2002

Combined effects of water chemistry, canopy cover, and stream size on benthic macroinvertebrates along a Central Appalachian stream continuum

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Combined effects of water chemistry, canopy cover, and stream size on benthic
macroinvertebrates along a Central Appalachian stream continuum

by

Jesse A. Bopp

A THESIS

Submitted to the Davis College of Agriculture, Forestry, and Consumer Sciences
at
West Virginia University

in partial fulfillment of the requirements
for the degree of

Master of Science
in
Wildlife and Fisheries Resources

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2002

Keywords: acidity, alkalinity, Appalachian, benthic, canopy, function, macroinvertebrate,
river continuum, stream size, structure

Abstract

Combined effects of water chemistry, canopy cover, and stream size on benthic macroinvertebrates along a Central Appalachian stream continuum

Jesse Adam Bopp

I sampled benthic macroinvertebrates along a 25.2 km stream continuum (flow 0.01 to 2.36 m³ s⁻¹) in the Central Appalachian Mountains of West Virginia from May - October 2000. Six components of macroinvertebrate structure and function were measured: density, biomass, richness, metric composition, community taxa similarity, and feeding group composition. I quantified these components to determine if general changes in macroinvertebrate communities associated with stream size were significantly altered by reach-scale variation in water chemistry and light. I specifically determined how site-specific variation in alkalinity and canopy cover would modify the predictions of: (1) an increase in density, biomass, and richness with increasing stream size; (2) a decrease in community taxa similarity as distance between two sites increased; and (3) a shift in the percent and absolute biomass of feeding group composition as energy inputs shift from riparian leaf litter to instream algal growth. Site-specific changes in alkalinity and canopy cover significantly affected macroinvertebrate structure and function and modified stream continuum predictions. Results indicated that alkalinity was the primary determinant of macroinvertebrate structure and function, and that the effects of canopy cover and stream size were secondary and tertiary determinants, respectively. General findings were as follows: (1) alkalinity and canopy cover determined macroinvertebrate density, biomass, and metric composition along the continuum; (2) alkalinity and basin area determined family richness patterns; (3) basin area determined community similarity with local variation from alkalinity and canopy cover; and (4) alkalinity and canopy cover determined the percent biomass of feeding group composition whereas canopy cover and basin area determined the absolute biomass of feeding group composition. Evaluation of these results suggests that small-scale variation in the geology and riparian character of Central Appalachian watersheds can modify stream continuum predictions at a continuum-specific level.

DEDICATION

I dedicate the efforts herein to my family whose love, support, and laughter is ingrained within the pages of this document.

“People hand in hand
Have I lived to see the milk and honey land?
Where hate’s a dream and love forever stands
Or is this a vision in my mind”

- Stevie Wonder, *Innervisions*

ACKNOWLEDGMENTS

I sincerely thank all committee members for their suggestions during the development, collection, analyses, and writing of this research. A special thanks is given to Todd Petty for mentoring a former terrestrial wildlifer through a stream ecology project. Of course, this project would not have been possible without funding from the West Virginia Division of Natural Resources, the Biological Resources Division of the United States Geological Survey, and the United States Fish and Wildlife Service.

Finally, I wish to thank: Ryan Gaujot, Peter Lamothe, Dan Nulph, Brock Reggi, and Matt Varner for field assistance; Donna Hartman, Mike Kaller, Adam Kane, and Matt Kraycar for laboratory assistance; and Jason Freund and John Sweka for statistical assistance.

Because if it truly were not for appearances such as the likes of “Danbo”, the “Rail Fans”, the “Ghost Gobbler”, my “Private Tecky”, the “Second Fork Iron Chefs”, and the “Laboratory Groovers”, I do not know if I would have kept sane. So thanks folks, as it was an honor to laugh, learn, and party with you all.

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Introduction

The River Continuum Concept (RCC) is a working hypothesis that attempts to describe the spatial and temporal variation in stream ecosystem structure and function (Cushing, 1994). The RCC focuses on changes in energy inputs (i.e. allochthonous versus autochthonous) and aquatic metabolism (i.e. ratio of gross primary productivity to community respiration) with movement from small headwater streams to large basin area rivers (Vannote et al., 1980). For example, the ratio of productivity to respiration should be < 1 in headwater reaches and > 1 in downstream reaches due to an increase in light and gross primary productivity (GPP). The RCC also makes explicit predictions of how the benthic macroinvertebrate community, which is comprised of primary and secondary consumers, should change along a stream continuum (Figure 1). Specific predictions for macroinvertebrate communities are as follows: (1) shredders and gatherers should dominate percent (%) biomass composition in 1st-2nd order streams; (2) grazers, gatherers, and filterers should dominate % biomass composition in 3rd-5th order streams; (3) gatherers and filterers should dominate % biomass composition in 6th or higher order streams; and (4) % biomass composition of predators should remain relatively unchanged as stream size increases.

The RCC advanced stream ecosystem theory by providing a holistic outline for the testing of physical, chemical, and biological variables along a continuum (Minshall et al., 1985; Cushing, 1994). Yet immediately following publication, the RCC was criticized as being too general for most riverine ecosystems. For example, Winterbourne et al. (1981) contended that New Zealand streams do not experience a similar seasonality and

temporal succession of taxa as do North American streams. Indeed, when several of the original authors conducted a large-scale North American test of several RCC predictions, their results determined that temporal variability and variability among regions often overwhelmed many observable changes along a stream continuum (Minshall et al., 1983). In particular, departures from RCC predictions occurred as a result of: (1) watershed elevation, latitude, and geography; (2) riparian condition; (3) tributary confluences; and (4) localized lithology and channel morphology. Consequently, their findings questioned the ability of the RCC to explain patterns in the structure and function of many stream continua.

Since that time other researchers observed numerous deviations and proposed refinements. Hawkins et al. (1982) found that open canopy headwater conditions indiscriminately increased the abundance of all feeding groups, not just grazers. Bruns et al. (1984) assessed tributary effects and concluded that downstream of small tributaries functional composition approximated large stream reaches, while downstream of large tributaries functional composition approximated small stream reaches. Minshall et al. (1985) discussed how channel dredging, dams, and industry-related thermal inputs shifted, obscured, or eliminated expected responses. Statzner and Higler (1985) suggested that removing the postulates regarding: (1) continual downstream increases in kinetic (i.e. moving) energy; (2) seasonally induced species replacement; (3) absence of instream successional events; and (4) greatest variation in temperature, flow, and habitat type of mid-order reaches, would result in a more flexible application of the RCC. They contended that removing these postulates would reduce criticism yet still allow the testing of predictions concerning GPP, community respiration, organic matter processing, and

structural and functional composition. Others suggested that a reach-level perspective based on local channel morphology is necessary to compliment entire longitudinal patterns (Brussock and Brown, 1991), since overall functional composition results from the relative contribution of each habitat type to total stream area (Huryn and Wallace, 1987). Meyer and Edwards (1990) determined that a south temperate, low gradient, blackwater river having extensive floodplain connectedness contained communities that were increasingly dependent upon allochthonous organic matter as stream size increased, despite concomitant increases in GPP in the central stream channel.

Concurrent to these modifications and refinements, several studies provided support for RCC predictions. In Oregon, Naiman and Sedell (1980) found that production to respiration ratios supported the postulate of a downstream increase in GPP. Also in Oregon, Hawkins and Sedell (1981) substantiated the hypothesis that functional group composition varies predictably along a stream continuum. Shredders dominated shaded upper reaches, scrapers peaked in mid-order reaches, gatherers and filterers increased downstream, and predator abundance remained relatively constant along a 1st- 7th order continuum. In a boreal watershed of eastern Quebec, Canada, Naiman (1983) reported a production to respiration ratio of < 1 in 1st order reaches and > 4 in 9th order reaches. Indeed, streams of 4th or higher order comprised $< 13\%$ of the watershed, but produced $> 86\%$ of the GPP. In southern Appalachian streams, Huryn and Wallace (1987) observed that functional group composition reflected the dominance of allochthonous energy inputs, an RCC expectation for forested headwater streams. Grubaugh et al. (1996) also concluded that, along a 65 km southern Appalachian stream gradient, the % biomass of functional group composition conformed to RCC predictions. More recently, Carpenter

(2000) demonstrated that a 77,000 ha continuum in western West Virginia and Pennsylvania compared closely to predictions for productivity/ respiration and macroinvertebrate community structure and function, and that outliers were explained through physical, chemical or ecological alterations linked to human influences.

Acid precipitation represents one such example of a human influence upon stream ecosystem communities. Potential impacts of stream acidification include a decrease in organic matter decomposition (Burton et al., 1985; Kimmel et al., 1985), a resulting decrease in sediment-nutrient exchange due to organic matter layering, an increase in acid-tolerant fungal growth (Wright et al., 1975), and a decrease in macroinvertebrate (e.g. Simpson et al., 1985) and fish (Lacroix, 1989; Carline et al., 1992; Fiss and Carline, 1993; Gagen et al., 1993; Marschall and Crowder, 1996; Kwak and Waters, 1997; Clayton et al., 1998) structure and function. The onsets of such impacts vary and depend upon the acute severity or chronic duration of pH reductions, as well as the buffering potential of the system; however, ecosystem alterations generally begin at a stream pH of 5.0 (Allan, 1995).

Given that acid precipitation occurs over much of the eastern United States (NADP, 2000) (Figure 2), numerous studies have described the effects of acidification on macroinvertebrate communities (Hall et al., 1982; Kimmel et al., 1985; Miller, 1985; Simpson et al., 1985; Hall and Ide, 1987; Feldman and Connor, 1992; Rosemond et al., 1992; Kobuszewski and Perry, 1993; Clayton and Menendez, 1996; Madarish and Kimmel, 1999). In particular, because effects on water chemistry are most severe in low order streams, the structure and function of headwater communities have received most of the attention. Withstanding variation in methodology (i.e. qualitative kicknet versus

quantitative Surber and Hess collection, or sample and mesh size), acidification has been shown to consistently decrease macroinvertebrate biomass (Miller, 1985), production (Groom and Hildrew, 1989), species richness (Kimmel et al., 1985), evenness (Simpson et al., 1985), habit (Allard and Moreau, 1987), and feeding group composition (Rosemond et al., 1992). In contrast, density may be unaltered (Kobuszewski and Perry, 1993; Clarke and Scruton, 1997) or increase (Madarish and Kimmel, 1999) due to an increased abundance of acid-tolerant taxa. Indeed, taxa response to acidity is highly variable with particular orders (e.g. decrease of Ephemeroptera), families (e.g. increase of Rhyacophilidae:Trichoptera), genera (e.g. increase of *Leuctra* spp:Plecoptera), and species (e.g. increase of *Ameletus lineatus*:Ephemeroptera) exhibiting differential growth and survivorship (Bell, 1971; Simpson et al., 1985; Peterson and Eeckhaute, 1991; Rosemond et al., 1992).

In addition to descriptive studies, experimental research suggests that acidification negatively affects both macroinvertebrate physiology (Allard and Moreau, 1987; Hopkins et al., 1989; Kiffney and Clements, 1996) and organic matter processing (Burton et al., 1985; Kimmel et al., 1985; Groom and Hildrew, 1989). Increased concentrations of hydrogen ions catalyze the extraction of heavy metal precipitant. In particular, acidification increases aluminum, calcium, magnesium, potassium, manganese, iron, and cadmium (Hall et al., 1980), and significant, positive correlations between acute (8 d) pH reductions (5.8 - 6.4 to 3.2 - 4.8), and inorganic monomeric Al and Ca concentrations are reported (Hall, 1990). Furthermore, elevated concentrations occur during high discharge events (Madarish and Kimmel, 1999) and with progression downstream (Hall et al., 1980). Direct physiological effects include improper ion regulation, respiration, and

acid/base balance (Havas, 1981; Hermann and Andersson, 1986; Rowe et al., 1989; Rockwood et al., 1990), with epi-benthic, external gill, emerging/immature, and comparatively small-sized macroinvertebrates primarily expressing higher sensitivity (Bell, 1971; Hall et al., 1980; Allan and Burton, 1986; Allard and Moreau, 1987; Hopkins et al., 1989; Kiffney and Clements, 1996). Delayed indirect effects include a reduction in the quality and processing of organic matter. Allochthonous matter is central to macroinvertebrate feeding and nutrition (Egglishaw, 1968; Minshall et al., 1983; Huryn and Wallace, 1987), and acidification slows decomposition via reductions in microbial activity and macroinvertebrate colonization (Burton et al., 1985; Kimmel et al., 1985; Garden and Davies, 1989). Individuals inhabiting such conditions exhibit hindered development, biomass, and fecundity (Soderstrom, 1988; Groom and Hildrew, 1989; Schell and Kerekes, 1989).

Objectives

Despite considerable efforts to test predictions of the RCC and to quantify the effects of acidification on stream macroinvertebrates, to my knowledge, no studies in this region have attempted to investigate the simultaneous effects of these processes on macroinvertebrates at a watershed scale. Thus my overall objective was to quantify the spatial and temporal variation in macroinvertebrate structure and function along a stream continuum in the Upper Shavers Fork watershed. I specifically quantified macroinvertebrate density, biomass, richness, relative abundance, among-site community taxa similarity, and feeding group composition.

The first objective was to compare observed patterns with those predicted by the RCC and its subsequent modifications. However, I did not measure energy inputs,

primary production, or community respiration, rather I used RCC predictions for macroinvertebrate structure and function as a guiding framework for sampling and analyses. The second objective was to examine how reach-to-reach variability in water chemistry and canopy cover, not correlated to position along the continuum, influenced macroinvertebrate structure and function. Here, I intended to determine if general changes in macroinvertebrate communities associated with stream size were overwhelmed by small-scale changes in alkalinity or light.

Finally, my objectives are embedded within a larger, integrated study of aquatic ecosystem processes in the Upper shavers Fork watershed. The ultimate objective of the larger study is to identify factors potentially limiting biological productivity in this historically important watershed. Research herein will provide an indication of how water chemistry, canopy cover, and stream size affect macroinvertebrate communities. Furthermore, macroinvertebrate dynamics, along with physical habitat variables, influence the distribution patterns (Schlosser and Angermeier, 1995; Petty and Grossman, 1996) and productivity of fish communities (Elliot, 1976; Fausch, 1984; Hughes and Dill, 1990; Facey and Grossman, 1992; Hill and Grossman, 1993; Baker and Coon, 1997; Hughes, 1998; Nislow, 1999). Consequently, an understanding of the factors influencing macroinvertebrates may contribute to an understanding of the role that food availability has in limiting fish productivity at a watershed scale.

Materials and Methods

Study Area

Shavers Fork is a major tributary of the Cheat River within the Ohio River basin. The Shavers Fork flows north, and its watershed (55,167 ha) comprises a part of Pocohontas, Randolph, and Tucker counties in the Eastern Allegheny Plateau of the Central Appalachian Mountains of West Virginia. The Eastern Allegheny Plateau is a primarily forested, high elevation (≥ 900 m) upland composed of sandstone, shale, conglomerate and coal (Waite et al., 2000). In particular, the Shavers Fork watershed is approximately 42% deciduous, 29% conifer, 26% mixed, 1% crop/hay pasture, 1% wetland, and 1% low intensity human disturbance (WVDNR, 2000).

The Upper Shavers Fork watershed (13,856 ha, 38.5° N 79.9 ° W) is the southern section of the Shavers Fork (Figure 3). With exception to three kilometers of headwater stream, the Upper Shavers Fork flows entirely within the Monongahela National Forest. The mainstem lies in an elevated (>1000 m), low gradient basin with eastern and western confinement by Shavers and Cheat Mountains, respectively. The Upper Shavers Fork originates at nearly 1400 m, flows north for 32 km, and increases to fourth order. Tributaries enter at near perpendicular angles (i.e. trellised network pattern) (OSM, 1981), and their gradients are often stair-stepped with low-high-low gradient segments.

The watershed is primarily forested and, along the stream continuum, a minimum of eighty years separates prior riparian harvest (Clarkson, 1964). Remnant effects of harvest, however, include deficiencies in large (>15 m) red spruce (*Picea ruben*) along the mainstem channel. In contrast, many headwater reaches have low gradient bogs that support naturally open canopies. A dense shrubby understory (e.g.

Rhododendron spp.) is generally absent, and a mixed deciduous-coniferous overstory primarily shades the stream continuum. In total, these riparian conditions provide variations in light that are not necessarily related to stream size. Headwater bogs, narrow and broad-leafed species composition, sparse shrubby understory, and downed overstory from ice and wind expose the stream to localized variations in canopy cover.

The watershed averages 122 cm to 152 cm of precipitation yearly (OSM, 1981; Clayton et al., 1998). Snow is common from November through April and thunderstorms occur about 50 days per year, mostly during June through August (WVU, 1965; OSM, 1981). Precipitation is acidic, averaging pH 4.1 - 4.5, and reflects a common pattern throughout the northeastern United States (Cogbill, 1976; Carline et al., 1992; Clayton et al., 1998; Stribling et al., 1998; NADP, 2000).

