Late-summer drawdown and invertebrate assemblages in intermittent Alabama streams

Evelyn Boardman
Environmental Science, University of Vermont

Abstract:

Intermittent streams of the southeastern US and elsewhere have traditionally been considered ephemeral habitats, and thus less focus has been placed on their ecological significance, either in research or management than that of permanent streams. Feminella (1996) developed an index of stream permanence to rank relative intermittency in six streams within the Talladega National Forest of Alabama. For the 1996 study, the streams were not sampled repeatedly over the summer period of intermittence to assess temporal variation in benthic response to drying. The goal of my research was to describe in more detail for these streams (a) how benthic fauna respond to a gradient of stream permanence; (b) differences in the abundance and composition of invertebrate assemblages during wet and dry periods of stream flow; and (c) watershed conditions besides permanence that may influence invertebrate assemblages. Invertebrates were collected first during late May through early June and again in late July, a drier portion of the summer. The water level drawdown in 2012 was unprecedented compared to in previous years. As a result, the majority of our July samples needed to be excavated from dry streambeds. For the first time, pressure transducers were installed in the streams for use in calculating physical metrics from continuous stage data that were previously unavailable. Additionally, I supplemented in-stream physical measurements with variables derived from geospatial analyses of the intermittent streams' watersheds.

Riffle drawdown was associated with greater invertebrate densities and greater proportions of assemblages made up of predators. Communities may be concentrated as water levels decrease, creating conditions favorable to predators seeking prey. Sites with higher flow were associated with filtering organisms, higher diversity, and evenly distributed assemblages. Sustained flow could create conditions favorable to diverse assemblages, including organisms requiring flow to filter out organic matter, that are not dominated by one or a few tolerant species. Watershed slope and area were good predictors of a number of metrics describing invertebrate assemblages. The possibility that these watershed characteristics could be related to hydrologic permanence suggests the need for further assessment of discharge and other physical variables pertaining to these streams. Such data would enhance our understanding of the factors driving invertebrate assemblage composition within intermittent streams.

Literature Review:

Stream ecosystems connect landscapes longitudinally, laterally, and vertically (Allan & Castillo, 2009). The ecology of streams in temperate northern latitudes has been well studied compared to that of streams in the tropics or arid climates. Intermittent streams of the southeastern US and elsewhere have traditionally been considered ephemeral habitats, and thus less focus has been placed on their ecological significance, either in research or management. Ephemeral streams flow mostly during, and for a short period of time following, storm events, whereas intermittent streams flow most of the year but experience seasonal temporary drying (Hansen 2001).

Intermittent and ephemeral streams comprise ~60%, or 32,000,000 km, of total stream length in the contiguous US (Nadeau and Rains 2007). While intermittent streams were found to have ecologically significant invertebrate communities, a case study of the Chattooga watershed in Georgia found that USGS topographic contour maps identified only ~20% of the stream network, which included perennial, intermittent, and ephemeral streams (Hansen 2001). In the Chattooga Basin, ~17% of the streams are intermittent; 28% are perennial; and the rest are ephemeral (Hansen 2001). Thus, intermittent streams comprise a significant portion of the flowing streams in a watershed.

Investigations of terrestrial and aquatic ecosystems are often treated as separate studies, and this is appropriate considering the complex interactions within these ecosystems and the physical separation between them. However, distinguishing between aquatic and terrestrial ecosystems, as they are traditionally defined, is problematic in intermittent streams, which exhibit characteristics of both ecosystems as they transition between wet and dry phases (Fritz and Feminella 2011).

Individual physical and chemical measurements provide a “snapshot” of stream conditions at the time of sample collection. Biological measurements, such as invertebrate sampling, on the other hand, provide insight into the recent history of a stream integrated over the age of the organisms (Resh et al. 1996). Specifically, macroinvertebrates are particularly useful in biological monitoring because of their sensitivity to in-stream disturbance over their life cycles (Resh et al. 1996). Several biotic measures documenting invertebrate tolerances as they relate to pollution and other sources of degradation of stream ecosystems have been developed (Hilsenhoff 1988).

Hydrologic differences in stream ecosystems are reflected in the response of biotic communities to stream flow. For example, invertebrate production has been shown to decrease with the drying of intermittent stream channels in Maine (Chadwick and Huryn 2007), while research on invertebrate assemblages in intermittent Piedmont streams in Alabama’s Talladega National Forest indicated that benthic fauna differed relatively little along a gradient of flow permanence within the same basin, although overall taxa richness and diversity increased with increasing stream permanence (Feminella 1996). Seventy five percent of the species found in the latter study occurred at all sample sites, whereas 7% of species were unique to intermittent streams, thus suggesting a subtle biological signal in response to drying (Feminella 1996). Spatial and hydrologic factors such as land use and stream permanence have been demonstrated to account for some of the variation in invertebrate assemblages. In western Georgia, land use-land cover and associated physicochemical measures, as well as habitat characteristics, explained stream macroinvertebrate assemblage characteristics (Helms et al. 2009). Further, percentage of impervious surface and of deciduous forest cover were found to be significantly related to macroinvertebrate metrics, with the highest integrity in areas of low impervious surface and high deciduous forest cover (Helms et al. 2009).

Feminella (1996) developed an index of stream permanence to rank relative intermittency in six streams within the Talladega National Forest of east-central Alabama. The Feminella (1996) study demonstrated seasonal relationships between macroinvertebrate assemblages and permanence in these streams. As part of an NSF-supported Research Experience for Undergraduates (REU), I studied invertebrate assemblages during this dynamic but poorly studied period, and measured short-term variation in water level with pressure transducers. Finally, I supplemented in-stream physical measurements with variables derived from geospatial analyses of the intermittent streams' watersheds to gain a perspective on watershed conditions influencing invertebrate assemblages.

