville station, $r = 0.79$, $p < 0.001$, $n = 33$ y) of the study sites (National Climatic Data Center records).

Benthic invertebrate sampling

For each stream, benthic invertebrates were sampled from riffles over a 0.5–1-km reach during March, August, and December 1994 and 1995. These months were chosen to assess seasonal differences in benthos (i.e., spring, summer and winter assemblages, respectively), as well as to provide a summary of year-round assemblage structure that would include most taxa. Riffles were chosen (vs. pools or runs) because these habitats typically have the highest species richness and abundance of benthic invertebrates (Hynes 1970, Minshall and Minshall 1977, Brown and Brussock 1991), and thus are likely to harbor the majority of benthic species present. Furthermore, because riffle assem-

blages are most directly affected by intermittent (non-flowing) conditions, examination of their dynamics across streams and years would likely provide the most direct test of hypotheses regarding among-stream variation in permanence.

I collected invertebrates with a Surber sampler (mesh size 250 μm), pooling 4 Surber samples from each of 5 riffles per stream (sampled area: 0.372 m²/riffle and 1.86 m²/stream). During times when flow in riffles was insufficient for direct Surber sampling (e.g., S–2 and S–6 in August 1995, see below), I excavated all substrate from the Surber quadrat, and then elutriated this material using a wash basin and 250-μm sieve. Samples were preserved in the field with 95% ethanol. In the laboratory, I used a 2-phase sorting method. Samples were sorted 1) macroscopically for 30 min to remove large and rare organisms, and 2) microscopically for smaller, more numerous organisms, using a volumetric (i.e., 25 ml aliquot) subsampling method, with 3–5 aliquots taken from a total suspended sample volume of 1000 ml. Sorting of subsamples was done by removing at least 200 organisms from at least 3 aliquots per sample (within-sample coefficient of variation usually <10–15%, J. W. Feminella, unpublished data).

Organisms were identified, counted, and their numbers extrapolated to the total number of individuals contained in the entire microscopic sample fraction. These were then combined with those organisms identified and counted from the macroscopically sorted fraction. Invertebrates were identified to the lowest possible taxonomic level (usually genus or 'morphospecies' sensu Mayr 1969), and taxon-specific density was determined. Assignment of some taxa to morphospecies was necessary because most of the species were immatures and therefore not identifiable to species given current taxonomy (Thorp and Covich 1991, Merritt and Cummins 1996). However, use of invertebrate morphospecies appears a reasonable surrogate for true species in community-level analyses (see Oliver and Beattie 1996).

Response variables, predictions, and statistical analyses

I used total benthic density, total invertebrate richness, EPT richness (i.e., total number of taxa in the insect orders Ephemeroptera, Plecoptera, and Trichoptera), Shannon's diversity (Shannon 1948, Magurran 1988), and percent of the assemblage as non-insect invertebrates as response variables. Because sampled area was approximately equal for all streams and dates, total and EPT richness measures were considered not subject to species–area bias (Douglas and Lake 1994, Vinson and Hawkins 1996), and therefore were more directly comparable among streams and seasons. Benthic macroinvertebrate density, diversity, and total richness have long been used in freshwater systems as community attributes (Hellawell 1986, Rosenberg and Resh 1993). Use of EPT richness in community assessments has been more recent, although it is fast becoming a standard measure because it 1) includes the insect orders thought the least tolerant of environmental perturbations in streams (Plafkin et al. 1989), 2) can accurately classify benthic assemblages under a variety of disturbance regimes (Resh et al. 1995), and 3) can serve as a useful indicator of complex ecosystem attributes such as macroinvertebrate secondary production (Wallace et al. 1996).

Differences in response variables among seasons and between years were analyzed with ANOVA and Student's *t*-tests, respectively (Zar 1984). Response variables also were used in simple linear regression analyses (Zar 1984) to test hypotheses about relationships, if any, between assemblage variables and stream permanence. All response variables except Shannon diversity and % non-insect taxa were log-transformed prior to analyses to stabilize variance; arcsine transformation was used for % non-insect taxa. Specifically, I predicted that density, richness, and diversity would all show positive relationships with stream permanence, resulting from the increased hydrologic stability and hence increased amount of favorable habitats for rheophilic invertebrate taxa (Boulton and Suter 1986, Boulton and Lake 1992b, Closs and Lake 1994). In contrast, I predicted that proportions of non-insect invertebrates (e.g., crustaceans, arachnids, etc.) would be negatively related to permanence, because these taxa tend to decrease as permanence increases while insect abundance tends to increase in these more benign hydrologic environments (sensu Williams and Hynes 1977, Williams 1987).

Streams also were compared to each other using a combination of community similarity estimates and regression. Similarity of stream faunal composition within and between years was estimated using Jaccard's coefficient (C_j, Southwood 1978, Magurran 1988). C_j was determined between the stream with the highest permanence score and each of the other 5 streams, and these values were regressed against the individual permanence scores of each of these streams. I predicted a positive relationship between permanence score across the 5 streams and their individual similarity to the stream with the highest permanence score in the group.

In addition to the community measures I also quantified and compared densities of selected summertime populations of invertebrates along the permanence gradient. I did this to determine the degree to which stream permanence influenced the abundance and distribution of common taxa occurring during summer, the season when populations were most likely to be affected by riffle intermittence.

For all regressions, because of low replication (i.e., usually $n = 5$ or 6 streams, depending on analysis) and hence limited statistical power to reject a false null hypothesis of no relationship among variables, I used an α-level of 0.10 to better balance risks of committing type I and II errors (Toft and Shea 1983, Peterman 1990).

