

Recovery of Aquatic Macroinvertebrate Communities from Drought in Georgia Piedmont Headwater Streams

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ABSTRACT.—Drought is an important disturbance in stream ecosystems. From 1998–2002 Georgia suffered a major drought, causing many headwater streams to experience reduced flows or to dry completely. Six headwater streams in the Georgia Piedmont were selected and paired based on similarities in substrate structure (sand, bedrock or gravel substrate). Each pair consisted of a stream that dried completely during the drought and one that retained at least some surface water. Riffles were sampled with a core sampler, runs and pools were sampled with a Hess sampler and wood was sampled by randomly collecting pieces of at least 1 cm diameter. Samples were collected within 15 d of reflooding, then after 45, 75, 165, 255, 345 and 435 d. Cluster analyses were used to assess the relative effects of drought history (dried or residual water), stream condition and temporal change. In terms of drought recovery, all streams followed the same pattern of recovery, with a rapid recolonization period following the onset of surface flow. Community compositions were initially similar in most streams, but after 15 d each stream began to develop unique recovery patterns. The number of new taxa colonizing these streams began to level off around 165 d after rewetting. Neither the presence nor absence of residual water nor substrate composition appeared to significantly influence drought recovery patterns of invertebrates.

INTRODUCTION

Drought is an important disturbance to invertebrates in stream ecosystems. Studies have shown that invertebrate fauna of intermittent and perennial streams differ (Feminella, 1996). However, only a few studies have described the process of community recovery from temporary drying of perennial streams (Larimore *et al.*, 1959; Williams and Hynes, 1976b; Minshall *et al.*, 1983; Wood and Petts, 1999; Shivoga, 2001).

Williams and Hynes (1977b) concluded that aquatic invertebrates employ several basic methods of dealing with drought: burying in surface sediments, burying in deep sediment, burying under rocks, burying under leaf litter, persisting in standing pools, using crayfish burrows as refuge and escaping as aerial adults. Several invertebrates avoid desiccation by retreating to areas of the substrate that are still moist (Larimore *et al.*, 1959); *e.g.*, larvae of Plecoptera, Ephemeroptera, Coleoptera, Trichoptera and Diptera have been found in damp surface materials. Decapoda, Gerridae and Corydalidae have been observed retreating to wet chambers underneath flat rocks. Physiological tolerance of drought occurs mainly as diapause or dormancy (Larimore *et al.*, 1959; Williams, 2001). Life history modifications to cope with drying include rapid growth, short life cycles, small size, high powers of dispersal and generalist feeding habits (Williams, 1997). Some taxa are capable of using multiple methods to survive drought, whereas others are limited to a single method.

Following a period of drying, invertebrates may recolonize via active or passive migration (Williams, 1997). Active migration requires flight (*e.g.*, Hemiptera adults). Species that do not possess the powers of flight necessary to migrate unassisted use passive migration. Examples of taxa that migrate passively are bivalves and water mites, which can migrate

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attached to a host (Stehr and Branson, 1938; Williams, 2001). Colonization may occur by the adult insect itself, in the case of aquatic Coleoptera and Hemiptera or via laying eggs (*e.g.*, Ephemeroptera, Plecoptera, Trichoptera, Diptera) (Williams and Feltmate, 1992). Many insects migrate from nearby permanent water bodies, especially weak fliers such as Ephemeroptera and Plecoptera.

Invertebrates that burrow into the substrate to avoid desiccation return to the surface by vertical migration. Organisms that are known to migrate vertically from the sediment include Cyclopoida, Chironomidae, Oligochaeta, Cladocera, Coleoptera, Gastropoda, Decapoda and Acari (Williams and Hynes, 1976b). The importance of vertical migration would likely depend on the ability of invertebrates to burrow into the substrate (Minshall *et al.*, 1983), as well as the ability to persist in the substrate during drying. Minshall *et al.* (1983) found no invertebrates in the substrate up to a depth of 50 cm in the North Fork of the Teton River, whereas Larimore *et al.* (1959) observed that Plecoptera, Ephemeroptera, Coleoptera, Trichoptera and Diptera nymphs, as well as Gastropoda burrowed 30 cm or more into the substrate. Vertical migration may also occur from crayfish burrows (Williams, 2001). Microcrustacea, Oligochaeta, Amphipoda, Collembola and Chironomidae are capable of cohabiting with crayfish and migrating out of the burrow upon stream rewetting.

Many of the same organisms that migrate vertically also migrate upstream to colonize new areas (Williams and Hynes, 1976b). This includes Oligochaeta, Cyclopoida, Chironomidae, Cladocera and Acari. Williams and Hynes also note that Ostracoda, Bivalvia and Ephemeroptera migrate upstream (1976b). Upstream migration has been shown to be at its maximum during the summer in the Speed River in Ontario, with numbers of invertebrates peaking in August (Bishop and Hynes, 1969). Elmidae beetle larvae that had recently hatched and early instar Baetinae mayflies were two of the main contributors to the August peak in numbers.

When streamflow stops, some streams may still retain surface water in stagnant pools (Lake, 2000). The importance of residual pools to the colonization process of aquatic macroinvertebrates in dried streams has not been adequately assessed. Larimore *et al.* (1959) observed Ephemeroptera nymphs as well as larval and adult Coleoptera in the organic matter surrounding residual pools. During a period of intermittent streamflow, they also found that taxa typically inhabiting riffles had moved into pools to survive the dry period. Residual pools also provided refugia for algae in streams that dried (Robson and Matthews, 2004) and streams that retained pools of water during a drought had high densities of algae after flow returned. Streams without residual pools had slower algal growth, limiting this valuable food source for invertebrates. Williams and Hynes (1976a) emphasized the importance of algae as a food source for early colonizers.