Goals and Objectives:

The goal of my thesis research was to describe in more detail for these streams (a) how benthic fauna respond to a gradient of stream permanence; (b) the abundance and composition of invertebrate assemblages during wet (early summer) and dry (late summer) periods of stream flow; and (c) the degree to which watershed conditions besides permanence influence invertebrate assemblages. Specific objectives and hypotheses are as follows:

1. Quantify benthic faunal assemblages within streams based on stream-specific variation in hydrologic permanence.

Hypothesis A: Benthic assemblages differ along a gradient of stream permanence in richness, composition, and feeding guild metrics.

2. Determine if there are differences in abundance and composition of summer invertebrate assemblages during wet (early summer) vs. dry (late summer) periods.

Hypothesis B: Benthic assemblages differ between wet and dry sites in richness, composition, and feeding guild metrics.

3. Determine if invertebrate assemblage composition is related to watershed slope, area, and forest cover.

Hypothesis C: Benthic assemblages will differ along gradients of watershed slope, area, and forest cover in richness, composition, and feeding guild metrics.

Methods:

Site Selection

The six, small, unnamed tributaries of Shoal Creek and its tributary, Choccolocco Creek, in the Talladega National Forest used by Feminella (1996) to study of macroinvertebrate assemblages and stream permanence were selected for this study. The watersheds were within the Talladega National Forest of east-central Alabama (Figure 1).

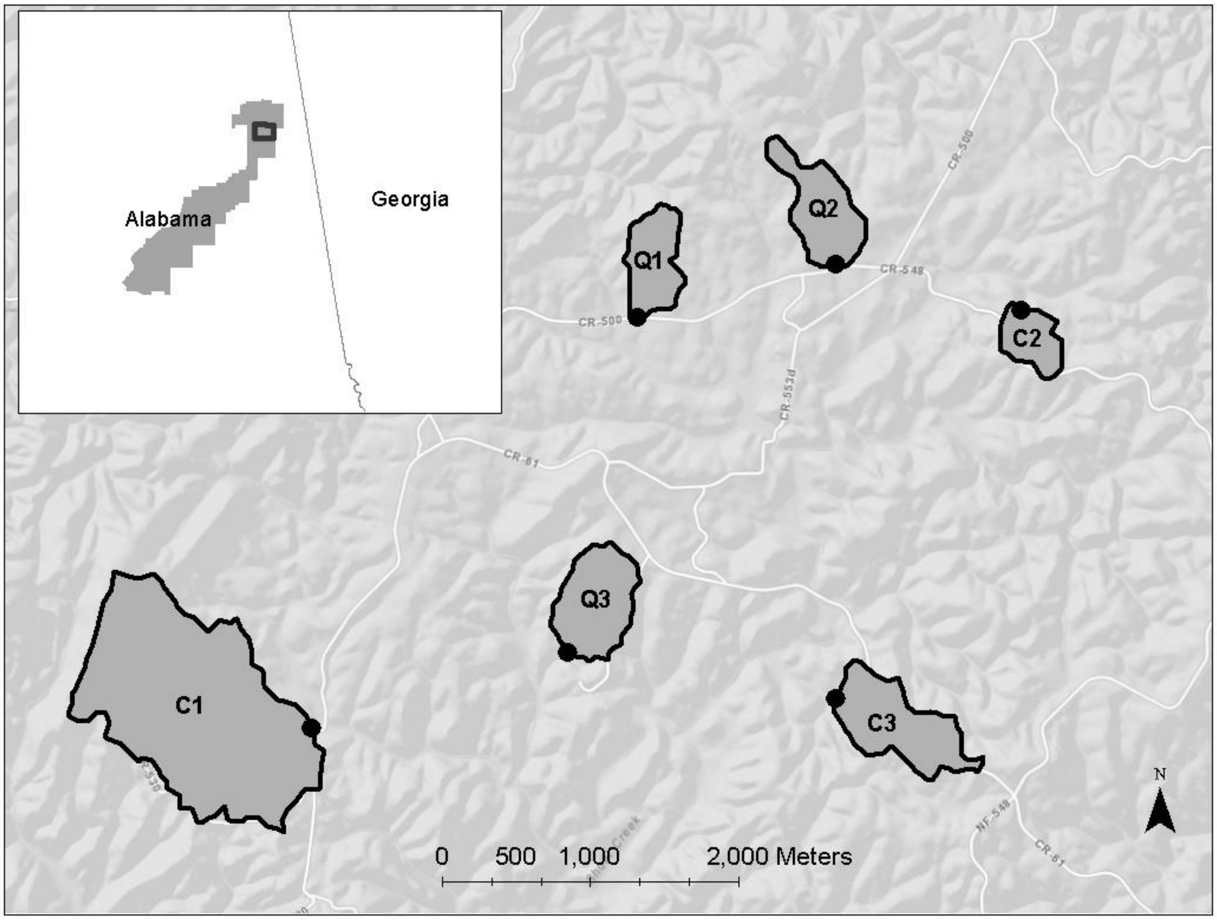

Figure 1. Map of study streams (C1-3, Q1-3) within the Talladega National Forest, AL (inset).

Benthic Sampling

Invertebrate sampling was conducted using a Surber sampler (244 um mesh) on May 29 and 7 June 2012, representing early summer (wet) conditions, and on 19 and 20 July 2012, representing late-summer (drying or dry conditions). The sampler was placed at 3 random locations within a riffle to obtain a composite sample (total substrate area per sample = 0.279 m^2). Substrate collected in the net of the 0.093 m^2 frame had been hand-scrubbed to dislodge organisms and the rocks and debris tossed aside. When all large substrate was scrubbed, finer sediments were agitated to ensure organisms in the area had been dislodged into the net.

Sampling was replicated in three riffles per stream, for a total of 0.837 m^2 of stream sampled per site.