TABLE 2. Hydrological variables used to derive an index of permanence for the 6 study streams (S–1 to S–6), March 1994–December 1995. Discharge measurements ($n = 25$) were made every 4–6 wk. Measurements of 2-y minimum discharge and riffle area were made during summer baseflow (on 26 July 1995); all streams flowed continuously during summer 1994. Streams are ordered in terms of increasing flow permanence, determined by summing the stream-specific ranks of median stream discharge, minimum discharge at baseflow, and mean wetted riffle area at baseflow for each stream (summarized by permanence scores in last column).

Stream	Median discharge (L/s)	Minimum discharge at baseflow (L/s)	$\bar{x}$ Wetted riffle area at baseflow (m²)	Permanence score (Σ ranks)
S-2	1.12	0	1.34	3.5
S-6	1.58	0	1.46	6.5
S-5	2.17	0.37	1.38	8.0
S-4	3.27	0.42	2.03	13.0
S-3	2.84	0.53	3.00	14.0
S-1	10.38	0.93	4.15	18.0

Results

Stream permanence and historical precipitation regimes

Hydrology.—Based on summer baseflow discharge measurements alone, riffle intermittence differed both between years (1994 and 1995) and among streams. All 6 streams flowed continuously during 1994, but 2 streams (S–2 and S–6) became intermittent in late July through August 1995 (Fig. 1). In these 2 streams, riffles ceased flowing but in places remained moist or contained small pockets (<1 cm depth) of surface water, and pools became isolated. Discharge was measurable at only a few points in each of these reaches, but no surface flow was evident in study riffles during this period. Continuous flows were observed in all 6 streams after the onset of autumn rains. S–1 usually had higher discharge (often by an order of magnitude) than any other stream (Fig. 1). It is important to note, however, that none of the streams dried entirely during 1994 or 1995.

Stream permanence.—According to the combined flow- and habitat-related criteria, permanence scores differed among the 6 streams (Table 2). S–1 had the highest permanence score, S–2 and S–6 had the lowest and 2nd-lowest scores

respectively, and S–5, S–4, and S–3 showed intermediate permanence scores. This classification matched summer baseflow discharge measurements alone as S–1 had the highest baseflow discharge, and S–2 and S–6 were the only streams to become intermittent during the study (i.e., in 1995, see Fig. 1).

Long-term precipitation patterns.—Visual inspection of the overall ranks of summer rainfall patterns over the 26-y period yielded 4 climatological categories classifiable as drought, dry, normal, or wet summers (Fig. 2). Four of the 26 years (15%) were considered wet summers, 15 years (58%) were normal, 4 years (15%) were dry, and 3 years (11%) were extremely dry or drought summers. Using this classification I considered 1993, 1994, and 1995 to be dry, wet, and normal summers respectively (Fig. 2). I classified 1994 as a wet summer because its overall rank (60) was closer to the median ranks of the wet years (75) than to the median of the normal years (44, Fig. 2).

Benthic invertebrate assemblages

Faunal composition.—A total of 510,846 invertebrates in 171 taxa was quantified from 170 samples during the 2-y study. Like assemblages in permanent streams, most taxa were aquatic insects (83–87% of total, depending on stream) and the rest, in order of decreasing richness, were represented by aquatic mites, crustaceans, annelids, bivalve and gastropod molluscs, nematodes, and turbellarian flatworms.

Examination of faunal composition using presence–absence data for streams ordered by increasing permanence revealed 3 broad habitat groupings of taxa: 1) those taxa restricted to stream riffles with high permanence scores (Fig. 3A); 2) those restricted to stream riffles with low permanence scores (Fig. 3B); and 3) those found in all 6 streams or showing no conspicuous pattern with regard to stream permanence (Fig. 3C). Most taxa (128, 75% of the total) were in this last group. Of the other 2 groups of taxa, fewest (12 taxa, 7% of the total) occurred only in streams with low permanence scores (Fig. 3B).

Numerically dominant families of invertebrates were generally similar among streams in a given year but were more variable within streams between years. In spring 1994, peltoperlid stoneflies (*Tallaperla*) and chironomid midges (mostly Orthocladiinae) were the most
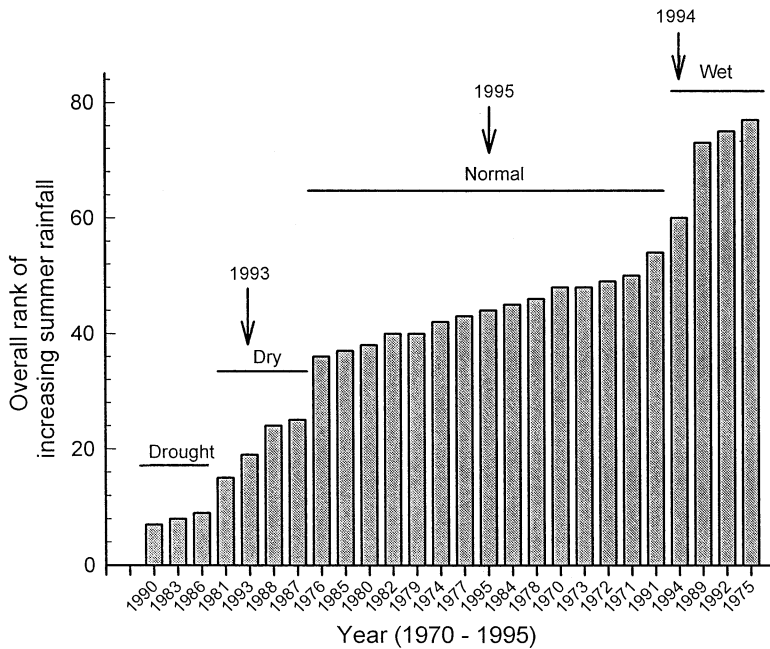
FIG. 2. Classification of summer (June–September) rainfall over a 26-y period, 1970–1995. Years were ordered on the x-axis by summing each year's rank of the following 3 summer rainfall parameters: 1) total summer rainfall; 2) lowest single summer month's rainfall; and 3) lowest rainfall during 2 consecutive summer months. According to this classification, 1993, 1994, and 1995 were considered dry, wet, and normal summers, respectively. Rainfall data were based on monthly means from a US National Oceanic and Atmospheric Administration climatological station in Anniston, Alabama, 25 km SW of the study sites.

