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Effects of Hydrologic Gradients on Woody Debris Breakdown and Macroinvertebrate Colonization in a Cumberland Plateau Watershed, Eastern Kentucky, U.S.A.

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EFFECTS OF HYDROLOGIC GRADIENTS ON WOODY DEBRIS
BREAKDOWN AND MACROINVERTEBRATE COLONIZATION IN A
CUMBERLAND PLATEAU WATERSHED, EASTERN KENTUCKY, U.S.A.

A Thesis

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In Partial Fulfillment

Of the Requirements for the Degree

Master of Science in Biology

By

Robin Rae Bernal

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EFFECTS OF HYDROLOGIC GRADIENTS ON WOODY DEBRIS
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CUMBERLAND PLATEAU WATERSHED, EASTERN KENTUCKY, U.S.A.

Date Recommended __April 2, 2010_____

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Date

DEDICATION

I would like to dedicate this thesis to my wonderful parents who have always supported me in all my endeavors. To my loving husband, who was always supportive, understanding, and was always by my side helping me and cheering me on.

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This research assessed the influence of hydrologic gradients on woody debris dynamics in a Cumberland Plateau watershed, eastern Kentucky, U.S.A. Although the breakdown of wood can be attributed to several different processes, including leaching, biological decay, fragmentation, and transport, the influence of differing flow regimes has been unstudied. The objectives of this study were to examine how stream channel type (temporary vs. perennial) affected wood processing dynamics (i.e., mass loss and macroinvertebrate colonization and standing stock patterns). Two questions were addressed: (1) do mass loss rates of wood differ across hydrological gradients in stream channels?, and (2) do macroinvertebrate colonization and standing stock patterns vary in relation to hydrologic gradients? Although within each channel type both dry mass and ash free dry mass loss followed a negative exponential model ($p < 0.05$), there wasn't a significant between-channel difference in mass loss rates ($p > 0.05$). Breakdown rates ($-k$) ranged from $0.133 - 0.194\text{year}^{-1}$ for perennial streams compared to $0.103 - 0.170\text{year}^{-1}$ in the temporary streams. Collector-gathers comprised the greatest proportion of macroinvertebrates, accounting for 65.5% (temporary) and 59.3% (perennial) of all taxa colonizing wood bundles, followed by shredders (16.1%, 16.8%), predators (16.8%,

20.1%), (scrapers < 0.1% in both reaches) and filtering collectors (1.2%, 3.7%). Overall, there were no significant between-channel differences for total macroinvertebrate abundance, total macroinvertebrate biomass, and similarly for abundance and biomass of all functional groups. There was a trend, however, of decreasing density and biomass over time of collector-gathers and shredders on wood. Overall, hydrological gradients had no effects on short-term breakdown rates of woody debris or macroinvertebrate colonization patterns. Studies of wood breakdown have been shown to require long study periods (≥ 5 years), therefore, future studies of hydrological gradient may show differing results for woody debris breakdown.

INTRODUCTION

Headwater streams and hydrologic gradients

The structure and function of headwater streams draining forested basin are tied to their adjacent landscapes and organic matter supplies through allochthonous inputs (Benfield 1997, Abelho and Graca 1998, Webster et al. 1999, Acuna 2004, Richardson et al. 2005, McNeely et al. 2007, Wipfli et al. 2007). The terrestrial vegetation along stream margins can limit primary production by blocking sunlight, but the organic material that falls into the streams can provide high amounts of allochthonous carbon (Gessner and Chauvet 1993). This litter, or coarse particulate organic matter (CPOM), is comprised mainly of leaves but also includes seeds, flowers, fruits, nuts, bark, and wood (Benfield 1997, Abelho 2001).

Abscised leaves and wood, in particular, are transformed by abiotic and biotic factors while undergoing continuous movement downstream (Simon and Benfield 2001). Allochthonous matter is stored in various structures in headwater streams and with hydrological events may be transported downstream (Abelho 2001). Studies have shown CPOM standing stocks decline both with increasing stream order and decreasing elevational gradient (Benfield et al. 2000). Transport and retention of CPOM along a hydrological gradient from temporary to perennial streams may in turn affect aquatic invertebrate communities.

The River Continuum Concept (RCC) presented a riverine system as a unidirectional gradient of physical conditions with consistent longitudinal patterns of organic matter loading, transport, and storage (Vannote et al. 1980). At a finer scale community shifts from within only the headwater reaches are subtle (Delucchi and

Peckarsky 1989, Feminella 1996, Proger and Moldenke 2002) since environmental gradients from temporary to 1st- and 2nd-order perennial channels are relatively shallow. Temporary streams may be underestimated in terms of biodiversity in macroinvertebrate assemblages, and many studies have shown high levels of taxonomic richness in these systems (Feminella 1996; Dietrich and Anderson 2000; Chadwick and Huryn 2005, Grubbs *unpublished data*). Whiles and Goldowitz (2005) showed that mean annual invertebrate abundance and biomass increased with hydroperiod length across a hydrologic gradient in four wetlands, yet, taxon richness and diversity were greatest at intermittent sites and concluded that a diversity of habitat with varying hydrologic regimes will maximize macroinvertebrate abundance and diversity.

Hydrological variation is commonly used as a means to suggest differences in ecosystem structure and function in streams (Diaz et al. 2008). Variations in flow can greatly influence macroinvertebrate communities, and flow heterogeneity and substratum size influence habitat types for stream insects (Merritt et al. 2008). High flow events are accompanied by increased velocity and hydraulic forces on the stream bed (Lancaster 1999), who identified several mechanisms by which macroinvertebrates may use refugia during flow disturbances. She investigated if lotic invertebrates move (either actively or passively) away from microhabitats where near-bed hydraulic forces increase with discharge towards areas that maintain lower flows and act as refugia. Schlosser and Ebel (1989) found that the density of benthic and drifting invertebrates increased significantly with elevated flow.

The importance of microbes and macroinvertebrate consumers varies both seasonally and across stream size gradients. Graca et al. (2001) revealed a decrease in

shredder densities downstream, yet this did not decrease litter processing rates and suggested increased microbial processing downstream due to parallel downstream increases in temperature and nitrogen and phosphorous levels. These results support RCC predictions (Vannote et al. 1980) that stream temperatures and nutrient content increase with distance from the source while shredder densities decrease in importance.

Acuna et al. (2004) showed that hydrological regimes significantly modified the influence of ecosystem respiration through its direct effect on the amount of allochthonous material stored. Their study found that high discharges had a cleaning effect by removing benthic organic matter and allowing light to reach benthic primary producers, further concluding that the best single predictor of gross primary production was discharge.

Woody debris

Forested headwater streams typically receive large volumes of woody debris from the surrounding riparian forest (Wipfli et al. 2007). The recruitment of wood from mass movement is highly variable over space and time (Hassan et al. 2005). Wood input into streams may greatly affect local-scale hydrological gradients and rate of wood decomposition. Stream size and hydrologic condition may influence the amount of woody debris stored in streams (Anderson et al. 1978, Collier and Halliday 2000). In headwater streams, large woody debris is too big to be moved by water and therefore affects channel form by providing sites for sediment storage and contributing to changes in flow hydraulics and high flow protection (Ehrman and Lamberti 1992, Gippel 1995, Hassan et al. 2005). Woody debris provides habitat complexity by the creation of pools

and retention of organic matter (Lemly and Hilderbrand 2000, Gullis et al. 2004). Woody debris and other organic matter breakdown are also affected by hydrological conditions of streams, since higher flow rates may cause increased physical fragmentation that in turn may increase surface area/volume ratios to enhance microbial growth (Benfield et al. 2000, Fowler and Scarsbrook 2002).

The contribution of woody debris to stream food webs as an energy and carbon source (Dudley and Anderson 1982, Gullis et al. 2008) to nutrient cycling (Spanhoff and Gessner 2004) is of particular interest because information on this function remains limited, which can be contributed to the necessity for long term studies due to a slow rate of breakdown (Harmon et al. 1986, Webster et al. 1999, Dahlstrom and Nilsson 2006).

Woody debris contributes to several important biological and physical processes and can influence biological communities in stream habitats. Although research on wood breakdown have shown how nutrient cycling, invertebrate communities, tree species, and chemical properties can influence rates of mass loss (Dudley and Anderson 1982, Golladay and Webster 1988, Gullis et al. 2004, Scherer 2004), few studies have assessed the influence of hydrological gradients.

Many studies have shown the importance of leaf breakdown to stream ecosystems (e.g., Webster and Benfield 1986, Webster et al. 1999), but relatively few studies have assessed the importance of wood processing. Although the input rates of wood are typically lower than that of leaves (Webster et al. 1999), the standing crop of wood is usually higher (Tank and Webster 1998). Some studies have shown that wood as a carbon resource may be an important resource for times when leaf detritus is unavailable, either seasonally or if excluded completely (Eggert and Wallace 2007). Wood breakdown can

also be attributed to other factors, including piece size, stream temperature, and water chemistry (e.g., nitrogen levels) (Harmon et al. 1986, Scherer 2004).

Similar to leaves, woody debris breakdown is affected by four main processes, namely leaching (i.e., chemical), microbial decay, macroinvertebrate feeding, and physical fragmentation (Harmon et al. 1986). Wood breakdown begins with a relatively rapid mass loss that is attributed to the leaching of soluble substances (Díez et al. 2002). Leaching of dissolved material accounts for 10–30% of initial weight loss from most leaf species, but it is likely that very little material is leached directly from wood (Webster et al. 1999). However, Díez et al. (2002) suggested that leaching of wood may occur at similar rates to those of leaf litter but extended over a longer period of time (e.g., several weeks).

Woody debris possesses both lower nutrient and higher lignin contents compared to leaves (Gulis et al. 2004). Lignins belong to a class of complex aromatic polymers formed from phenyl propanoid units, protect cellulose against microbial enzymes, and comprise 20–30% of woody tissue (Wallace et al. 1999). Lignin also complexes with cellulose forming lignocelluloses, representing more than one-half the total carbon present in wood (Aumen et al. 1983). Lignin decays slower than cellulose and hemicelluloses, leading to an increase in the lignin to cellulose ratio as wood decay proceeds (Harmon et al. 1986). Wood decaying fungi are of importance because they can break down lignins in cellular walls (Blanchette 1991).

Oxygen is required for significant rates of microbial decomposition of lignin (Harmon et al. 1986). Wood breakdown occurs mainly at the surface via fungal (e.g., aquatic hyphomycetes) and bacterial activity (Tank and Winterbourn 1996, Crenshaw et

al. 2002), allowing for a more suitable habitat and food supply for stream macroinvertebrates. The fact that wood decays at a much slower rate than other organic matter allows microbes to recolonize after grazing by macroinvertebrates, showing that wood can be a long standing carbon resource for stream organisms (Eggert and Wallace 2007). Although abrasion and fragmentation are two means of physical breakdown in wood that allow for increased surface area for microbial colonization, yet the chemical constituents of wood can affect decomposition rates by making them resistant to abrasion and fragmentation (Sedell et al. 1988). The decay of intact wood is limited typically to the surfaces because high water content and low oxygen levels within the wood limit microbial penetration (Richardson et al. 2005).

Microbial communities that colonize wood are an important biotic processing component. Gulis (2001) showed that wood has a distinctly different fungal community from those found on leaf litter. Aquatic hyphomycetes are a major fungi colonizer of woody tissues. Wood can promote extensive biofilm development as a carbon source and as a surface for microbial colonization, therefore playing a significant role in supporting stream community metabolism (Tank and Winterbourn 1996). The slow decomposition of wood also provides a stable surface for microbial colonization. Few freshwater organisms consume wood directly so microbial colonization serves as a primary vector of wood carbon transfer to higher trophic levels in stream food webs (Tank et al. 1998, Tank and Dodds 2003).