Geology consists of the Pennsylvanian Pottsville Group and Mississippian Mauch Chunk Group (OSM, 1981; Clayton et al., 1998). The Pennsylvanian Pottsville Group includes sandstones, shales, and limited coal. The Mississippian Mauch Chunk Group includes sandstones, shales and limestone. Consequently, streams flowing through this latter group receive increased buffering potential. Superficial distributions of Mauch Chunk, however, are inconsistent (OSM, 1981; Gaujot, 2002) and, at best, provide short longitudinal sections of slightly buffered water with no correlation to stream size. Furthermore, when placed in the perspective of all geologic groups, the Pottsville and Mauch Chunk groups are minimally alkaline (USEPA, 1986) and provide low buffering potential for acidic input into stream waters (Reger, 1931; Galloway et al., 1976).

Site Selection

I sampled a 25.2 km continuum (flow 0.01 to 2.36 m³ s⁻¹) that incorporated a principal headwater tributary, Second Fork, and the mainstem of the Upper Shavers Fork (Figure 4). Ten sites were selected to investigate the effects of changes in basin area, canopy cover, alkalinity, and secondary parameters such as channel width and water temperature (Table 1). I was particularly interested in reach-scale variation in alkalinity and canopy cover occurring along the continuum (Figure 5). For instance, moving downstream, and thus as an overlay upon increasing stream size, selected sites had: high alkalinity and low canopy (site I), high alkalinity and high canopy (II), low alkalinity and high canopy (III, IV, and V), low alkalinity and low to high canopy (VI and VII), and high alkalinity and low canopy (VIII, IX, and X). Consequently, these sites allowed complete depiction of the relationship between spatio-temporal changes in physico-chemical variables and macroinvertebrate structure and function.

Field Procedures

Sampling Regime

Benthic samples were collected from sites III – X in spring (May 15th - 25th), summer (July 25th - August 10th), and fall (October 7th - 26th) 2000. Benthic samples for sites I and II were collected in fall (October 7th - 26th) 2000 only (see section on macroinvertebrates for explanation). I quantified microhabitat and measured pH immediately prior to sampling the benthos at each site each season. Additional pH measurements were collected whenever on site (May 15th 2000 to December 5th 2001). I quantified macrohabitat from May 10th - 25th 2000. Instream temperatures were recorded from April 1st - October 26th 2000. I quantified percent canopy cover at each site on

September 1st - 2nd 2000. Water samples for alkalinity estimates were collected on Nov. 6th and Dec. 05th 2001.

Physical Habitat

Macrohabitat was quantified to assess the degree of change in macro-scale features with position along the stream continuum. Using Arcview 3.2, I estimated basin area, distance below headwater, and link number for each site. A link number indicates the number of 1st order perennial streams upstream of a given site along the continuum. I used this descriptor because it represents stream size more accurately than Strahler's stream ordering system (Statzner and Higler, 1985; Childers, 2000). Channel width was measured by judging bank-full discharge (i.e. the maximum streamflow that can be incorporated within the channel without over topping the banks and spreading onto the floodplain) (Armantrout, 1998). I quantified channel width from transects spaced every one mean stream width (MSW) in the tributary (sites I-VII) and every two MSW's in the Shavers Fork mainstem (sites VIII-X). Dissimilarity between the spacing of tributary and mainstem transects was justified by the increased heterogeneity of tributary habitat versus the comparatively homogenous mainstem habitat. In addition, the increased spacing of transects in the mainstem allowed for accurate representation of the comparatively longer pool-riffle-glide habitat units. Following guidelines of Simonson et al. (1994), estimates of channel width are composites of twenty-one transects at each site.

Microhabitat was quantified to assess variation in micro-scale features among benthic sampling points. For a given sampling point, I measured bottom and average (0.6 total depth) current velocities with a Marsh-McBirney (model 201) electronic velocity

meter. Substrate composition was then measured by placing a 40 cm² viewing quadrat on the water's surface and visually estimating % bedrock, boulder (> 256 mm), cobble (6-256 mm), gravel (2-64 mm), sand (1-2 mm), silt (< 1 mm), and organic debris (Petty and Grossman, 1996). Particle classification followed a modified Wentworth scale (Minshall, 1984). Estimates of riffle microhabitat features are composites of five points from each site each season.

Water Chemistry

Alkalinity and pH were measured to assess the relationship between changes in water chemistry and macroinvertebrate structure and function along the stream continuum. I estimated alkalinity by sampling each site on two dates. On each date, I would triple dip and rinse 2-3 acid-bathed polyethylene bottles, then cap each below the water's surface. Samples were immediately placed in ice then titrated within 48 hr to pH 4.5 using a 0.02 N H₂SO₄ solution (USEPA, 1979). Estimates of alkalinity are composites of 4-6 water samples from each site.

Preceding macroinvertebrate collections, I measured pH with an Oakton (model 100) handheld meter. Additional measurements were collected whenever on-site (May 15th 2000 to Dec. 5th 2001). Estimates of pH are composites of 10 measurements from each site.

Canopy Cover

Canopy cover was measured to assess the relationship between changes in light and macroinvertebrate structure and function along the stream continuum. Using a

spherical densiometer, measurements were conducted from the midstream point of transects spaced every 10 m immediately upstream of benthos sites. For a given point, four directional readings (i.e. upstream, downstream, left bank, right bank) were recorded from approximately 30 cm above the water's surface (Bain and Stevenson, 1999). Additionally at each midstream point, I visually estimated the % composition of the overstory as either deciduous or coniferous. Estimates of % canopy cover are composites of ten points from 100 m of stream reach at each site.

Macroinvertebrates

Benthic samples were collected to assess the relationship among physico-chemical variables and macroinvertebrate structure and function along the stream continuum. For a given sample, I hand-scoured cobble and stirred smaller substrate within a modified Hess sampler (0.10 m², 250 µm mesh net). I preserved samples on-site with a 95% ethanol and Rose Bengal solution (William and Williams, 1974). Estimates of macroinvertebrate communities are composites of five random samples from riffles within each site each season. I collected benthic samples from sites III-X in spring, summer, and fall 2000. However, because I was initially unaware of the presence of high alkalinity tributaries in the headwaters of Second Fork, macroinvertebrates were collected from sites I and II in fall 2000 only.

Laboratory Procedures

Benthic samples were flushed with water and sorted into 1.0 and 0.25 mm sieves. All 1.0 mm sieve contents were separated from organic matter by dissecting microscope (Leica, model MZ6) and fully counted. I subsampled and counted 0.25 mm sieve contents

by removing 100 ml from 500 ml of stirred, aerated water (Feminella, 1996; Angradi, 1999). Macroinvertebrates were identified to family, or genera of concern (i.e. *Epeorus* spp., Heptageniidae:Ephemeroptera; *Eurylophella* spp., Ephemerellidae:Ephemeroptera; and *Parapysche* spp., Hydropsychidae:Trichoptera), using Merrit and Cummins (1996), Peckarsky et al. (1990), and Wiggins (1998). Exceptions occurred for Oligocheata and Nematomorpha, which were identified to order only. Independent verifications (i.e. < 10% of total collection) were performed by Janet Clayton (West Virginia Division of Natural Resources) and a verified reference collection (West Virginia University, Department of Wildlife & Fisheries) was used for comparison. With an ocular micrometer, I measured head capsule width to the nearest 0.1 mm and then used regression equations (Smock, 1980; Benke et al., 1999) to convert size measurements to biomass (mgDM/m²).

Statistical Analyses

Analyses were conducted to determine whether macroinvertebrate structure and function depended more on position along the stream continuum or on site-specific changes in alkalinity and canopy cover. To measure if spatio-temporal variation in macroinvertebrate communities resulted from changes in alkalinity, canopy cover, or basin area, I performed stepwise multiple regressions, analyses of variance, coefficients of community similarity (i.e. Jaccard's coefficient), and metrics of relative and absolute abundance. In order to meet normality assumptions and reduce heteroskedasticity, I transformed density ($\log_{10}$), biomass [$\log_{10}(x + 1)$], and percent (arcsine) data (Zar, 1996). Due to the high degree of variability inherent in macroinvertebrate distributions (Downes et al., 1993), a critical alpha (α) value of less than 0.10 was used in all multiple means

comparison, whereas as a critical alpha (α) value of less than 0.15 was used in stepwise regression analyses.

Comparisons were conducted on five replicate benthic samples taken from each site each season. However, not all benthic macroinvertebrate larva and aquatic adults were included in analyses. Decapoda ($n = 61$), Oligocheata ($n = 3,071$), and Nematomorpha ($n = 210$) were removed. Such removals constituted 7% of the total macroinvertebrate community ($N = 47,737$). I removed Decapoda because they can significantly increase the variance of biomass estimates (Miller, 1985). I removed Oligocheata and Nematomorpha because individuals were often in parts, and since I could not distinguish posterior and anterior regions, abundance was potentially overestimated, thereby increasing the variance of density estimates.

Physical Microhabitat

Depth (m), bottom and average current velocities (m/s), and substrate composition (%) were measured at each benthos sampling point (0.1 m^2). With exception to riparian debris, I expected all variables to remain consistent throughout riffles along the continuum. The amount of riparian debris should decrease as canopy cover decreases. To test for significant differences among sites along the continuum, I used one-way analysis of variance with a Tukey-Kramer Honestly Significant Difference (HSD) multiple means comparison.

Macroinvertebrate Density and Biomass

Density and biomass were measured as the number and milligrams of dry mass per meter squared, respectively. I expected density and biomass to increase as alkalinity (e.g. Miller, 1985) and basin area increased or canopy cover decreased (e.g. Vannote et al., 1980). To test for significant differences among sites along the continuum, I used one-way analysis of variance with a Tukey-Kramer HSD multiple means comparison. Stepwise multiple regressions were then performed to rank the relative influences of alkalinity, canopy cover, and basin area on seasonal and annualized patterns in density and biomass (annualized patterns refer to the mean of a given site for spring, summer, and fall 2000).

Family Richness

Family Richness was measured as the total number of families present per site. I expected family richness to increase as alkalinity (e.g. Kimmel et al., 1985) and basin area increased or canopy cover decreased (e.g. Vannote et al., 1980). Stepwise multiple regressions were performed to rank the relative influences of alkalinity, canopy cover, and basin area on the annualized pattern in family richness.

Community Similarity

Community similarity was measured as the percent congruency (i.e. 0 - 100 %) of family-level taxa occurring among sites. I expected community similarity to decrease as the distance from a focal site increased (e.g. Vannote et al., 1980). Hence, when moving from small to large basin area sites, community similarity should progressively decrease

(e.g. Grubaugh et al., 1996). Additionally, when moving among adjacent sites at the reach-scale, community similarity should vary with changes in alkalinity (e.g. Simpson et al., 1985) and canopy cover (e.g. Vannote et al., 1980). Thus, small-scale variability in alkalinity or canopy cover should change taxa composition and modify stream continuum predictions for community similarity at affected points along the continuum.

Jaccard Coefficients were calculated to assess the degree of similarity in community composition among sites along the continuum. This procedure has been used to determine patterns in community composition along elevation and stream size gradients (Allan, 1975; Grubaugh et al., 1996; Stribling et al., 1998). The equation is as follows:

$$C_j = j / (a + b - j)$$

where:

j = the number of taxa common to both samples

a = the number of taxa in sample A

b = the number of taxa in sample B

The coefficient decreases (i.e. C_j approaches zero) as the similarity in community composition among sites decreases. Furthermore, large decreases in the similarity coefficient, represented graphically through steep angles connecting adjacent sites, indicate an area where the rapid addition or replacement of taxa has occurred.

Feeding Group Composition

The % biomass of each feeding group was calculated from the total biomass at each site. I used Merritt and Cummins (1996) to assign a feeding group to each family, then referenced these classifications with published results from previous studies in the region (Miller, 1985; Kobuszewski and Perry, 1993; Stribling et al., 1998). The function

established for local genera was used as decisive criteria to categorize family-level feeding guilds. Following predictions of the RCC (Vannote et al., 1980), I expected highly predictable changes in the % biomass composition of feeding groups with movement from small to large basin area sites. Specifically, I expected a shift from the dominance of % shredder and gatherer feeding groups to the dominance of % scraper and filterer feeding groups. In comparison, I expected % predator biomass to remain consistent along the continuum (Vannote et al., 1980). Stepwise multiple regressions were performed to rank the relative influences of alkalinity, canopy cover, and basin area on the seasonal and annualized patterns in % biomass of individual feeding groups.

Second, the % biomass of each family within a feeding group was calculated at each site. I expected the contribution of a given family to vary spatially according to alkalinity (Rosemond et al., 1992), canopy cover, and basin area (Vannote et al., 1980). I additionally expected the contribution of each family to vary seasonally (Georgian and Wallace, 1983). These family level calculations are descriptive and provide a measure of the relative biomass contribution to the absolute biomass of each feeding group. Tests of statistical significance were not performed.

Third, the seasonal and annualized mean biomass (mgDM/m^2) of each feeding group was calculated from the total biomass at each site. I expected all feeding groups to have greater biomass as alkalinity increased (e.g. Miller, 1985). Similarly, I expected all feeding groups to have greater biomass as light increased (e.g. Hawkins et al., 1982). Stepwise multiple regressions were performed to rank the relative influences of alkalinity, canopy cover, and basin area on the seasonal and annualized patterns in absolute biomass of individual feeding groups.

Community Metrics

The relative abundance of particular orders, families, and genera were measured at each site. In low alkalinity sites, I expected abundances of the comparatively acid-tolerant Plecoptera to increase, while abundances of the comparatively acid-intolerant Ephemeroptera and Trichoptera decrease (e.g. Simpson et al., 1985; Allard and Moreau, 1987). Abundances of the acid-intolerant Leptophlebiidae (Ephemeroptera) should also decrease in low alkalinity sites (e.g. Rosemond et al., 1992;). In contrast, I expected an increased abundance of the acid-tolerant genera *Epeorus*, *Eurylophella*, *Parapsyche* within their respective families (e.g. Kobuszewski and Perry, 1993; Clayton and Menendez, 1998).

Community metrics should change again as basin area increases and canopy cover decreases (e.g. Vannote et al., 1980). Specifically, Ephemeroptera and Trichoptera should increase due to an increase in scraper, gatherer and filterer taxa with increasing stream size. Similarly, the abundance of Leptophlebiid gatherers should increase within Ephemeroptera. The genera *Epeorus*, *Eurylophella*, *Parapsyche* should decrease in relative abundance as additional genera in each respective family increase in abundance. These community metrics are descriptive and provide a measure of relative and absolute abundance. Tests of statistical significance were not performed.

Results

Benthic samples from ten sites over three seasons contained macroinvertebrates from fifty families and eight orders (Appendix I). Chironomidae (Diptera) comprised 49% of all individuals (N = 43,395). Excluding Chironomidae, the orders Ephemeroptera

(40%), Plecoptera (36%), Diptera (12%), and Trichoptera (10%) were numerically dominant, comprising 98% of all non-chironomidae taxa.

Physical Microhabitat

No significant differences occurred among sites along the continuum in mean depth, average or bottom current velocity, and % bedrock, boulder, cobble, gravel, or sand. In fall, silt and debris significantly differed in sites II and III, respectively. Site II had increased riparian litter ($P < 0.01$, $F = 6.38$, $DF = 49$) and site III had increased silt ($P < 0.01$, $F = 15.25$, $DF = 49$). Mean values among sites in all three seasons were: depth 0.2 ± 0 m; average current velocity 0.28 ± 0 m/s; bottom current velocity 0.14 ± 0 m/s; bedrock 0 %; boulder 1 ± 0 %; cobble 44 ± 3 %; gravel 29 ± 2 %; sand 20 ± 2 %; silt 4 ± 1 %; and debris 2 ± 0 %.

Macroinvertebrate Density and Biomass

I detected significant differences in mean macroinvertebrate density (Figure 6) and biomass (Figure 7) among sites in all three seasons of the study. These seasonal patterns are summarized by the annualized mean density and biomass for each site (except for sites I and II which represent fall 2000 only) (Figure 8). The essential patterns were as follows: (1) macroinvertebrate density and biomass tended to be lower in the middle reaches of the tributary (sites III-V); whereas (2) macroinvertebrate density and biomass tended to be higher in the upper reaches of the tributary (I and II) and the Shavers Fork mainstem (VIII and IX). An exception to this pattern was the significantly lower annualized density observed in site X (Figure 8). Comparison of these spatio-temporal patterns with estimates of alkalinity and canopy cover for each site indicated a

strong influence of physico-chemical variables upon benthic macroinvertebrate density and biomass (Figure 5). Multiple regression analyses provided further evidence for such influences (Table 2). Alkalinity was the only significant predictive variable throughout every season; hence, it explained 67% of the spatial variation in annualized density. Alkalinity primarily affected biomass distributions as well. Yet, canopy cover and basin area also affected biomass, thus all three variables explained 88% of the spatial variation in annualized biomass (Table 2).

Family Richness

Macroinvertebrate family richness increased dramatically in downstream reaches, particularly with passage from the tributary into the Shavers Fork mainstem (Figure 9). Across seasons, diversity ranged from 17 families in the most upstream acidic site in Second Fork (site III in summer) to 32 families in the downstream reaches of the Shavers Fork mainstem (site X in spring, and site IX in fall). The variability in family richness resulted from changes in alkalinity and basin area (Table 3). Basin area explained 92% and 72% of the spatial variation in family richness during the spring and summer seasons, respectively. Alkalinity explained 78% and 63% of the spatial variation in family richness during the fall season and the annualized distribution, respectively.