At non-flowing sites, an area equivalent to that sampled with the Surber during wet periods was excavated (Feminella 1996). Water was added to the sediment, which was agitated and poured through a 250-um sieve to collect floating invertebrates and organic matter. When the water was clear of organic matter, sediments were examined for remaining invertebrates.

Field samples of invertebrates were preserved in ethanol and taken to the laboratory for identification. Substrate composition was determined by measuring the maximum diameter of 100 individual particles, selected randomly within sample riffles, and expressed as median substrate size at each site. Measurements of mean riffle area, depth, velocity, and discharge were also made at each site during each sampling period (EPA 2004).

Laboratory Identification

Benthic samples of invertebrates were processed in the laboratory. The samples were washed through a stack of 2 mm and 250 um sieves. The portion of the sample that did not pass through the 2 mm sieve was spread in a tray and sorted for large and rare organisms. In order to select a representative sample of organisms with a manageable size for thorough identification, sub-sampling was performed on the remainder of the samples collected in the 250 um sieve. The smaller sample material was diluted to 1000 mL in a large beaker and homogenized by stirring. Two 25 mL aliquots were removed as a single subsample and sorted until at least 300 organisms from at least 2 subsamples were collected. Invertebrates were counted and identified using Merritt, Cummins, and Berg (2008). The numbers of organisms found in the subsamples were extrapolated to account for the entire portion of the sample that passed through a 2 mm sieve. These were added with the large and rare organisms for data analysis.

Watershed Spatial Analysis

GPS coordinates were taken at the upstream and downstream riffles sampled at each site. A 10-m (1/3 arc second) digital elevation model (DEM) and stream layer, both obtained from USGS, were used to delineate each watershed area and slope from the downstream GPS point. The 2006 land use-land cover data from the USGS National Land Cover Dataset (NLCD) were used to estimate relative abundance (as %) of deciduous and evergreen land cover in each watershed.

Data Analysis

A suite of benthic macroinvertebrate metrics was used to represent different features of the community from each site and date (Table 1). The North Carolina Biotic Index assigns a value calculated by multiplying the tolerance values assigned to the taxa by the number of individuals within each group, and then dividing the sum of the products for all individuals by the total number of individuals for which tolerance values were assigned (Lenat 1993). The lower the North Carolina Biotic Index value, the more sensitive the assemblage composition is. Regression and analysis of variance (ANOVA) were performed on the set of independent variables consisting of physical and landscape measures and dependent biological metrics (Table 1).

Objective 1. Quantify benthic faunal assemblages among streams based on site-specific variation in hydrologic permanence.

ANOVA was used to examine the invertebrate assemblage characteristics of early and late summer samples from the six streams separately. Simple regression analyses were performed in order to examine the relationships between invertebrate metrics and physical variables representing permanence measured at each site. The physical gradients used included mean stream depth, velocity, and discharge. Multidimensional scaling ordination, performed with SAS, was used to spatially represent the invertebrate assemblages of different sites.

Objective 2. Determine if there are differences in abundance and composition of invertebrate assemblages during wet vs. dry periods of stream flow.

ANOVA was used to examine invertebrate metrics in order to compare richness, composition, feeding guild, and habitat metrics during wet and dry periods.

Objective 3. Determine if invertebrate assemblage composition is related to watershed slope, area, and forest cover.

Regression analyses were performed in order to examine the relationships of invertebrate metrics to landscape variables. . The physical gradients used included watershed area, watershed slope, deciduous forest cover, and evergreen forest cover.

Table 1. Metrics used in statistical tests.

Measure	**Metrics**
Abundance	Density
Functional Feeding Group Composition	Percent Collector-Filterers
	Percent Predators
	Percent Collector-Gatherers

	Percent Shredders
	Percent Scrapers
Richness	Number of EPT Taxa
	Total Number of Taxa
Composition	Percent Non-Insect Taxa
	Percent *Lirceus*
Tolerance	North Carolina Biotic Index (Lenat 1993)
Diversity	Shannon' *H*
	Simpson' *D*
	Pielou's *J*
Stream Permanence	Riffle Depth
	Riffle Flow
	Riffle Width
	Riffle Area
	Riffle Volume
	1996 Permanence Score
	Discharge
Watershed Characteristics	Slope
	Area
	Percent Deciduous
	Percent Evergreen
Substrate Characteristics	D50 (median substrate size)
	Dominant Substrate Size

Results:

The observed water level drawdown in the summer of 2012 was unprecedented. As a result, the majority of the July samples needed to be excavated from dry streambeds. Pressure transducers were installed in the streams for use in calculating metrics from continuous stage data that were previously unavailable. Samples collected in the summer of 2012 included >96,000 invertebrates after correction for subsampling. In early summer (late May to early June), all sites except C2 had flowing surface water, whereas in late summer (late July), C1 and C3 were the only sites with enough flowing water to sample the riffles without excavation. The most abundant taxa throughout the study were the isopod *Lirceus*, the chironomid groups Tanytarsini, Orthocladiinae and Tanypodinae, and Elmidae of the genus *Oulimnius* (Table 2).

Table 2. Density (individuals per m^2) of most abundant organisms for early, late and combined summer samples.

	May-June	July	Combined
Lirceus	69480	9247	78728
Oulimnius	27581	24993	52573
Orthocladiinae	27584	13208	40792
Tanypodinae	14681	10849	25530
Tanytarsini	20122	7921	28043

Objective 1. Quantify benthic faunal assemblages among streams based on site-specific variation in hydrologic permanence.

I hypothesized that benthic assemblages would differ in richness, composition, feeding guild, and habitat metrics along a gradient of stream permanence. In early summer samples, the most permanent site (C1) had a significantly higher percentage of filtering invertebrates than all other sites (Figure 2A), and the second-most permanent site (C3) had a higher percentage of shredding invertebrates than other sites (Figure 2B). Overall, Q1 and Q2 had the smallest proportion of predators, the lowest richness and diversity, and were dominated by the isopod *Lirceus* (Figure 2C,D,E,F).