abundant taxa in most streams, whereas in spring 1995 peltoperlids were replaced as the dominant group by several other taxa (Table 3). In summer, hydropsychid caddisflies, orthoclads, and elmid beetles (mostly *Optioservus* and *Oulimnius*) were usually the major groups, together making up at least 30% of the total fauna. Of these, hydropsychids and elmids were the most numerically abundant groups in 1994 whereas chironomids were numerically dominant in all 6 streams in 1995 (Table 3). In winter, all streams contained mostly orthoclad chironomids and elmids (usually >30% of assemblage). Peltoperlids, although numerically dominant in winter 1995 samples, were less abundant in 1994 (Table 3).

Community attributes.—Total invertebrate densities did not differ between years (seasons combined) or among seasons (years combined), yet the degree of difference in density between years varied with season (i.e., significant year × season interaction, Table 4). Stream-specific densities in 1994 usually were lowest in summer

except for S–1, the stream with the highest permanence score (Fig. 4). This trend was reversed in 1995 when densities were highest in summer, particularly for S–2 and S–6, streams with lowest permanence scores. However, there were no significant relationships between density and permanence in either year (Table 5). Shannon diversity (H' usually between 2.7 and 3.1) did not differ between seasons but was significantly higher in 1995 (Table 4, Fig. 4). In only one season (spring 1994) was diversity significantly related with permanence (Table 5). Percent of the benthic assemblage as non-insect taxa was not different between years but was significantly higher in spring than winter in most streams (ANOVA and Tukey's HSD test; Table 4, Fig. 4). This measure was significantly related to permanence (i.e., negative in summer and winter, positive in spring) only in 1994 (Table 5).

Total invertebrate richness was significantly higher in 1995, although the magnitude of this difference varied with season (i.e., significant year × season interaction, Table 4, Fig. 4). In

FIG. 3. Presence (shaded bars) and absence (clear bars) of invertebrate taxa collected from riffle habitats in 6 streams (S–1 to S–6), March, August, and December 1994 and 1995. Streams are ordered by increasing flow permanence (see Table 2). Taxa are divided into 3 groups: A) those found in more permanent streams; B) those found in streams with low permanence scores (i.e., normally intermittent streams); and C) those ubiquitous in all streams or showing no pattern with respect to stream permanence. Specific names, where known, were omitted to save space, and alphabetic characters after generic names (e.g., "sp. a", "sp. b", "sp. b'", "sp. c'", etc.) are the author's morphospecies designations. Taxonomic identifications were made from Stewart and Stark (1988), Thorp and Covich (1991), Merritt and Cummins (1996), and Wiggins (1996).

C. Ubiquitous or no pattern

Family	Taxon
Ephemerellidae	Eurylophella
Ephemerellidae	Ephemerella
Leptophlebiidae	Paraleptophlebia
Ephemeridae	Ephemera
Ameletidae	Ameletus
Baetidae	Fallceon
Baetidae	Baetis sp. c
Baetidae	Baetis sp. d
Baetidae	Baetis sp. e
Baetidae	Centroptilum
Heptageniidae	Stenonema sp. a
Heptageniidae	Stenonema sp. b
Heptageniidae	Leucrocuta
Aeshnidae	Boyeria
Gomphidae	Gomphus sp. b
Cordulegastridae	Cordulegaster
Calopterygidae	Calopteryx
Nemouridae	Amphinemura
Capniidae	Allocapnia
Leuctridae	Leuctra
Leuctridae	Tallaperla
Perlidae	Acroneuria
Perlidae	Eccoptura
Perlidae	Beloneuria
Perlodidae	Isoperla sp. a
Perlodidae	Isoperla sp. b
Perlodidae	Remenus
Chloroperlidae	Sweltsa
Chloroperlidae	Paraperla
Hydropsychidae	Diplectrona
Hydropsychidae	Hydropsyche
Philopotamidae	Chimarra
Philopotamidae	Dolophilodes
Hydroptilidae	Hydroptila
Calamoceratidae	Anisocentropus
Glossosomatidae	Glossosoma
Glossosomatidae	Agapetus
Molannidae	Molanna
Psychomyiidae	Lype
Leptoceridae	
Polycentropodidae	Polycentropus
Odontoceridae	Psiloreta sp. a
Odontoceridae	Psiloreta sp. b

Increasing permanence →
S-2 S-6 S-5 S-4 S-3 S-1

Family	Taxon
Rhyacophilidae	Rhyacophila sp. b
Limnephilidae	Pycnopsyche sp. a
Limnephilidae	Pycnopsyche sp. b
Rhyacophilidae	Rhyacophila sp. d
Uenoidae	Neophylax sp. b
Uenoidae	Neophylax sp. c
Goeridae	Goera
Lepidostomatidae	Lepidostoma
Simuliidae	Simulium
Simuliidae	Prosimulium
Dixidae	Dixella
Dixidae	Dixa
Empididae	Clinocera
Ceratopogonidae	Bezzia
Ceratopogonidae	Dasyhelea (?)
Ceratopogonidae	Atrichopogon
Tipulidae	Tipula sp. a
Tipulidae	Tipula sp. b
Tipulidae	Pilaria
Tipulidae	Pedicia
Tipulidae	Hexatoma sp. b
Tipulidae	Hexatoma sp. c
Tipulidae	Antocha
Tipulidae	Pseudolimnophila
Tipulidae	Dicranota sp. a
Tipulidae	Leptotarsus
Tipulidae	Cryptolabis
Tabanidae	Tabanus
Psychodidae	Pericoma
Chironomidae	Tanypodinae sp. a
Chironomidae	Tanypodinae sp. b
Chironomidae	Tanypodinae sp. c
Chironomidae	Corynoneurini sp. a
Chironomidae	Corynoneurini sp. b
Chironomidae	Corynoneurini sp. c
Chironomidae	Corynoneurini sp. d
Chironomidae	Tanytarsini sp. a
Chironomidae	Tanytarsini sp. b
Chironomidae	Chironominae sp. a
Chironomidae	Chironominae sp. b
Chironomidae	Chironominae sp. c
Chironomidae	Chironominae sp. f
Chironomidae	Chironominae sp. h