The microbial activity on the substrate can increase the palatability of the substrate to detritus feeders (Nikolcheva et al. 2003). Many studies have been performed to address the relationships between macroinvertebrate colonization and level of

microbial conditioning. For example, Eggert and Wallace (2007) measured assimilation efficiencies of three detritivores (*Pycnopsyche gentilis* (Trichoptera), *Tipula abdominalis* (Diptera), and *Tallaperla* spp. (Plecoptera)) for grazed versus ungrazed wood epixylon to determine its use by detritivores and to see what extent wood biofilm is a food resource for stream invertebrates. All three detritivores fed on epixylon and wood had significantly lower microbial respiration rates plus lower fungal and bacterial densities and biomass (Eggert and Wallace 2007).

There have been several studies (e.g., Hax and Golladay 1993, Kaller and Kelso 2006) focusing on macroinvertebrate colonization patterns on wood substrates. Invertebrates will colonize wood based on substrate quality (Harmon et al. 1986). All functional feeding groups can be found on wood substrates. Some macroinvertebrate use wood as a preferred food source, while others may only incidentally ingest wood when feeding on other detritus (Dudley and Anderson 1982, Sedell et al. 1988). Factors that influence macroinvertebrate colonization patterns include species, size, texture, and degree of conditioning (Magoulick 1998). Dudley and Anderson (1982) and Magoulick (1998) both summarized that invertebrate density, diversity, and richness were correlated to wood decay. A few studies (e.g., Kaller and Kelso 2006), however, have produced contrasting results.

Sedell et al. (1988) indicated that invertebrates colonize wood according to successive stages of decay. New wood serves mainly as habitat that is then colonized by microbes and algae, providing a direct food source for grazers but this feeding does not affect the structure of the wood. Colonization by fungi eventually softens the wood enough to be incidentally ingested by scrapers, and also the wood becomes suitable for

wood grazers and wood shredders (Sedell et al. 1988).

Collier and Halliday (2000) showed varying preferences by different macroinvertebrates at different stages of decay for wood, signifying that invertebrate community changes as wood goes through various stages of breakdown. They found that *Austroclima sepia* (Ephemeroptera: Leptophlebiidae) preferred wood at early to intermediate stages and *Pycnocentria funerea* (Trichoptera: Conoesucidae) and *Zephlebia dentata* (Ephemeroptera: Leptophlebiidae) preferred wood at intermediate to advanced stages, while *Coloburiscus humeralis* (Ephemeroptera: Coloburiscidae) and *Eukiefferiella* (Diptera: Chironomidae) preferred severely decayed substrate. Overall, Collier and Halliday (2000) found that *P. funerea* larva became more xylophagous throughout larval growth and there was significantly more FPOM produced by macroinvertebrates on wood at a highly decomposed state than from early or intermediate stages.

The availability of nutrients, specifically nitrogen (N) and phosphorus (P), in wood for microorganisms can contribute to the decomposition process. Recent studies (Tank and Webster 1998, Gulis et al. 2004) have shown that experimentally-augmented nutrient content significantly increased microbial biomass and activity. In general, breakdown rates have been found to be higher in nutrient-rich and lower in nutrient-poor systems (Gulis et al. 2004). Other studies (Tank and Dodds 2003) have demonstrated nutrient-limitation, with fungal biomass increasing 26% with N additions, 43% for P additions, and increasing 157% with both N and P supplements.

There is considerable variability between tree species in decomposition rates due to differing chemical contents. For example, gymnosperm wood typically degrades more slowly than angiosperms due to the higher proportion of lignin and lower nutrient levels

(Harmon et al. 1986, Golladay and Webster 1988, Spanhoff and Gessner 2004).

Magoulick (1998) analyzed how wood hardness, condition, and texture influenced colonization of stream macroinvertebrates, showing found that taxa richness was greater on rough conditioned wood compared to rough unconditioned wood. Magoulick (1998) concluded that wood condition and hardness can influence community structure on wood substrates. Druryl and Kelso (2000) showed differences in invertebrate colonization dynamics due to wood type and underlying substrate type, indicating that a higher rate of decomposition means more surface area for invertebrate colonization.

Spanhoff et al. (2001) stated that determining wood decay state based on external characteristics (e.g., hardness) may be misleading because it does not represent the physical state of the wood. Surface texture may be influenced by abiotic and biotic factors, including invertebrates scraping off the top layers and darkening of wood due to burial by sediment or by microbial colonization. Spanhoff et al. (2001) determined decay state based on relative density of wood, finding a correlation of decreasing wood density and increasing water content.

Wood size plays an important role because small pieces of wood have high surface-to-volume ratios causing them to breakdown at a faster rate (Webster and Benfield 1996). Simon and Benfield (2001) suggested that their study may have overestimated natural wood breakdown rates due to the use of wood veneer strips with high surface area to volume ratios. Spanhoff and Meyer (2004) summarized wood breakdown rates in streams from various studies, finding that natural wood (e.g. twigs and branches) decayed at a slower rate compared to commercial wood products and that deciduous versus coniferous wood had varying breakdown rates.

Although research on wood breakdown have shown how nutrient cycling, invertebrate communities, tree species, and chemical properties can influence breakdown rates (Dudley and Anderson 1982, Golladay and Webster 1988, Gulis et al. 2004, Scherer 2004), few studies have assessed the influence of hydrological gradients. Hydrological gradients may influence stream functions, including water chemistry, nutrient content, breakdown of allochthonous materials, and plant and animal communities (Fowler and Scarsbrook 2002) and influence the rate of organic matter breakdown of biomass in streams.

Study purpose and statement of hypothesis

As stated previously, although there have been several studies examining the effects of varying hydrological regimes on leaf processing (e.g., Leff and McArthur 1989), comparatively little research has been done to study woody debris breakdown across flow gradients. This research assessed woody debris breakdown dynamics across a temporary-perennial hydrological stream gradient in a Cumberland Plateau watershed in eastern Kentucky, U.S.A. Although the temporary and perennial streams are linked longitudinally in the same watershed, it was hypothesized that the woody debris would breakdown at a faster rate and would be colonized by a more abundant and diverse macroinvertebrate fauna in the perennial reaches due to the perpetual flow conditions.

A specific series of *a priori* hypothesis were established for woody debris breakdown rates and all macroinvertebrate variables. Woody debris breakdown was proposed to breakdown at a faster rate in perennial channels due to continual flow conditions compared to temporary streams when comparing $-k$ values. I also expected to

find that comparing all total abundance and biomass, as well as abundance and biomass for all functional feeding groups, that there would be a significant difference from month one of sampling to month 13 due to greater time in stream. For macroinvertebrate richness, it was anticipated that perennial streams would hold a more diverse macroinvertebrate fauna due to higher breakdown rates. For macroinvertebrate abundance, it was proposed for total abundance and abundance for all functional feeding groups that perennial streams would hold a higher abundance of macroinvertebrates in perennial streams also due to perpetual flow conditions. For macroinvertebrate biomass, it was similarly assumed that total biomass and biomass for all functional feeding groups in perennial streams would hold a higher biomass of macroinvertebrates in perennial streams due to perpetual flow conditions in these reaches.

METHODS and MATERIALS

Study site description

All research was performed during autumn-spring 2007–2008 and 2008–2009 in a 1545 ha, 3rd-order watershed, Clemons Fork, that is located in the Kentucky River Basin of eastern Kentucky and is part of a series of tracts at Robinson Forest (Fig. 1) that are owned and managed in part by the University of Kentucky. Robinson Forest is positioned in portions of Breathitt, Knott and Perry counties (Fig. 1). Clemons Fork is positioned in the Central Appalachians-Dissected Appalachian Plateau Level IV Ecoregion, characterized by Pennsylvanian-aged shale, sandstone, and coal (Woods et al. 2002). The main underlying bedrock and stream substrates within both watersheds are sandstone, with occasional exposed coal seams and shale.

Clemons Fork was last logged during the early part of the 1900's and currently supports mature second-growth mixed mesophytic forests (Cherry 2006). Forest stand age and disturbance history are virtually identical both across the watershed and along a hydrologic continuum from temporary downslope to perennial channels. Tree and woody shrub species commonly located along study streams and the adjacent upland slopes include American beech (*Fagus grandifolia* Ehrh.), black oak (*Q. velutina* Lamb.), chestnut oak (*Q. prinus* L.), northern red oak (*Q. rubra* L.), white oak (*Q. alba* L.), hickory (*Carya* spp.), yellow-poplar (*Liriodendron tulipifera* L.), sugar maple (*Acer saccharum* Marshall), red maple (*A. rubrum* L.), white ash (*Fraxinus americana* L.), American rhododendron (*Rhododendron maximum* L.), mountain laurel (*Kalmia latifolia* L.), and common spicebush (*Lindera benzoin* L.). Dekalb-Marowbone-Lantham,

Cloverick-Shelocata-Cutshin, Shelocata-Gilpin-Hazleton, and Shelocata-Gilpin-Kimper soil series underlay the forest (Cherry 2006).

A series of seven similar-sized 1st-2nd order tributaries were established as *a priori* replicates (Fig. 1). Each tributary drains a small subwatershed (34–109 ha), is positioned within a narrow altitudinal band (Table 1–2), and was divided longitudinally into temporary, intermittent and upland perennial reaches based on annual flow permanence. Only temporary and perennial reaches were employed in this study. All stream reaches were 50 m in length and composed mainly of coarse sandstone substrates intermixed with small accumulations of large woody debris and an occasional shallow bedrock run. Pools were mainly associated with woody debris.

In-stream physical and chemical parameters were analyzed monthly during 2008. Conductivity ($\mu\text{s}/\text{cm}$) and pH (S.U.) were measured in the field with an YSI 556 multiprobe system. Automated ISCO and grab samples were taken for quantifying alkalinity, dissolved organic carbon, and total organic carbon levels according to standard methods (APHA 1992). Alkalinity (mg/L) was analyzed with an Orion 940/960 autotitrator and both organic carbon parameters were quantified with a Shimadzu TOC-5000A.

Field and laboratory methods

Untreated wood strips (1.3 cm x 1.3 cm x 7.6 cm; = 12.3 cm³) from freshly-harvested red maple heartwood were used as substrates for measuring mass loss and macroinvertebrate colonization patterns. Wood strips were placed in plastic mesh holders (5 mm mesh; Conweb Plastics, LLC, Minneapolis, MN) to make wood bundles (WB)

weighing approximately 10 g. Mesh holders were attached to aluminum nails using cable-ties (6 holders per nail), fully submerged, and staked to the stream bed of all 14 study reaches in January 2008.

Three bundles were collected monthly from each study reach between February 2008 and February 2009. A 500- μ m sieve was placed immediately downstream of each collected bundle to obtain any dislodged macroinvertebrates. The bundle and associated biota were placed in individual plastic bags and then immediately in a cooler.

In the laboratory, macroinvertebrates were gently washed off the wood strips with a soft brush and preserved in 75% ethanol. Macroinvertebrates were identified to the lowest practical level, namely genus or species, and assigned to individual functional feeding groups according to Merritt et al. (2008). Body lengths for macroinvertebrates were measured digitally with SIMAGIS®3.0 (Smart Imaging Technologies, Houston, TX). Mass-body length regressions were taken from Benke et al. (1999), Matousek (2007) and McNeely et al. (2007) to calculate macroinvertebrate biomass with the equation $M=aL^b$, where M = mass (mg), L = length (cm), and b = logarithmic slope of the line.