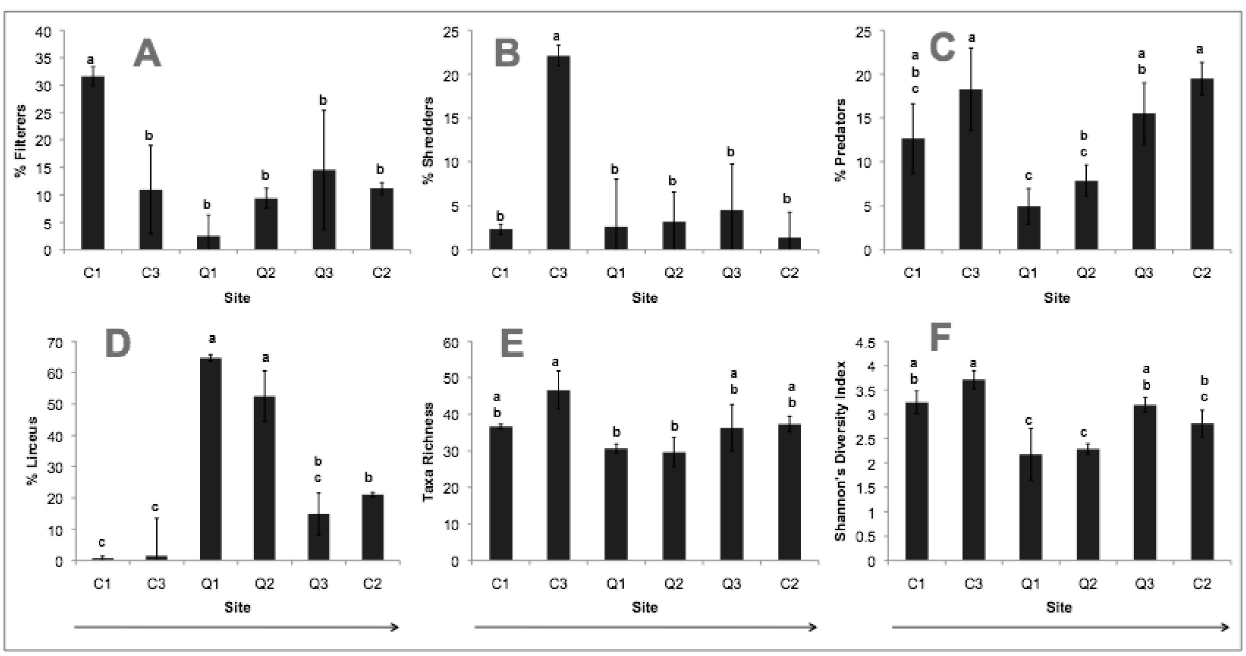

Fig. 2. ANOVA results for selected benthic response variables from early-summer samples (n=3 for each site). Sites (C1-3. Q1-3) are arranged in order of increasing riffle intermittence (Feminella 1996). Bars with the same letters were not significantly different (α = 0.05).

In late summer, the percentage of predators was significantly lower at C1 than other sites (Figure 3A). Site C3 no longer had a significantly higher proportion of shredding invertebrates and C1 no longer had a significantly higher proportion of filtering invertebrates than all other sites (Figure 3A,D). C3 had the lowest biotic index of all sites (Figure 3C). There was no significant difference in benthic density among streams in early and late summer samples, although this measure was highly variable among riffles at each site (Figure 4).