Community Similarity

For brevity, the results of sites I, III, VI, VIII, and X are presented. I focus on these sites because they cover the complete range of variability in alkalinity, canopy cover, and stream size. The greatest similarity in community taxa occurred among adjacent sites (Figure 10). Thus as the distance from a given focal site increased, steady

reductions were observed in community similarity. Indeed, basin area was the primary determinant of community similarity along the stream continuum as sites I, III, VI, VIII, and X decreased in similarity when compared to sites of increasing distance. Taxa composition in site I, for example, was more similar to sites II and VI than to sites XII - X, despite the similarity of sites I and VIII - X in alkalinity and canopy cover.

I also observed an interactive effect of alkalinity and canopy cover on community similarity. In particular, a large replacement and addition of taxa occurred when moving from the lower tributary to the Shavers Fork mainstem (site VIII) (Figure 10). Between sites VII and VIII, alkalinity and canopy cover varied greatly, while basin area did not. Such change in alkalinity, canopy cover, and channel width reduced the similarity of the communities despite a relatively small change in basin area. In fact, site VIII was more similar to sites IX and X than it was to site VII, even though basin area increased by several thousand hectares (sites VIII and X) (Figure 10).

Feeding Group Composition

Alkalinity, canopy cover, and basin area significantly influenced the spatial variation in % biomass of feeding group composition (Table 4). However, alkalinity and canopy cover better explained the seasonal spatial variation in % biomass of feeding group composition than did basin area. Specifically, alkalinity explained: (1) 78% of the spatial variation in % gatherer biomass in spring; (2) 59% of the spatial variation in % shredder biomass in summer; and (3) 45% of the spatial variation in % predator biomass in summer. Canopy cover explained: (1) 10% of the spatial variation in % gatherer biomass in spring; (2) 83% of the spatial variation in % filterer biomass in summer; and (3) 29% of the spatial variation in % shredder biomass in fall. In contrast, basin area

explained 54% of the spatial variation in % shredder biomass in spring. Yet as these findings suggest, no consistent relationship occurred between the % biomass of any feeding group and predictive variable.

The annualized distribution of % feeding group biomass further supported these seasonal results (Table 4). Basin area did not significantly explain variation in the annualized % biomass of any feeding group. However, canopy cover and alkalinity explained 63% and 26% of the annualized spatial variation in % shredder and scraper biomass, respectively.

The contribution of an individual family to feeding group biomass varied spatially and temporally (Table 5). For example, Corydalidae (Megaloptera) contributed to predator biomass only in sites VIII - X, and in site VI, Heptageniidae (Ephemeroptera) substantially contributed to scraper biomass in spring and fall, but not in summer. Therefore, a very general summary of the top biomass contributors is as follows: Leuctridae (Plecoptera) contributed the greatest biomass to the shredder group; Heptageniidae contributed the greatest biomass to the scraper group; Chironomidae (Diptera) contributed the greatest biomass to the gatherer group; Polycentropodidae and Hydropsychidae (Trichoptera) contributed the greatest biomass to the filterer group; and Chloroperlidae and Perlodidae (Plecoptera) contributed the greatest biomass to the predator group. Appendix II contains a full account of the % biomass, total biomass, abundance, and richness of taxa comprising feeding groups in each site each season.

Alkalinity, canopy cover, and basin area significantly influenced the spatial variation in absolute biomass of feeding group composition (Table 6). However, alkalinity and canopy cover better explained the seasonal spatial variation in absolute

biomass of feeding group composition than did basin area. Specifically, alkalinity explained: (1) 95% and 45% of the spatial variation in gatherer and filterer biomass in spring, respectively; (2) 37%, 48%, 79%, and 80% of the spatial variation in scraper, gatherer, filterer, and predator biomass in summer, respectively; and (3) 56% and 51% of the spatial variation in gatherer and filterer biomass in fall, respectively. Canopy cover explained: (1) 34% and 42% of the spatial variation in scraper and predator biomass in spring, respectively; and (2) 40% and 62% of the spatial variation in scraper and predator biomass in fall, respectively. In contrast, basin area explained 25% of the spatial variation in gatherer biomass in summer.

The annualized distribution of absolute feeding group biomass supported seasonal results for canopy cover, but not for alkalinity (Table 6). Indeed, basin area was more important than alkalinity in explaining the spatio-temporal variation in annualized biomass of all feeding groups. Basin area explained 32%, 41%, 29%, 71% and 78% of the annualized variation in shredder, scraper, gatherer, filterer, and predator biomass, respectively. Canopy cover explained 54%, 58%, 22%, and 17% of the annualized variation in scraper, gatherer, filterer, and predator biomass, respectively. Alkalinity was not retained in any annualized model explaining the spatio-temporal variation in absolute biomass of feeding groups. Yet as these findings suggest, basin area and canopy cover consistently predicted the annualized absolute biomass of all feeding groups.

Community Metrics

In low alkalinity sites (III - VII), absolute abundances of Ephemeroptera and Trichoptera (Figure 11), Leptophlebiidae (Figure 12), and Hydropsychidae (Figure 13) decreased, while the absolute abundance of *Parapsyche* increased (Figure 13). In

contrast, in more alkaline sites upstream and downstream of III - VII, the absolute abundance of Ephemeroptera, Trichoptera, Leptophlebiidae, and Hydropsychidae increased while *Parapsyche* decreased. The absolute abundance of *Eurylophella* varied spatially and temporally and appeared unaffected by distributions in alkalinity (Figure 14). With exception to the fall season, the absolute abundance of *Epeorus* also did not appear to be affected by distributions in alkalinity (Figure 15).

The greatest change in annualized relative abundances occurred in the two least alkaline sites (sites III and IV) (Table 7). For example, Trichoptera were 12% (N = 18,867) of Ephemeroptera:Plecoptera:Trichoptera (EPT) along the stream continuum, yet just 4% (N = 2,565) of EPT in sites III and IV. Such decline increased the relative abundance of Plecoptera from 42% (N = 18,867) of EPT along the stream continuum to 87% (N = 2,565) of EPT in sites III and IV.

Upstream from these sites, alkalinity increased, canopy cover and basin area decreased, and relative abundances changed (Table 7). In particular, Ephemeroptera increased to 56% of EPT, and *Eurylophella* and *Parapsyche* contributed 1% or less to their respective family abundance. *Epeorus*, however, increased from 38% (N = 61) in sites III and IV to 50% (N = 538) of Heptageniidae in sites I and II.

In Shavers Fork mainstem sites (VIII – X) with high alkalinity, low canopy, and increasing stream size, *Epeorus*, *Eurylophella* and *Parapsyche* contributed less to their respective families (Table 7). Zero *Parapsyche*, for example, occurred within the family Hydropsychidae (N = 535). In contrast, the relative abundances of Leptophlebiidae, Ephemeroptera, and Trichoptera increased. The relative abundance of Plecoptera to EPT decreased in comparison to sites III and IV, and in turn, was nearly identical to sites I and

II. Indeed, the smallest two sites most closely approximated the largest three sites in all measurements of relative abundance except % *Epeorus*.

Discussion

Alkalinity was the most significant determinant of benthic macroinvertebrate community structure and function along the stream continuum. Alkalinity affected density and biomass regardless of position along the continuum. Furthermore, spatial variation in alkalinity significantly explained the annualized % biomass of shredders as well as the seasonal patterns in absolute biomass of all feeding groups but shredders. Finally, the distribution and occurrence of several orders, families, and genera were determined more by their tolerance level to acidity than by position along the continuum.

Canopy cover was the second most significant determinant of community structure and function along the stream continuum. The effect of canopy was independent of stream size, as small tributary sites with high light had significantly higher density and biomass. Furthermore, spatial variation in canopy cover significantly explained the annualized % biomass of scrapers as well as the annualized absolute biomass of all feeding groups but shredders. Yet the effect of canopy may not be independent of alkalinity, as the one high light / low alkalinity site (site VI) had increased density and biomass but significant differences were not seasonally consistent. Nevertheless, combinations of alkalinity and canopy cover were dominant factors affecting community structure and function along the stream continuum.

Stream size influenced community structure and function least, though effects of basin area were observed. Results of community similarity indicated that stream size was independent of alkalinity and canopy cover. Specifically, the smallest site was more

similar to other tributary sites than it was to the Shavers Fork mainstem sites, which it most closely approximated in terms of alkalinity and canopy cover. In mainstem sites, family richness was also higher than in the smallest site, suggesting that position along the continuum affected richness more strongly than alkalinity or canopy cover.

In addition, the annualized absolute biomass of all feeding groups increased with increasing basin area. Thus, alkalinity, canopy cover, and stream size interacted to affect different components of macroinvertebrate structure and function. Furthermore, because results for individual components of macroinvertebrate structure and function are complex, a more detailed synthesis follows.

Macroinvertebrate Density and Biomass

In agreement with predications of Vannote et al. (1980), significant increases in macroinvertebrate density and biomass occurred downstream. These results also support Grubaugh et al. (1996) who found large increases in density and biomass with transition from small ($< 1,000$ ha) to middle ($> 1,500$ ha) sized streams. Along their continuum, however, density and biomass showed the largest increase with transition into the Little Tennessee River ($> 36,000$ ha) of North Carolina.

In the smallest (< 100 ha) sites of my study, changes in alkalinity and canopy cover presumably caused an increase in density and biomass. The significantly higher density and biomass of site II likely resulted from increased alkalinity (Feldman and Connor, 1992). The further increase in density and biomass of site I likely resulted from that site being more alkaline plus a large reduction in canopy (Hawkins et al., 1982). In fact, biomass at this smallest site was significantly higher than at all other tributary sites, and only differed significantly from the largest site. Both of these small sites (I and II)

flow through Mauch Chunk formation (Gaujot, 2002) which, in southwestern Pennsylvania (Madarish and Kimmel, 1999) and western Virginia (Miller, 1985), was found to cause similar improvements in alkalinity and localized macroinvertebrate structure.

Relatively high macroinvertebrate density and biomass in the least alkaline site (site III) along the continuum was unanticipated since these measurements declined in pH-depressed sites of southwestern Pennsylvania (Kimmel et al., 1985), western Virginia (Feldman and Connor, 1992), north central Virginia (Miller, 1985), and western North Carolina (Rosemond et al., 1992). Unaltered or increased density and biomass, however, is reported for more acidic sites of other tributaries in the Shavers Fork (Kobuszewski and Perry, 1993) and in southwestern Pennsylvania (Madarish and Kimmel, 1999). Thus, the observed increase in density and biomass likely reflects a competition release from colonizing, marginally acid-sensitive taxa and, in turn, a dominance of acid-tolerant taxa (Hall and Ide, 1987; Clayton and Menendez, 1998). In addition, downstream sites may have had greater fluctuations in water chemistry and a less stable chemical environment for resident macroinvertebrates (Madarish and Kimmel, 1999).

Although inconsistent across seasons, the low alkalinity / high light site (site VI) had a significantly higher density and biomass in comparison to upstream tributary sites with low alkalinity and light. Thus, alkalinity may have acted as a template upon which variations in light secondarily affected macroinvertebrate density and biomass. Specifically, low alkalinity may have indirectly reduced nutrient potential (Allan, 1995), and thereby limited the response of macroinvertebrates to light (Rosemond et al., 1993).

The most alkaline site also had an open canopy and significantly higher density and biomass every season. Here, however, concurrent changes in stream size (Minshall et al., 1983) and instream temperature (Benke and Jacobi, 1986; Hauer and Benke, 1987; Stites and Benke, 1989) likely increased macroinvertebrate density and biomass. Therefore, the effects of alkalinity and canopy cover were likely interacting with other stream continuum predictions regarding increasing channel width and temperature (Vannote et al., 1980).

Results for the largest site were unexpected since prior research has predicted (Vannote et al., 1980) and found higher density and biomass in large sites ($\geq 4^{\text{th}}$ order) of the Ozark Plateau (Brussock and Brown, 1991) and Southern Appalachians (Grubaugh et al., 1996). Yet, the range of alkalinity in our largest site was near the USEPA (1986) minimum threshold of 20mg/L CaCO_3 , and thus acidic episodes may have occurred during large storm events. Furthermore, winter ice-scour (Naiman et al., 1987), critical summer temperatures in excess of 25° C (Cada et al., 1987; Peterson and Eeckhaute, 1991; Allan, 1995), epi-benthic predation from stocked populations of brown (*Salmo trutta*) (Bechara et al., 1993) and rainbow (*Oncorhynchus mykiss*) (Feltmate, et al., 1986) trout, resulting sub-optimal habitat use by benthic macroinvertebrates (Feltmate et al., 1986; McIntosh and Townsend, 1994; Forrester, 1994), and a large principal tributary (> 1,500 ha) (Bruns et al., 1984) upstream of this site may have also added to the observed significant reduction in density and biomass.

Family Richness

Family richness followed predictions of Vannote et al. (1980), as all tributary sites had reduced family numbers in comparison to Shavers Fork mainstem sites. In particular,

the successive increase in richness of mainstem sites likely indicated a blending of heterotrophic and autotrophic conditions (Minshall et al., 1983), and these results agree well with the findings of Brussock and Brown (1991) and Grubaugh et al. (1996) who also observed peaks in richness at 3rd – 5th order sites. Furthermore, the largest tributary site had more families than the adjacent site upstream that received more light but was smaller in size. These findings suggest position along the continuum significantly affected family richness.

In addition to stream size, alkalinity also affected family richness, as the two smallest sites had more families than all other tributary sites. In fact, several acid-intolerant families reappeared such as Pteronarcyid and Perlodid stoneflies (Stribling et al., 1998) (Table 8). Thus, distributions of family richness indicated significant effects of alkalinity and supported findings in other tributaries of southwestern Pennsylvania (Kimmel et al., 1985) and western Virginia (Feldman and Connor, 1992). Here, however, the effect of alkalinity on family richness was secondary to the effect of basin area.

Against expectations (Vannote et al., 1980), variation in canopy cover did not significantly affect family richness along the continuum. As with macroinvertebrate density and biomass, I believe alkalinity indirectly constrained the potential increase in family richness with increasing light (Kimmel et al., 1985; Rosemond et al., 1993; Allan, 1995). Specifically, if site VI were more alkaline, it likely would have had increased family richness (Kobuszewski and Perry, 1993; Kimmel et al., 1985; Feldman and Connor, 1992). I then believe this would have produced a significant result in the regression analyses of canopy cover. Yet, this finding may also suggest that the common observation of increased family richness with decreasing canopy cover may result from

the typical correlation between canopy cover and basin area (but see Hawkins et al., 1982).

Community Similarity

Longitudinal changes in community taxa generally supported patterns predicted by Vannote et al. (1980). Macroinvertebrate community similarity decreased sharply with increasing distance between sites. Allan (1975) also observed communities to be more similar when less difference in elevation occurred among sites along a stream continuum in Colorado. He attributed specific areas of taxa replacement to gradual changes in the physical gradient. In comparison, the Shavers Fork has much less elevation loss along its continuum, yet localized variation in alkalinity and canopy cover produced several areas of rapid taxa replacement. For example, tributary sites I, III, and VI differed considerably from adjacent sites in all seasons. Nevertheless, localized variation in alkalinity and canopy cover was not necessarily the primary determinant of community similarity along the stream continuum. The smallest site, which is most similar in alkalinity and canopy cover to the mainstem sites, had a very dissimilar community composition from those sites. Therefore, it is likely that community similarity is influenced simultaneously by the local characteristics of alkalinity (Feldman and Connor, 1992) and canopy cover (Hawkins et al., 1982) as well as by position along the stream continuum (Allan, 1975).

Although basin area among the mainstem sites was very different, these sites were more similar to each other than they were to tributary sites. Yet a large change in community similarity occurred with transition between 3rd order sites of the tributary and Shavers Fork mainstem. This difference occurred despite a small change in basin area. Grubaugh et al. (1996) observed a similarly large change in community taxa in two 3rd

order stream sites in western North Carolina. As with Allan (1975), they attributed their findings to a transition from steeply sloped mountain streams into shallow-sloped alluvial river reaches, since this represented a transitional point between two geomorphic conditions and an overlap of ecotones between the habitat tolerances of many taxa (Statzner and Higler, 1986). The transition from tributary to Shavers Fork mainstem, however, is low gradient ($< 2\%$) and thus it is likely that the observed changes in community similarity resulted from differences in alkalinity and canopy cover, more so than from geomorphic processes dictated by position along the continuum. Furthermore, in eastern deciduous-coniferous forests the onset of autotrophy depends upon the degree of shading (Minshall 1978), which likely occurs at the 3rd stream order (Vannote et al., 1980).