Studies have shown great variation in the period of time required for the process of recolonization to be complete (Larimore *et al.*, 1959; Williams and Hynes, 1977a; Gore, 1979; Minshall *et al.*, 1983; Malmqvist *et al.*, 1991; Feminella, 1996; Wood and Petts, 1999; Shivoga, 2001). The amount of time largely depends on the size of the area affected, distance from sources of colonizers, length of dry period, degree of impact and season (Larimore *et al.*, 1959; Minshall *et al.*, 1983; Wood and Petts, 1999). Studies of larger streams have shown that invertebrate abundance and taxa richness can level off anywhere from 86 to 400 d (Minshall *et al.*, 1983; Shivoga, 2001). Smaller streams often show shorter recovery times from drought (Williams and Hynes, 1977a; Gore, 1979; Malmqvist *et al.*, 1991) and rapid colonization was observed in newly created artificial channels, with invertebrate densities leveling off after 90 to 200 d.

This study assessed the invertebrate recovery process in six Georgia headwater streams subjected to an extreme drought. Goals included: (1) assessing the period of time needed

for recovery in terms of taxa richness and invertebrate abundance, (2) determining the impact of residual pools on drought impacts and recovery time and (3) examining how drought impact and community recovery varied in streams with different substrates (gravel, sand, bedrock). We expected that recovery time would be similar to the studies mentioned above for smaller streams (Williams and Hynes, 1977a; Gore, 1979; Malmqvist *et al.*, 1991), with recovery occurring between 90 and 200 d. The recovery time was expected to be shorter in the streams that retained residual pools than in the streams that dried completely, due to these pools acting as refugia for organisms. Lastly, we expected streams with similar substrates to behave in similar ways as far as drought impact and community recovery.

METHODS

STUDY SITES

We studied headwater streams of the Upper Oconee River watershed in northcentral Georgia. The Oconee River Basin is divided into two physiographic regions: the Piedmont and the Coastal Plain. The streams used in this study were all located in the Piedmont region, which makes up about 60% of the 8576 sq km basin. The predominant soil types are sandy loam clay to fine sandy loam. This area has a temperate climate with an average annual precipitation of about 127 cm. Evapotranspiration rates range from 66–89 cm per year and average annual runoff is between 30.5 and 76 cm (Georgia Department of Natural Resources, 1998).

A severe drought occurred in the study region from 1998 to 2002. Annual precipitation for the state of Georgia fell to 103.84 cm in 1999 (normal ~147 cm per year), making it the sixth driest year in a 104-y period (NOAA). Precipitation remained well below normal throughout 2000 and 2001. Streamflow in the Oconee River Basin, as estimated from local surface-water monitoring stations, dropped to 12–34% of normal flow by August 2002 (USGS records). In September 2002, rainfall from Tropical Storm Hanna ended the drought. Rainfall over a 3-d period (September 13–15) ranged from 6.5 cm (Eatonton, GA) to 10.7 cm (Watkinsville, GA) (Georgia Automated Environmental Monitoring Network, 2005). Immediately after the storm, streamflow in the Oconee River Basin increased to 50 to 100% of normal.

We selected six small streams (drainage area = 1.02 to 3.40 sq km) in the Upper Oconee River Watershed for this study (Fig. 1). All streams were in areas that were owned by government agencies and had been protected for 40 to 100 y. Although pristine streams are very rare in the Piedmont, the six study streams were perhaps among the best protected in the Georgia Piedmont. Sites were chosen on the basis of streamflow and substrate. Three streams had dried completely during the drought and three streams had retained some residual water in the form of isolated pools.

Streams that had dried or retained water during the drought were paired by substrate characteristics. Table 1 shows the descriptive metrics for each stream. Gravel-Wet and Gravel-Dry were located in the Oconee National Forest, Putnam County. These streams were sandy and gravel bottomed with a thick layer of silt and clay and some small cobble. Sand-Wet and Sand-Dry were both located near each other in the Oconee National Forest of Greene County. These streams were predominantly sandy-bottomed with a small amount of gravel, but no cobble. Bedrock-Wet was located in the State Botanical Garden of Georgia in Clarke County and Bedrock-Dry was located in the Rock Eagle 4-H Center in Putnam County. These streams were the only pair not located in close proximity. The bedrock streams both had predominantly large cobble as their substrate.