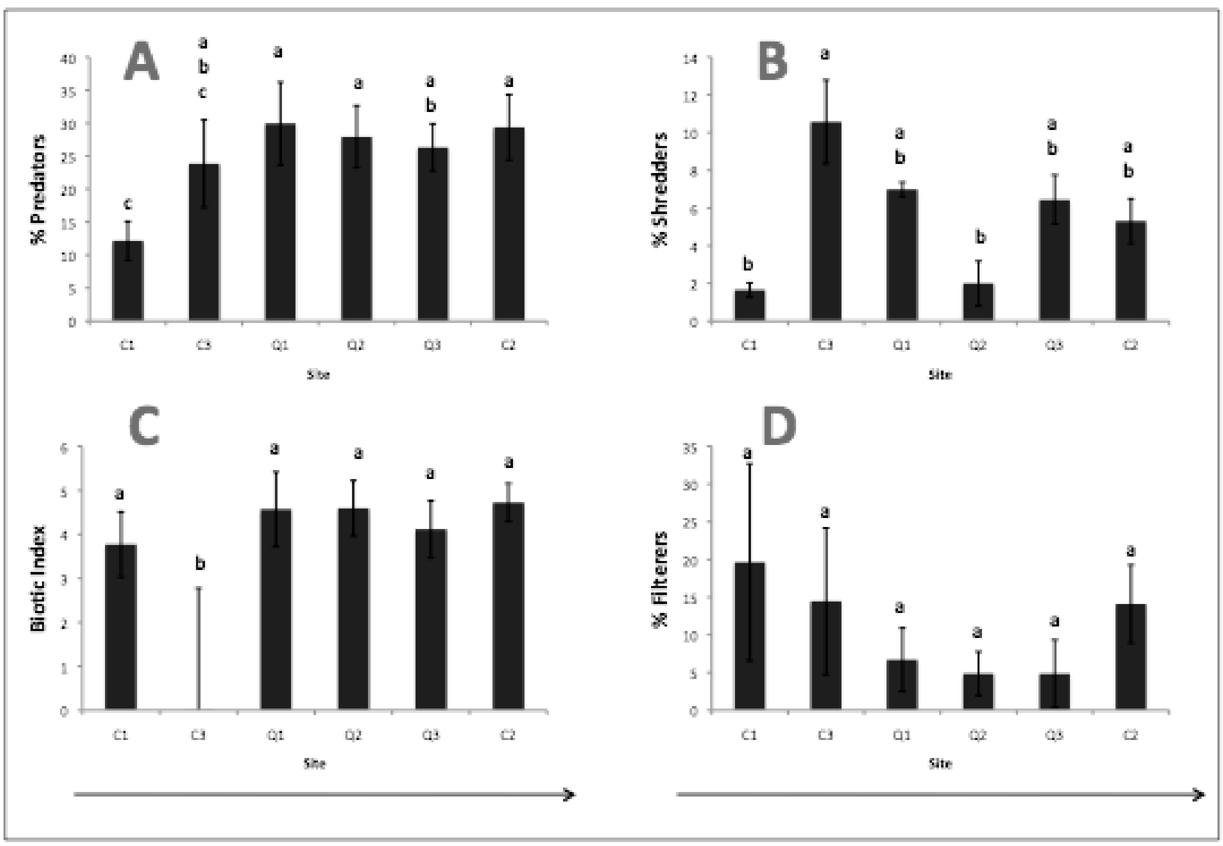

Figure 3. ANOVA results for selected benthic response variables from late-summer samples (n=3 for each site). Sites (C1-3. Q1-3) are arranged in order of increasing riffle intermittence (Feminella 1996). Bars with the same letters were not significantly different (α = 0.05).

Regression analyses were performed to examine the relationships between invertebrate metrics and physical variables representing permanence at each site. Regressions analyses of the Feminella (1996) scores and all invertebrate metrics yielded no significant relationships. Sites with greater discharge were associated with an increased proportion of filtering organisms (Table 3). A decrease in the proportion of predators in each assemblage was correlated with increasing average flow and riffle width (Table 3). Shannon's *H* and Pielou's *J* increased with increased mean riffle length and area (Table 3). When invertebrate density and discharge were averaged over early and late summer, discharge was negatively related to density (R^2=0.724, p=0.032) and positively related to the proportion of collector-filterers (R^2=0.861 p=0.008).

Table 3. Summary of relationships between assemblages and measurements of permanence in early and late summer.

X	**Y**	**R^2**	**p**	**Slope Sign**
Discharge	% Filterers	0.7277	0.0004	Positive
Average Flow	% Predators	0.3836	0.0317	Negative
Average Riffle Width	% Predators	0.4661	0.0144	Negative
Riffle Length	Shannon	0.4249	0.0216	Positive
Riffle Length	Pielou	0.5616	0.0050	Positive
Riffle Area	Shannon	0.4498	0.0170	Positive
Riffle Area	Pielou	0.3732	0.0348	Positive

Multidimensional scaling showed similarity among streams of relatively low permanence. The assemblages at the higher permanence sites, C1 and C3, separated out from the others (Figure 4). C1 and C3 assemblages were also separate from one another, as would be expected, based on their significantly different proportions of filtering and shredding taxa.

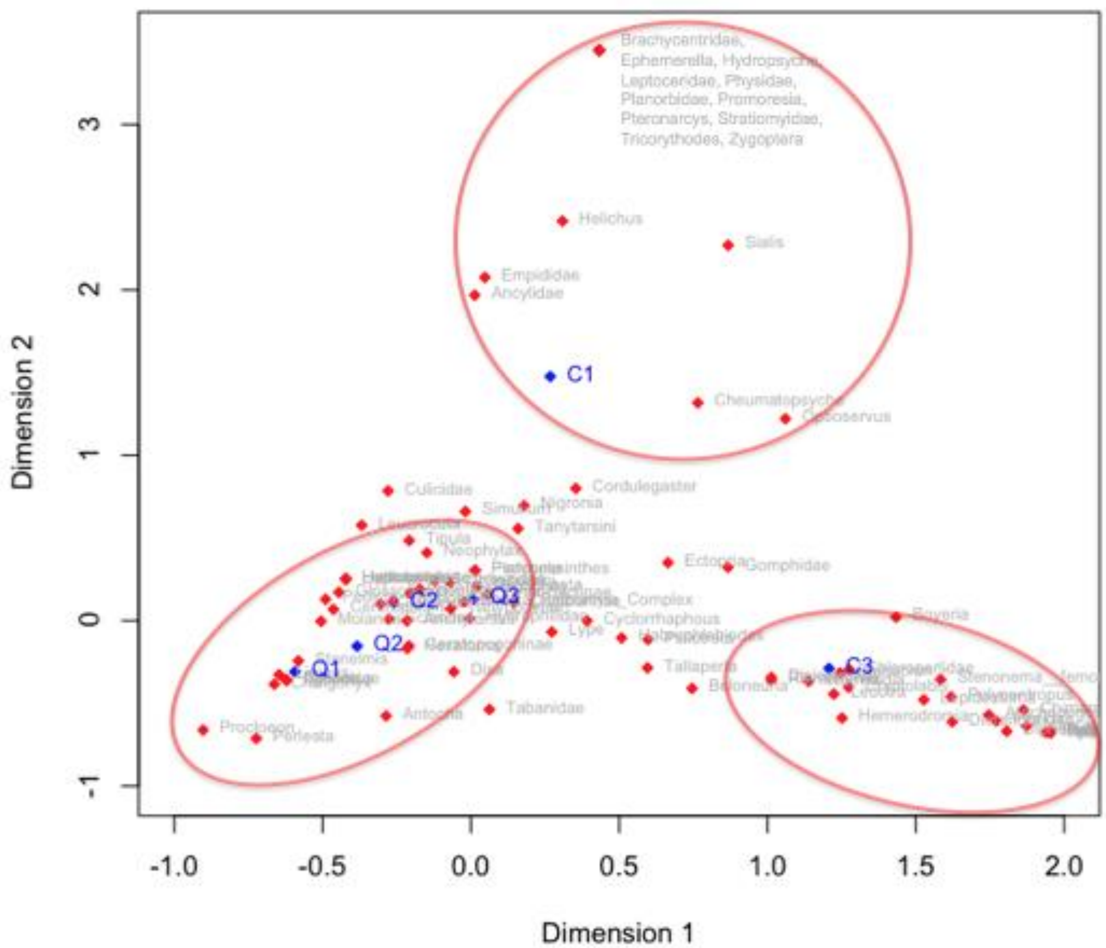

Figure 4. Multidimensional scaling analysis of sites based on their invertebrate assemblages. Sampling sites are colored blue. Specific taxa are represented by red points. Taxa spatially close to a site were present at relatively high abundance at that site. Taxa spatially distant from a site were not associated with that site.