Feeding Group Composition

Against predictions of Vannote et al. (1980), stream size did not explain the spatial variation in annualized % biomass of feeding group composition. Rather, alkalinity and canopy cover explained the spatial variation in annualized % biomass of shredders and scrapers, respectively. Direct comparison of these results with prior findings is difficult, as several studies have used benthic abundance and density to measure feeding group composition (e.g. Hawkins and Sedell, 1981; Hawkins et al., 1982; Cushing et al., 1983; Minshall et al., 1983; Rosemond et al., 1992; Kobuszewski and Perry, 1993; Madarish and Kimmel, 1999). Others have used annual macroinvertebrate production ($\text{gDM}/\text{m}^2/\text{yr}$) to compare feeding group composition (e.g. Smock et al., 1985; Hury and Wallace, 1987). Estimates of feeding composition based on abundance, density, biomass, or production can differ significantly (Miller, 1985;

Lugthart and Wallace, 1992; Grubaugh et al., 1996). For instance, the % composition of shredders may be overestimated by density, predators underestimated by density, grazers and collectors more prominent than predators as production, yet less prominent than predators as biomass (Miller, 1985). Furthermore, no studies to my knowledge have investigated the % biomass of feeding groups along large (50 – 10,000 ha) stream continua having localized variation in alkalinity and canopy cover. Miller (1985), for example, conducted a comprehensive study of macroinvertebrate feeding groups including annual monthly samples that calculated density, biomass, and production estimates, yet all five sites along the stream continuum were $\leq 2^{\text{nd}}$ order (< 1900 ha). A pH gradient did exist, however, and his finding that less grazer taxa attained $2.0 \text{ mgDM}/\text{m}^2$ in smaller sites of lower pH was not supported. Yet his comparisons were for 1^{st} to 2^{nd} order sites, while in this study, a comparable pH gradient existed only for 2^{nd} to 3^{rd} order sites. This study does support Miller's (1985) finding that Leuctrid stoneflies accounted for the largest % of shredder biomass across most sites, and that when Pteronarcyid stoneflies were present Leuctrid stonefly biomass was notably reduced (see Appendix II: site X in summer, and sites II, IX, and X in fall).

The ability of alkalinity to predict distributions in % shredder biomass may suggest that shredders are high in headwater sites not simply because of allochthonous litter but rather: (1) headwater reaches in Central Appalachia are often acidic (Kimmel et al., 1985; Miller, 1985; Menezes et al., 1996; Madarish and Kimmel, 1999), and thus the absolute biomass of all acid-intolerant taxa are reduced regardless of feeding group; and (2) high canopy cover further decreases the absolute biomass of taxa in feeding groups

other than shredders. Consequently, the majority of remaining taxa are acid-tolerant Plecopteran shredders (e.g. Leuctridae) (Simpson et al., 1985; Miller, 1985).

The annualized absolute biomass of feeding groups provided support for the notion that localized variation in light indiscriminately affects all feeding groups. With exception to shredders, canopy cover significantly influenced the annualized absolute biomass of all feeding groups. Although based upon macroinvertebrate abundance, Hawkins et al. (1982) observed similar results regarding the effects of light on feeding groups in open canopy stream sections of Oregon. Streams without shading had higher abundances of macroinvertebrates than did shaded streams. Specifically, open stream sites had higher abundances in the gatherer, filterer, and predator groups, while shredder abundance did not differ among shaded and open canopy stream sites (Hawkins et al., 1982).

The finding that basin area significantly influenced the annualized absolute biomass of all feeding groups may explain the lack of support for RCC predictions regarding % biomass composition of feeding groups. In particular, the absolute biomass of all feeding groups was indiscriminately influenced by stream size. Thus the % biomass composition of feeding groups did not change in support of RCC predictions.

Community Metrics

Longitudinal changes in the relative and absolute abundances of selected orders, families, and genera indicated that the effects of alkalinity, canopy cover, and stream size interacted along the continuum. Yet, alkalinity was the primary determinant of taxa abundance. Ephemeroptera were greater than 50% of EPT in sites with alkalinity near or above the USEPA (1986) minimal standard of 20 mg/L CaCO₃, and the transition from

Ephemeroptera to Plecoptera dominated communities is a well documented finding for benthic community structure in acidified sites (Kimmel et al., 1985; Miller, 1985; Simpson et al., 1985; Allard and Moreau, 1987; Hall and Ide, 1987; Peterson and Eeckhaute, 1991; Feldman and Connor, 1992; Rosemond et al., 1992; Clayton and Menendez, 1998; Madarish and Kimmel, 1999). Similarly, distributions of Trichoptera abundance further supported the ability of the EPT metric to depict alterations in water chemistry (Rosemond et al., 1992; Kobuszewski and Perry, 1993; Wallace et al., 1996).

The increase in Leptophlebiidae in upstream, more alkaline sites supports the findings of Rosemond et al. (1992) and Clayton and Menendez (1998). The decrease in the relative abundance of *Eurylophella* and *Parapsyche* with increasing alkalinity also supports previous findings (Kobuszewski and Perry, 1993; Clayton and Menendez, 1998). In contrast, the increase in the relative and absolute abundance of *Epeorus* in upstream, more alkaline sites was not expected. However, species within *Epeorus* have differential tolerance to acidity (Feldman and Connor, 1992), and perhaps such variation was responsible for the unexpected observation.

Low canopy and increasing stream size also affected community metrics. In particular, the relative and absolute abundances of acid-sensitive taxa increased incrementally from sites III to I. Thus, the interaction of alkalinity and light were apparent upon community structure. Furthermore, these taxa were most abundant in large, highly alkaline, low canopy mainstem sites. Thus, the additional effect of increasing stream size with a wider variance in mean daily temperature was likely observed (Vannote et al., 1980).

Conclusions

Influences on macroinvertebrate structure and function in the Upper Shavers Fork watershed are a complex interaction of factors such as water chemistry, canopy cover, and stream size. At a given point along the continuum, these factors may covary, as suggested by the RCC, and at other points they do not. When these factors do not covary, observed patterns on macroinvertebrate structure and function are quite complex and difficult to predict. Furthermore, the general idea of predictable changes along a stream continuum may be biased by the fact that water chemistry, canopy cover, and basin area can covary along a given longitudinal continuum in Central Appalachian streams. Thus, evaluation of these results suggests that small-scale variation in the geology and riparian character of Central Appalachian watersheds can modify stream continuum predictions at a continuum-specific level.

Management Implications

Stream ecosystem restoration is a scale-dependent process often requiring mitigation from outside the stream-bank such as in the riparian and surrounding watershed (Allan, 1995). Yet, the Upper Shavers Fork flows within the Monongahela National Forest and largely evades such impact. Nevertheless, problems existing within the watershed are: (1) the wet (e.g. precipitation) and dry (e.g. settling of coarse particulates and aerosols) deposition of atmospheric sulfuric and nitric acids (Clayton et al., 1998); and (2) a wide, shallow channel structure in the mainstem which decreases habitat complexity, such as the frequency of pools, and increases instream temperatures.

Headwater Tributaries

Headwater tributaries of the Upper Shavers Fork are most affected by acid precipitation, as the confluence of buffered stream segments may not occur until further downstream. Furthermore, the influence of water chemistry on habitat suitability is significant (Angradi, 1999), as its effects on resident biota may override interrelated influences of current velocity (Mackay, 1992), depth (Huryn and Wallace, 1987), substrate (Rabeni and Minshall, 1977), and cover (Hill et al., 1995). Potential consequences of acidification include a decrease in bacterial composition (Kimmel, 1985), a resulting decrease in sediment-nutrient exchange due to organic layering, an increase in acid-tolerant fungal growth (Wright et al., 1975), and a decrease in macroinvertebrate (Kobuszewski and Perry, 1993; Clayton and Menendez, 1998) and fish structure and function (Clayton et al., 1998).

In general, macroinvertebrate communities display greater tolerances to acidification than do fish (Bell, 1971). Yet, brook trout are among the most acid-tolerant North American fish, and in comparison to cool-water species their rank increases further (Packer and Dunson, 1970). Nevertheless, in headwater tributaries of the Upper Shavers Fork brook trout productivity is likely limited by a combination of indirect (i.e. prey availability) and direct (i.e. physiology) influences. Specifically, sites affected by acidification in this study had reduced macroinvertebrate taxa richness and biomass, as well as an overrepresentation of acid-tolerant taxa. Of particular importance to fisheries management was the loss or decline of large, potentially free swimming mayflies susceptible to predation (e.g. Ameletidae, Baetidae, and Leptophlebiidae). As well, any opportunistic epi-benthic feeding of fleshy caddisflies (e.g. Philopotamidae), and large

stoneflies (e.g. Pteronarcyidae, and Perlodidae) and dragonflies (e.g. Gomphidae) was not available. In turn, the remaining dominance of comparatively small-sized stoneflies (e.g. Leuctridae) and trueflies (e.g. Chironomidae) likely cannot provide a comparable energetic content per unit feeding effort. Furthermore, feeding may become secondarily important as acidification directly affects brook trout physiology. Effects of acidification on physiology may include: (1) excessive gill mucous production which lowers blood oxygen concentrations (Power, 1995); (2) reductions in the ability of dissolved oxygen to bind to hemoglobin (Packer and Dunson, 1970); and (3) improper cellular regulation of sodium due to excessive efflux and deficient influx from the absence of supportive oxidative processes (Wood and McDonald, 1982).

As a counter-treatment, the application of limestone to road-accessible headwater streams is generally inexpensive, improves water chemistry, and restores structure and function to macroinvertebrate and fish communities (Lacroix, 1992; Milner and Aston, 1995; Clayton and Menendez, 1996; Clayton and Menendez, 1998). Furthermore, the effects of liming generally last three years with streams of pH 5.0 either attaining pH 6.0 for more than 90% of the year (Clayton et al., 1998) or expressing an average increase of 0.4 pH units (range 0.1-1.3 pH units) (Lacroix, 1992). Biological responses should include: (1) an increase in macroinvertebrate taxa richness (Clayton and Menendez 1996; Milner and Aston, 1995), and evenness (Clayton and Menendez, 1998); and (2) an increase in fish species richness, biomass (Clayton et al., 1998), growth, survivorship, and density (Lacroix, 1992). Thus, headwater limestone additions will likely reduce indirect and direct limitations on brook trout productivity as prey availability increases and physiology improves. Furthermore, vital ecological links should be restored as

trophic-level interactions are renewed and habitat suitability is improved throughout the longitudinal gradient.

Mainstem Channel

Limitations on brook trout productivity in the mainstem channel of the Upper Shavers Fork likely results from the direct influences of habitat structure and instream temperature, whereas indirect influences of food availability do not appear problematic. When compared to its tributaries, deficiencies in instream structure characterize the mainstem of the Upper Shavers Fork. In general, the wide, shallow low-gradient character of the mainstem channel likely decreases structural density, depth and flow (Lyons, 1992), while simultaneously increasing water temperature. In addition, heavy riparian logging and instream boulder removal into the 1920's (Clarkson, 1964) further reduced instream structure and cover by limiting the addition of large woody debris and boulder frequency. Resulting effects on brook trout likely include: (1) increased energetic demands while feeding without the use of velocity shelters (Everest and Chapman, 1972; Fausch and White, 1981; Hayers and Jowett, 1994); (2) a reduction in pool area, frequency, and use (Beechie and Sibley, 1997); and (3) an increased metabolism (Elliot, 1976; Cada et al., 1987) from instream temperatures that readily exceed 20° Celsius, and may even exceed 25° Celsius, throughout summer (Petty et al., unpublished data).

To improve physical habitat structure and thereby reduce direct limitations on brook trout productivity in the Shavers Fork mainstem, sections (i.e. ≤ 0.5 km) of stream channel could be restructured and the adjacent riparian replanted with red spruce (*Picea ruben*). By confining the stream channel and increasing boulder frequency, trout will

receive the direct benefits of increased depth, flow, and cover. Furthermore, by replanting the adjacent riparian, future (i.e. 50-100 years) additions of large woody debris should increase pool area, particulate organic matter and sediment retention, juvenile trout survival, and overall fish community diversity (Beechie and Sibley, 1997). As well, both management scenarios will likely reduce critically high summer temperatures.

Literature Cited

- Allan, J.D. 1975. The distribution ecology and diversity of benthic insects in Cement Creek, Colorado. *Ecology* 56:1040-1053.
- Allan, J.D. 1995. Stream ecology: structure and function of running waters. Kluwer Academic Publishers, Norwell, MA.
- Allan, J.W. and T. M. Burton. 1986. Size-dependent sensitivity of three species of stream invertebrates to pH depression. In B.G. Isom, S.D. Dennis, and J.M. Bates (eds.), *Impact of acid rain and deposition on aquatic biological systems*. ASTM STP 928, Philadelphia, PA.:54-66.
- Allard, M. and G. Moreau. 1987. Effects of experimental acidification on a lotic macroinvertebrate community. *Hydrobiologia* 144: 37-50.
- Angradi, T. R. 1999. Fine sediment and macroinvertebrate assemblages in Appalachian streams: a field experiment with biomonitoring implications. *Journal North American Benthological Society* 18(1):49-66.
- Armantrout, N.B., compiler. 1998. Glossary of aquatic habitat inventory terminology. American Fisheries Society, Bethesda, Maryland.
- Bain, M.B., and N.J. Stevenson, editors. 1999. Aquatic habitat assessment: common methods. American Fisheries Society, Bethesda, Maryland.
- Baker, E.A., and T.G. Coon. 1997. Development and evaluation of alternative habitat suitability criteria for brook trout. *Transactions of the American Fisheries Society* 126:65-76.
- Bechara, J.A., G. Moreau, and L. Hare. 1993. The impact of brook trout (*Salvelinus fontinalis*) on an experimental stream benthic community: the role of spatial and size refugia. *Journal of Animal Ecology* 62:451-464.
- Beechie, T.J., and T.H. Sibley. 1997. Relationships between channel characteristics, woody debris, and fish habitat in northwestern Washington streams. *Transactions of the American Fisheries Society* 126:217-229.
- Bell, H.L. 1971. Effects of low pH on the survival and emergence of aquatic insects. *Water Resources* 5:313-319.
- Benke, A.C., and D.J. Jacobi 1986. Growth rates of mayflies in a subtropical river and their implications for secondary production. *Journal of North American Benthological Society* 5:107-114.

- Benke, A. C., A.D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of North American Benthological Society* 18(3):308-343.
- Bruns, D.A., G.W. Minshall, C.E. Cushing, K.W. Cummins, J.T. Brock, and R.L. Vannote. 1984. Tributaries as modifiers of the river continuum concept: analysis by polar ordination and regression models. *Archivfur Hydrobiologie* 99(2): 208-220.
- Brussock, P.P., and A.V. Brown. 1991. Riffle-pool geomorphology disrupts longitudinal patterns of stream ecosystems. *Hydrobiologia* 220:109-117.
- Burton, T.M., R.M. Stanford, and J.W. Allan. 1985. Acidification effects on stream biota and organic matter processing. *Canadian Journal of Fisheries and Aquatic Science* 42:669-675.
- Cada, G.F., J.M. Loar, and M.J. Sale. 1987. Evidence of food limitation of rainbow and brown trout in southern Appalachian soft-water streams. *Transactions of the American Fisheries Society* 116:692-702.
- Carline, R.F., D.R. Dewalle, W.E. Sharpe, B.A. Dempsey, C.J. Gagen, and B. Swistock. 1992. Water chemistry and fish community responses to episodic stream acidification in Pennsylvania. *Environmental Pollution* 78:45-48.
- Carpenter, D.A. 2000. Testing the river continuum concept: exploring ecological processes in the Wheeling Creek watershed. Master's Thesis. West Virginia University. 80 pp. http://etd.wvu.edu/ETDS/E1879/Carpenter_Deborah_Thesis.pdf
- Childers, H.M. 2000. Scale, ecological fallacy, and the river continuum concept. Master's Thesis. West Virginia University. 49 pp. http://etd.wvu.edu/ETDS/E1849/Childers_H_Thesis.pdf
- Clarke, K.D. and D.A. Scruton. 1997. The benthic community of stream riffles in Newfoundland, Canada and its relationship to selected physical and chemical parameters. *Journal of Freshwater Ecology* 12(1):113-121.
- Clarkson, R.B. 1964. Tumult on the mountains, lumbering in West Virginia, 1770-1920. 8th edition. McClain Printing Company, Parsons, West Virginia.
- Clayton, J.L., and R. Menendez. 1996. Macroinvertebrate responses to mitigative liming of Dogway Fork, West Virginia. *Restoration Ecology* 4:234-246.

- Clayton, J.L., E.S. Dannaway, R. Menendez, H.W. Rauch, and P.E. Zurbuch. 1998. Application of limestone to restore fish communities in acidified streams. *North American Journal of Fisheries Management* 18:347-360.
- Clayton, J.L., and R. Menendez. 1998. Macroinvertebrate response to instream applications of fine-grained limestone to mitigate acid deposition. WVDNR Project Report to United States Fish and Wildlife Service.
- Cogbill, C.V. 1976. The history and character of acid precipitation in eastern North America. *Water, Air and Soil Pollution* 6:407-413.
- Cushing, C.E., C.D. McIntire, K.W. Cummins, G.N. Minshall, R.C. Petersen, J.R. Sedell, and R.L. Vannote. 1983. Relationships among chemical, physical, and biological indices along a river continua based on multivariate analyses. *Archiv Fur Hydrobiologie* 98:317-326.
- Cushing, C.E. 1994. The conception and testing of the river continuum concept. *Bulletin of the North American Benthological Society*. 11(2):225-229.
- Downes, B.J., P.S. Lake, and E.S.G. Schrieber. 1993. Spatial variation in the distribution of stream invertebrates: implication of patchiness for models of community organization. *Freshwater Biology* 30:119-132.
- Egglishaw, H.J. 1968. The quantitative relationship between bottom fauna and plant detritus in streams of different calcium concentrations. *Journal of Applied Ecology* 5:731-740.
- Elliot, J.M. 1976. The energetics of feeding, metabolism, and growth of the brown trout (*Salmo trutta* L.) in relation to body weight, water temperature, and ration size. *Journal of Animal Ecology* 45:923-948.
- Everest, F.H., and D.H. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. *Journal of the Fisheries Research Board of Canada* 29:91-100.
- Facey, D.E., and G.D. Grossman. 1992. The relationship between water velocity, energetic costs, and microhabitat use on four North American stream fishes. *Hydrobiologia* 239:1-6.
- Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology* 62:441-451.
- Fausch, K.D., and R.J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1220-1227.