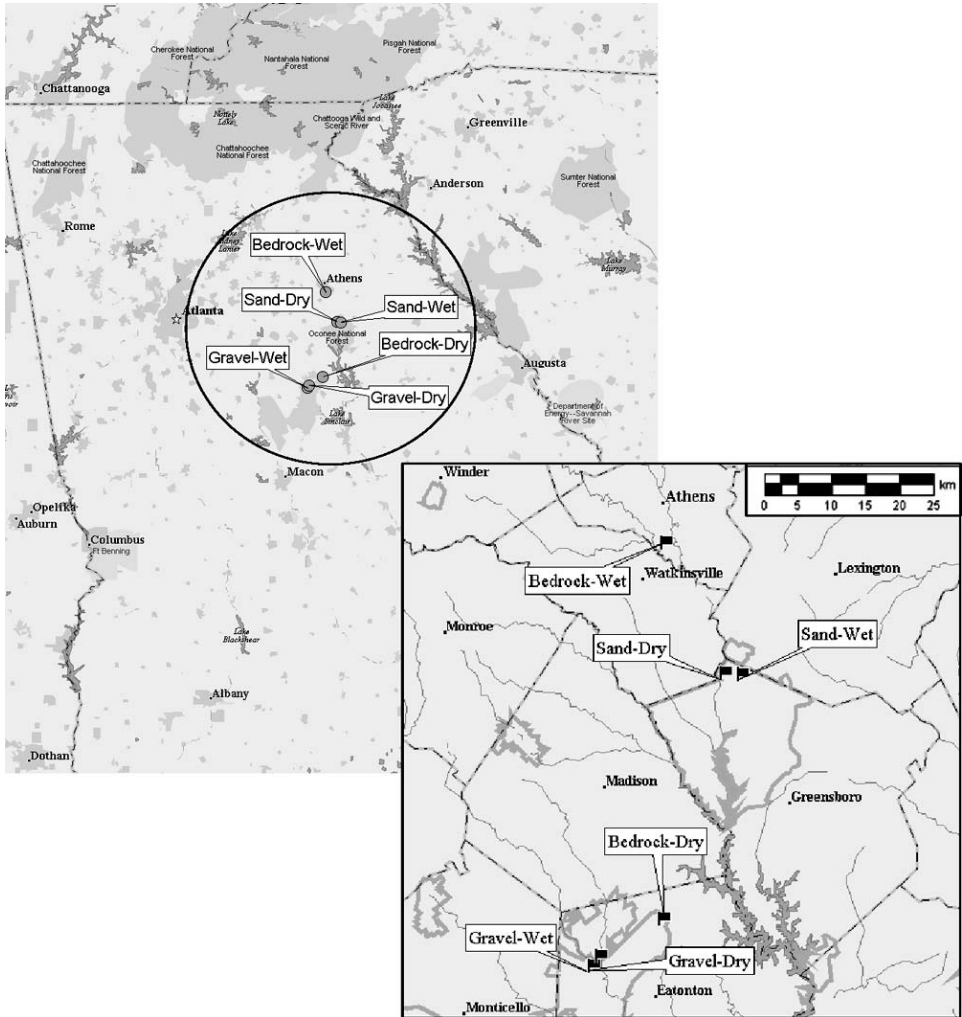


FIG. 1.—Study stream locations in the Piedmont physiographic region of Georgia

SAMPLING METHODS

Sampling was initiated in late September 2002 during the first 15 d after tropical rains had ended the drought. Streams were then sampled after 45 (October) and 75 (November) d and then every 3 mo for 1 y (February, May, August, November 2003). In gravel and sand streams, three subhabitats existed – riffles, runs and pools. Three randomly selected locations for each of the three subhabitats were sampled in each of these streams ($N=9$ per stream). Two subhabitats existed in bedrock streams – riffles and runs. Four randomly selected locations for each of the two subhabitats were sampled in each bedrock stream ($N=8$ per stream).

Riffles were sampled with a core sampler (27.5 cm^2) that was forced into the streambed and all of the contents down to 7.5 cm were removed. The water in the core was removed

TABLE 1.—Descriptive metrics of 6 study streams. Standard deviation ($n = 10$) for stream width and bankfull width measurements is given in parentheses

	Gravel-Wet	Gravel-Dry	Sand-Wet	Sand-Dry	Bedrock-Wet	Bedrock-Dry
Stream Width (m)	1.12 (0.11)	1.15 (0.02)	2.51 (0.37)	1.87 (0.08)	1.49 (0.15)	1.79 (0.11)
Bankfull Width (m)	2.8 (0.65)	2.43 (0.47)	5.05 (0.68)	3.15 (0.35)	2.22 (0.26)	2.62 (0.32)
Drainage Area (sq km)	1.14	1.03	3.4	1.39	1.02	3.19
Substrate Composition:						
% <12 mm	42	34	96	99	35	24
% 12–48 mm	51	55	4	1	29	33
% >48 mm	7	11	0	0	36	43

and filtered through a 250 μm sieve and the contents were rinsed into the rest of the collection. Because the corer was relatively small, three core sub-samples were taken in each riffle and combined into a single composite sample (9 subsamples used to create 3 samples). Runs and pools were sampled with a Hess sampler (860 cm^2 , 250 μm mesh, Wildlife Supply Co., Buffalo, NY, U.S.A.). The Hess sampler was forced into the streambed and the top 15 cm of substrate and water were washed into the mesh collection bag. Residual water was filtered through the bag as the sampler was removed from the substrate. Because the Hess samples a large area, only one collection was gathered for each of the runs or pools sampled.

Wood can be an important habitat for invertebrates in southeastern streams and neither a corer nor Hess sampler samples this material adequately. Wood samples were collected in each of these streams by gathering randomly selected pieces of woody debris that were at least 1 cm in diameter. Large wood snags were rare and were not sampled. Wood pieces were measured and surface area was calculated.

All samples were preserved in 95% ethanol and returned to the lab. Hess and core samples were elutriated to separate the organic and inorganic material and the organic material was divided into >1 mm and <1 mm sized portions by sieving. Large samples were sub-sampled as needed and macroinvertebrates were removed from the organic material under a dissecting microscope. Wood pieces were scrubbed to remove all organisms and all macroinvertebrates were removed from debris under a dissecting microscope. Macroinvertebrates were identified to genus or the lowest taxonomic category possible using keys (*see* Pennak, 1989; Peckarsky *et al.*, 1990; Eppler, 1996; Merritt and Cummins, 1996).

To justify our pairing of streams by substrate, pebble counts were performed in each stream based on the method developed by Wolman (1954). The study reach was divided into 10 transects and 10 substrate particles were randomly selected at each transect for a total sample of 100 grains. Particles were only sampled from within the stream channel. The intermediate axis of each grain was measured and placed into size categories.