Objective 2. Determine if there are differences in abundance and composition of invertebrate assemblages during wet vs. dry periods of stream flow.

I hypothesized that benthic assemblages would differ between wet and dry sampling events in richness, composition, feeding guild, and habitat metrics. Invertebrate density declined significantly over the summer months only at C2, the least permanent site (Figure 5). There was no significant decline in EPT richness at any site during dry periods. Taxa richness declined significantly from early to late summer at C3 and C1, the most permanent sites. All sites except

C1 and C3 showed declines from early to late summer in the proportion of collector-gatherer taxa in their assemblages. Q1 and Q2 showed significant declines in numbers of the isopod *Lirceus,* which did not dominate any of the assemblages during dry sampling events. Q1 and Q2 had a greater proportion of predatory taxa in their late summer assemblages compared to other sites.

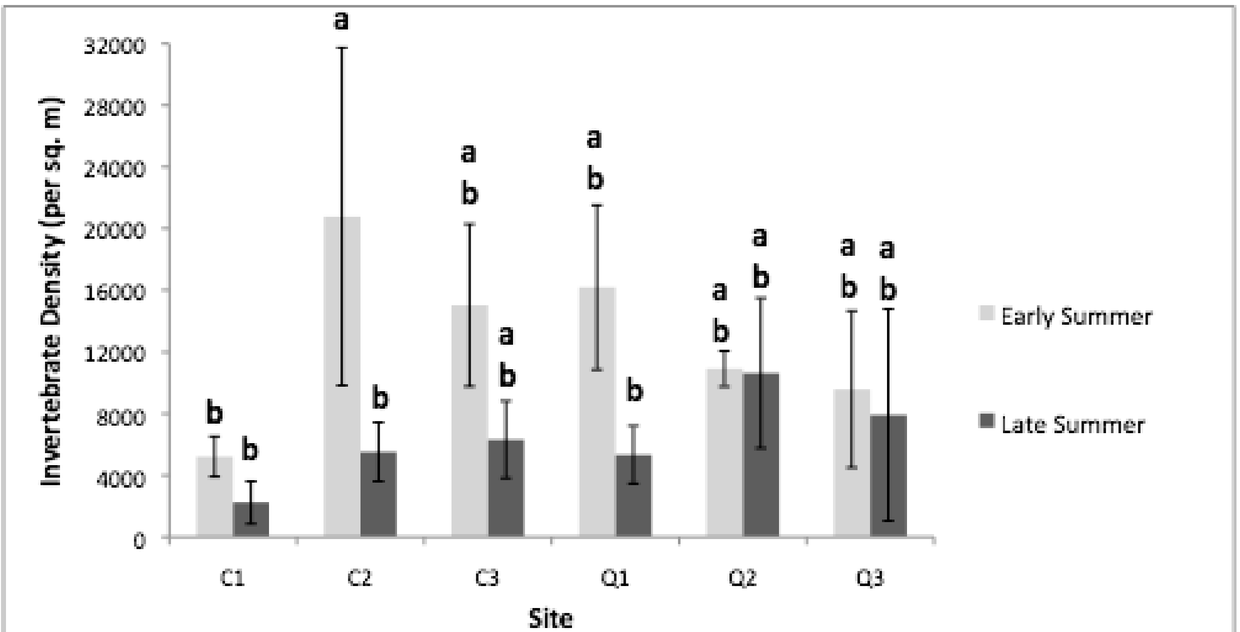

Figure 5. ANOVA results for invertebrate density (n=3 for each site). Sites (C1-3. Q1-3) are arranged in order of increasing intermittency (Feminella 1996). Bars with the same letters were not significantly different (α = 0.05).

Objective 3. Determine if invertebrate assemblage composition is related to watershed slope, area, and forest cover.

I hypothesized that benthic assemblages would differ along gradients of watershed slope, area, and forest cover in richness, composition, and feeding guild metrics. Watershed area was significantly related to abundance, % collector-filterer taxa, % predatory taxa, and % scraper taxa when early and late summer results were averaged (Table 4). Watershed average slope was significantly related to % collector-gatherers, % isopod *Lirceus,* and Shannon's *H*, Simpson's *D,* and Pielou's *J* (Table 4). Percent forest cover was not significantly related to any of the chosen invertebrate metrics.

Table 4. Summary of relationships between watershed and assemblage characteristics and combined summer samples.

X	**Y**	R^2	**p**	**Slope Sign**
Watershed Area	Density	0.8796	0.0057	Negative
Watershed Area	% Filterers	0.8190	0.0131	Positive
Watershed Area	% Predators	0.6499	0.0527	Negative
Watershed Area	% Scrapers	0.8592	0.0079	Positive
Watershed Slope	Taxa Richness	0.6942	0.0392	Positive
Watershed Slope	% Gatherers	0.6742	0.0449	Negative
Watershed Slope	% *Lirceus*	0.7367	0.0287	Negative
Watershed Slope	Shannon	0.7870	0.0184	Positive
Watershed Slope	Simpson	0.7906	0.0177	Negative
Watershed Slope	Pielou	0.8251	0.0122	Positive

Discussion:

Goal A. Describe in more detail for these streams how benthic fauna respond to a gradient of stream permanence.