- Feldman, R.S., and E.F. Connor. 1992. The relationship between pH and community structure of invertebrates in streams of the Shenandoah National Park, Virginia, U.S.A. *Freshwater Biology* 27:261-276.
- Feltmate, B.W., R.L. Baker, and P.J. Pointing. 1986. Distribution of the stonefly nymph *Paragnetina media* (Plecoptera: Perlidae): influence of prey, predators, current speed, and substrate composition. *Canadian Journal of Fisheries and Aquatic Sciences* 43:1582-1587.
- Feminella, J.W. 1996. Comparison of benthic macroinvertebrate assemblages in small streams along a gradient of flow permanence. *Journal North American Benthological Society* 15(4):651-659.
- Fiss, F.C., and R.F. Carline. 1993. Survival of brook trout embryos in three episodically acidified streams. *Transactions of the American Fisheries Society* 122:268-278.
- Forrester, G.E. 1994. Influences of predatory fish on the drift dispersal and local density of stream insects. *Ecology* 75(5):1208-1218.
- Gagen, C.J., W.E. Sharpe, and R.F. Carline. 1993. Mortality of brook trout, mottled sculpins, and slimy sculpins during acidic episodes. *Transactions of the American Fisheries Society* 122:616-628.
- Galloway, J.N., G.E. Likens, and E.S. Edgerton. 1976. Hydrogen ion speciation in the acid precipitation of the northeastern U.S. in *Proceedings on the first international symposium on acid precipitation and the forest ecosystem*. Forest Service General Technical Report. NE-23. pp. 383-396.
- Garden, A. and R.W. Davies. 1989. Decomposition of leaf litter exposed to simulated acid rain in a buffered lotic system. *Freshwater biology* 22:33-44.
- Gaujot, R.C. 2002. Geology, surface hydrology, and fish habitat relationships in the upper Shaver Fork drainage basin, West Virginia. Master's Thesis. West Virginia University. 95 pp.
- Georgian, T., and J.B. Wallace. 1983. Seasonal production in a guild of periphyton-grazing insects in a southern Appalachian stream. *Ecology* 64(5):1236-1248.
- Grubaugh, J.W., J.B. Wallace, and E.S. Houston. 1996. Longitudinal changes in macroinvertebrate communities along an Appalachian stream continuum. *Canadian Journal Fisheries Aquatic Sciences* 53:896-909.
- Groom, A.P., and A.G. Hildrew. 1989. Food quality for detritivores in streams of contrasting pH. *Journal of Animal Ecology* 58:863-881.

- Hall, R.J., G.E. Likens, S.B. Fiance, and G.R. Hendrey. 1980. Experimental acidification of a stream in the Hubbard Brook experimental forest, New Hampshire. *Ecology* 61(4):976-989.
- Hall, R.J., M.J. Pratt, and G.E. Likens. 1982. Effects of experimental acidification on macroinvertebrate drift diversity in a mountain stream. *Water, Soil, and Air Pollution* 18:273-287.
- Hall, R.J. and F.P. Ide. 1987. Evidence of acidification effects on stream insect communities in central Ontario between 1937 and 1985. *Canadian Journal of Fisheries and Aquatic Science* 44:1652-1657.
- Hall, R.J. 1990. Relative importance of seasonal, short term pH disturbances during discharge variation on a stream ecosystem. *Canadian Journal of Fisheries and Aquatic Science* 47:2261-2274.
- Hauer F.R. and A.C. Benke. 1987. Influence of temperature and river hydrograph on black fly growth rates in a subtropical blackwater river. *Journal of North American Benthological Society*. 6:251-261.
- Havas, M. 1981. Physiological response of aquatic animals to low pH. In R. Singer (ed.), *Effects of acid precipitation on benthos. Proceedings of a regional symposium on benthic biology*. North American Benthological Society, Springfield, IL.:49-65.
- Hawkins, C.P., and J.R. Sedell. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. *Ecology* 62(2):387-397.
- Hawkins, C.P., M.L. Murphy, N.H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology* 63:1840-1856.
- Hayes, J.W., and I.G. Jowett. 1994. Microhabitat models of large drift feeding brown trout in three New Zealand streams. *North American Journal of Fisheries Management* 14:710-725.
- Hermann, J. and K.G. Andersson. 1986. Aluminum impact on respiration of lotic mayflies at low pH. *Water, Air, and Soil Pollution*. 30:703-709.
- Hill, J., and G.D. Grossman. 1993. An energetic model of microhabitat use for rainbow trout and rosyzide dace. *Ecology* 74(3):685-698.
- Hill, W.R., M.G. Ryon, and E.M. Schilling. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. *Ecology* 76(4):1297-1309.

- Hopkins, P.S., K.W. Kratz, and S.D. Cooper. 1989. Effects of experimental pulse on invertebrates in a high altitude Sierra Nevada stream. *Hydrobiologia* 171:45-58.
- Hughes, N.F., and L.M. Dill. 1990. Position choice by drift-feeding salmonids: model and test for arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2039-2048.
- Hughes, N.F. 1998. A model of habitat selection by drift-feeding stream salmonids at different scales. *Ecology* 79(1):281-294.
- Huryn, A.D. and J.B. Wallace. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. *Ecology* 68(6):1932-1942.
- Kimmel, W.G., and D.J. Murphey, W.E. Sharpe, and D.R. Dewalle. 1985. Macroinvertebrate community structure and detritus processing rates in two southwestern Pennsylvanian streams acidified by atmospheric deposition. *Hydrobiologia* 124:97-102.
- Kiffney, P.M., and W.H. Clements. 1996. Effects of metals on stream macroinvertebrate assemblages from different altitudes. *Ecological Applications* 6(2):472-481.
- Kobuszewski, D.M. and S.A. Perry. 1993. Aquatic insect community structure in an acidic and a circumneutral stream in the Appalachian Mountains of West Virginia. *Journal Freshwater Ecology* 8(1):37-45.
- Kwak, T.J., and T.F. Waters. 1997. Trout production and water quality in Minnesota streams. *Transactions of the American Fisheries Society* 126:35-48.
- Lacroix, G.L. 1989. Production of juvenile Atlantic salmon (*Salmo salar*) in two acidic rivers in Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences* 46:2003-2018.
- Lacroix, G.L. 1992. Mitigation of low stream pH and its effects on salmonids. *Environmental Pollution*, 157-163. 0269-7491/92 Elsevier Science Publishers Ltd. England.
- Lugthart, G.J., and J.B. Wallace. 1992. Effects of disturbance on benthic functional structure and production in mountain streams. *Journal of the North American Benthological Society* 11:138-164.
- Lyons, J. 1992. Length of stream to sample with a towed electrofishing unit when fish species richness is estimated. *North American Journal of Fisheries Management* 12:198-203.

- Mackay, R.J. 1992. Colonization by lotic macroinvertebrates: a review of patterns and processes. *Canadian Journal of Fisheries and Aquatic Sciences* 49:617-628.
- Madarish, D.M. and W.G. Kimmel. 1999. Benthic macroinvertebrate community structure in relation to seasonal and geochemical changes in a chronically acidified stream. *Journal of Freshwater Ecology* 14(3):13-26.
- Marschall, E.A. and L.B. Crowder. 1996. Assessing population responses to multiple anthropogenic effects: a case study with brook trout. *Ecological Applications* 6(1):152-167.
- McIntosh, A.R., and C.R. Townsend. 1994. Interpopulation variation in mayfly antipredator tactics: differential effects of contrasting predatory fish. *Ecology* 75(7):2078-2090.
- Meritt, R. W., and K. W. Cummins. 1996. An introduction to the aquatic insects of North America. 3rd edition. Kendall and Hunt. Dubuque, Iowa.
- Milner, A.G.P., and R.J. Aston. 1995. Pre and post liming of aquatic communities and trout diets. *Chemistry and Limnology* 9:193-205.
- Miller, C. 1985. Correlates of habitat favourability for benthic macroinvertebrates at five stream sites in an Appalachian Mountain drainage basin, U.S.A. *Freshwater Biology* 15:709-733.
- Minshall, G.W. 1978. Autotrophy in stream ecosystems. *Bioscience* 28:767-771.
- Minshall G.W., R.C. Peterson, K.W. Cummins, T.L. Bott, J.R. Sedell, C.E. Cushing and R.L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. *Ecological Monographs* 53(1):1-25.
- Minshall, G. M. 1984. Aquatic insect – substratum relationships. *In the ecology of aquatic insects*. Edited by V. H. Resh and D. M. Rosenberg, Preager, New York, N.Y. pp. 358-400.
- Minshall, G.W., K.W. Cummins, R.C. Petersen, C.E. Cushing, D.A. Bruns, J.R. Sedell, and R.L. Vannote. 1985. Developments in stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1045-1055.
- Meyer, J.L., and R.T. Edwards. 1990. Ecosystem metabolism and turnover of organic carbon along a blackwater river continuum. *Ecology* 71(2):668-677.
- NADP. 2000. <http://nadp.sws.uiuc.edu>. National Atmospheric and Deposition Program.

- Naiman, R.J., and J.R. Sedell. 1980. Relationships between metabolic parameters and stream order in Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 37:834-847.
- Naiman, R.J. 1983. The annual pattern and spatial distribution of aquatic oxygen metabolism in boreal forest watersheds. *Ecological Monographs* 53(1):73-94.
- Naiman, R.J., J.M. Melillo, M.A. Lock, and T.E. Ford. 1987. Longitudinal patterns of ecosystem processes and community structure in a sub-arctic river continuum. *Ecology* 68(5):1139-1156.
- Nislow, K.H., C.L. Folt, and D.L. Parrish. 1999. Favorable foraging locations for young atlantic salmon: application to habitat and population restoration. *Ecological Applications* 9(3):1085-1099.
- OSM. 1981. Shavers Fork Petition Evaluation. Office of Surface Mining. Final 522 SMCRA Evaluation. OSM-PE-3.
- Packer, R.K., and W.A. Dunson. 1970. Effects of low environmental pH on blood pH and sodium balance of brook trout. *Journal of Experimental Zoology* 174:65-71.
- Peckarsky, B.L., P.R. Faissinet, M.A. Penton, and D.J. Conklin, Jr. 1990. Freshwater macroinvertebrates of the northeastern United States. Cornell University Press. Ithica, New York.
- Peterson, R.H., and L.V. Eeckhaute. 1991. Distributions of Epemeroptera, Plecoptera, and Trichoptera of three maritime catchments differing in pH. *Freshwater Biology* 21:67-77.
- Petty, J. T., and G. D. Grossman. 1996. Patch selection by mottled sculpin (Pisces: Cottidae) in a southern Appalachian stream. *Freshwater Biology* 35:261-276.
- Power, G. 1995. The brook charr, *Salvelinus fontinalis*. in E.K. Balon editor, Charrs: salmonid fishes of the genus *Salvelinus*. Dr W. Junk bv Publishers. pp. 141-203.
- Rabeni, C.F. and G.M. Minshall. 1977. Factors affecting the microdistribution of stream benthic insects. *Oikos* 29:33-43.
- Reger, D.B. 1931. West Virginia Geological Survey, County Reports, Randolph County. Morgantown Printing and Binding, Morgantown, WV.
- Rockwood, J.P., D.S. Jones, and R.A. Coler. 1990. The effect of aluminum in soft water at low pH on oxygen consumption by the dragonfly *Libellula Julia*. *Hydrobiologia* 190:55-59.

- Rosemond, A.D., P.J. Mulholland, and J.W. Elwood. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology* 74(4):1264-1280.
- Rosemond, A.D., S.R. Reice, J.W. Elwood, and P.J. Mulholland. 1992. The effects of stream acidity on benthic invertebrate communities in the south-eastern United States. *Freshwater Biology* 27:193-209.
- Rowe, L.M., M. Berrill, L. Hollett, and R.J. Hall. 1989. The effects of short-term laboratory pH depressions on molting, mortality, and major ion concentrations in the mayflies *Stenonema femoratum* and *Leptophlebia cupida*. *Hydrobiologia* 184:89-97.
- Schell, V.A and J.J. Kerekes. 1989. Distribution, abundance and biomass of benthic macroinvertebrates relative to pH and nutrients in eight lakes of Nova Scotia, Canada. *Water, Air and Soil Pollution* 46:359-374.
- Schlosser, I.J., and P.L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implication for conservation. *American Fisheries Society Symposium* 17:392-401.
- Simonson, T.D., J. Lyons, and P.D. Kanehl. 1994. Quantifying fish habitat in streams: spacing, sample size, and a proposed framework. *North American Journal of Fisheries Management* 14:607-615.
- Simpson, K.W., R.W. Bode, and J.R. Colquhoun. 1985. The macroinvertebrate fauna of an acid-stressed headwater stream system in the Adirondack Mountains, New York. *Freshwater Biology* 15:671-687.
- Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. *Freshwater Biology* 10:375-383.
- Smock, L.A., E. Gilinsky, and D.L. Stoneburner. 1985. Macroinvertebrate production in a southwestern United States blackwater stream. *Ecology* 66(5):1491-1503.
- Soderstrom, O. 1988. Effects of temperature and food quality on life-history parameters in *Parameletus chelifera* and *P. minor* (Ephemeroptera): a laboratory study. *Freshwater Biology* 20:295-303.
- Statzner, B., and B. Higler. 1985. Questions and comments on the river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1038-1044.
- Statzner, B., and B. Higler 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology* 16:127-139.

- Stites, D.L., and A.C. Benke. 1989. Rapid growth rates of chironomids in three habitats of a subtropical blackwater river and their implications for *P-B* ratios. *Limnological Oceanography* 34:1278-1289.
- Stribling, J.B., B.K. Jessup, J.S. White, D. Boward, and M. Hurd. 1998. [Development of a benthic index of biotic integrity for Maryland streams](#), Tetra Tech, Inc., Owings Mills, MD and Maryland Department of Natural Resources, Resource Assessment Service, Monitoring and Non-Tidal Assessment Division. CBWP-EA-98-3, NTIS No. PB99-240223.
- USEPA. 1979. Methods for chemical analysis of water and wastes. 600/4-79-020. Washington, DC. U.S. Environmental Protection Agency.
- USEPA. 1986. Quality criteria for water 1986. U.S. Environmental Protection Agency, Office of water regulations and standards, EPA 440/5-86-001, Washington DC.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. *The Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Waite, I.R., A.T. Herlihy, D.P. Larsen, and D.J. Klemm. 2000. Comparing strengths of geographic and non-geographic classifications of stream benthic macroinvertebrates in the Mid-Atlantic Highlands, USA. *Journal of the North American Benthological Society* 19(3):429-441.
- Wallace, J.B., J.W. Grubaugh, and M.R. Whiles. 1996. Biotic indices and stream ecosystem processes: results from an experimental study. *Ecological Applications* 6(1): 140-151.
- Wiggins, G.B. 1998. Larvae of the North American caddisfly genera. 2nd edition. University of Toronto Press. Toronto, Ontario.
- Williams D.D. and Williams, N.E., 1974. A counter staining technique for use in sorting benthic samples. *Limnology and Oceanography* 19:152-154.
- Winterbourne, M.J., J.S. Rounick, and B. Cowie. 1981. Are New Zealand stream ecosystems really different? *New Zealand Marine and Freshwater Resources* 15:321-328.
- Wood, C.M., and D.G. McDonald. 1982. Physiological mechanisms of acid toxicity to fish. in R.E. Johnson editor, *Acid rain / fisheries*. American Fisheries Society Northeastern Division, Bethesda, Maryland. pp. 197-226.
- Wright, R.F., T. Dale, E.T. Gjessing, G.R. Hendrey, A. Henriksen, M. Johannessen, and I.P. Muniz. 1975. Impact of acid precipitation on freshwater ecosystems in Norway. *Water, Air, and Soil Pollution* 6:483-499.

WVDNR. 2000. <http://www.dep.state.wv.us/watershed/w5020004.html>. West Virginia Division of Natural Resources.

WVU. 1965. Agricultural Experiment Station, West Virginia University. Climatological Survey #20-46-2, Morgantown, West Virginia, USA.

Zar, J.H. 1996. Biostatistical Analysis. 3rd Edition. Prentice-Hall Inc.

Table 1. Macroinvertebrate sampling sites and corresponding values for physical and chemical parameters along a 25.2 km continuum of the Upper Shavers Fork, WV, May - October 2000.