STATISTICAL ANALYSES

Cumulative and total numbers of taxa were plotted for each stream for all seven sampling dates. Logarithmic trendlines were plotted on the total number of taxa graph and polynomial trendlines were plotted on the cumulative number of taxa graph to assess colonization patterns. Hierarchical, polythetic, agglomerative cluster analyses with a Euclidean distance measure and Ward's linkage method were used to assess variation in substrate composition and taxa abundances among streams or sampling periods. Cluster analyses were completed using PC-ORD Version 4.1 (MJM Software Design, Glenden Beach, OR, U.S.A.).

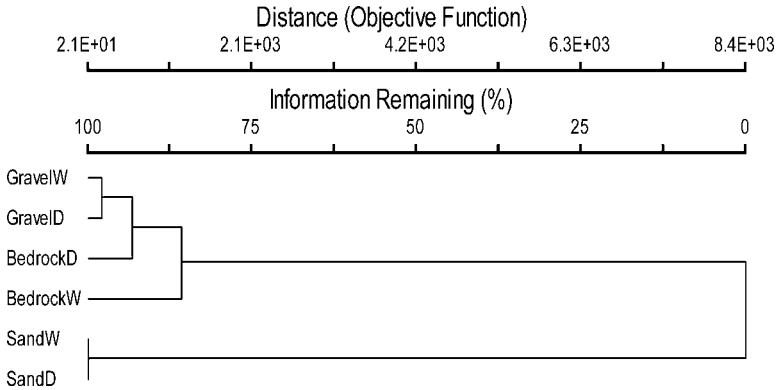


FIG. 2.—Cluster analysis of pebble counts in all 6 streams

Rare taxa (those that occurred in only one sample) were not included in cluster analyses. Those individuals that could not be identified were dealt with in two ways. If there was an individual that could not be identified and only one identifiable subgrouping existed (*e.g.*, one genus in a family), the unknown individual was combined with the others using the higher taxon (*e.g.*, family). If there was an individual that could not be identified and multiple groupings existed (*e.g.*, several genera from a family), the individual was deleted from the analysis. Habitat-weighted invertebrate abundances were calculated for each stream. All habitat-weighted abundances were $\log_{10}(x + 1)$ transformed to meet normality and equalize variance assumptions.

We first analyzed the pebble counts to examine similarities and differences in substrate composition among the six streams. We then analyzed invertebrate communities in all six streams by month (September- 15 d, October- 45 d, November- 75 d) for the first 3 mo after rains returned. We also assessed invertebrate communities in all streams in November 2002 and November 2003 to assess recovery after 1 y.

RESULTS

SUBSTRATE COMPOSITION

Cluster analysis of the pebble counts separated the six streams into two distinct groups (Fig. 2). The two sand streams clustered together as being very similar to each other in substrate composition and markedly different from the other four streams. The gravel and bedrock streams generally clustered together, with the gravel streams being more similar to each other than the bedrock streams.

INVERTEBRATE COMMUNITY COMPOSITION

We collected and identified a total of 136 taxa (including 32 rare taxa which were not used for statistical analysis). The orders with the highest taxa richness were Diptera, with 18 families and 25⁺ genera and Trichoptera, with 12 families and 15⁺ genera. The most diverse families were Gomphidae, Elmidae and Tipulidae with 6, 6 and 7 genera, respectively. The most abundant taxon was Chironomidae, composing 66% of the total. Other abundant taxa included: an unknown family of Plecoptera (5%), Ceratopogonidae (3%), Acari (2%), Ostracoda (2%), Ancylidae (2%) and Cyclopoida (2%).

RECOVERY PATTERNS

Invertebrate communities in all six streams recovered quickly following the return of water flow. Within 15 d of rewetting, the number of taxa present in the gravel, sand and bedrock streams that previously had no surface water was 19, 39 and 17, respectively. The number of taxa present in the streams that retained pools was 30, 23 and 10. Only in the pair of gravel streams did the channel that retained water have more taxa than the channel that dried. Thereafter, streams exhibited different patterns by substrate (Fig. 3A). The gravel and bedrock streams had a large increase in the total number of taxa during the first 75 d of rewetting. Total numbers of taxa then began to level off, with only slight increases in taxa apparent throughout the remainder of the study. The sand streams on the other hand, showed no change in the total number of taxa present over time.

Cumulative taxa curves (Fig. 3B) provided some additional information. In every stream, there was a large increase in the number of colonizing taxa from 15 d to 45 d, with 14 to 21 new taxa being found per stream. Because total numbers of taxa in the sand streams did not change temporally, the increase in cumulative taxa reflected some taxa replacements. In the gravel and bedrock streams, this increase represented taxa additions. From 45 d to 75 d, only 2 to 9 new taxa per stream were collected and by February (165 d), the number of new taxa colonizing these streams leveled off. Within this short time, the available pool of colonists had already been largely exhausted. Accumulation rates of taxa in all streams were similar regardless of substrate or the presence or absence of water during the drought.

INITIAL RECOVERY PERIOD

The cluster analysis of invertebrate communities for the first 3 mo indicated two clear groupings (Fig. 4). The first grouping (lower cluster in dendrogram) included the September samples, which were taken within 15 d of the resumption of flow, for all streams except the Gravel-Dry stream. The initial communities found in these five streams were more similar to each other than to the communities found within the same streams in the following months. Early colonizers that were found in all five streams included: Ceratopogonidae, Chironomidae and *Hexatoma* (Table 2). Invertebrates that were found in some of these five streams, but that were unique to September included: *Ancyronyx*, *Crangonyx*, *Eccoptura*, *Glutops*, *Psychoda* and *Rhagovelia*.

The second grouping in the cluster analysis (upper portion of dendrogram) included mainly the October and November samples. Within this grouping, clustering occurred by stream instead of by month for the Bedrock-Wet, Gravel-Wet, Bedrock-Dry and Sand-Dry streams. The invertebrate communities present after 45 days and 75 d were similar within each of these streams. New taxa that were found in October and November included: *Pisidium*, *Tipula*, Cladocera, Ostracoda, Leptophlebiidae, *Molophilus* and one family of Gastropoda.