Increasing permanence →
S-2 S-6 S-5 S-4 S-3 S-1

Family	Taxon
Chironomidae	Chironominae sp. i
Chironomidae	Chironominae sp. j
Chironomidae	Chironominae sp. k
Chironomidae	Chironominae sp. l
Chironomidae	Orthocladiinae sp. a
Chironomidae	Orthocladiinae sp. c
Chironomidae	Orthocladiinae sp. e
Chironomidae	Orthocladiinae sp. f
Chironomidae	Orthocladiinae sp. g
Chironomidae	Orthocladiinae sp. h
Chironomidae	Orthocladiinae sp. i
Chironomidae	Orthocladiinae sp. j
Corydalidae	Nigronia
Sialidae	Sialis
Psephenidae	Psephenus
Psephenidae	Ectopria
Elmidae	Optioservus
Elmidae	Dubiraphia
Elmidae	Stenelmis sp. a
Elmidae	Oulimnius
Dryopidae	Macronychus
Ptilodactylidae	Helichus
Ancylidae	Anchytarsus
Sphaeriidae	Laevapex
Asellidae	Pisidium
Crangonyctidae	Lirceus
Gammaridae	Crangonyx
Harpactacoida	Gammarus
Cyclopoida	
Chydoridae	
Ostracoda	
Cambaridae	Cambarus
Stygothrombiidae	Katharinera
Rhynchohydracaridae	Clathrosperchon
Oribatida	
Halacaridae	Lobohalacarus
Aeolosomatidae	sp. a
Haplotaxidae ?	sp. a
Haplotaxidae ?	sp. b
Planariidae	
Merminthidae	sp. a

Increasing permanence →
S-2 S-6 S-5 S-4 S-3 S-1

FIG. 3. Continued.

TABLE 3. Percentage composition of the 2 most numerically abundant families of invertebrates present in streams S-1 through S-6 during spring (March), summer (August), and winter (December) for 1994 and 1995. Streams are ordered by increasing permanence scores. $n = 5$ riffles per stream.

Stream	Spring	Summer	Winter
1994			
S-2	Peltoperlidae (44)	Elmidae (33)	Chironomidae (32)
	Elmidae (12)	Asellidae (10)	Elmidae (21)
S-6	Peltoperlidae (38)	Elmidae (18)	Chironomidae (29)
	Nemouridae (9)	Chironomidae (16)	Simuliidae (11)
S-5	Chironomidae (28)	Elmidae (20)	Chironomidae (27)
	Peltoperlidae (23)	Chironomidae (18)	Elmidae (22)
S-4	Peltoperlidae (21)	Hydropsychidae (16)	Chironomidae (37)
	Chironomidae (19)	Elmidae (14)	Elmidae (11)
S-3	Peltoperlidae (38)	Hydropsychidae (20)	Chironomidae (35)
	Chironomidae (18)	Chironomidae (19)	Capniidae/Leuctridae (13)
S-1	Chironomidae (26)	Elmidae (20)	Chironomidae (27)
	Peltoperlidae (15)	Chironomidae (15)	Simuliidae (12)
1995			
S-2	Chironomidae (23)	Chironomidae (24)	Peltoperlidae (29)
	Asellidae (18)	Hydropsychidae (14)	Chironomidae (11)
S-6	Chironomidae (22)	Chironomidae (38)	Chironomidae (17)
	Capniidae/Leuctridae (9)	Hydropsychidae (9)	Peltoperlidae (15)
S-5	Chironomidae (26)	Chironomidae (26)	Chironomidae (35)
	Asellidae (24)	Elmidae (17)	Elmidae (19)
S-4	Chironomidae (28)	Chironomidae (38)	Chironomidae (33)
	Elmidae (16)	Hydropsychidae (12)	Elmidae (16)
S-3	Chironomidae (25)	Chironomidae (22)	Chironomidae (28)
	Peltoperlidae (17)	Hydropsychidae (18)	Peltoperlidae (14)
S-1	Chironomidae (27)	Chironomidae (24)	Chironomidae (17)
	Simuliidae (14)	Elmidae (15)	Elmidae (15)

only one case (winter 1994) was total richness significantly related to permanence (Table 5). Surprisingly, the stream with the highest total richness (93 taxa) on any date was S-2 during summer 1995 (Fig. 4B), the stream with the lowest permanence score (see Table 2). Although EPT richness was not different between years or among seasons (Table 4, Fig. 4), of all community attributes it showed the strongest relationship with permanence (4 of 6 seasons), particularly in 1994 when all 3 seasons were significant. All significant relationships between richness (total and EPT) were positive.

Between-year comparisons of summer assemblages.—Density in summer 1995 showed a 3-fold, and highly significant, increase over that of 1994 (i.e., 16,573 ± 7188 vs. 5212 ± 2612 individuals/m², x̄ ± 1 SD; $t = -4.42$, $p = 0.001$, $n = 6$). Significant increases in total richness also were found during summer 1995 (i.e., 81.5 ± 6.74 taxa/stream vs. 64.5 ± 8.54 in 1994; $t = -3.83$, $p = 0.003$, $n = 6$).