Site	Basin Area (ha)	DBHW (km)	Link Number	Mean Channel Width (m)	Mean Canopy Cover (%)	Deciduous/ Coniferous (%)	Mean Alkalinity (range)	Mean pH (range)
I	48	1.2	01	3.9 ± 0.0	31 ± 6	44 / 56	22.4 (22.0 – 22.8)	6.8 (5.5 – 7.4)
II	98	1.9	02	5.4 ± 0.0	92 ± 1	88 / 12	17.2 (16.3 – 18.0)	6.7 (6.1 – 7.2)
III	469	3.0	03	7.9 ± 2	92 ± 1	78 / 22	4.2 (4.0 – 4.3)	5.6 (4.5 – 6.6)
IV	540	3.8	03	9.5 ± 2	92 ± 2	71 / 29	7.6 (7.2 – 8.0)	6.0 (4.5 – 6.8)
V	1043	4.8	07	9.9 ± 2	84 ± 3	92 / 08	8.3 (8.0 – 8.5)	6.3 (5.8 – 6.8)
VI	1225	5.5	09	9.8 ± 2	54 ± 5	69 / 31	8.9 (7.0 – 10.8)	6.5 (5.7 – 7.3)
VII	1464	6.6	11	11.8 ± 3	74 ± 7	54 / 36	10.0 (10.0 – 10.2)	6.5 (6.0 – 7.1)
VIII	1640	9.5	17	16.0 ± 4	44 ± 5	45 / 55	66.7 (30.0 – 136.0)	6.9 (6.4 – 7.4)
IX	5106	18.1	38	20.8 ± 5	21 ± 4	95 / 05	47.0 (24.0 – 92.0)	6.8 (6.6 – 7.1)
X	10300	26.4	75	26.9 ± 6	7 ± 1	79 / 21	39.7 (22.0 – 80.0)	6.4 (6.2 – 6.9)

DBHW = Distance Below Headwater. Link Number = The number of 1st order perennial streams comprising a given site along the continuum. Mean (n = 20) Channel Width. Mean (n = 10) Canopy Cover. Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). Mean (n = 10) pH.

Table 2. Response of macroinvertebrate density and biomass to the effects of alkalinity, canopy cover, and basin area along a 25.2 km continuum of the Upper Shavers Fork, WV, May – October 2000.

Season	Response Variable	Predictor Variable	DF	F-value	R ²	P-value
Spring	Density	Alkalinity	7	25.7	0.81	0.002
		Canopy Cover				NS
		Basin Area				NS
		Full Model	7	25.7	0.81	0.002
	Biomass	Alkalinity	7	17.9	0.75	0.006
		Canopy Cover				NS
		Basin Area				NS
		Full Model	7	17.9	0.75	0.006
Summer	Density	Alkalinity	7	8.8	0.60	0.025
		Canopy Cover				NS
		Basin Area				NS
		Full Model	7	8.8	0.60	0.025
	Biomass	Alkalinity	7	11.1	0.65	0.016
		Canopy Cover	7	3.3	0.10	0.145
		Basin Area	7	3.0	0.13	0.145
		Full Model	7	9.7	0.88	0.026
Fall	Density	Alkalinity	9	10.4	0.57	0.012
		Canopy Cover				NS
		Basin Area				NS
		Full Model	9	10.4	0.57	0.012
	Biomass	Alkalinity	9	16.8	0.68	0.003
		Canopy Cover	9	2.7	0.0900	0.144
		Basin Area				NS
		Full Model	9	11.6	0.77	0.006
Annual	Density	Alkalinity	9	16.2	0.67	0.004
		Canopy Cover				NS
		Basin Area				NS
		Full Model	9	16.2	0.67	0.004
	Biomass	Alkalinity	9	13.6	0.63	0.006
		Canopy Cover	9	4.9	0.10	0.069
		Basin Area	9	6.9	0.14	0.074
		Full Model	9	13.9	0.88	0.004

NS = no significance in model ($P > 0.15$).

Table 3. Response of macroinvertebrate family richness to the effects of alkalinity, canopy cover, and basin area along a 25.2 km continuum of the Upper Shavers Fork, WV, May – October 2000.

Season	Response Variable	Predictor Variable	DF	F-value	R ²	P-value
Spring	Richness	Alkalinity				NS
		Canopy Cover				NS
		Basin Area	7	72.3	0.92	< 0.001
		Full Model	7	72.3	0.92	< 0.001
Summer	Richness	Alkalinity				NS
		Canopy Cover				NS
		Basin Area	7	15.2	0.72	0.008
		Full Model	7	15.2	0.72	0.008
Fall	Richness	Alkalinity	9	29.0	0.78	0.001
		Canopy Cover				NS
		Basin Area				NS
		Full Model	9	29.0	0.78	0.001
Annual	Richness	Alkalinity	9	13.5	0.63	0.006
		Canopy Cover				NS
		Basin Area				NS
		Full Model	9	13.5	0.63	0.006

NS = no significance in model ($P > 0.15$)

Table 4. Response of percent biomass of feeding groups to the effects of alkalinity, canopy cover, and basin area along a 25.2 km continuum of the Upper Shavers Fork, WV, May – October 2000.

Season	Response Variable	Predictor Variable	DF	F-value	R ²	P-value
Spring	% Shredder	Alkalinity				NS
		Canopy Cover				NS
		Basin Area	7	7.2	0.54	0.037
		Full Model	7	7.2	0.54	0.037
Summer		Alkalinity	7	8.5	0.59	0.027
		Canopy Cover				NS
		Basin Area				NS
		Full Model	7	8.5	0.59	0.027
Fall		Alkalinity				NS
		Canopy Cover	9	3.2	0.29	0.111
		Basin Area				NS
		Full Model	9	3.2	0.29	0.111
Annual		Alkalinity				NS
		Canopy Cover	9	13.8	0.63	0.006
		Basin Area				NS
		Full Model	9	13.8	0.63	0.006
Spring	% Scraper	Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS
Summer		Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS
Fall		Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS
Annual		Alkalinity	9	2.8	0.26	0.134
		Canopy Cover				NS
		Basin Area				NS
		Full Model	9	2.8	0.26	0.134
Spring	% Gatherer	Alkalinity	7	21.6	0.78	0.004
		Canopy Cover	7	3.8	0.10	0.101
		Basin Area				NS
		Full Model	7	17.7	0.88	0.005
Summer		Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS

Table 4. Continued.

Season	Response Variable	Predictor Variable	DF	F-value	R ²	P-value
Fall	% Gatherer	Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS
Annual		Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS
Spring	% Filterer	Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS
Summer		Alkalinity				NS
		Canopy Cover	7	28.5	0.83	0.002
		Basin Area				NS
		Full Model	7	28.5	0.83	0.002
Fall		Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS
Annual		Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS
Spring	% Predator	Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS
Summer		Alkalinity	7	5.0	0.45	0.067
		Canopy Cover				NS
		Basin Area				NS
		Full Model	7	5.0	0.45	0.067
Fall		Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS
Annual		Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS

NS = no significance in model ($P > 0.15$).

Table 5. Contribution of individual families to the percent biomass of feeding groups along a 25.2 km continuum of the Upper Shavers Fork, WV, May – October 2000.

Site	Season	Shredder Family	%	Scraper Family	%	Gatherer Family	%
I	Spring	ND		ND		ND	
	Summer	ND		ND		ND	
	Fall	Leuctridae	65	Heptageniidae	87	Ephemerellidae	59
II	Spring	ND		ND		ND	
	Summer	ND		ND		ND	
	Fall	Pteronarcyidae	62	Psychomyiidae	56	Chironomidae	32
III	Spring	Leuctridae	88	Heptageniidae	99	Chironomidae	60
	Summer	Leuctridae	68	Heptageniidae	50	Chironomidae	47
	Fall	Leuctridae	47	Heptageniidae	59	Ephemerellidae	82
IV	Spring	Leuctridae	89	Heptageniidae	99	Chironomidae	90
	Summer	Leuctridae	90	Heptageniidae	99	Chironomidae	79
	Fall	Capniidae	30	Elmidae	59	Chironomidae	74
V	Spring	Leuctridae	62	Heptageniidae	36	Chironomidae	96
	Summer	Leuctridae	99	Heptageniidae	99	Chironomidae	73
	Fall	Leuctridae	69	Heptageniidae	79	Chironomidae	45
VI	Spring	Leuctridae	89	Heptageniidae	83	Chironomidae	73
	Summer	Leuctridae	99	Heptageniidae	53	Chironomidae	87
	Fall	Peltoperlidae	47	Heptageniidae	97	Chironomidae	46
VII	Spring	Leuctridae	97	Heptageniidae	92	Tiplulidae	53
	Summer	Leuctridae	95	Heptageniidae	75	Chironomidae	75
	Fall	Leuctridae	43	Heptageniidae	49	Tipulidae	45
VIII	Spring	Leuctridae	99	Heptageniidae	69	Ephemeridae	37
	Summer	Leuctridae	97	Heptageniidae	93	Ephemeridae	36
	Fall	Leuctridae	85	Heptageniidae	86	Leptophlebiidae	42
IX	Spring	Leuctridae	97	Heptageniidae	93	Chironomidae	35
	Summer	Leuctridae	94	Psephenidae	50	Chironomidae	64
	Fall	Pteronarcyidae	82	Heptageniidae	92	Leptophlebiidae	37
X	Spring	Leuctridae	71	Heptageniidae	73	Chironomidae	52
	Summer	Pteronarcyidae	84	Odontoceridae	61	Chironomidae	39
	Fall	Pteronarcyidae	95	Heptageniidae	90	Ephemerellidae	25

% = Percent of total biomass (mgDM/m²).

(ND = no data. Sites I-II data collected and presented for the fall season only.)

Table 5. Continued.

Site	Season	Filterer Family	%	Predator Family	%
I	Spring	ND		ND	
	Summer	ND		ND	
	Fall	Hydropsychidae	67	Perlodidae	56
II	Spring	ND		ND	
	Summer	ND		ND	
	Fall	Polycentropodidae	86	Chloroperlidae	51
III	Spring	Polycentropodidae	94	Perlodidae	91
	Summer	Polycentropodidae	100	Ceratopogonidae	53
	Fall	Hydropsychidae	82	Perlodidae	73
IV	Spring	Polycentropodidae	100	Perlodidae	75
	Summer	Polycentropodidae	100	Chloroperlidae	56
	Fall	Polycentropodidae	90	Chloroperlidae	58
V	Spring	Polycentropodidae	100	Chloroperlidae	65
	Summer	Polycentropodidae	100	Chloroperlidae	74
	Fall	Polycentropodidae	100	Gomphidae	84
VI	Spring	Hydropsychidae	61	Gomphidae	64
	Summer	Polycentropodidae	99	Chloroperlidae	92
	Fall	Polycentropodidae	75	Chloroperlidae	61
VII	Spring	Polycentropodidae	100	Gomphidae	71
	Summer	Hydropsychidae	56	Chloroperlidae	81
	Fall	Hydropsychidae	67	Chloroperlidae	63
VIII	Spring	Polycentropodidae	69	Chloroperlidae	37
	Summer	Isonychiidae	72	Corydalidae	57
	Fall	Hydropsychidae	75	Perlidae	37
IX	Spring	Isonychiidae	59	Perlidae	29
	Summer	Hydropsychidae	62	Corydalidae	41
	Fall	Hydropsychidae	73	Perlodidae	33
X	Spring	Polycentropodidae	53	Corydalidae	61
	Summer	Polycentropodidae	37	Gomphidae	38
	Fall	Hydropsychidae	50	Perlidae	61

% = Percent of total biomass (mgDM/m²).

(ND = no data. Sites I-II data collected and presented for the fall season only.)

Table 6. Response of absolute biomass of feeding groups to the effects of alkalinity, canopy cover, and basin area along a 25.2 km continuum of the Upper Shavers Fork, WV, May – October 2000.

Season	Response Variable	Predictor Variable	DF	F-value	R ²	P-value
Spring	Shredder	Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS
Summer		Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS
Fall		Alkalinity				NS
		Canopy Cover				NS
		Basin Area				NS
		Full Model				NS
Annual		Alkalinity				NS
		Canopy Cover				NS
		Basin Area	9	3.7	0.32	0.091
		Full Model	9	3.7	0.32	0.091
Spring	Scraper	Alkalinity				NS
		Canopy Cover	7	3.1	0.34	0.127
		Basin Area				NS
		Full Model	7	3.1	0.34	0.127
Summer		Alkalinity	7	3.5	0.37	0.110
		Canopy Cover				NS
		Basin Area				NS
		Full Model	7	3.5	0.37	0.110
Fall		Alkalinity				NS
		Canopy Cover	7	5.3	0.40	0.050
		Basin Area				NS
		Full Model	7	5.3	0.40	0.050
Annual		Alkalinity				NS
		Canopy Cover	9	79.0	0.54	< 0.001
		Basin Area	9	5.6	0.41	0.045
		Full Model	9	69.7	0.95	< 0.001
Spring	Gatherer	Alkalinity	7	110.1	0.95	< 0.001
		Canopy Cover				NS
		Basin Area				NS
		Full Model	7	110.1	0.95	< 0.001
Summer		Alkalinity	7	5.5	0.48	0.057
		Canopy Cover				NS
		Basin Area	7	4.7	0.25	0.082
		Full Model	7	6.8	0.73	0.037

Table 6. Continued.

Season	Response Variable	Predictor Variable	DF	F-value	R ²	P-value
Fall	Gatherer	Alkalinity	7	10.1	0.56	0.13
		Canopy Cover				NS
		Basin Area				NS
		Full Model	7	10.1	0.56	0.13
Annual		Alkalinity				NS
		Canopy Cover	9	30.2	0.58	0.001
		Basin Area	9	3.3	0.29	0.108
		Full Model	9	22.7	0.87	0.001
Spring	Filterer	Alkalinity	7	4.9	0.45	0.068
		Canopy Cover				NS
		Basin Area				NS
		Full Model	7	4.9	0.45	0.068
Summer		Alkalinity	7	23.1	0.79	0.003
		Canopy Cover				NS
		Basin Area				NS
		Full Model	7	23.1	0.79	0.003
Fall		Alkalinity	7	8.5	0.51	0.020
		Canopy Cover				NS
		Basin Area				NS
		Full Model	7	8.5	0.51	0.020
Annual		Alkalinity				NS
		Canopy Cover	9	19.9	0.22	0.003
		Basin Area	9	19.2	0.71	0.002
		Full Model	9	42.2	0.92	< 0.001
Spring	Predator	Alkalinity				NS
		Canopy Cover	7	4.3	0.42	0.082
		Basin Area				NS
		Full Model	7	4.3	0.42	0.082
Summer		Alkalinity	7	23.8	0.80	0.003
		Canopy Cover				NS
		Basin Area				NS
		Full Model	7	23.8	0.80	0.003
Fall		Alkalinity				NS
		Canopy Cover	7	12.9	0.62	0.007
		Basin Area				NS
		Full Model	7	12.9	0.62	0.007
Annual		Alkalinity				NS
		Canopy Cover	9	22.2	0.17	0.002
		Basin Area	9	28.5	0.78	0.001
		Full Model	9	63.3	0.95	< 0.001

NS = no significance in model ($P > 0.15$).

Table 7. Annualized abundance of taxa in sites having the largest variation in alkalinity, canopy cover, and basin area along a 25.2 km continuum of the Upper Shavers Fork, WV, May - October 2000.

Sites I - II

Tolerant of Acidity	Order	Family	Genera	% Contribution	N
No	Ephemeroptera	-	-	56	2,312 (EPT)
Yes	Plecoptera	-	-	37	2,312 (EPT)
No	Trichoptera	-	-	07	2,312 (EPT)
No	Ephemeroptera	Leptophlebiidae	-	22	1,304 (Order)
Yes	Ephemeroptera	Heptageniidae	Epeorus	50	538 (Family)
Yes	Ephemeroptera	Ephemerellidae	Eurylophella	01	130 (Family)
Yes	Trichoptera	Hydropsychidae	Parapsyche	00	53 (Family)

Sites III - IV

Tolerant of Acidity	Order	Family	Genera	% Contribution	N
No	Ephemeroptera	-	-	09	2,565 (EPT)
Yes	Plecoptera	-	-	87	2,565 (EPT)
No	Trichoptera	-	-	04	2,565 (EPT)
No	Ephemeroptera	Leptophlebiidae	-	02	228 (Order)
Yes	Ephemeroptera	Heptageniidae	Epeorus	38	61 (Family)
Yes	Ephemeroptera	Ephemerellidae	Eurylophella	70	88 (Family)
Yes	Trichoptera	Hydropsychidae	Parapsyche	100	16 (Family)

Sites VIII - X

Tolerant of Acidity	Order	Family	Genera	% Contribution	N
No	Ephemeroptera	-	-	55	8,259 (EPT)
Yes	Plecoptera	-	-	30	8,259 (EPT)
No	Trichoptera	-	-	15	8,259 (EPT)
No	Ephemeroptera	Leptophlebiidae	-	56	4,563 (Order)
Yes	Ephemeroptera	Heptageniidae	Epeorus	11	454 (Family)
Yes	Ephemeroptera	Ephemerellidae	Eurylophella	08	472 (Family)
Yes	Trichoptera	Hydropsychidae	Parapsyche	00	535 (Family)

Sites I - II data collected and presented for fall season only, N = total abundance from five 0.1 m² benthic samples. For all other sites, N = total abundance from fifteen 0.1 m² benthic samples.

EPT = Ephemeroptera:Plecoptera:Trichoptera.

Table 8. Comparison of the abundance of acid-sensitive taxa occurring in four headwater sites differing in alkalinity in the Upper Shavers Fork, WV, October 2000.