An anomaly occurred in the October–November subgrouping, with all samples for the Gravel-Dry stream clustering together, including September. Taxa that were common to all months for the Gravel-Dry stream included: *Pisidium*, *Dubiraphia*, *Stenelmis*, *Anchytarsus*, Cyclopoida, Harpacticoida, Cecidomyiidae, Chironomidae, Ceratopogonidae, Oligochaeta, Ostracoda, Acari and one genus of Plecoptera. The Gravel-Dry stream had similar invertebrate communities during all 3 months, indicating that it was less affected by the drought.

The September, October and November samples for the Sand-Wet stream also clustered together as having similar communities, indicating that the invertebrate community changed relatively little over the first 3 mo. The invertebrate community present in September was initially similar to the communities present in the other six streams, but the

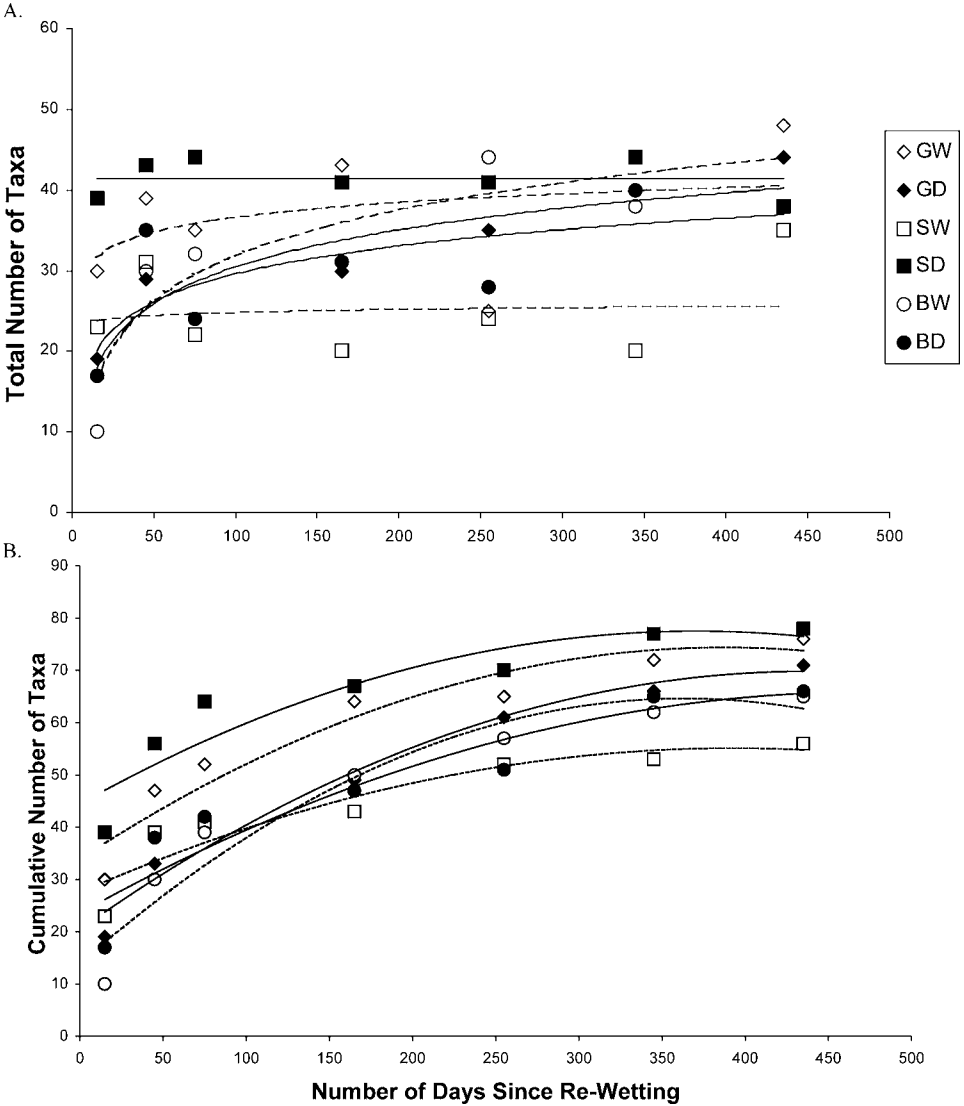


FIG. 3.—Total (A) and cumulative (B) number of taxa found in 6 study sites over the period studied. Streams had either gravel (G), sand (S) or bedrock (B) substrates, and had either dried (D) completely during the drought (filled symbols and solid trendlines) or retained some water (W) (open symbols and broken trendlines)

communities present in October and November differed from the other streams with several normally dominant taxa being rare, including *Pisidium*, *Stenelmis*, *Allocapnia*, Copepoda, Cladocera, Cecidomyiidae, Gastropoda, Oligochaeta and Acari. Chironomidae was the dominant taxa in this stream comprising 91% of the total abundance in October and 96% of the total abundance in November.