Densities of several invertebrate populations common in summer showed patterns related to stream permanence (Fig. 5). Density of the mayfly *Stenonema* increased with increasing stream permanence during 1994 and 1995. Although more variable, densities of simuliid larvae (usually *Simulium*) also were higher in streams with higher permanence scores, and larvae were absent from S-2, the stream with the lowest permanence score (Fig. 5). The caddisflies *Cheumatopsyche* and *Chimarra* were restricted mainly to S-1, the stream with the highest permanence

TABLE 4. Results of ANOVA on differences in benthic invertebrate density, Shannon diversity (H'), percent of non-insect taxa, total number of taxa, and total number of taxa within the orders Ephemeroptera, Plecoptera, and Trichoptera (EPT) between years (1994 and 1995) and seasons (spring, summer, and winter). $n = 36$.

Source of variation	SS	df	MS	F	p
Density					
Year	0.148	1	0.148	2.53	0.122
Season	0.011	2	0.006	0.10	0.907
Year × season	0.748	2	0.374	6.37	0.005
Error	1.761	30	0.059		
H'					
Year	0.286	1	0.286	4.35	0.046
Season	0.262	2	0.131	1.99	0.155
Year × season	0.270	2	0.135	2.05	0.146
Error	1.970	30	0.066		
% Non-insect taxa					
Year	0.274	1	0.274	0.08	0.779
Season	39.656	2	19.828	5.82	0.007
Year × season	0.542	2	0.271	0.08	0.924
Error	102.175	30	3.406		
Total taxa					
Year	0.021	1	0.021	10.29	0.003
Season	0.011	2	0.005	2.68	0.085
Year × season	0.014	2	0.007	3.48	0.044
Error	0.061	30	0.002		
Total EPT taxa					
Year	<0.001	1	<0.001	0.01	0.928
Season	0.019	2	0.010	1.86	0.173
Year × season	0.014	2	0.007	1.36	0.271
Error	0.155	30	0.005		

score, whereas the caddisfly *Diplectrona* and the isopod *Lirceus* were both restricted to streams of intermediate or low permanence scores (Fig. 5).

Faunal similarity.—The extent of faunal similarity among the 6 streams differed between years. Streams were more similar to each other (i.e., had significantly higher C_j values) in 1995 ($\bar{x} = 0.651$) than in 1994 ($\bar{x} = 0.599$, $t = -3.05$, $p = 0.005$, $n = 18$). Moreover, streams differed not only in similarity between years, but also in their degree of relationship between permanence scores and individual similarity to S–1, the stream with the highest permanence score. In 1994, there was no relationship between stream permanence score and similarity to S–1 (Fig. 6A), whereas in 1995 there was a significant, positive relationship (Fig. 6B).

Discussion

In this study I focused on flow permanence as the basis for explaining distributional pat-

terns of benthic invertebrates inhabiting riffles of 6 small upland streams. Observed faunal differences among streams and between years likely reflected variation in stream permanence, rather than that of other sources of variation, for 3 reasons. First, all streams showed similar ranges of physico-chemical variables such as conductivity, dissolved oxygen, substrate size, and temperature—factors commonly considered important to benthic invertebrates (e.g., Mackay and Kalff 1969, Vannote and Sweeney 1980, Minshall 1984, Boulton and Lake 1990), but whose levels were relatively invariant among streams in the present study. Second, benthic sampling efforts were equivalent across sites and seasons, thereby minimizing errors in community characterization typically problematic of unbalanced sampling designs (Elliott 1977, Resh 1979). Third, all 6 streams are within 5 km of each other and are tributaries of the same basin; therefore variation in assemblages (par-
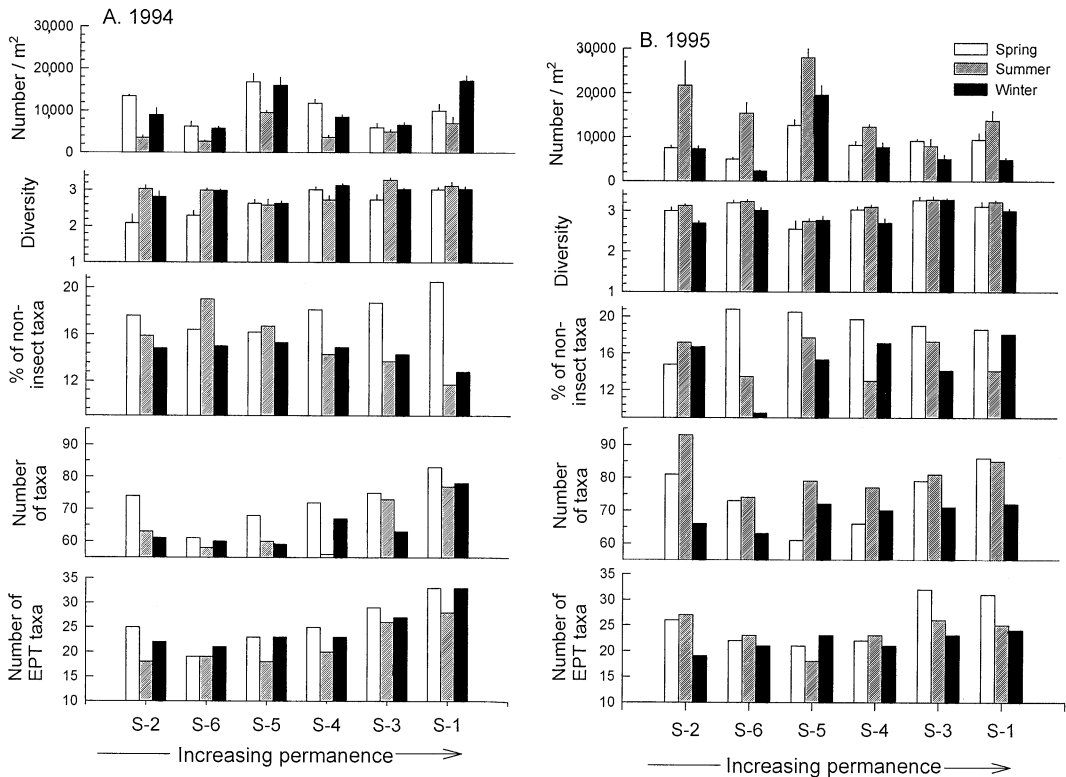
FIG. 4.   Benthic macroinvertebrate density, Shannon diversity, percent of non-insect taxa in the community, total number of taxa, and total number of EPT taxa in A) 1994, a wet year following a dry year (1993), and B) 1995, a normal rainfall year following a wet year (1994). Spring, summer, and winter correspond to late-March, August, and late-December sampling periods, respectively. Bars represent means, and error bars (+1 SE) for density and H' are included to display within-stream variation.