To quantify dry mass loss, each wood bundle was dried for at 70°C for 72 h, cooled to room temperature, and weighed to the nearest 0.01 g. The bundle was then combusted at 550°C for 24 h in a muffle furnace, cooled to room temperature, and reweighed to the nearest 0.01 g. Wood breakdown rates, as processing coefficients ($-k$), were calculated with ash free dry mass (AFDM) using a negative exponential model (Webster and Benfield 1986). All AFDM data were log-transformed and the negative exponential model calculated $-k$ by taking the slope of the regression line for the natural

log mean of percent AFDM remaining per time in-stream.

Statistical methods

To assess differences between temporary and perennial reaches, paired sample t-tests were used to compare wood processing rate coefficients ($-k$), total macroinvertebrate taxa richness, and all macroinvertebrate abundance (no./WB) and biomass variables (mg/WB). Macroinvertebrate variables included total abundance and biomass, and abundance and biomass individually for the shredders, scraper, filtering-collector, gathering-collector, and predator functional feeding groups. The t-tests were analyzed using STATISTICA 9.1 and SPSS 18.0.

RESULTS

Physiochemical characteristics

All study reaches were weakly acidic and generally exhibited both low alkalinity and conductivity levels. All reaches also had both low total and dissolved organic carbon levels (Table 3).

Hydrologic gradients

Woody debris breakdown

The range of woody debris mass loss rates ($-k$, calculated with ash free dry mass) overlapped between stream reach types (temporary (T): 0.103 – 0.170 year⁻¹ vs. perennial (P): 0.133 – 0.194 year⁻¹; Table 4). Although the mean rate of mass loss was slightly lower in the temporary (0.133 year⁻¹) compared to the perennial reaches (0.160 year⁻¹), there were no significant between-reach differences ($t = 1.71$, $p = 0.11$).

Macroinvertebrate colonization patterns

In total, 48 macroinvertebrate taxa colonized the wood bundles from both stream reaches (Tables 5–6). The number of taxa found on wood bundles in the temporary ($n = 43$) and perennial ($n = 48$) reaches was similar. Both the overall mean abundance (no./WB: 9.5 > 7.2) and mean biomass (mg/WB: 2.8 > 2.5) were marginally greater on wood bundles in the temporary compared to the perennial reaches. Non-tanypod Chironomidae, (T = 45.1%, P = 36.6%) were the most abundant group of macroinvertebrates colonizing the wood bundles in both reaches. *Amphinemura* sp.

(T = 5.7%, P = 6.4%), *Ameletus* sp. (T = 5.5%, P = 7.5%), Oligochaeta (T = 5.4%, P = 3.7%), *Ephemerella* sp. (T = 4.5%, P = 6.1%), *Isoperla* spp. (T = 3.8%, P = 4.6%), tanypod Chironomidae (T = 3.5%, P = 3.6%) and *Peltoperla arcuata* (T = 3.4%, P = 3.2%) were the next most numerically-abundant taxa obtained from the wood bundles. These eight taxa comprised 76.9% and 71.7% of the total macroinvertebrate abundance on the wood bundles in the temporary and perennial reaches, respectively.

Macroinvertebrate biomass patterns on wood bundles were similar to abundance. Oligochaete worms (T = 27.0%, P = 19.6%) constituted the highest biomass of macroinvertebrates colonizing the wood bundles in both reaches. *Lepidostoma* spp. (T = 13.6%, P = 16.0%), *Ameletus* spp. (T = 10.0%, P = 10.4%), *Ephemerella* sp. (T = 8.0%, P = 8.8%), immature Taeniopteryginae (T = 5.0%, P = 4.3%), *Eurylophella* sp. (T = 4.9%, P = 7.8%), *Amphinemura* sp. (T = 3.6%, P = 3.2%), and *Rhyacophila* sp. (T = 3.0%, P = 3.7%) had the next highest biomass taxa obtained from the wood bundles. These eight taxa comprised 75.1% and 73.8% of the total macroinvertebrate biomass on the wood bundles in the temporary and perennial reaches, respectively.

Comparisons between the first (February 2008) and last (February 2009) months for total macroinvertebrate abundance and biomass, plus both shredder and gathering-collector abundance, were significantly different ($p < 0.05$; Table 11). Between-month differences for shredder and gathering-collector biomass, plus both abundance and biomass of filtering-collectors and predators, were not significant ($p > 0.05$).

Although there was considerable between-reach variability, gathering collectors, predators and shredders dominated the wood bundles in terms of both abundance and biomass (Tables 7–8). Overall, gathering-collectors were the most numerically-abundant

individual functional feeding group colonizing wood bundles, comprising 65.5% (temporary) and 59.3% (perennial) of the total macroinvertebrates obtained (Table 9). Predators (T = 16.8%, P = 20.1%) and shredders (T = 16.1%, P = 16.8%) were also moderately abundant while filtering-collectors (T = 1.2%, P = 3.7%) and scrapers (T = 0.4%, P = 0.2%) were comparatively rare. Gathering-collectors, shredders, and predators similarly comprised the majority of macroinvertebrate biomass colonizing wood bundles in both reach types (T = 98.3%, P = 97.8%; Table 7).

Overall, there was a trend of declining macroinvertebrate abundance and biomass on woody bundles in both the temporary and perennial reaches (Figs. 3 and 4). This trend was particularly evident with both gathering-collector (Figs. 5 and 6) and shredder (Figs. 7 and 8) functional groups. Predator abundance and biomass, however, did not decline with in-stream colonization time (Figs. 9 and 10).

There was only one between-reach difference comparing macroinvertebrate richness, abundance and biomass on wood bundles (Table 10). Mean filtering-collector biomass was significantly greater, albeit marginally, on wood bundles in the perennial reaches ($t = 2.17$, $p = 0.049$).

DISCUSSION

This study compared breakdown dynamics of red maple (*Acer rubrum*) heartwood between temporary and perennial sections of a forested, headwater stream continuum. Although mean breakdown rates ($-k$) in the perennial reaches (0.160 year^{-1}) were higher than from the temporary reaches (0.133 year^{-1}), this difference was not significant ($p = 0.09$ or 0.11). Hence, the hypothesis that woody debris would breakdown at a faster rate in the perennial reaches due to perennial flow conditions was refuted.

Breakdown rates in this study ranged from $0.103 - 0.194 \text{ year}^{-1}$, which was similar to rates published from previous studies (Table 11). Specifically, this range of breakdown rates is comparable to prior research using wood derived from other *Acer* species. Fisher, Wold and Hershey (1999) reported that sugar maple (*Acer saccharum*) wood was processed at rates ($0.133 - 0.140 \text{ year}^{-1}$) comparable to this study. Shearer and von Bodman (1983) also found that silver maple (*A. saccharinum*) was processed at a rate (0.16 year^{-1}) similar to this study. The woody debris used by both Fisher Wold and Hershey (1999) and Shearer and von Bodman (1983) used natural maple wood products. There is ample evidence, however, from various studies (e.g., Spanhoff and Gessner 2004, Spanhoff and Meyer 2004) suggesting that breakdown rates differ among wood products (e.g., commercial vs. natural or differing species). Many prior studies have used commercial wood substrates (e.g. ice-cream sticks and tongue depressors) that differ unlike the natural heartwood used in the present study. Spanhoff and Meyer (2004) found that natural wood exhibited slower breakdown rates than commercial products. Differing surface area: volume ratios can also lead to great differences in breakdown rates,

implying that the mean surface or volume per woody debris piece should be reported with studies of wood processing dynamics.

Studies have shown that temporary streams may harbor macroinvertebrate abundance and diversity of equal or greater value when compared to downstream perennial reaches (Alvarez et al. 2001). This study showed no clear distinction in total macroinvertebrate richness, abundance and biomass, and abundance and biomass of individual functional feeding groups, on decay woody debris.

Studies comparing permanent and temporary reaches through random sampling with kick nets (Halwas and Church 2005) found that the majority of taxonomic groups were abundant in perennial rather than ephemeral or intermittent streams. Other studies (Feminella 1996) have found taxa to be similar between reaches, similar to the present study.

Decaying leaves in streams draining forested watersheds are typically characterized by high macroinvertebrate densities, particularly as shredder and gathering-collector functional groups (Webster and Benfield 1986). Wood substrates, however, may maintain lower densities, because few macroinvertebrates consume wood directly. Whereas both wood and leaves first require microbial activity to improve the palatability of each organic carbon resource prior to transfer to higher trophic levels (Webster and Benfield 1986, Tank and Winterbourn 1996, Tank et al. 1998), the former is more resistant to ecosystem-level processing (Tank and Winterbourn 1996, Gulis et al. 2004). Hofer and Richardson (2007) compared macroinvertebrate colonization on plastic leaves and several species of wood and leaves, finding that there was no significant difference in colonization of wood versus plastic leaves or between various species of wood,

suggesting that macroinvertebrates may colonize wood for physical features (i.e., habitat) initially, or when they have developed surface biofilm and fungal colonization. Anderson et al. (1978) and Drury and Kelso (2000) showed similar macroinvertebrate colonization patterns, specifically that wood supported higher richness but low mean abundance values.

The greatest proportion of macroinvertebrates colonizing wood bundles in both reach types were gathering-collector Chironomidae. Overall, gathering-collectors (all) comprised 66% (temporary) and 59% (perennial) of the total number of taxa found on the wood bundles while Chironomidae (minus Tanypodinae), in particular, constituted 45% (temporary) and 36% (perennial). Anderson et al. (1978) and Magoulick (1998) similarly found high chironomid densities colonizing decaying woody debris in headwater streams. Several other taxa, namely Oligochaete worms, Ephemeroptera (*Ameletus* and *Ephemerella*), and Plecoptera (*Amphinemura*, *Isoperla* and *Peltoperla arcuata*), were also found in relatively high abundance and biomass numbers on wood bundles. Anderson et al. (1978) also reported that *Ameletus*, *Ephemerella*, and *Yoraperla* (reported as *Peltoperla*) were common colonizers of woody debris. Johnson and Kennedy (2003) reported highest invertebrate densities on newly submerged wood, comparable to this study with a trend of initial high invertebrate densities that gradually decreased over the time of the study.

Gathering-collectors and shredders exhibited marked declines in both abundance and density with increasing instream colonization time. Magoulick (1988), O'Connor (1991), and Kaller and Kelso (2006) similarly have shown the same trend for taxa densities stabilizing after a few weeks and then decreasing over time on wood substrata.

In contrast, Tank and Winterbourn (1996) have reported that mean densities of invertebrates colonizing wood increased over time and Wooster and DeBano (2006) found high scraper and shredder densities on woody debris.

CONCLUSION

Environmental gradients have been shown to have affect detritus processing rates and macroinvertebrate colonization patterns (Graca et al. 2001). This study, however, showed little difference in either wood breakdown or macroinvertebrate abundance and diversity between perennial and temporary reaches. Wood is a resilient organic matter resource for forested, headwater stream foodwebs (Tank and Webster 1998). The importance of this food resource can be easily overlooked due to the long time commitment required to fully assess processing dynamics and few studies have dedicated long term (> 5 yrs) research on this topic. The slow breakdown rates of wood compared to other substrata may require a longer study to get a better understanding of breakdown processes and macroinvertebrate community structure.