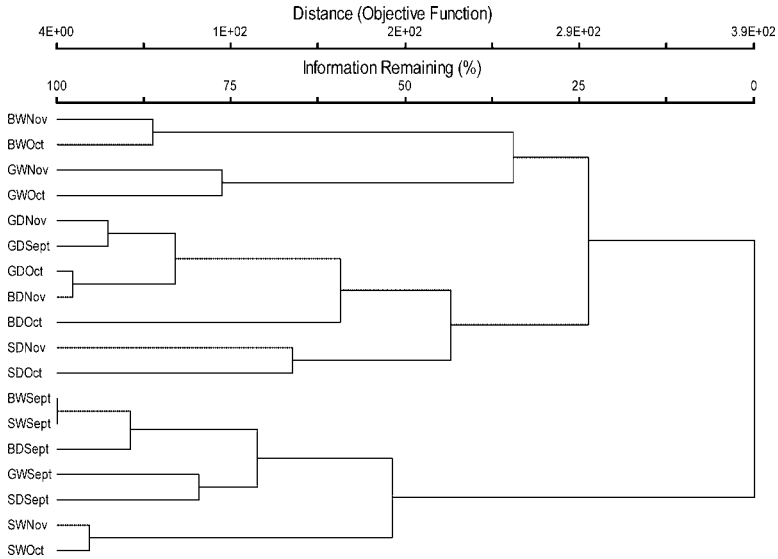


FIG. 4.—Cluster analysis of invertebrate abundances in all 6 streams for the first 3 mo after resumption of flow

LONG-TERM RECOVERY

The cluster analysis of the November samples for 2002 (75 d of recovery) and 2003 (1 y of recovery) showed grouping by stream and by year (Fig. 5). The first major division separates out the November 2003 samples for Bedrock-Wet, Gravel-Wet and Gravel-Dry (lower cluster on dendrogram) as having different communities than the November 2002 samples in these streams (upper cluster on dendrogram). Eleven taxa common to all three streams in November 2003 were absent or rare in November 2002 (*Dixa*, *Hemerodromia*, *Tallaperla*, *Eccoptura*, *Lepidostoma*, *Tipula*, *Stenonema*, *Cheumatopsyche*, *Allocapnia*, Simuliidae and Baetidae). Even after a year, recovery was ongoing in those three habitats.

Two streams, Sand-Wet and Sand-Dry, clustered together by year, indicating similar invertebrate communities in November 2002 and November 2003 (Fig. 5). Chironomidae was the most abundant taxon in both streams during both years. Non-biting midges composed 73% of the 2002 sample and 70% of the 2003 sample in the Sand-Dry stream. In the Sand-Wet stream, Chironomidae composed 96% of the 2002 sample and 92% of the 2003 sample. These two streams recovered the most rapidly. The Bedrock-Dry stream had an anomalous pattern, sharing characteristics with the gravel and Bedrock-Wet streams in the initial stages of recovery and with the sand streams after 1 y of recovery.

DISCUSSION

This study focused on the recovery of invertebrate communities from drought in six headwater streams. In terms of taxa richness, all streams followed a similar pattern of recovery, with a rapid recolonization period occurring in the initial months following the onset of surface flow. We had expected that the streams that retained some water during the drought would be less impacted and would recover more quickly, but this was not the case. Taxa that survive drought in or around isolated pools (*see* Larimore *et al.*, 1959; Williams and Hynes, 1977b) did not appear to buffer impacts of drying in our study streams.

TABLE 2.—Habitat-weighted abundances of major taxa collected in September, October and November 2002 and November 2003