Family	Tol. Val.	I (n)	II (n)	III (n)	IV (n)
Pteronarcyidae	2	0	1	0	0
Glossosomatidae	0-2	1	0	0	0
Philopotamidae	0-4	4	1	0	0
Gomphidae	4-6	2	3	0	0
Perlodidae	1-2	15	34	3	9

Tol.Val. = Range of tolerance values for each family (0 = no tolerance) (Stribling et al., 1998).

I - IV (n) = Total abundance from five, 0.1m², benthic samples at sites I-IV.

Mean alkalinity (mg/L CaCO₃) for Site I = 22.4; Site II = 17.2; Site III = 4.2; and Site IV = 7.6.

Figure 1. The River Continuum Concept with predicted changes in stream ecosystem communities along a hypothetical longitudinal gradient (From Vannote et al., 1980).

Figure 2. Hydrogen ion wet deposition for the United States in 2000. (From NADP, 2000).

Figure 3. The Shavers Fork watershed with the Upper Shavers Fork subsection, WV, 2000.

Figure 4. The Upper Shavers Fork watershed with sampling sites along a 25.2 km stream continuum, WV, 2000.

Figure 5. Relationship between basin area, canopy cover (+SE), and alkalinity (+SE) along a 25.2 km continuum of the Upper Shavers Fork, WV, May – October, 2000.

Figure 6. Mean ($n = 5$) density ($\pm$ SE) of benthic macroinvertebrates along a 25.2 km continuum of the Upper Shavers Fork, WV, May - October 2000. Sites sharing a common letter do not significantly differ ($P < 0.10$). (ND = no data collected).

Figure 7. Mean ($n = 5$) biomass ($\pm$ SE) of benthic macroinvertebrates along a 25.2 km continuum of the Upper Shavers Fork, WV, May - October 2000. Sites sharing a common letter do not significantly differ ($P < 0.10$). (ND = no data collected).

Figure 8. Annualized mean (n = 15) density ($\pm$ SE) and biomass ($\pm$ SE) for benthic macroinvertebrates along a 25.2 km continuum of the Upper Shavers Fork, WV, May – October 2000. Sites sharing a common letter do not significantly differ ($P < 0.10$). (Sites I-II data collected and presented for fall season only, n = 5).

Figure 9. Annualized mean ($n = 3$) macroinvertebrate family richness ($\pm$ SE) along a 25.2 km continuum of the Upper Shavers Fork, WV, May – October 2000. (Sites I-II data collected and presented for fall season only, $n = 1$).

Figure 10. Annualized Jaccard coefficient for sites I, III, VI, VIII, and X of the Upper Shavers Fork, WV, May - October 2000. (Site I data collected and presented for fall season only).

Figure 11. Abundance of Ephemeroptera, Plecoptera, and Trichoptera along a 25.2 km continuum of the Upper Shavers Fork, WV, May – October 2000. (ND = no data. Sites I-II data collected and presented for fall season only.)

Figure 12. Abundance of Leptophlebiidae to Ephemeroptera along a 25.2 km continuum of the Upper Shavers Fork, WV, May – October 2000. (ND = no data. Sites I-II data collected and presented for fall season only.)

Figure 13. Abundance of *Parapsyche* spp. to Hydropsychidae along a 25.2 km continuum of the Upper Shavers Fork, WV, May – October 2000. (ND = no data. Sites I-II data collected and presented for fall season only.)

Figure 14. Abundance of *Eurylophella* spp. to Ephemerellidae along a 25.2 km continuum of the Upper Shavers Fork, WV, May - October 2000. (ND = no data. Sites I-II data collected and presented for fall season only.)

Figure 15. Abundance of *Epeorus* spp. to Heptageniidae along a 25.2 km continuum of the Upper Shavers Fork, WV, May – October 2000. (ND = no data. Sites I-II data collected and presented for fall season only.)

Appendices.

Appendix I. Macroinvertebrate Orders and Families collected along a 25.2 km continuum of the Upper Shavers Fork, WV, May – October, 2000.

Order	Family	Order	Family
Amphipoda	Gammaridae	Megaloptera	Corydalidae Sialidae
Coleoptera	Elmidae Hydrophilidae Psephenidae	Odonata	Aeshnidae Gomphidae
Diptera	Athericidae Blepharicidae Ceratopogonidae Chironomidae Dixidae Empididae Muscidae Simuliidae Tabanidae Tipulidae	Plecoptera	Capniidae Chloroperlidae Leuctridae Nemouridae Peltoperlidae Perlidae Perlodidae Pteronarcyidae Taeniopterygidae
Ephemeroptera	Ameletidae Baetiscidae Baetidae Caenidae Ephemerellidae Ephemeridae Heptageniidae Isonychiidae Leptophlebiidae Siphonuridae	Trichoptera	Brachycentridae Glossosomatidae Hydropsychidae Hydroptilidae Lepidostomatidae Leptoceridae Limnephilidae Odontoceridae Polycentropodidae Philopotamidae Psychomyiidae Rhyacophilidae Uenoidae

Appendix II. Contribution of individual families to feeding group biomass in the Upper Shavers Fork, WV, May – October 2000. (Families contributing ≥ 0.5 % of biomass are listed.)

Spring Shredder Functional Group

Site Description				FFG Family and Characteristics				Total Family Richness
B.A.	C.C.	Alk.	pH	Shredder	%	mgDM/m ²	n	
48	31	22.4	5.5	ND	ND	ND	ND	ND
98	92	17.2	6.1	ND	ND	ND	ND	ND
469	92	4.2	4.5	Leuctridae	88	17.6	352	06
				Nemouridae	06	1.1	03	
				Lepidostomatidae	05	1.1	02	
540	92	7.6	4.5	Leuctridae	89	7.7	106	06
				Lepidostomatidae	05	0.6	02	
				Peltoperlidae	03	0.3	20	
				Capniidae	02	0.1	15	
1043	84	8.3	5.8	Leuctridae	62	7.4	129	05
				Limnephilidae	19	2.3	03	
				Lepidostomatidae	15	1.8	04	
				Capniidae	04	0.5	71	
1225	54	8.9	5.7	Leuctridae	89	3.9	111	04
				Capniidae	10	0.4	60	
1464	74	10.0	6.0	Leuctridae	97	2.2	88	03
				Capniidae	02	0.1	10	
				Gammaridae	01	0.02	20	
1640	44	66.7	6.4	Leuctridae	99	53.2	751	04
				Capniidae	01	0.5	07	
5106	21	47.0	6.6	Leuctridae	97	4.2	203	03
				Nemouridae	02	0.1	07	
				Capniidae	01	0.1	06	
10300	07	39.7	6.2	Leuctridae	71	2.1	91	05
				Capniidae	12	0.4	10	
				Nemouridae	08	0.2	05	
				Pteronarcyidae	07	0.2	01	
				Taeniopterygidae	01	0.1	04	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Summer Shredder Functional Group

Site Description				FFG Family and Characteristics				Total Family Richness
B.A.	C.C.	Alk.	PH	Shredder	%	mgDM/m ²	n	
48	31	22.4	5.5	ND	ND	ND	ND	ND
98	92	17.2	6.1	ND	ND	ND	ND	ND
469	92	4.2	4.5	Leuctridae	68	8.4	365	04
				Capniidae	30	3.8	258	
				Lepidostomatidae	02	0.2	01	
540	92	7.6	4.5	Leuctridae	90	11.8	264	06
				Capniidae	08	1.0	34	
				Peltoperlidae	01	0.2	01	
1043	84	8.3	5.8	Leuctridae	99	12.5	221	02
1225	54	8.9	5.7	Leuctridae	99	25.1	237	02
1464	74	10.0	6.0	Leuctridae	95	3.1	47	03
				Capniidae	05	0.2	10	
1640	44	66.7	6.4	Leuctridae	97	7.3	82	03
				Capniidae	03	0.2	15	
5106	21	47.0	6.6	Leuctridae	94	3.7	41	02
				Limnephilidae	06	0.2	05	
10300	07	39.7	6.2	Pteronarcyidae	84	14.0	03	04
				Leuctridae	13	2.1	24	
				Lepidostomatidae	03	0.5	01	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Fall Shredder Functional Group

Site Description				FFG Family and Characteristics				Total Family Richness
B.A.	C.C.	Alk.	pH	Shredder	%	mgDM/m ²	n	
48	31	22.4	5.5	Leuctridae	65	8.9	248	05
				Capniidae	34	4.6	44	
				Gammaridae	01	0.1	39	
98	92	17.2	6.1	Pteronarcyidae	62	29.0	01	05
				Leuctridae	28	13.2	204	
				Nemouridae	07	3.3	36	
				Capniidae	03	1.2	06	
469	92	4.2	4.5	Leuctridae	47	9.0	216	06
				Capniidae	42	8.0	109	
				Taeniopterygidae	10	1.9	17	
				Nemouridae	02	0.3	40	
540	92	7.6	4.5	Capniidae	30	3.9	85	07
				Limnephilidae	27	3.5	03	
				Peltoperlidae	25	3.2	02	
				Leuctridae	18	2.3	92	
1043	84	8.3	5.8	Leuctridae	69	2.5	52	05
				Capniidae	28	1.0	30	
				Taeniopterygidae	02	0.1	01	
1225	54	8.9	5.7	Peltoperlidae	47	5.0	03	06
				Leuctridae	28	3.0	76	
				Capniidae	18	1.9	49	
				Lepidostomatidae	07	0.7	01	
1464	74	10.0	6.0	Leuctridae	43	2.4	83	06
				Peltoperlidae	33	1.8	01	
				Capniidae	22	1.2	62	
				Lepidostomatidae	01	0.1	01	
1640	44	66.7	6.4	Leuctridae	85	3.9	195	05
				Capniidae	08	0.4	04	
				Taeniopterygidae	05	0.2	01	
				Gammaridae	02	0.1	66	
5106	21	47.0	6.6	Pteronarcyidae	82	15.6	01	05
				Capniidae	13	2.4	198	
				Leuctridae	05	0.9	81	
10300	07	39.7	6.2	Pteronarcyidae	95	101.1	01	05
				Limnephilidae	04	4.3	02	
				Capniidae	01	0.1	20	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Spring Scraper Functional Group

Site Description				FFG Family and Characteristics			Total Family Richness	
B.A.	C.C.	Alk.	PH	Scraper	%	mgDM/m ²	n	Richness
48	31	22.4	5.5	ND	ND	ND	ND	ND
98	92	17.2	6.1	ND	ND	ND	ND	ND
469	92	4.2	4.5	Heptageniidae	99	14.6	05	02
540	92	7.6	4.5	Heptageniidae	99	6.6	10	02
1043	84	8.3	5.8	Heptageniidae	36	1.4	09	05
				Ameletidae	29	1.1	01	
				Glossosomatidae	23	0.9	05	
				Uenoidae	10	0.4	10	
				Elmidae	01	0.03	08	
1225	54	8.9	5.7	Heptageniidae	83	29.2	27	06
				Ameletidae	12	4.2	05	
				Brachycentridae	02	0.9	01	
				Hydrophilidae	02	0.8	10	
1464	74	10.0	6.0	Heptageniidae	92	22.5	06	03
				Ameletidae	08	1.8	01	
1640	44	66.7	6.4	Heptageniidae	69	10.5	65	03
				Ameletidae	30	4.7	02	
				Elmidae	01	0.1	13	
5106	21	47.0	6.6	Heptageniidae	93	26.0	36	05
				Blepharicidae	04	1.1	53	
				Elmidae	01	0.4	16	
				Glossomatidae	01	0.4	02	
10300	07	39.7	6.2	Heptageniidae	73	13.8	31	09
				Ameletidae	13	2.4	05	
				Brachycentridae	06	1.1	01	
				Psychomiidae	04	0.8	01	
				Elmidae	02	0.3	23	
				Psephenidae	01	0.2	01	
				Blepharicidae	01	0.2	18	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Summer Scraper Functional Group

Site Description				FFG Family and Characteristics			Total Family Richness	
B.A.	C.C.	Alk.	pH	Scraper	%	mgDM/m ²	n	Richness
48	31	22.4	5.5	ND	ND	ND	ND	ND
98	92	17.2	6.1	ND	ND	ND	ND	ND
469	92	4.2	4.5	Heptageniidae	50	4.2	03	03
				Ameletidae	49	4.1	03	
540	92	7.6	4.5	Heptageniidae	99	11.0	26	03
1043	84	8.3	5.8	Heptageniidae	99	7.2	36	04
				Uenoidae	01	0.1	05	
1225	54	8.9	5.7	Heptageniidae	53	3.4	03	03
				Elmidae	32	2.1	52	
				Ameletidae	15	1.0	01	
1464	74	10.0	6.0	Heptageniidae	75	1.6	12	07
				Hydrophilidae	10	0.2	10	
				Elmidae	12	0.2	118	
				Glossomatidae	03	0.1	02	
				Ameletidae	01	0.03	01	
1640	44	66.7	6.4	Heptageniidae	93	31.9	73	05
				Psephenidae	03	1.2	01	
				Uenoidae	03	0.9	15	
				Elmidae	01	0.3	23	
5106	21	47.0	6.6	Psephenidae	50	2.8	05	04
				Heptageniidae	46	2.6	13	
				Elmidae	03	0.1	24	
				Blepharicidae	01	0.04	09	
10300	07	39.7	6.2	Odontoceridae	61	7.2	02	05
				Heptageniidae	33	3.9	18	
				Elmidae	07	0.8	42	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Fall Scraper Functional Group

Site Description				FFG Family and Characteristics				Total Family Richness
B.A.	C.C.	Alk.	pH	Scraper	%	mgDM/m ²	n	
48	31	22.4	5.5	Heptageniidae	87	24.4	295	04
				Glossosomatidae	05	1.5	01	
				Ameletidae	04	1.2	06	
				Elmidae	03	1.1	34	
98	92	17.2	6.1	Psychomyiidae	56	8.3	03	04
				Heptageniidae	41	6.1	243	
				Ameletidae	03	0.4	04	
469	92	4.2	4.5	Heptageniidae	59	12.0	12	05
				Ameletidae	28	5.8	12	
				Psychomyiidae	12	2.4	04	
				Hydroptilidae	01	0.1	02	
540	92	7.6	4.5	Elmidae	59	0.04	03	03
				Psychomyiidae	24	0.02	01	
				Heptageniidae	17	0.01	05	
1043	84	8.3	5.8	Heptageniidae	79	2.7	06	05
				Psychomyiidae	14	0.5	03	
				Glossosomatidae	03	0.1	06	
				Ameletidae	03	0.1	01	
				Elmidae	01	0.04	14	
				Heptageniidae	97	18.0	50	
Elmidae	02	0.3	39					
Glossosomatidae	01	0.2	01					
1464	74	10.0	6.0	Heptageniidae	49	0.6	53	05
				Psychomyiidae	21	0.3	06	
				Hydrophilidae	15	0.2	05	
				Elmidae	12	0.1	31	
				Glossosomatidae	03	0.03	05	
				Heptageniidae	86	42.8	75	
Brachycentridae	12	6.1	01					
Psephenidae	01	0.4	03					
Uenoidae	01	0.3	05					
5106	21	47.0	6.6	Heptageniidae	92	23.7	76	05
				Hydroptilidae	06	1.5	03	
				Elmidae	01	0.2	12	
				Psephenidae	01	0.2	02	
10300	07	39.7	6.2	Heptageniidae	90	39.8	68	05
				Odontoceridae	08	3.6	01	
				Glossosomatidae	01	0.4	01	
				Elmidae	01	0.3	31	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Spring Gatherer Functional Group

Site Description				FFG Family and Characteristics				Total Family Richness
B.A.	C.C.	Alk.	pH	Gatherer	%	mgDM/m ²	n	
48	31	22.4	5.5	ND	ND	ND	ND	ND
98	92	17.2	6.1	ND	ND	ND	ND	ND
469	92	4.2	4.5	Chironomidae	60	9.3	282	04
				Ephemerellidae	39	6.1	16	
				Tipulidae	01	0.2	08	
540	92	7.6	4.5	Chironomidae	90	12.4	507	04
				Ephemerellidae	09	1.2	02	
				Tipulidae	01	0.1	04	
1043	84	8.3	5.8	Chironomidae	96	10.3	396	05
				Tipulidae	03	0.3	01	
1225	54	8.9	5.7	Chironomidae	73	12.9	618	03
				Tipulidae	27	4.7	21	
1464	74	10.0	6.0	Tipulidae	53	11.3	11	07
				Chironomidae	35	7.5	568	
				Ephemeridae	09	1.9	01	
				Ephemerellidae	02	0.5	19	
				Baetidae	01	0.1	15	
1640	44	66.7	6.4	Ephemeridae	37	49.8	15	07
				Chironomidae	23	31.3	946	
				Ephemerellidae	18	23.5	46	
				Leptophlebiidae	10	13.9	160	
				Tipulidae	06	8.5	97	
				Baetidae	05	6.9	17	
5106	21	47.0	6.6	Chironomidae	35	25.2	1007	07
				Tipulidae	26	18.4	04	
				Leptophlebiidae	23	16.5	313	
				Ephemeridae	13	9.1	36	
				Baetidae	02	1.5	20	
				Ephemerellidae	02	1.1	16	
10300	07	39.7	6.2	Chironomidae	52	21.3	735	07
				Leptophlebiidae	16	6.5	189	
				Ephemerellidae	16	6.5	09	
				Baetidae	06	2.5	16	
				Tipulidae	06	2.3	49	
				Ephemeridae	04	1.6	03	
				Siphonuridae	01	0.2	28	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Summer Gatherer Functional Group