TABLES AND FIGURES

Table 1. Summary of physical characteristics of the seven study subwatersheds in the Clemons Fork watershed. Adapted from Cherry (2006).

Tributary	Drainage area (ha)	Drainage density (m/m ²)	Elevational range (m)
Little Millseat	77.9	0.0038	304–451
Shelly Rock Fork South	34.5	0.0032	304–426
Shelly Rock Fork West	69.0	0.0045	304–426
Booker Fork	59.6	0.0041	304–451
Wet Fork	108.7	0.0036	316–451
Goff Hollow	34.3	0.0043	316–451
Falling Rock Branch	92.3	0.0040	304–445

Table 2. GPS for each study reach in the Clemons Fork watershed. T = temporary, P = perennial.

Tributary	Reach	Latitude	Longitude
Little Millseat	T	N 37 28.673'	W 83 10.007'
	P	N 37 28.445'	W 83 09.218'
Shelly Rock Fork South	T	N 37 28.816'	W 83 09.583'
	P	N 37 28.911'	W 83 09.188'
Shelly Rock Fork West	T	N 37 28.993'	W 83 09.737'
	P	N 37 29.010'	W 83 09.262'
Bookers Fork	T	N 37 29.223'	W 83 08.445'
	P	N 37 28.809'	W 83 08.418'
Wet Fork	T	N 37 29.760'	W 83 07.246'
	P	N 37 29.160'	W 83 07.876'
Goff Hollow	T	N 37 28.925'	W 83 07.168'
	P	N 37 28.946'	W 83 07.556'
Falling Rock	T	N 37 28.403'	W 83 07.694'
	P	N 37 28.509'	W 83 08.199'

Table 3. Mean in-stream chemical parameters within the Clemons Fork watershed during 2008. T = temporary, P = perennial. n.a. = data not obtained.

Tributary	Reach	Parameter				
		pH (s.u.)	Cond ($\mu\text{s/m}$)	Alk (mg/L)	TOC (mg/L)	DOC (mg/L)
Little Millseat	T	6.24	42.5	23.8	4.5	4.4
	P	6.36	49.7	41.8	3.1	2.8
Shelly Rock Fork South	T	6.18	44.3	24.0	3.5	3.2
	P	6.37	46.8	30.4	3.8	3.4
Shelly Rock Fork West	T	6.11	41.0	15.9	3.0	2.5
	P	6.27	50.7	22.7	3.8	3.2
Booker Fork	T	6.44	32.8	15.3	n.a.	n.a.
	P	6.35	45.6	34.6	3.5	3.2
Wet Fork	T	6.49	61.7	46.4	7.1	5.7
	P	6.44	51.2	32.3	4.0	3.3
Goff Hollow	T	6.16	40.6	18.2	5.2	3.7
	P	6.03	42.4	18.4	2.9	2.4
Falling Rock Branch	T	6.23	41.8	18.5	2.7	2.5
	P	6.35	47.2	34.1	2.7	2.5

Table 4. Comparison of woody debris ash-free dry mass loss rates ($-k$) between temporary and perennial study reaches in the Clemons Fork watershed during 2008–2009. n.a. = not enough data collected. All mass loss models were significant ($p < 0.05$).

Tributary	Temporary		Perennial	
	$-k$	r^2	$-k$	r^2
Little Millseat	n.a.	n.a.	0.14	0.77
Shelly Rock Fork South	0.10	0.77	0.16	0.92
Shelly Rock Fork West	0.10	0.75	0.15	0.76
Booker Fork	0.17	0.87	0.19	0.54
Wet Fork	0.15	0.81	0.16	0.84
Goff Hollow	0.15	0.51	0.19	0.87
Falling Rock Branch	0.13	0.80	0.13	0.90

Table 5. Overall mean individual macroinvertebrate taxa abundance (no.) and biomass (mg) values per wood bundle by stream reach type and functional feeding group (FFG). SHR = shredders, SCR = scrapers, FC = filtering-collectors, CG = collector-gathers, PR = predators.

FFG	Taxa			Temporary		Perennial	
				no.	mg	no.	mg
SHR	Plecoptera	Capniidae	<i>Allocapnia sp.</i>	0.28	0.02	0.21	0.02
		Leuctridae	<i>Leuctra sp.</i>	0.06	0.01	0.01	< 0.01
		Nemouridae	<i>Amphinemura sp.</i>	0.54	0.10	0.46	0.08
		Taeniopterygidae	Taeniopteryginae (immature)	0.18	0.14	0.14	0.11
		Peltoperlidae	<i>Peltoperla arcuata</i>	0.32	0.09	0.23	0.11
	Trichoptera	Lepidostomatidae	<i>Lepidostoma sp.</i>	0.12	0.38	0.13	0.39
		Limnephilidae	<i>Pycnopsyche sp.</i>	0.02	0.01	0.01	0.05
	Coleoptera	Dryopidae	<i>Helichus sp.</i>	0.01	0.02	0.02	0.04
	Diptera	Tipulidae	<i>Tipula abdominalis</i>	0.01	0.01	0.02	0.01
SCR	Trichoptera	Glossosomatidae	<i>Agapetus sp.</i>	0.03	0.04	< 0.01	0.05
		Molannidae	<i>Molanna sp.</i>	0	0	< 0.01	< 0.01
	Coleoptera	Psephenidae	<i>Ectopria nervosa</i>	0.01	0.01	< 0.01	0.01
FC	Bivalvia	Sphaeriidae	<i>Sphaerium sp.</i>	0.09	0.01	0.22	0.03
	Trichoptera	Hydropsychidae	<i>Diplectrona modesta</i>	0	0	0.01	0.01
		Philopotamidae	<i>Wormaldia moestus</i>	0	0	< 0.01	0.01
	Diptera	Simuliidae	<i>Prosimulium sp.</i>	0.02	< 0.01	0.03	< 0.01
CG	Oligochaeta			0.51	0.75	0.27	0.48
	Collembola	Poduridae		0.10	< 0.01	0.08	< 0.01
	Ephemeroptera	Ameletidae	<i>Ameletus sp.</i>	0.52	0.28	0.54	0.26
		Baetidae	<i>Centropilum sp.</i>	0	0	0.02	0.01
		Ephemerellidae	<i>Ephemerella sp.</i>	0.42	0.22	0.44	0.22
			<i>Eurylophella sp.</i>	0.05	0.14	0.08	0.19
			Leptophlebiidae	<i>Habrophlebia vibrans</i>	0.10	0.04	0.01
	<i>Paraleptophlebia sp.</i>	0.05	0.03	0.04	0.02		

	Coleoptera	Elmidae	<i>Stenelmis</i> sp.	0.12	0.03	0.11	0.03
			<i>Macronychus glabratus</i>	0.02	0.01	0	0
	Diptera	Chironomidae	non-Tanypodinae	4.29	0.06	2.63	0.04
		Stratiomyiidae	<i>Nemotelus</i> sp.	0.01	< 0.01	0.01	< 0.01
PR	Plecoptera	Chloroperlidae	<i>Sweltsa</i> sp.	0.01	0.01	0.01	< 0.01
		Perlodidae	<i>Clioperla clio</i>	0.07	< 0.01	0.05	< 0.01
			<i>Diploperla robusta</i>	0.05	< 0.01	0.09	< 0.01
			<i>Isoperla</i> spp.	0.36	0.02	0.33	0.02
			<i>Remenus bilobatus</i>	0.08	0.01	0.03	0.02
			<i>Yugus kirchneri</i>	0.04	< 0.01	< 0.01	0.01
			Perlodidae (immature)	0.22	0.00	0.28	< 0.01
	Hemiptera			0	0	0.01	< 0.01
	Megaloptera	Corydalidae	<i>Nigronia</i> sp.	0.03	0.03	0.02	0.01
	Trichoptera	Rhyacophilidae	<i>Rhyacophila</i> sp.	0.05	0.08	0.04	0.09
	Coleoptera	Dytiscidae		< 0.01	< 0.01	0.01	0.03
	Diptera	Ceratopogonidae	<i>Ceratopogon</i> sp.	0.15	0.02	0.08	0.01
			<i>Bezzia</i> sp.	0.12	0.02	0.12	0.02
		Chironomidae	Tanypodinae	0.33	0.01	0.26	0.01
		Dolichopodidae	<i>Rhaphium</i> sp.	< 0.01	< 0.01	0.01	< 0.01
		Empididae	<i>Clinocera</i> sp.	< 0.01	< 0.01	0.01	< 0.01
		Tabanidae	<i>Chrysops</i> sp.	0.01	< 0.01	< 0.01	< 0.01
			<i>Tabanus</i> sp.	0.01	< 0.01	0.02	0.01
		Tipulidae	<i>Hexatoma</i> sp.	0.01	0.01	0.01	< 0.01
			<i>Limnophila</i> sp.	0.03	0.18	0.02	0.01
			<i>Pilaria</i> sp.	0.03	< 0.01	0.07	0.02

Table 6. Overall mean individual macroinvertebrate taxa abundance (no.) and biomass (mg) values per ash-free dry mass wood bundle by stream reach type and functional feeding group (FFG). SHR = shredders, SCR = scrapers, FC = filtering-collectors, CG = collector-gathers, PR = predators.

FFG	Taxa			Temporary		Perennial	
				no.	mg	no.	mg
SHR	Plecoptera	Capniidae	<i>Allocapnia sp.</i>	0.09	0.01	0.07	0.01
		Leuctridae	<i>Leuctra sp.</i>	0.02	< 0.01	< 0.01	< 0.01
		Nemouridae	<i>Amphinemura sp.</i>	0.18	0.03	0.16	0.03
		Taeniopterygidae	Taeniopteryginae (immature)	0.06	0.05	0.05	0.04
		Peltoperlidae	<i>Peltoperla arcuata</i>	0.11	0.03	0.08	0.04
	Trichoptera	Lepidostomatidae	<i>Lepidostoma sp.</i>	0.04	0.13	0.04	0.13
		Limnephilidae	<i>Pycnopsyche sp.</i>	0.01	< 0.01	< 0.01	0.02
	Coleoptera	Dryopidae	<i>Helichus</i>	< 0.01	0.01	0.01	0.01
	Diptera	Tipulidae	<i>Tipula abdominalis</i>	< 0.01	< 0.01	0.01	0.01
SCR	Trichoptera	Glossosomatidae	<i>Agapetus sp.</i>	0.01	0.01	< 0.01	0.02
		Molannidae	<i>Molanna sp.</i>	0	0	< 0.01	< 0.01
	Coleoptera	Psephenidae	<i>Ectopria nervosa</i>	< 0.01	< 0.01	< 0.01	< 0.01
FC	Bivalvia	Sphaeriidae		0.03	< 0.01	0.08	0.01
	Trichoptera	Hydropsychidae	<i>Diplectrona modesta</i>	0	0	< 0.01	< 0.01
		Philopotamidae	<i>Wormaldia moestus</i>	0	0	< 0.01	0.01
	Diptera	Simuliidae	<i>Prosimulium sp.</i>	0.01	< 0.01	0.01	< 0.01
CG	Oligochaeta			0.17	0.25	0.09	0.16
	Collembola	Poduridae		0.03	< 0.01	0.03	< 0.01
	Ephemeroptera	Ameletidae		0.17	0.09	0.18	0.09
		Baetidae	<i>Centroptilum sp.</i>	0	0	0.01	< 0.01
		Ephemerellidae	<i>Ephemerella sp.</i>	0.14	0.07	0.15	0.07
			<i>Eurylophella sp.</i>	0.02	0.05	0.03	0.06
		Leptophlebiidae	<i>Habrophlebia vibrans</i>	0.03	0.01	< 0.01	0.01
<i>Paraleptophlebia sp.</i>	0.02	0.01	0.01	0.01			