			September						October					
			GW	GD	SW	SD	BW	BD	GW	GD	SW	SD	BW	BD
Non-Insects														
Acari			13	98	0	5	0	0	854	223	13	376	63	276
Amphipoda	Crangonyctidae	<i>Crangonyx</i>	0	0	0	3	0	0	0	0	0	1	1	0
Bivalvia	Sphaeriidae	<i>Pisidium</i>	0	67	0	2	0	1	101	136	1	50	5	119
Cladocera			0	0	0	0	0	0	19	5	0	0	8	56
Copepoda	Calanoid		0	0	0	0	0	0	115	1	0	0	0	0
	Cyclopoida		7	20	0	0	0	1	427	63	35	5	13	656
	Harpacticoida		0	19	0	0	0	12	62	62	6	132	8	151
Decapoda	Cambaridae		1	1	1	1	0	11	1	8	1	3	0	7
Gastropoda	Ancylidae		0	0	0	0	0	0	12	0	0	0	0	0
	Physidae		0	2	0	1	0	0	0	0	10	168	0	4
	Planorbidae		0	0	0	0	0	0	0	0	4	3	0	1092
	Unknown1		0	1	0	0	0	0	0	0	0	0	99	0
Oligochaeta			0	41	1	9	3	4	287	588	94	140	53	654
Ostracoda			0	4	0	0	0	0	226	116	28	0	9	43
Insects														
Collembola	Entomobryidae	<i>Seira</i>	0	6	1	0	0	0	0	0	1	0	0	20
	Sminthuridae		0	0	0	0	0	0	0	0	0	0	0	0
Ephemeroptera	Baetidae		0	12	1	0	0	4	16	0	2	5	0	0
	Ephemerellidae	<i>Ephemerella</i>	0	0	0	0	0	0	0	0	0	0	0	0
	Ephemeridae	<i>Hexagenia</i>	0	0	0	0	0	0	0	0	0	0	0	0
	Heptageniidae	<i>Stenonema</i>	3	1	0	0	0	0	20	3	0	7	4	4
	Leptophlebiidae		0	0	0	0	0	0	24	0	103	17	3	43
Plecoptera	Capniidae	<i>Allocapnia</i>	0	27	0	0	0	0	0	0	0	0	0	0
	Peltoperlidae	<i>Tallaperla</i>	0	0	0	0	0	0	0	0	0	0	0	0
	Perlidae	<i>Eccoptura</i>	3	0	0	0	0	0	0	0	0	0	0	0
	Unknown1		29	35	8	2	5	33	111	80	586	29	280	331
Hemiptera	Veliidae	<i>Rhagovelia</i>	3	0	0	0	0	0	0	0	0	0	0	0
Trichoptera	Calamoceratidae	<i>Anisocentropus</i>	0	0	0	0	0	0	0	0	0	1	0	0
	Helicopsychidae	<i>Helicopsyche</i>	0	2	0	0	0	0	118	0	0	0	0	0
	Hydropsychidae	<i>Cheumatopsyche</i>	3	0	4	4	0	0	36	0	0	3	53	0
		<i>Diplectrona</i>	0	0	0	0	0	0	0	0	0	0	0	0
		<i>Unknown1</i>	0	0	0	0	0	0	0	0	0	0	8	0
	Lepidostomatidae	<i>Lepidostoma</i>	3	0	0	0	0	0	0	0	0	0	0	0
	Odontoceridae	<i>Psilotreta</i>	25	0	0	10	0	0	113	0	0	2	0	12
	Philopotamidae		0	0	0	0	0	0	0	0	0	0	0	16
	Psychomyiidae	<i>Lype</i>	2	0	0	1	0	0	1	0	0	1	0	0
Coleoptera	Dytiscidae	<i>Neoporus</i>	0	1	0	0	0	7	15	16	8	17	1	25
	Elmidae	<i>Ancyronyx</i>	0	0	1	18	0	0	0	0	2	2	0	0
		<i>Dubiraphia</i>	18	5	6	35	0	0	5	59	6	42	0	3
		<i>Gonielmis</i>	0	15	0	0	0	0	0	0	0	1	0	0
		<i>Macronychus</i>	4	0	0	0	0	0	0	0	0	5	0	0
		<i>Microcyloepus</i>	0	0	0	58	0	0	0	0	0	200	0	4
		<i>Stenelmis</i>	34	23	2	42	9	0	102	52	2	23	178	57
	Psephenidae	<i>Ectopria</i>	0	0	0	0	8	0	10	0	1	0	49	8
	Ptilodactylidae	<i>Anchytarsus</i>	56	8	4	108	22	0	161	16	0	28	33	25
Diptera	Cecidomyiidae		0	44	8	12	14	111	0	43	15	148	81	676
	Ceratopogonidae		18	50	104	151	56	33	295	383	151	115	386	197
	Chironomidae		293	386	1309	779	576	28	705	151	11401	962	1724	492
	Dixidae	<i>Dixa</i>	1	2	0	1	0	0	0	0	0	0	0	0
	Empididae	<i>Hemerodromia</i>	0	0	0	0	0	0	0	0	4	0	0	0
	Pelecorynchidae	<i>Glutops</i>	0	3	0	3	0	4	0	0	0	1	0	0
	Simuliidae	<i>Simulium</i>	0	0	0	0	0	4	0	0	0	0	4	0
	Tabanidae	<i>Chrysops</i>	0	0	25	2	0	9	0	1	14	11	0	4
	Tipulidae	<i>Hexatoma</i>	88	5	60	8	8	14	171	0	24	27	33	70
		<i>Molophilus</i>	0	6	0	1	0	0	0	0	7	0	0	4
		<i>Tipula</i>	0	1	0	1	0	0	0	0	3	10	8	4

TABLE 2.—Extended

November 2002						November 2003					
GW	GD	SW	SD	BW	BD	GW	GD	SW	SD	BW	BD
969	201	1	427	76	125	1419	314	0	291	414	639
0	0	0	0	0	1	0	6	0	0	0	5
124	45	2	64	22	124	30	21	1	26	19	5
452	51	0	0	0	10	10	192	0	159	0	0
0	0	0	0	0	0	0	0	0	0	0	0
190	13	82	68	8	118	908	345	251	59	121	587
166	37	0	78	16	115	291	329	25	214	10	743
0	0	0	5	0	0	8	4	0	17	1	4
0	0	1	194	0	0	257	217	31	3892	0	254
0	0	4	55	0	0	0	0	28	71	0	0
0	0	0	1	0	118	0	0	5	0	0	0
0	0	0	6	74	24	0	0	0	66	9	0
487	107	16	88	85	401	7	38	23	82	19	18
125	18	19	39	257	44	26	10	5	81	4772	2
1	0	0	15	112	0	5	0	0	11	220	177
0	0	0	1	0	0	0	26	0	112	0	0
3	0	1	25	20	0	4547	56	19	0	147	1
0	0	0	0	0	0	52	0	0	0	0	0
0	0	0	13	0	0	1	2	17	84	0	21
13	0	0	48	8	0	2467	263	200	1148	773	438
0	0	0	19	0	0	269	7	75	105	0	0
0	0	1	9	1016	0	1876	627	135	0	3359	0
0	0	0	0	0	0	7	33	0	0	8	0
0	0	0	0	0	0	13	10	0	0	12	0
110	65	44	64	134	41	0	0	468	362	2	424
0	0	0	0	0	0	0	0	0	0	8	0
0	0	0	12	0	0	2	16	0	25	0	3
16	0	0	0	0	0	109	0	0	0	0	0
10	0	5	3	8	0	633	3	88	17	41	86
0	3	0	0	0	0	0	29	0	0	464	667
0	0	0	0	33	0	1139	0	0	0	0	0
0	0	0	5	0	0	3	29	1	0	367	1
26	0	0	1	20	0	23	0	0	0	0	0
0	0	0	0	12	0	92	115	0	0	0	1263
1	0	1	2	17	0	51	0	1	8	36	0
0	3	0	11	0	22	14	11	12	34	0	6
0	0	0	0	0	0	0	0	0	0	0	0
41	6	2	33	0	20	46	285	1	302	0	45
0	0	0	65	0	0	0	0	0	0	0	0
5	0	1	21	0	0	38	0	0	72	8	4
0	0	0	0	0	0	0	0	0	0	0	0
73	33	1	4	71	38	180	131	0	1	71	0
7	6	0	0	18	0	0	0	0	0	0	49
75	13	0	8	33	0	220	574	0	10	70	12
17	113	38	90	100	204	25	38	62	125	115	4
1154	243	417	143	376	268	407	184	397	201	633	23
1276	78	17492	4633	3138	1176	16269	6066	26025	18473	11623	10864
0	0	0	0	0	0	137	74	36	1	46	53
0	0	2	2	0	0	84	32	58	152	33	18
0	0	0	1	0	1	0	26	0	0	0	0
0	0	1	0	12	0	295	52	111	3	61	0
13	0	4	6	0	0	2	1	11	17	0	11
91	1	81	2	43	16	282	0	93	8	118	0
0	10	8	16	8	4	0	0	4	5	0	0
0	5	1	28	8	0	30	67	77	36	51	107