ANOVA showed little separation among the assemblage characteristics of each site likely because of high within-site variability among riffles. Metric separation among sites, when it occurred, did not follow the previously established permanence gradient. In the early summer, sites Q1 and Q2 separated from the remaining sites of higher and lower permanence for many metrics. The second-most permanent site, C3, had a higher number of shredders. These results suggest something other than permanence may affect assemblages at these sites.

Alternatively, characterization of true hydrologic permanence requires further study. Stage data collected in the summer of 2012 showing variable drying among all sites except C3, previously considered the second most permanent site, suggest the permanence scores established in 1996 may require revalidation. For example, in my regression analyses, I used proxies for permanence when the 1996 scores yielded no significant relationships. These short-term measures, such as discharge and depth, can vary widely temporally, especially with the frequency and intensity of late-summer storms. A full time series of stage data would also help differentiate between sites that all had low discharge at the time of sampling.

As late summer drawdown progressed from May to July, assemblages at the sites changed. Early summer significant differences in assemblages among streams were no longer detectable. This pattern was, in part, due to high variability among riffles at each site in late-summer samples. Continuous water level data collected at each site (data not shown) suggested that even the riffles at C1, the most permanent site, might have gone dry during July. The stress of drawdown in late summer could account for the lowered proportion of filtering organisms at C1, which rely on flowing water carrying fine particulate organic matter downstream for them to feed on (Thorp and Delong 1994). Depletion of leaf litter inputs or the lack of precipitation events to carry litter into C3 could account for the diminished proportion of shredding organisms at this site. C3 did not show any instances of flow falling below the riffle surface in stage data collected over the sampling season, however.

The lower biotic index values at C3, indicating an assemblage composition with more sensitive species than other sites, could be a result of fewer stressors from low flow conditions, such as desiccation of intolerant species or increased predation pressure. As water levels draw down, prey may be more concentrated, facilitating predation by aquatic and possibly terrestrial organisms. C1 and C3, the only sites with water levels above the riffle surface in late summer, had the lowest proportion of predators in their assemblages. The concentration of prey at other sites may have created conditions favorable for predation, and these invertebrate predators may have lowered the abundance of other organisms. Conditions unfavorable to filtering taxa, for instance, would also lower the number of types of functional feeding groups that could possibly inhabit dry riffles.

Overall invertebrate density and several functional feeding group metrics were not significantly different among streams in early or late summer. Levels of stream permanence at the study sites may not affect many invertebrate groups during early summer sampling, when they have not yet experienced the stress of riffle drawdown. As the water level lowers, less permanent sites may be more affected by drying, temperature increases, decreases in dissolved oxygen, or predation pressure than sites with consistent flowing water. However, the assemblages at the least permanent sites may be concentrated with riffle drawdown. The degree of assemblage concentration may obscure any negative influence of physical or biological stress on invertebrate density.

Sites with higher discharge, a feature associated with more hydrologic permanence, appeared to provide conditions favorable for filtering taxa. The proportion of predatory taxa was greater at sites with decreased flow and riffle width, variables indicative of more wetted riffles. As less permanent sites experiencing drawdown may have concentrated prey populations for predators to exploit, density of organisms was seen to increase in sites with lower discharge. Decreased discharge passing through riffles may concentrate biotic communities and increase densities in some streams. This may benefit predatory organisms, while negatively affecting their prey. Drawdown may also increase the competition for space and resources, such as for biofilm on the substrate.

Higher diversity and evenness were associated with greater riffle length and area. Sampling a larger area will generally yield more species (Vinson and Hawkins 1996). However, larger riffles could also be associated with more permanent streams, as they indicate areas where large flows have consistently established the stream channel. If so, a stable system could result in a relatively diverse community where stressful conditions do not favor the dominance of one or a few tolerant species.

Multidimensional scaling showed similarity in invertebrate assemblages among sites of low permanence. C1 and C3 were separated from the grouping of low permanence sites and also from one another because of their different assemblages. The discharge at C1 supported filterers that were uncommon at other sites. Certain taxa, such as the stonefly *Pteronarcys,* were found only at C1. All but three of the beetle *Psephenus* were found at C3, while another relatively less tolerant genus *Ectopria* was found at all sites but Q2.

Goal B. Describe in more detail for these streams the abundance and composition of invertebrate assemblages during wet (early summer) and dry (late summer) periods of stream flow.

With the variability of the data collected among riffles of the same streams during the summer months, density was difficult to differentiate among sites using ANOVA. Assemblage density at C2 significantly declined between early and late summer. Late-summer drawdown could be concentrating assemblages and obscuring the effects of drying, such as desiccation or increased ease of predation. C2, the site identified by Feminella in 1996 as least permanent, was already dry and needed to be excavated to collect samples in the early summer. With sustained drying of riffles, the early summer samples could have been representative of a concentrated community, while the late summer samples could have described assemblages affected by the stress of drawdown. Concentration may result in greater competition for resources, as well as physical stress from desiccation, high temperatures, and lower dissolved oxygen. Additional temporal sampling and targeting more sites with permanence similar to C2 could establish this relationship between drying and population dynamics over the summer months.

Over the summer, taxa richness declined only at C1 and C3. These sites may have experienced increasing physical stress from drawdown as the summer progressed. Other sites may have already experienced this reduction in richness by the time of early summer sampling. The lowering of richness from early to late summer at these sites made C3 comparable to the other sites and kept C1 at a level comparable to other sites.

As *Lirceus* no longer dominated Q1 and Q2, these sites had an increase in the proportion of predatory organisms in their assemblages. *Lirceus* is in the collector-gatherer functional feeding group. Lower abundance of this taxon at sites where it was dominant, particularly Q1 and Q2, would contribute to the lower proportion of gatherers observed in late summer at all but the most permanent sites. Depletion of labile organic matter at the surface without storm events to replenish allochthonous matter could cause collector-gatherer mortality or migration deeper into the hyporheic zone. The more permanent sites, C1 and C3, may have had the flow to support these organisms' feeding strategies. These sites also had the highest median substrate diameter in the Feminella study (1996), which may have provided better habitat for a variety of species needing shelter or a hard surface for anchoring onto.