	Coleoptera	Elmidae	<i>Macronychus</i> sp.	0.01	< 0.01	0	0
			<i>Stenelmis</i> sp.	0.04	0.01	0.04	0.01
	Diptera	Chironomidae	non-Tanypodinae	1.41	0.02	0.90	0.01
		Stratiomyiidae	<i>Nemotelus</i> sp.	0.01	, <	< 0.01	< 0.01
PR	Plecoptera	Chloroperlidae	<i>Sweltsa</i> sp.	0.01	< 0.01	< 0.01	< 0.01
		Perlodidae	<i>Clioperla clio</i>	0.02	< 0.01	0.02	< 0.01
			<i>Diploperla robusta</i>	0.02	< 0.01	0.03	< 0.01
			<i>Isoperla</i> spp.	0.12	0.01	0.11	0.01
			<i>Remenus bilobatus</i>	0.03	< 0.01	0.01	0.01
			<i>Yugus kirchneri</i>	0.01	< 0.01	0	0
			Perlodidae (immature)	0.07	< 0.01	0.10	< 0.01
	Hemiptera			0	0	< 0.01	< 0.01
	Megaloptera	Corydalidae	<i>Nigronia</i> sp.	0.01	0.01	0.01	0.01
	Trichoptera	Rhyacophilidae	<i>Rhyacophila</i> sp.	0.02	0.03	0.01	0.03
	Coleoptera	Dytiscidae		< 0.01	< 0.01	< 0.01	0.01
	Diptera	Ceratopogonidae	<i>Bezzia</i> sp.	0.04	0.01	0.04	0.01
			<i>Ceratopogon</i> sp.	0.05	0.01	0.03	< 0.01
		Chironomidae	Tanypodinae	0.11	0.01	0.09	< 0.01
		Dolichopodidae	<i>Rhaphium</i> sp.	< 0.01	< 0.01	< 0.01	< 0.01
		Empididae	<i>Clinocera</i> sp.	< 0.01	< 0.01	< 0.01	< 0.01
		Tabanidae	<i>Chrysops</i> sp.	0.01	< 0.01	< 0.01	< 0.01
			<i>Tabanus</i> sp.	< 0.01	< 0.01	0.01	< 0.01
		Tipulidae	<i>Hexatoma</i> sp.	< 0.01	< 0.01	< 0.01	< 0.01
			<i>Limnophila</i> sp.	0.01	0.06	< 0.01	< 0.01
			<i>Pilaria</i> sp.	0.01	< 0.01	0.02	0.01

Table 7. Overall mean functional feeding group abundance (no.) and biomass (mg) per wood bundle (WB) by individual stream reach. T = temporary, P = perennial, SHR = shredders, SCR = scrapers, FC = filtering-collectors, CG = collector-gathers, PR = predators.

Reach	Tributary	no./WB					mg/WB				
		SHR	SCR	FC	GC	PR	SHR	SCR	FC	GC	PR
T	Little Millseat	3.7	0	0.1	7.0	1.9	4.1	0	< 0.1	1.1	0.5
	Shelly Rock Fork South	1.2	< 0.1	0.1	6.5	1.8	0.3	0.1	< 0.1	2.8	0.3
	Shelly Rock Fork West	1.6	< 0.1	0.2	6.2	3.5	0.9	< 0.1	< 0.1	1.7	0.2
	Booker Fork	2.3	0.5	0	7.2	1.5	2	0.2	0	1.4	0.1
	Wet Fork	1.9	0	0.4	8.3	1.9	1.4	0	0.1	1.6	0.5
	Goff Hollow	0.4	0	< 0.1	4.1	0.4	0.3	0	0	1.3	< 0.1
	Falling Rock Branch	1.3	0	0.1	6.1	1.1	0.9	0	0	1.7	0.2
P	Little Millseat	0.8	0	0.5	3.4	2.8	0.5	0	0.1	0.9	0.3
	Shelly Rock Fork South	1.3	0	0.2	5.2	0.9	0.7	0	< 0.1	1.2	0.2
	Shelly Rock Fork West	1.3	0	< 0.1	3.5	1.5	0.6	0	0	1.6	0.2
	Booker Fork	1.5	< 0.1	0	4.6	1.1	1.5	< 0.1	0	0.7	0.1
	Wet Fork	1.2	0	1.3	4.1	1.2	0.8	0	0.1	2.0	0.1
	Goff Hollow	1.1	0	0.1	4.5	1.0	0.4	0	0	1.1	0.1
	Falling Rock Branch	1.5	< 0.1	0.1	4.8	1.6	1.1	< 0.1	0.1	1.8	0.9

Table 8. Overall mean functional feeding group abundance (no.) and biomass (mg) per ash free dry mass (AFDM) wood bundle by individual stream reach. T = temporary, P = perennial, SHR = shredders, SCR = scrapers, FC = filtering-collectors, CG = collector-gathers, PR = predators.

Reach	Tributary	no./AFDM					mg/AFDM				
		SHR	SCR	FC	GC	PR	SHR	SCR	FC	GC	PR
T	Little Millseat	1.3	0	< 0.1	2.4	0.7	1.2	0	< 0.1	0.3	0.1
	Shelly Rock Fork South	0.4	< 0.1	< 0.1	2.2	0.6	0.1	< 0.1	< 0.1	0.9	0.1
	Shelly Rock Fork West	0.5	< 0.1	0.1	2.0	1.1	0.3	< 0.1	< 0.1	0.6	0.1
	Booker Fork	0.8	0.2	0	2.5	0.5	0.7	0.1	0	0.5	< 0.1
	Wet Fork	0.6	0	0.1	2.4	0.6	0.5	0	< 0.1	0.5	0.2
	Goff Hollow	0.1	0	< 0.1	1.4	0.1	0.1	0	< 0.1	0.4	< 0.1
	Falling Rock Branch	0.5	0	< 0.1	2.0	0.4	0.3	0	< 0.1	0.6	< 0.1
P	Little Millseat	0.3	0	0.2	1.2	1.0	0.2	0	< 0.1	0.3	0.1
	Shelly Rock Fork South	0.4	0	0.1	1.2	0.3	0.2	0	< 0.1	0.4	0.1
	Shelly Rock Fork West	0.5	0	< 0.1	1.3	0.5	0.2	0	< 0.1	0.6	0.1
	Booker Fork	0.5	< 0.1	0	1.6	0.4	0.5	< 0.1	0	0.2	< 0.1
	Wet Fork	0.4	0	0.4	1.3	0.4	0.2	0	< 0.1	0.6	< 0.1
	Goff Hollow	0.4	0	< 0.1	1.5	0.3	0.1	0	< 0.1	0.4	< 0.1
	Falling Rock Branch	0.5	< 0.1	< 0.1	1.6	0.5	0.4	0	0.1	0.6	0.3

Table 9. Overall relative percentage values for abundance (no.) and biomass (mg) by per wood bundle (WB) for each reach type and functional feeding group (FFG). SHR = shredders, SCR = scrapers, FC = filtering-collectors, CG = collector-gathers, PR = predators.

FFG	Temporary		Perennial	
	no./WB	mg/WB	no./WB	mg/WB
SHR	16.1 %	37.2%	16.8 %	32.9%
SCR	0.4 %	1.2%	0.2 %	0.1%
FC	1.2 %	0.5%	3.7 %	2.1%
GC	65.5 %	54.1%	59.3 %	53.4%
PR	16.8%	7.0%	20.1 %	11.5%

Table 10. Summary of paired t-tests comparing macroinvertebrate richness, abundance and biomass values per wood bundle between the temporary and perennial reaches. SHR = shredders, SCR = scrapers, FC = filtering-collectors, GC = gathering-collectors, PR = predators, * p = 0.05.

Variable	Temporary		Perennial		t-statistic
	Mean	1 S.E.	Mean	1 S.E.	
Total taxa richness	3.03	0.13	2.88	0.10	0.58
Total abundance	8.38	0.65	7.11	0.39	0.97
Total biomass	3.06	0.17	2.46	0.14	1.58
SHR abundance	1.40	0.13	1.23	0.08	0.56
SHR biomass	1.01	0.07	0.78	0.06	1.43
SCR abundance	0.07	0.01	0.01	< 0.01	1.05
SCR biomass	0.03	0.01	0.01	< 0.01	0.81
FC abundance	0.12	0.01	0.27	0.02	1.53
FC biomass	0.01	< 0.01	0.05	< 0.01	*2.52
CG abundance	5.59	0.42	4.34	0.25	1.16
CG biomass	1.58	0.10	1.33	0.08	0.67
PR abundance	1.49	0.11	1.35	0.08	0.66
PR biomass	0.20	0.01	0.27	0.01	1.19

Table 11. Summary of Student t-tests comparing macroinvertebrate abundance and biomass values per wood bundle between first month and last month of sampling between reaches. SHR = shredders, SCR = scrapers, FC = filtering-collectors, GC = gathering-collectors, PR = predators, * p = 0.05, ** = t-tests not performed due to zero data for both months

Variable	Month 1		Month 13		t-statistic
	Mean	1 S.E.	Mean	1 S.E.	
Total abundance	9.2	1.42	3.0	0.72	*3.3
Total biomass	3.5	0.68	1.8	0.46	*1.9
SHR abundance	1.9	0.39	0.5	0.17	*3.0
SHR biomass	1.1	0.41	0.5	0.20	1.5
SCR abundance	0	0	0	0	**
SCR biomass	0	0	0	0	**
FC abundance	0.1	0.09	0.1	0.09	0.1
FC biomass	0.1	0.05	< 0.1	0.01	1.3
CG abundance	5.9	0.95	1.5	0.35	*4.0
CG biomass	1.7	0.42	1.0	0.33	1.3
PR abundance	1.4	0.44	1.0	0.42	0.6
PR biomass	0.3	0.16	0.4	0.23	0.8

Table 12. Comparison of woody debris breakdown rates ($-k$) by species and wood piece size between published studies and the current study.