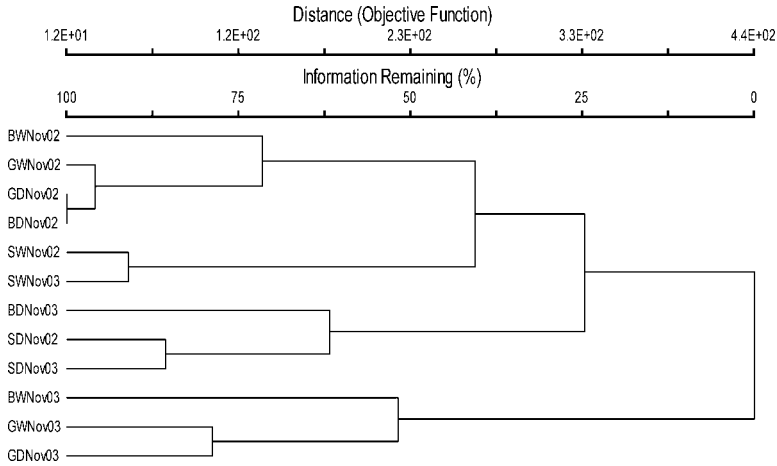


FIG. 5.—Cluster analysis of invertebrate abundances in all 6 streams for November 2002 and November 2003

Community compositions, however, changed markedly during the initial stages of recovery. In five of the six streams, similar invertebrate communities existed after 15 d of recovery. Several of the taxa found at this time are capable of surviving drought within the streambed. Oligochaetes survive drought by forming protective cysts (Williams, 2001), or by retreating down into the substrate (Williams and Hynes, 1976b). Crayfish retreat to wet areas under rocks (Larimore *et al.*, 1959) or in deep burrows (Williams and Hynes, 1976b). Riffle beetles, including *Stenelmis* and *Dubiraphia*, survive drought by burrowing into the moist substrate of exposed riffle subhabitats (Larimore *et al.*, 1959). Chironomidae, as well as other larval Diptera, also burrow into fine sediment to find moisture (Larimore *et al.*, 1959; Williams and Hynes, 1976b). However, after the first 15 d of recovery, each stream began to develop unique recovery patterns. The streams developed their own community structures, regardless of substrate or past presence of surface water during the drought.

Over the longer term, substrate composition appeared to have more of an effect on recovery. The sand streams had similar communities in November 2002 and 2003, indicating rapid recovery. On the other hand, the gravel streams and the Bedrock-Wet stream had different communities in November 2002 and 2003, indicating long-term impact by the drought. The sand streams may have recovered quickly because they were dominated by Chironomidae, which have the ability to burrow down through the sand to find moist areas in the substrate and also colonize aeri ally very rapidly. However, we did not identify Chironomidae genera and generic compositions of midges may have differed in sand streams between years. Wright and Symes (1999) also found that Chironomidae were abundant during periods of drought.

The Gravel-Dry stream exhibited the most anomalous recovery pattern. A similar invertebrate community existed throughout the first 3 mo of the study, indicating rapid recovery from the drought. However, very different communities existed in November 2002 and November 2003, indicating long-term recovery. We believe that recovery was ongoing in this stream due to the recovery pattern exhibited by this stream. In the absence of the October sample, total number of taxa increases linearly over time. The reason for a larger number of taxa being present in October than in November 2002 is unknown, but could be a smaller disturbance that occurred only in this stream.

The results of our study in many respects mirror those found by other researchers. Rapid colonization immediately following the resumption of flow had been reported by Williams and Hynes (1977b), Malmqvist *et al.* (1991), Miller and Golladay (1996), Shivoga (2001) and Wright *et al.* (2004). In our study, the cumulative number of taxa present in all six streams (Fig. 3B) began to level off around 165–255 d, which is in agreement with what Malmqvist *et al.* (1991) found in a man-made stream in Sweden where the number of cumulative taxa leveled out at around 200 d and what Minshall *et al.* (1983) found in the North Fork of the Teton River where colonization rates began to level off after 220 d. However, our finding that communities in some streams were still changing after 1 y suggests that recovery can be a longer-term process, as found by Wood and Petts (1999) and Wood and Armitage (2004).

Droughts, as categorized by Lake (2003), can be seasonal or “supra-seasonal” and the drought that we studied would be considered supra-seasonal. Supra-seasonal droughts are characterized by a longer duration, usually continuing through more than one season. Studies on supra-seasonal droughts have been limited, but have shown dramatic impacts on invertebrate communities (Boulton *et al.*, 1992; Wood and Petts, 1994, 1999; Wright and Symes, 1999; Wright *et al.*, 2004; Wood and Armitage, 2004). Longer droughts have been shown to have a greater effect of community composition than shorter droughts (Boulton, 2003; Fritz and Dodds, 2004). The extended recovery process as compared to some of the studies cited above may be due to the extended nature of the drought studied.

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