Goal C. Describe in more detail for these the degree to which watershed conditions besides permanence influence invertebrate assemblages.

Forest cover did not significantly explain the variation in benthic assemblages among sites. Forest cover may be more important during times of the year when leaf fall in deciduous watersheds is greater, or during times of the year where storm events are more frequent and terrestrial organic matter likely washes into the streams. The composition of the surrounding forest may also be more important relative to the dry summer months.

Watershed area was related to the proportion of filtering, predatory, and scraping taxa at each site. Filtering taxa were associated with sites of high discharge and predatory taxa with sites of low discharge. Greater watershed area could result in more water draining into stream channels, which is important to filterers. As previously discussed, predation could become easier as drawdown in streams concentrates assemblages. Scraping taxa are likely to inhabit streams with consistent flow that will support biofilms on the substrate.

The slope of a watershed could contribute to higher discharge, flushing water and organic matter into the stream at a greater rate and in larger quantities than watersheds with lower slope and slower release of water from the water table. Low residence time of organic matter in these high slope watersheds could prevent favorable feeding conditions for gathering taxa, such as *Lirceus*. Other variables influenced by slope, such as vegetative cover, could further influence the assemblage composition of a watershed.

Sites with higher flows resulting from greater watershed slope, which is not necessarily related to stream channel slope, might also have more continuous discharge. Systems with consistent flow and good water quality may support a relatively diverse community, with a variety of functional feeding groups and sensitive species that are excluded from drier sites. Assemblages at sites with lower slope and possibly less permanence are likely to be dominated by one or a few species tolerant of the stress of drying. Further study of the hydrographs of these systems could determine whether high slopes result in a flashier hydrograph or steadier flows.

Further exploration of invertebrate assemblage variation is necessary for full characterization of the benthic assemblage response to hydrologic permanence and watershed conditions. Watershed slope and area may relate to stream permanence and the hydrologic variation within streams likely plays a major role in determining the assemblages present at each site. Reconsideration of the 1996 permanence scores using stage-discharge currently being developed could better characterize the physical conditions of each site and provide more meaningful information on the factors affecting invertebrates in these and other hydrologically dynamic streams.

The density and diversity of benthic invertebrate assemblages present even in the smallest and driest streams sampled underscore the importance of considering these streams in scientific research and management decisions. Further exploration of the temporal dynamics of these streams may provide insight into effects of ongoing global changes in temperature and precipitation on aquatic ecosystems. Further study could examine whether the degree to which a gradient in hydrologic permanence influences the assemblages in intermittent streams predicts how assemblages change as climate becomes wetter or drier.

Acknowledgements:

Special thanks to Alan Wilson and the National Science Foundation for supporting this project through the Warm Water Ecology REU Program at Auburn University (Grant 0965272); Brad Schneid, Ely Kosnicki, and Jack W. Feminella of the Auburn University Biological Sciences department for their significant contributions to the planning and execution of this research; as well as Alan McIntosh and Suzanne Levine of the University of Vermont for their participation in the Honors Thesis committee.

Literature Cited:

Allan, J. D., and M.M. Castillo. 2009. Stream ecology: structure and function of running Waters. 2nd edition. Springer, Dortrecht, The Netherlands.
Chadwick, M. A. and A. D. Huryn. 2007. Role of habitat in determining macroinvertebrate production in an intermittent-stream system. Freshwater Biology **52**:240-251.
EPA. 2004. Wadeable Streams Assessment: Field Operations Manual. EPA841-B-04-004. U.S. Environmental Protection Agency, Office of Water and Office of Research and Development, Washington, DC.
Feminella, J. W. 1996. Comparison of benthic macroinvertebrate assemblages in small streams along a gradient of flow permanence. Journal of the North American Benthological Society **15**:651-669.
Fritz, K. M. and J. W. Feminella. 2011. Invertebrate colonization of leaves and roots within sediments of intermittent Coastal Plain streams across hydrologic phases. Aquatic Sciences **73**:459-469.
Hansen, W. F. 2001. Identifying stream types and management implications. Forest Ecology and Management **143**:39-46.
Helms, B. S., J. E. Schoonover, and J. W. Feminella. 2009. Seasonal variability of landuse impacts on macroinvertebrate assemblages in streams of western Georgia, USA. Journal of the North American Benthological Society **28**:991-1006.
Hilsenhoff, W. L. 1988. Rapid Field Assessment of Organic Pollution with a Family-Level Biotic Index. Journal of the North American Benthological Society **7**:65-68.
Lenat, D. R. 1993. A Biotic Index for the Southeastern United States: Derivation and List of Tolerance Values, with Criteria for Assigning Water-Quality Ratings. Journal of the North American Benthological Society **12**:279-290.
Nadeau, T.-L. and M. C. Rains. 2007. Hydrological Connectivity Between Headwater Streams and Downstream Waters: How Science Can Inform Policy1. Journal of the American Water Resources Association **43**:118-133.
Resh, V. H., M. J. Meyers, and M. J. Hannaford. 1996. Macroinvertebrates as Biotic Indicators of Environmental Quality. Pages 647-667 Methods in Stream Ecology. Academic Press, San Diego.
Thorp, J. H. and M. D. Delong. 1994. The Riverine Productivity Model: An Heuristic View of Carbon Sources and Organic Processing in Large River Ecosystems. Oikos **70**:305-308.
Vinson, M. R. and C. P. Hawkins. 1996. Effects of Sampling Area and Subsampling Procedure on Comparisons of Taxa Richness among Streams. Journal of the North American Benthological Society **15**:392-399.