Reference	Species	$-k$ (year ⁻¹)	Size of wood pieces
This Study	<i>Acer rubrum</i>	0.10 – 0.19	1.3 * 1.3 * 7.7 cm
Diez <i>et al.</i> (2002)	<i>Alnus glutinosa</i> (branch)	0.06 – 0.17	3 cm
Diez <i>et al.</i> (2002)	<i>Alnus glutinosa</i>	0.12 – 0.27	10 * 2.5 * 2.5 cm
Diez <i>et al.</i> (2002)	<i>Quercus robur</i>	0.07 – 0.18	3 cm
Diez <i>et al.</i> (2002)	<i>Pinus insignis</i>	0.02 – 0.07	3 cm
Diez <i>et al.</i> (2002)	<i>Eucalyptus globulus</i>	0.08 – 0.15	3 cm
Fisher Wold and Hershey (1999)	<i>Betula sp.</i>	0.13 – 0.22	0.6 cm
Fisher Wold and Hershey (1999)	<i>Acer saccharum.</i>	0.13 – 0.14	0.6 cm
Golladay and Webster (1988)	<i>Quercus rubra</i>	0.11 – 0.28	1 – 3 cm diameter
Shearer and Von Bodman (1983)	<i>Acer saccharinum</i>	0.16	20 * 1.6cm ^b
Spanhoff and Meyer (2004)	<i>Alnus glutinosa</i> (branch)	0.07 – 0.09	25.1 * 5 cm
Spanhoff and Meyer (2004)	<i>Pinus sylvestris</i> (branch)	0.07	28.6 * 4.6 cm
Tank <i>et al.</i> (1988)	<i>Liriodendron tulipifera</i>	1.71 – 3.10	15 * 2.5 * 0.1 cm
Tank and Webster (1988)	<i>Quercus rubra</i>	0.53	15 * 2.5 * 0.1 cm
Webster <i>et al.</i> (1999)	<i>Liriodendron tulipifera</i>	0.15 – 0.23	1.3 – 3.6 cm
Webster <i>et al.</i> (1999)	<i>Pinus strobus</i>	0.06 – 0.38	1.3 – 3.6 cm
Webster <i>et al.</i> (1999)	<i>Quercus rubra</i>	0.11 – 0.16	1.3 – 3.6 cm

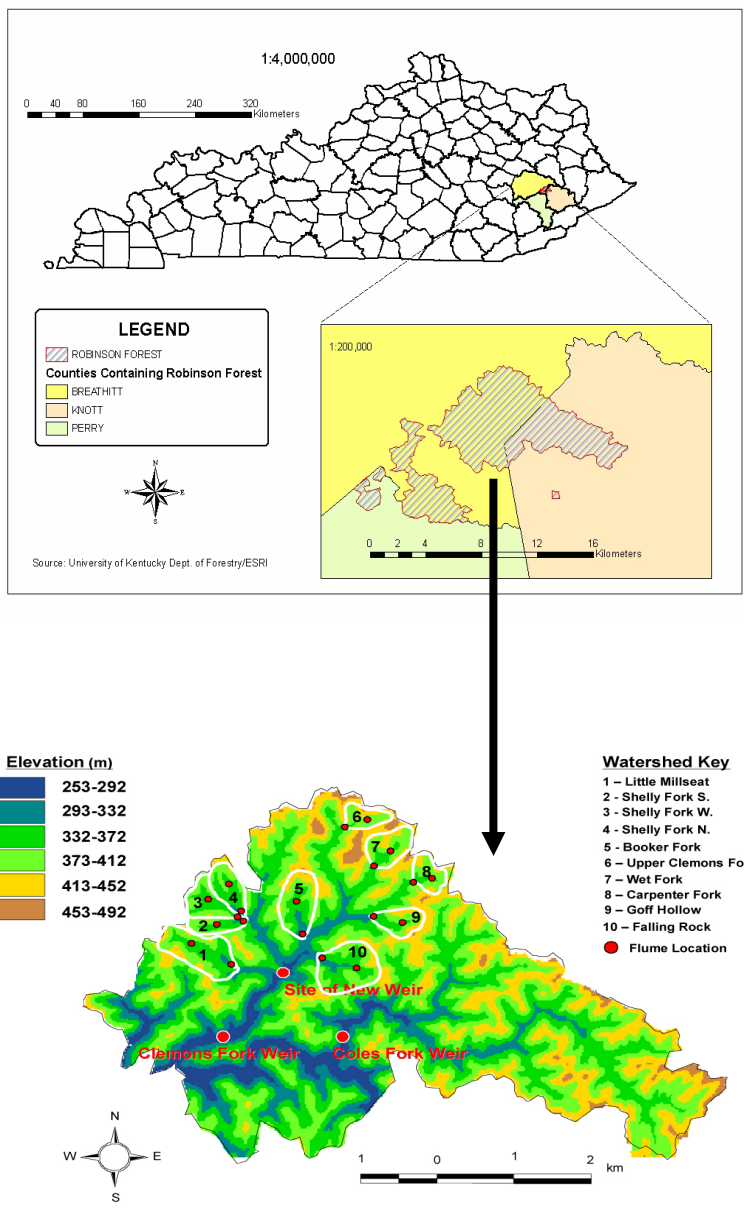


Figure 1. Location of Robinson Forest in eastern Kentucky, U.S.A. and specific location of the seven study streams. Adapted from Cherry (2006). Shelley Fork N. (4), Upper Clemons Fork (6), and Carpenter Fork (8) were not included in this study.

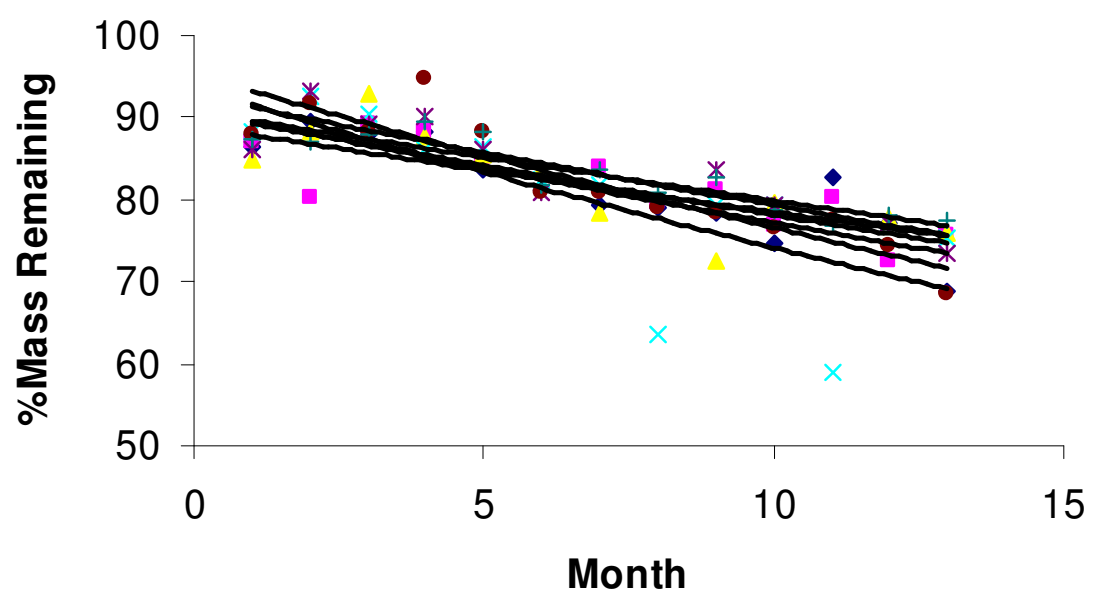


Fig. 2A

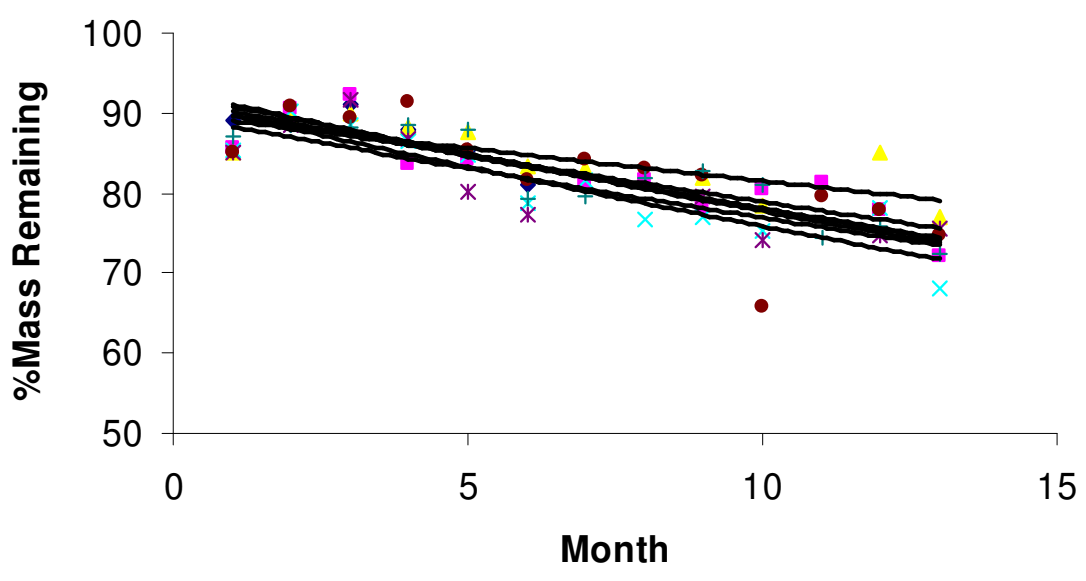


Fig. 2B
Figure 2. Comparison of percent AFDM remaining of wood bundles between temporary and perennial stream reaches. A = perennial, B = temporary, and symbols refer to individual stream reaches.

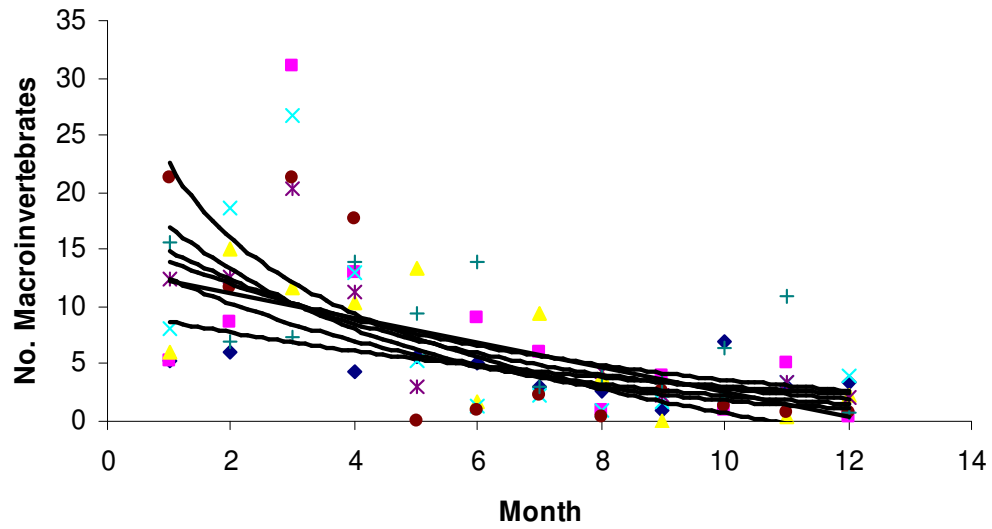


Fig. 3a.

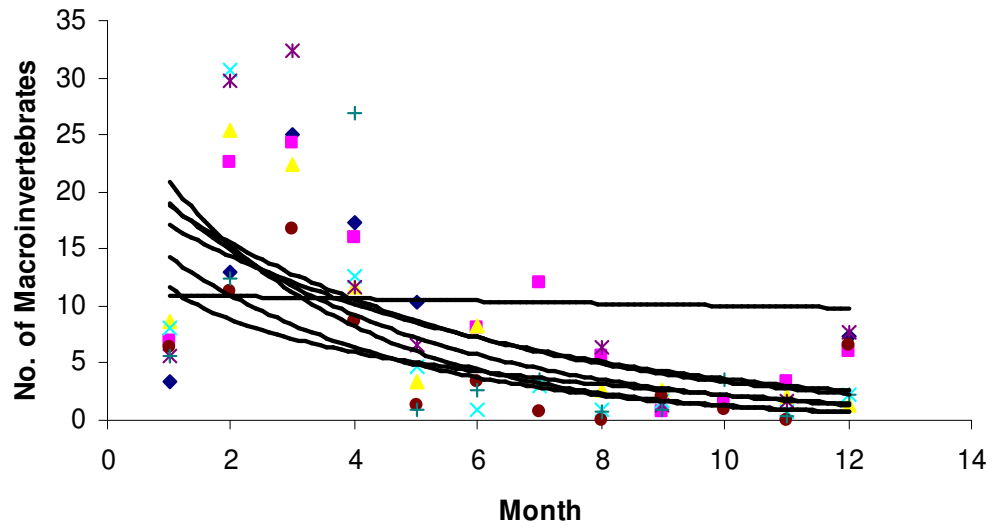


Fig. 3b.