ticularly for taxa richness and diversity) attributable to differences in stream zoogeography was probably minimal. In contrast, streams differed strongly in permanence, as indicated by the measures summarized by stream perma-

nence scores (Table 2). Because permanence score represented a combination of flow (i.e., discharge) and habitat (i.e., wetted riffle area) variables associated with intermittence, and scores reliably summarized these variables, they

TABLE 5.   Pearson product-moment coefficients showing the relationships between flow permanence (independent variable; see Table 2), and 5 biotic variables: benthic density, Shannon diversity (H'), % of non-insect taxa in samples, total taxa richness, and combined number of taxa within the insect orders Ephemeroptera, Plecoptera and Trichoptera (EPT). 1994 was a wet year following a dry year (1993) and 1995 was a normal rainfall year following a wet year (1994). $n = 6$. * $p < 0.10$; ** $p < 0.05$; *** $p < 0.01$; **** $p < 0.001$.

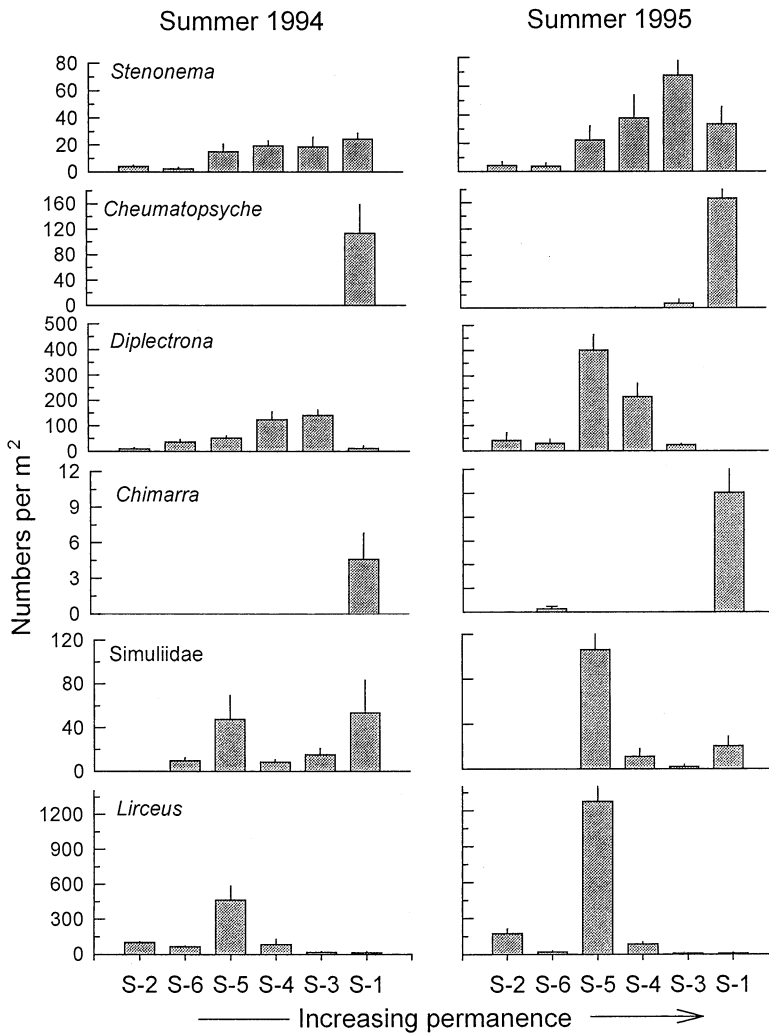| Feature	1994 (Wet year)			1995 (Normal year)		
	March	August	December	March	August	December
Density	−0.25	0.39	0.32	0.35	−0.64	−0.10
H'	0.92****	0.30	0.60	0.32	0.33	0.47
% Non-insect taxa	0.75*	−0.98****	−0.76*	0.50	−0.34	0.40
Total taxa	0.65	0.62	0.83**	0.28	−0.14	0.69
Total EPT taxa	0.76*	0.89**	0.88**	0.57	0.14	0.77*

Summer 1994   Summer 1995

FIG. 5. Summer densities of invertebrate populations showing patterns with respect to stream permanence for A) 1994, a wet year following a dry year (1993), and B) 1995, a normal rainfall year following a wet year (1994). Streams are ordered on the x axis by increasing permanence. ($\bar{x}$ + 1 SE, n = 5).

seemed a reasonable means of expressing permanence as a single variable useful in testing univariate hypotheses about relationships between permanence and invertebrate assemblages.