Site Description				FFG Family and Characteristics				Total Family Richness
B.A.	C.C.	Alk.	PH	Gatherer	%	mgDM/m ²	n	
48	31	22.4	5.5	ND	ND	ND	ND	ND
98	92	17.2	6.1	ND	ND	ND	ND	ND
469	92	4.2	4.5	Chironomidae	47	21.7	749	04
				Ephemerellidae	46	20.9	17	
				Baetidae	05	2.2	04	
				Tipulidae	03	1.2	23	
540	92	7.6	4.5	Chironomidae	79	12.3	643	04
				Baetidae	12	1.9	05	
				Ephemerellidae	08	1.3	01	
				Tipulidae	01	0.2	14	
1043	84	8.3	5.8	Chironomidae	73	14.8	515	06
				Baetidae	21	4.1	23	
				Caenidae	04	0.7	02	
				Ephemerellidae	01	0.2	05	
				Tipulidae	01	0.2	05	
				Siphonuridae	01	0.3	25	
1225	54	8.9	5.7	Chironomidae	87	31.7	1081	05
				Baetidae	12	4.4	13	
				Leptophlebiidae	01	0.2	07	
1464	74	10.0	6.0	Chironomidae	75	8.5	718	07
				Ephemerellidae	07	0.8	04	
				Baetiscidae	07	0.7	02	
				Baetidae	06	0.6	13	
				Leptophlebiidae	03	0.3	72	
				Tipulidae	02	0.2	14	
				Siphonuridae	01	0.03	08	
1640	44	66.7	6.4	Ephemeridae	36	65.9	21	09
				Caenidae	30	56.8	226	
				Chironomidae	25	46.6	1263	
				Leptophlebiidae	07	13.4	389	
				Baetidae	01	2.4	23	
				Tipulidae	01	1.2	75	
5106	21	47.0	6.6	Chironomidae	64	21.5	1574	09
				Baetidae	11	3.8	63	
				Leptophlebiidae	10	3.3	127	
				Tipulidae	10	3.2	53	
				Caenidae	03	0.9	32	
				Ephemerellidae	02	0.7	27	
				Siphonuridae	01	0.2	21	
10300	07	39.7	6.2	Chironomidae	39	10.2	744	09
				Ephemeridae	19	5.0	03	
				Baetidae	18	4.7	27	
				Leptophlebiidae	08	2.13	88	
				Tipulidae	07	1.9	82	
				Ephemerellidae	04	1.0	19	
				Baetiscidae	03	0.8	01	
				Caenidae	03	0.8	02	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Fall Gatherer Functional Group

Site Description				FFG Family and Characteristics				Total Family Richness
B.A.	C.C.	Alk.	pH	Gatherer	%	mgDM/m ²	n	
48	31	22.4	5.5	Ephemerellidae	59	64.7	121	05
				Tipulidae	16	17.7	78	
				Baetidae	16	17.5	186	
				Leptophlebiidae	05	5.9	158	
				Chironomidae	04	4.0	283	
98	92	17.2	6.1	Chironomidae	32	9.3	535	06
				Baetidae	25	7.2	138	
				Ephemerellidae	23	6.7	09	
				Tipulidae	16	4.7	20	
				Leptophlebiidae	04	1.2	125	
469	92	4.2	4.5	Ephemerellidae	82	26.1	17	05
				Chironomidae	16	5.2	598	
				Baetidae	01	0.3	35	
				Tipulidae	01	0.3	11	
540	92	7.6	4.5	Chironomidae	74	2.1	284	06
				Ephemerellidae	13	0.4	01	
				Tipulidae	04	0.1	09	
				Baetidae	04	0.2	08	
				Leptophlebiidae	03	0.1	05	
				Siphonuridae	01	< 0.01	10	
1043	84	8.3	5.8	Chironomidae	45	3.2	367	05
				Baetidae	24	1.7	190	
				Siphonuridae	17	1.2	52	
				Ephemerellidae	08	0.6	07	
				Tipulidae	06	0.4	06	
1225	54	8.9	5.7	Chironomidae	46	7.8	633	05
				Baetidae	32	4.2	442	
				Siphonuridae	21	3.5	196	
				Leptophlebiidae	01	0.1	10	
1464	74	10.0	6.0	Tipulidae	45	17.7	21	06
				Baetidae	18	6.9	551	
				Siphonuridae	11	4.1	414	
				Chironomidae	09	3.6	362	
				Leptophlebiidae	09	3.6	126	
				Ephemerellidae	08	3.2	17	
1640	44	66.7	6.4	Leptophlebiidae	42	88.2	301	09
				Chironomidae	23	49.5	2761	
				Ephemeridae	12	24.4	12	
				Baetiscidae	09	18.5	02	
				Ephemerellidae	07	13.9	197	
				Tipulidae	05	9.7	141	
				Baetidae	04	7.7	200	
5106	21	47.0	6.6	Leptophlebiidae	37	40.0	957	09
				Chironomidae	26	28.0	2086	
				Ephemerellidae	16	16.7	57	
				Baetiscidae	11	11.8	03	
				Tipulidae	09	10.0	169	
				Baetidae	01	0.9	33	

Fall Gatherer Functional Group continued.

Site Description				FFG Family and Characteristics				Total Family Richness
B.A.	C.C.	Alk.	pH	Gatherer	%	mgDM/m ²	n	
10300	07	39.7	6.2	Ephemerellidae	25	10.3	87	08
				Tipulidae	32	10.0	134	
				Chironomidae	21	8.4	568	
				Leptophlebiidae	18	7.5	47	
				Baetidae	05	2.2	23	
				Ephemeridae	04	1.7	02	
				Siphonuridae	02	0.7	32	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Spring Filterer Functional Group

Site Description				FFG Family and Characteristics			Total Family Richness	
B.A.	C.C.	Alk.	pH	Filterer	%	mgDM/m ²	n	
48	31	22.4	5.5	ND	ND	ND	ND	ND
98	92	17.2	6.1	ND	ND	ND	ND	ND
469	92	4.2	4.5	Polycentropodidae	94	3.5	11	02
				Simulidae	06	0.2	06	
540	92	7.6	4.5	Polycentropodidae	100	1.3	14	01
1043	84	8.3	5.8	Polycentropodidae	100	6.8	10	01
1225	54	8.9	5.7	Hydropsychidae	61	4.5	03	03
				Polycentropodidae	39	2.8	10	
1464	74	10.0	6.0	Polycentropodidae	100	0.01	12	01
1640	44	66.7	6.4	Polycentropodidae	69	10.7	19	03
				Hydropsychidae	31	4.7	23	
5106	21	47.0	6.6	Isonychiidae	59	20.1	03	03
				Hydropsychidae	36	12.4	18	
				Polycentropodidae	05	1.8	21	
10300	07	39.7	6.2	Polycentropodidae	53	6.4	38	03
				Hydropsychidae	46	5.6	16	
				Simulidae	01	0.1	01	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Summer Filterer Functional Group

Site Description				FFG Family and Characteristics			Total Family Richness	
B.A.	C.C.	Alk.	pH	Filterer	%	mgDM/m ²	n	
48	31	22.4	5.5	ND	ND	ND	ND	ND
98	92	17.2	6.1	ND	ND	ND	ND	ND
469	92	4.2	4.5	Polycentropodidae	100	1.2	09	01
540	92	7.6	4.5	Polycentropodidae	100	1.0	10	01
1043	84	8.3	5.8	Polycentropodidae	100	2.0	28	01
1225	54	8.9	5.7	Polycentropodidae	99	10.3	28	02
				Hydropsychidae	01	0.04	05	
1464	74	10.0	6.0	Hydropsychidae	56	2.1	07	03
				Polycentropodidae	38	1.4	32	
				Simulidae	06	0.2	11	
1640	44	66.7	6.4	Isonychiidae	72	39.3	12	03
				Polycentropodidae	18	9.9	81	
				Hydropsychidae	10	5.8	20	
5106	21	47.0	6.6	Hydropsychidae	62	9.2	45	03
				Isonychiidae	28	4.2	06	
				Polycentropodidae	10	1.5	23	
10300	07	39.7	6.2	Polycentropodidae	37	5.1	96	04
				Isonychiidae	37	5.0	02	
				Hydropsychidae	26	3.5	22	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Fall Filterer Functional Group

Site Description				FFG Family and Characteristics				Total Family Richness
B.A.	C.C.	Alk.	pH	Filterer	%	mgDM/m ²	n	
48	31	22.4	5.5	Hydropsychidae	67	25.9	52	04
				Polycentropodidae	20	7.7	12	
				Philopotamidae	11	4.2	04	
				Simulidae	03	1.0	12	
98	92	17.2	6.1	Polycentropodidae	86	19.5	18	04
				Simulidae	10	2.2	79	
				Hydropsychidae	04	4.2	01	
				Philopotamidae	01	0.2	01	
469	92	4.2	4.5	Hydropsychidae	82	11.2	08	02
				Polycentropodidae	18	2.4	07	
540	92	7.6	4.5	Polycentropodidae	90	12.3	04	02
				Hydropsychidae	10	1.3	06	
1043	84	8.3	5.8	Polycentropodidae	100	2.5	05	01
1225	54	8.9	5.7	Polycentropodidae	75	3.4	45	03
				Hydropsychidae	22	1.0	19	
				Simulidae	03	0.1	11	
1464	74	10.0	6.0	Hydropsychidae	67	7.4	80	03
				Polycentropodidae	30	3.3	37	
				Simulidae	03	0.3	109	
1640	44	66.7	6.4	Hydropsychidae	75	36.6	140	03
				Isonychiidae	21	10.3	06	
				Polycentropodidae	04	2.0	04	
5106	21	47.0	6.6	Hydropsychidae	73	23.3	78	02
				Polycentropodidae	27	8.6	17	
10300	07	39.7	6.2	Hydropsychidae	50	45.4	174	03
				Polycentropodidae	50	45.3	32	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Spring Predator Functional Group

Site Description				FFG Family and Characteristics			Total Family Richness	
B.A.	C.C.	Alk.	pH	Predator	%	mgDM/m2	n	Richness
48	31	22.4	5.5	ND	ND	ND	ND	ND
98	92	17.2	6.1	ND	ND	ND	ND	ND
469	92	4.2	4.5	Perlodidae	91	7.3	01	04
				Chloroperlidae	05	0.4	01	
				Tabanidae	03	0.3	01	
540	92	7.6	4.5	Perlodidae	75	5.8	01	06
				Chloroperlidae	23	1.7	15	
				Ceratopogonidae	01	0.1	43	
				Tabanidae	01	0.04	01	
1043	84	8.3	5.8	Chloroperlidae	65	6.2	84	05
				Rhyacophilidae	18	1.8	02	
				Gomphidae	13	1.2	10	
				Empididae	03	0.3	05	
1225	54	8.9	5.7	Gomphidae	64	13.1	01	05
				Chloroperlidae	36	7.4	100	
1464	74	10.0	6.0	Gomphidae	71	12.6	01	06
				Chloroperlidae	21	3.7	43	
				Perlodidae	07	1.3	01	
1640	44	66.7	6.4	Chloroperlidae	37	8.3	54	06
				Corydalidae	36	8.0	03	
				Gomphidae	26	5.9	05	
				Empididae	01	0.3	15	
5106	21	47.0	6.6	Perlidae	29	2.4	04	08
				Corydalidae	25	2.1	03	
				Gomphidae	20	1.7	03	
				Chloroperlidae	14	1.2	33	
				Sialidae	07	0.6	01	
				Perlodidae	05	0.5	33	
10300	07	39.7	6.2	Corydalidae	61	27.4	01	08
				Gomphidae	28	12.6	16	
				Perlidae	05	2.2	07	
				Chloroperlidae	04	1.7	17	
				Perlodidae	02	1.0	03	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Summer Predator Functional Group

Site Description				FFG Family and Characteristics				Total Family Richness
B.A.	C.C.	Alk.	pH	Predator	%	mgDM/m ²	n	
48	31	22.4	5.5	ND	ND	ND	ND	ND
98	92	17.2	6.1	ND	ND	ND	ND	ND
469	92	4.2	4.5	Ceratopogonidae	53	0.4	59	05
				Chloroperlidae	27	0.2	02	
				Perlodidae	08	0.1	02	
				Rhyacophilidae	07	0.1	08	
				Empididae	05	0.04	03	
540	92	7.6	4.5	Chloroperlidae	56	2.9	14	06
				Perlodidae	34	1.5	09	
				Ceratopogonidae	06	0.3	25	
				Rhyacophilidae	04	0.2	06	
				Gomphidae	01	0.03	02	
1043	84	8.3	5.8	Chloroperlidae	74	6.7	100	05
				Perlodidae	11	1.0	02	
				Gomphidae	06	0.6	01	
				Rhyacophilidae	05	0.5	06	
				Ceratopogonidae	04	0.4	33	
1225	54	8.9	5.7	Chloroperlidae	92	6.9	52	05
				Rhyacophilidae	05	0.4	02	
				Ceratopogonidae	02	0.2	27	
				Perlodidae	01	0.1	01	
1464	74	10.0	6.0	Chloroperlidae	81	5.0	66	05
				Ceratopogonidae	10	0.6	25	
				Rhyacophilidae	07	0.4	22	
				Perlodidae	01	0.03	02	
				Empididae	01	0.03	02	
1640	44	66.7	6.4	Corydalidae	57	50.0	08	07
				Perlidae	19	16.7	04	
				Gomphidae	19	16.5	06	
				Chloroperlidae	03	3.0	29	
				Perlodidae	01	1.2	06	
				Rhyacophilidae	01	0.6	06	
5106	21	47.0	6.6	Corydalidae	41	11.4	23	09
				Gomphidae	37	10.3	05	
				Perlodidae	13	3.7	21	
				Sialidae	04	1.1	02	
				Chloroperlidae	04	1.0	18	
				Rhyacophilidae	01	0.2	26	
10300	07	39.7	6.2	Gomphidae	38	5.5	06	09
				Corydalidae	21	3.0	05	
				Perlodidae	16	2.3	07	
				Chloroperlidae	08	1.2	07	
				Perlidae	07	1.0	02	
				Ceratopogonidae	05	0.6	42	
				Rhyacophilidae	04	0.6	17	
				Muscidae	01	0.1	02	

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.

Fall Predator Functional Group

Site Description				FFG Family and Characteristics				Total Family Richness
B.A.	C.C.	Alk.	pH	Predator	%	mgDM/m ²	n	
48	31	22.4	5.5	Perlodidae	56	45.1	15	06
				Gomphidae	21	16.7	02	
				Chloroperlidae	16	12.9	80	
				Rhyacophilidae	07	5.3	03	
98	92	17.2	6.1	Chloroperlidae	51	22.9	110	07
				Perlodidae	46	20.6	34	
				Gomphidae	01	0.6	03	
				Rhyacophilidae	01	0.4	01	
				Ceratopogonidae	01	0.2	17	
469	92	4.2	4.5	Perlodidae	73	2.6	03	04
				Chloroperlidae	21	0.7	21	
				Rhyacophilidae	04	0.1	05	
				Ceratopogonidae	02	0.1	03	
540	92	7.6	4.5	Chloroperlidae	58	4.1	102	05
				Perlodidae	23	1.6	09	
				Rhyacophilidae	18	1.3	02	
				Empididae	01	0.04	01	
1043	84	8.3	5.8	Gomphidae	84	31.5	01	04
				Chloroperlidae	16	5.9	82	
				Perlodidae	01	0.3	02	
1225	54	8.9	5.7	Chloroperlidae	61	27.9	158	06
				Perlidae	25	11.3	01	
				Rhyacophilidae	12	5.3	08	
				Perlodidae	01	0.6	03	
				Gomphidae	01	0.5	02	
1464	74	10.0	6.0	Chloroperlidae	63	11.0	126	04
				Perlodidae	33	5.8	09	
				Rhyacophilidae	03	0.5	35	
				Ceratopogonidae	01	0.2	11	
1640	44	66.7	6.4	Perlidae	37	45.1	05	08
				Rhyacophilidae	30	36.0	93	
				Corydalidae	11	13.1	03	
				Perlodidae	11	12.6	07	
				Aeshnidae	06	7.0	01	
				Chloroperlidae	05	6.4	108	
5106	21	47.0	6.6	Perlodidae	33	15.6	14	11
				Chloroperlidae	27	12.6	211	
				Rhyacophilidae	21	10.0	26	
				Aeshnidae	06	3.1	02	
				Perlidae	06	2.8	01	
				Corydalidae	05	2.3	01	
				Athericidae	01	0.6	01	
				Sialidae	01	0.3	01	

Fall Predator Functional Group continued.

Site Description				FFG Family and Characteristics			Total Family Richness
B.A.	C.C.	Alk.	pH	Predator	%	mgDM/m ²	n
10300	07	39.7	6.2	Perlidae	61	142.9	02
				Perlodidae	22	52.1	12
				Corydalidae	08	18.9	03
				Aeshnidae	04	9.9	17
				Rhyacophilidae	03	7.8	33
				Chloroperlidae	01	1.5	18

B.A. = Basin Area (ha). C.C. = Mean (n = 10) Canopy Cover (%).

Alk. = Mean (n = 4 - 6) Alkalinity (mg/L CaCO₃). pH = Minimum (n = 10) pH.