Figure 3. Comparison of total macroinvertebrate abundance per wood bundle between temporary and perennial stream reaches. A = perennial, B = temporary, and symbols refer to individual stream reaches.

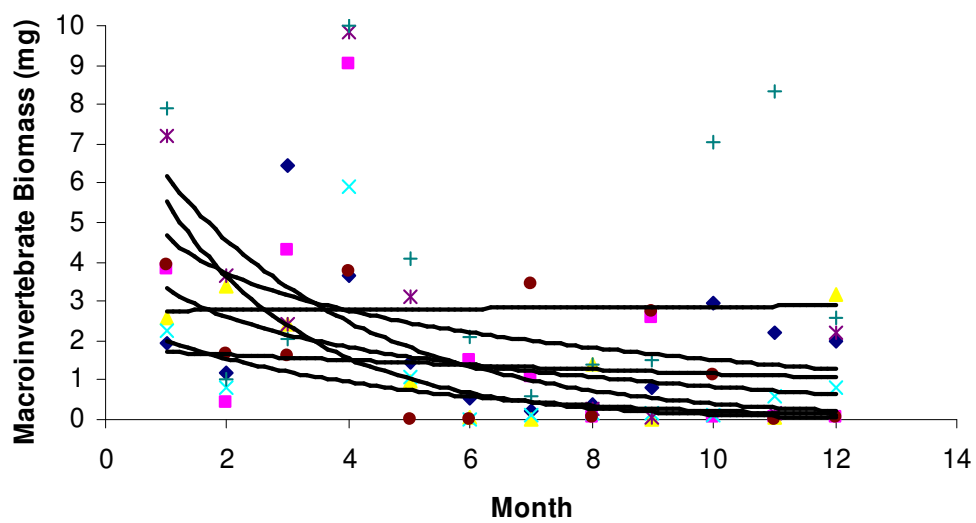


Fig. 4a.

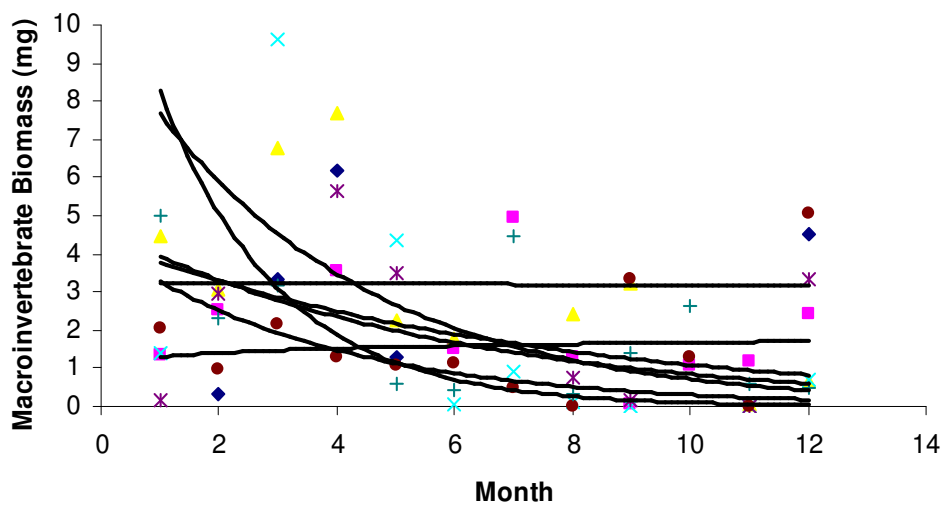


Fig. 4b.

Figure 4. Comparison of total macroinvertebrate biomass per wood bundle between temporary and perennial stream reaches. A = perennial, B = temporary, and symbols refer to individual stream reaches.

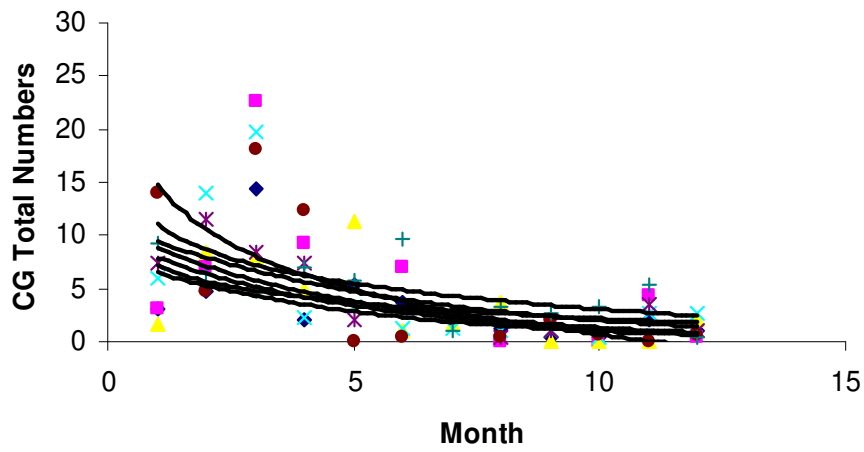


Fig. 5a.

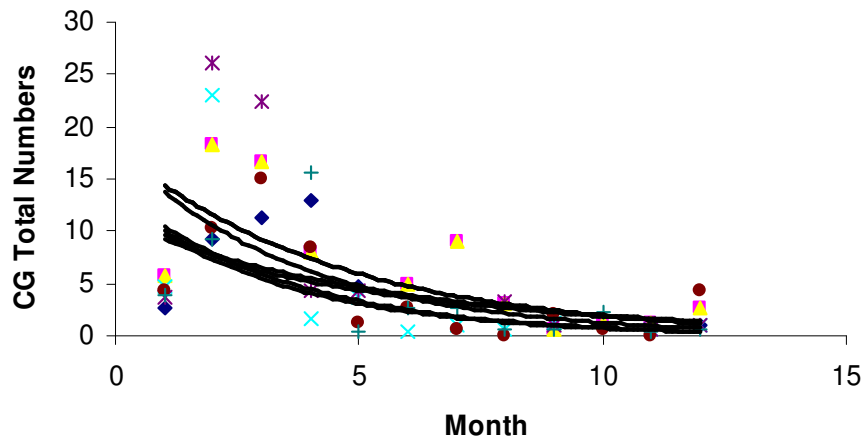


Fig. 5b.

Figure 5. Comparison of gathering-collector abundance per wood bundle between temporary and perennial stream reaches. A = perennial, B = temporary, and symbols refer to individual stream reaches.

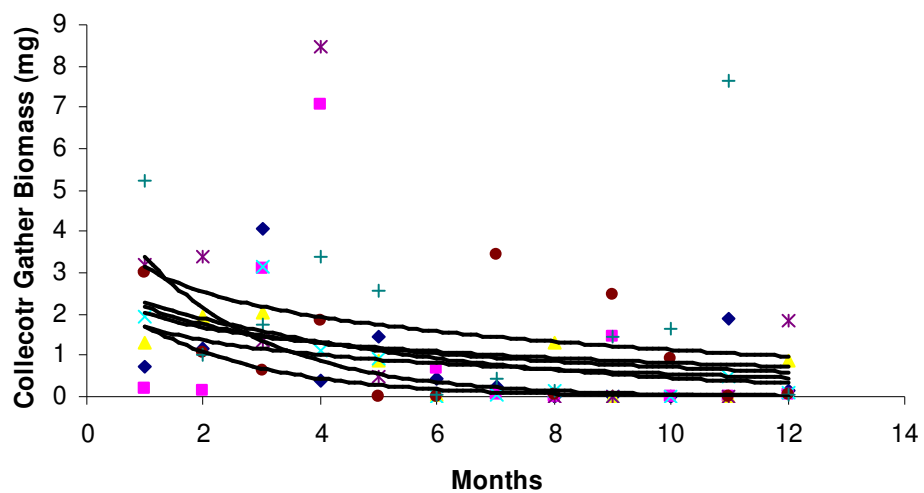


Fig. 6a.

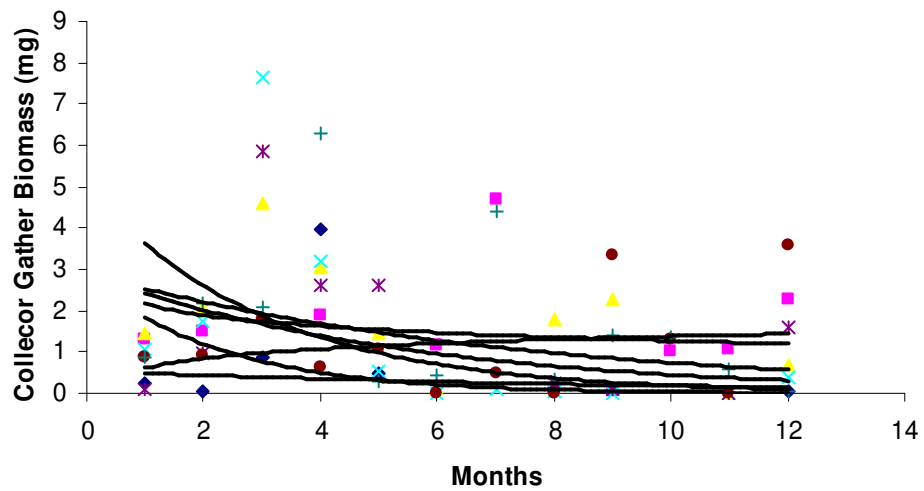


Fig. 6b.

Figure 6. Comparison of gathering-collector biomass per wood bundle between temporary and perennial stream reaches. A = perennial, B = temporary, and symbols refer to individual stream reaches.

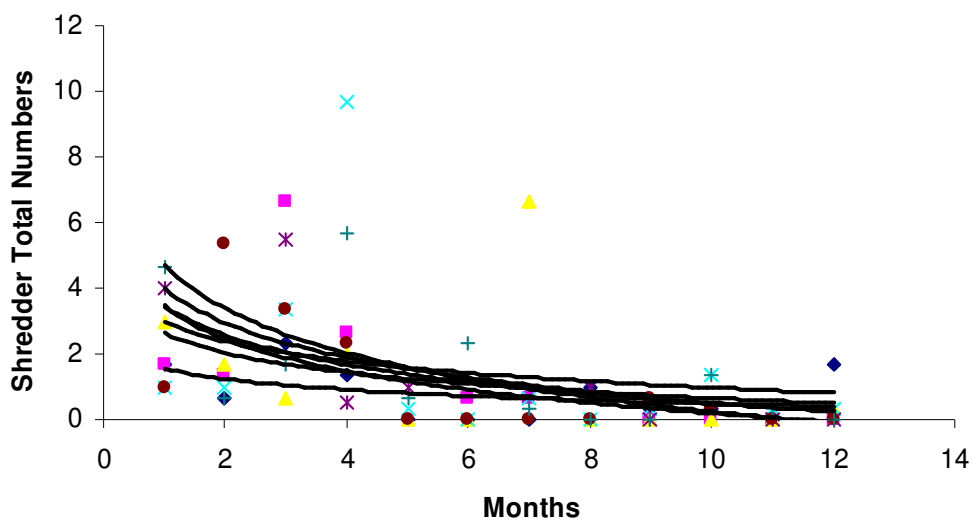


Fig. 7a.