In addition, the strongly contrasting summer rainfall patterns observed for 1993 (dry summer), 1994 (wet summer), and 1995 (normal summer), as determined from the long-term climatological records, provided the basis for evaluating the impact of intermittence frequency on benthic assemblages. Based on this classification and the observation of actual intermittence of S-

2 and S–6 riffles during 1995, S–2 and S–6 are probably normally intermittent (i.e., in most years), streams S–3, S–4, and S–5 are occasionally intermittent (i.e., only in dry years), and S–1, the stream with the highest permanence score, is probably rarely intermittent (i.e., ceasing to flow only in extremely dry or drought years). This would suggest that, if permanence influences invertebrate assemblages, invertebrates in riffles would be most dissimilar between the normally intermittent streams (i.e., S–2 and S–6) and the rarely intermittent stream (i.e., S–1), and streams with intermediate rank-
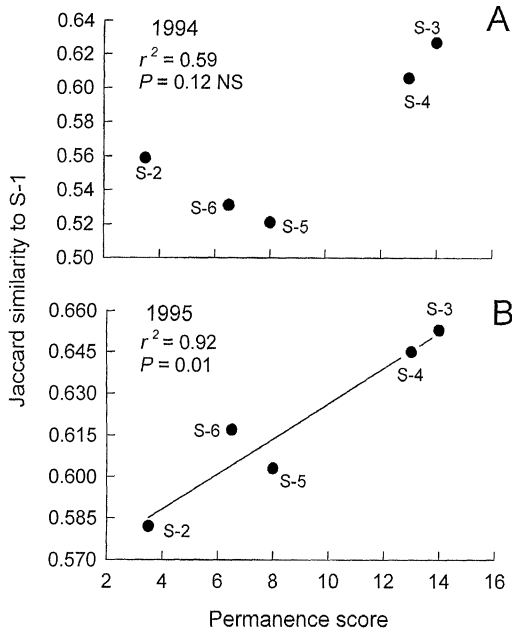
FIG. 6. Relationship between stream-specific Jaccard similarity to S–1, the stream with the highest permanence score, and permanence scores of the other 5 streams examined (i.e., S–2–S–6), for A) 1994, a wet year following a dry year (1993), and B) 1995, a normal rainfall year following a wet year (1994).

ings (i.e., S–3, S–4, and S–5) would have assemblages intermediate between these extremes. Given these differences in frequency of intermittence, how dissimilar were assemblages along this permanence gradient?

Surprisingly, despite large differences in permanence scores (e.g., up to 5-fold between S–1 and S–2, see Table 2), presence–absence data revealed that most taxa were ubiquitous across streams or at least showed no clear pattern with respect to permanence. Jaccard similarity values among streams also supported this result, with streams sharing an average of 60–65% of their taxa with other streams. Benthic invertebrates in intermittent streams have been partitioned into 3 groups of taxa: 1) permanent, 2) facultative (i.e., lotic/lentic generalists), and 3) temporary specialist species, based on their tolerance of or preference for non-flowing conditions (Williams and Hynes 1977). That most taxa in my study occurred in the ubiquitous/no pattern category suggests that the assemblage is composed mostly of "permanent stream species" displaying some tolerance of intermittent conditions (Wil-

liams and Hynes 1977) or an ability to recolonize intermittent riffles from permanent ones (McArthur and Barnes 1985, Jacobi and Cary 1996, Williams 1996). A smaller percentage of other "permanent" taxa (e.g., Ophiogomphus, Taeniopteryx, Pteronarcys, Neophylax, see Fig. 3) showed extremely limited tolerance of intermittence, being found only in the most permanent stream; but clearly these taxa were exceptions. In contrast, there were far fewer "temporary specialist species" in these streams (e.g., sensu Williams and Hynes 1977, see also Boulton and Lake 1992a, Dudgeon 1992), occurring only in normally intermittent streams, and some (e.g., Hexagenia, Chrysops, see Fig. 3) were probably pool species that colonized drying riffles during summer 1995 (personal observations, see also Williams and Hynes 1977). For the vast majority of rheophilic taxa, however, irregularity of flow in riffles, at least to the extent found within the 6 streams, appeared unimportant to their distribution. This pattern is consistent with that of other studies (Delucchi 1988, Boulton and Lake 1992a) where faunal differences between intermittent and permanent streams were minimal, with most taxa ostensibly having no specialized adaptations for surviving intermittence.

Schneider and Frost (1996) recently argued that persistence of many species in temporary aquatic systems with a wide range of wetted habitat duration may be possible largely through life history adaptations, rather than from random processes such as colonization or extinction, or from biotic interactions with other species. In this context, many species may persist in such habitats as long as they complete the aquatic stage of their life cycles before the loss of critical aquatic habitat (Schneider and Frost 1996, see also Wiggins et al. 1980, Williams 1996). In streams S–2 and S–6, the non-flowing period in August 1995 appeared to last only about 4–5 wk (Fig. 1), and the timing and duration of aquatic habitat was probably adequate for most species to complete development in these streams. Indeed, during the dry period several groups were found as late instars (e.g., Pycnopsyche, Psilotreta, Tipula) or pupal stages (e.g., Oulimnius, Glossosoma, Diplectrona, Rhyacophila, Hexatoma, personal observations).

Not only was the non-flowing period brief in S–2 and S–6 but other abiotic conditions in riffles may have allowed many species to persist. During the dry phase, the streambed remained

cool and moist, with an extensive wetted hyporheic zone (>25 cm depth, personal observations) that could provide a spatial refuge for surface benthos during drying (Williams and Hynes 1974, Boulton and Suter 1986, Jacobi and Cary 1996, but see Delucchi 1989, Stanley et al. 1994, Clinton et al. 1996). Furthermore, water temperatures and oxygen concentrations in the isolated pools showed no greater fluctuations than those in pools in other more permanent streams with extensive surface flow connections to adjacent riffles (J. W. Feminella, unpublished data), patterns that would be unlikely had isolated pools (and riffles) become disconnected from subsurface water. Apparently, favorable environmental conditions afforded by subsurface flows, water temperature and humidity buffered by high riparian shading, or some combination of these factors, maintained stream microclimate and thus facilitated the persistence of many species in these habitats. The high taxa richness observed for S–2 in summer 1995 (see Fig. 4B), when riffles were intermittent, further supports this idea. Such benign physico-chemical conditions are contrary to those reported for other intermittent streams where the non-flowing period may extend for several months (Snellen and Stewart 1979, Fisher et al. 1982, Hill and Gardner 1987, Bottorff and Knight 1988, Miller and Golladay 1996), and oxygen, temperature, or streamwater chemistry may exceed tolerance levels of many benthic species (Clifford 1966, Williams and Hynes 1976, Williams 1987, Boulton and Lake 1990, Towns 1991).

Despite the generally high faunal similarity among streams of contrasting permanence, I could not reject the hypothesis that assemblage structure and permanence were unrelated. First, both measures of taxa richness (total and EPT) and Shannon diversity were significantly (and always positively) correlated with permanence (Table 5), particularly during 1994, which fit predictions. Several of the explanations advanced by others for increases in richness and diversity with increasing permanence (e.g., increased hydrologic and habitat stability, increased colonization and survivorship by flow-dependent taxa, see Boulton and Suter 1986, Delucchi 1988) may apply to species in these streams. Second, the significant correlation between stream-specific Jaccard similarity to the normally perennial S–1 and permanence scores of the other 5 streams observed for 1995 coupled

with the borderline ($p = 0.12$), albeit non-significant, trend for 1994 (Fig. 6), suggest that degree of permanence may influence a stream's faunal similarity to that of other, more permanent streams. The small sample size ($n = 5$, df = 3), however, makes these regression analyses subject to high type I or type II error rates, even with an adjusted α-level of 0.10. That any relationships were detectable under these circumstances is remarkable given the limited statistical power, because error associated with even 1 data point can greatly influence significance. Assuming these relationships are valid, it is unclear whether the non-significant relationship observed for 1994 reflects type II error or the presence of some other unmeasured factor that influenced community similarity independently of stream permanence. Third, some of the more common invertebrate populations clearly displayed non-random distributions (Fig. 5), either being restricted to permanent or normally intermittent streams, or showing an increase in density along the permanence gradient.

There was circumstantial evidence to support the hypothesis that year-to-year differences in riffle permanence resulting from variable precipitation accounted for some of the year-to-year differences in assemblage structure. The significantly higher Shannon diversity and total richness across all seasons for 1995 compared with 1994 (Table 4, Fig. 4), and like increases in density and total richness observed across streams during summer 1995 (Fig. 4), may have been influenced by rainfall patterns of the previous summer. Lower density and total richness observed for summer 1994 occurred during a wet summer that followed a dry summer (1993, Fig. 2), whereas the higher summer densities and richness during 1995 occurred during a normal summer that followed a wet summer (1994). If riffles in most of the streams had become intermittent for an extended period during 1993, and flow-dependent taxa decreased in abundance or were excluded from these habitats, increases in density and richness observed over the 2-y period could signal a recovery by some populations after the return of flowing water. Indeed, others have reported reduced faunal similarity between permanent and temporary habitats as the duration of drying in temporary habitats increases (Wiggins et al. 1980, Delucchi 1988, Schneider and Frost 1996), a likely situation for intermittent stream riffles during summer 1993.

Increased diversity and total richness and summer densities during 1995 may have represented higher colonization and survivorship over this relatively benign hydrologic period. This pattern coupled with the generally significant relationships between diversity and richness variables and permanence observed in 1994 (5 of 9 cases, Table 5), and fewer significant relationships in 1995 (1 of 9 cases), suggest that many species remained depressed in 1994 but recovered in 1995. In contrast, the significant negative relationships between permanence and the percent of non-insect taxa for summer and winter 1994 (Table 5) suggest that some of these taxa were favored by intermittent conditions during summer 1993, which persisted through 1994. However, the precise mechanism accounting for this pattern, as well as why the March 1994 relationship was exactly opposite (i.e., positive, Table 5) that of later seasons, is unclear.

Although correlative, these data are consistent with the idea that some species in these communities are influenced by riffle permanence, with their presence and abundance varying with hydrologic features of the previous year. It also underscores the need highlighted by others (Boulton and Lake 1992a) for innovative, longer-term studies designed to quantify the degree to which invertebrate assemblages are shaped by antecedent environmental conditions. Such historical time lags in the effects of disturbance, while acknowledged as important structural components of aquatic communities (Poff and Ward 1989, Resh and Rosenberg 1989) rarely have been quantified in streams (but see Boulton and Lake 1992a, Resh 1992).

Conclusions

I conclude that 1) small intermittent and permanent streams in the present study displayed generally high similarity in benthic fauna, 2) differences in benthic assemblages, at least in part, can reflect spatial and temporal variation in stream permanence, and 3) year-to-year variation in assemblage structure within a single stream can be as great as differences between streams of contrasting permanence within a given year. The fact that assemblages of normally intermittent streams do not differ greatly from those of nearby permanent streams has important implications for stream management plans, which often fail to recognize intermittent habitats as contributing substantially to stream biodiversity (Allan and Flecker 1993). My study shows clearly that invertebrates inhabiting intermittent streams, because of their high diversity and faunal similarity to permanent streams, deserve consideration in conservation plans designed to protect species and their habitats (Williams 1996).

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