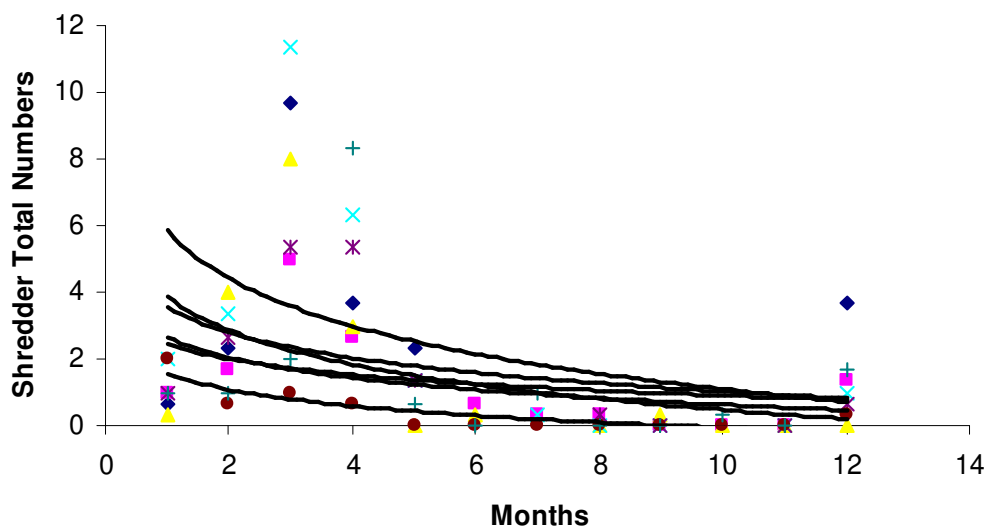


Fig. 7b.

Figure 7. Comparison of shredder abundance per wood bundle between temporary and perennial stream reaches. A = perennial, B = temporary, and symbols refer to individual stream reaches.

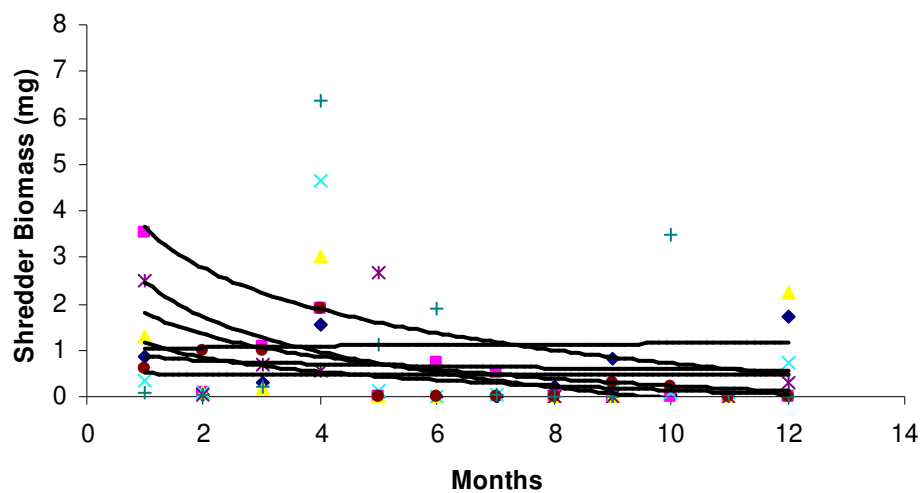


Fig. 7a.

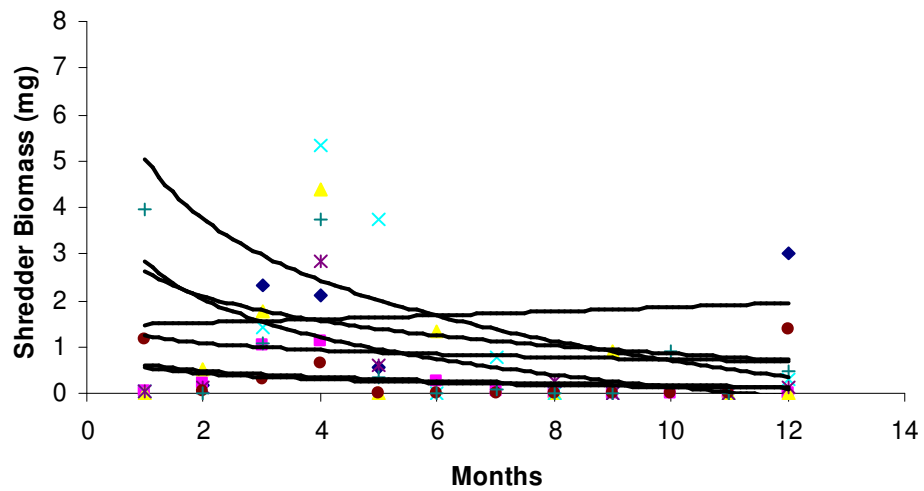


Fig. 7b.

Figure 8. Comparison of shredder biomass per wood bundle between temporary and perennial stream reaches. A = perennial, B = temporary, and symbols refer to individual stream reaches.

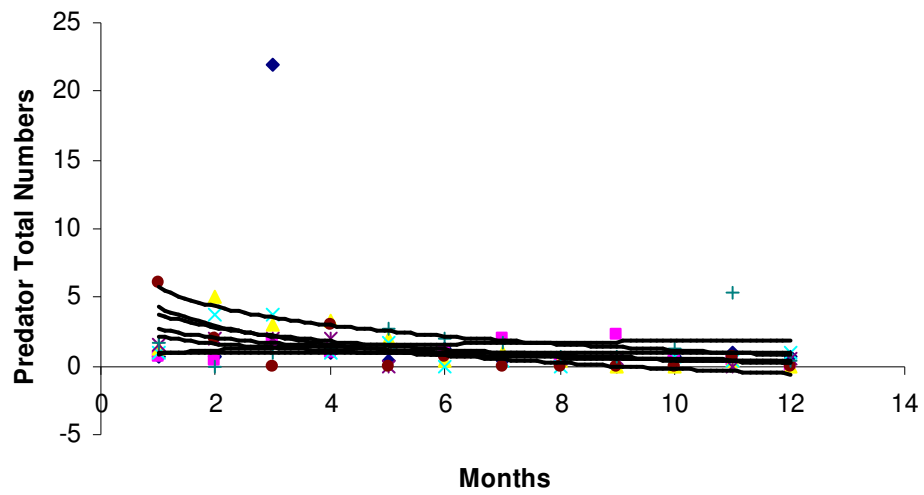


Fig. 9a.

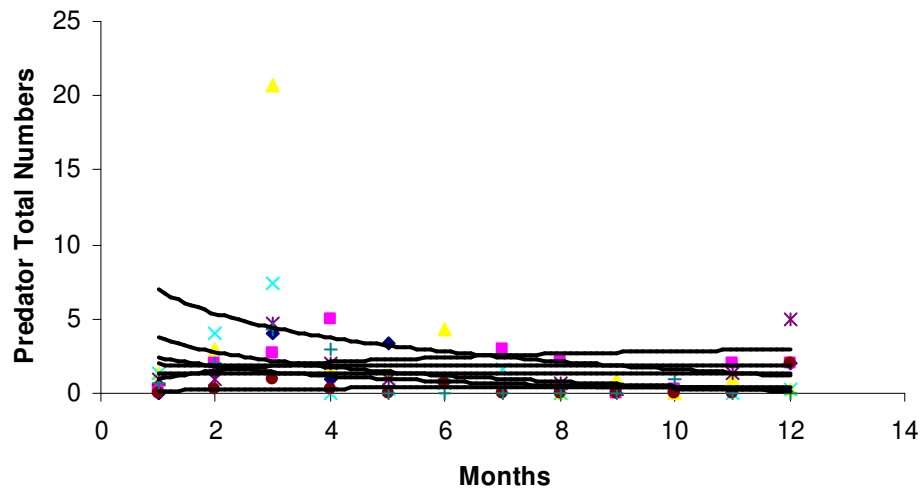


Fig. 9b.

Figure 9. Comparison of predator abundance per wood bundle between temporary and perennial stream reaches. A = perennial, B = temporary, and symbols refer to individual stream reaches.

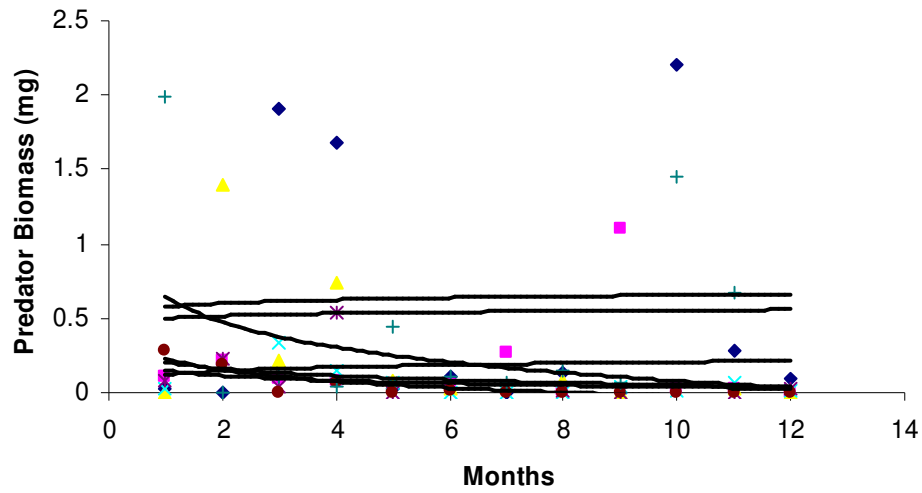


Fig. 10a.

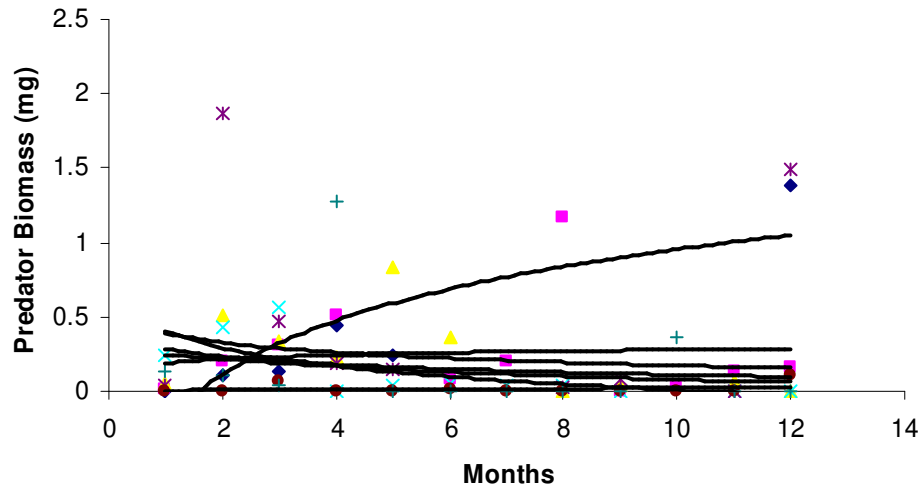


Fig. 10b.

Figure 10. Comparison of predator biomass per wood bundle between temporary and perennial stream reaches. A = perennial, B = temporary, and symbols refer to individual stream reaches.

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