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THE STRUCTURE OF LARVAL ODONATE ASSEMBLAGES IN THE ENOREE RIVER BASIN OF SOUTH CAROLINA

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ABSTRACT – Odonate larvae were collected at 127 sites in the Enoree River and nine of its tributaries in the summers of 1999 and 2000. Mean odonate abundance, species richness, and Simpson's diversity were compared across tributaries and the main channel of the Enoree River with one-way ANOVA. These indices were significantly lower in Brushy Creek, Rocky Creek, and the Upper Enoree than in the other streams (Tukey multiple comparison test, $p < 0.05$). These three streams also differed from the others in species composition (MANOVA $p < 0.0001$), as measured by changes in the relative abundances of the five most abundant species: *Progomphus obscurus*, *Boyeria vinosa*, *Macromia illinoiensis*, *Cordulegaster maculata*, and *Ophiogomphus mainensis*. For example, *O. mainensis* was nearly absent from Brushy, Rocky, and the Upper Enoree, but was a significant component of the assemblages in other streams. *Cordulegaster maculata* was rare in Rocky Creek but dominated the Upper Enoree where other species were less abundant. Brushy, Rocky, and the Upper Enoree are areas of either rapid residential development or known industrial contamination. The different structure of odonate assemblages in these streams may reflect the impact of these local anthropogenic effects.

INTRODUCTION

Dragonflies and damselflies (order Odonata) are important components of stream communities. Odonates prey upon other stream invertebrates and are consumed by fish and birds, so they are an important trophic link between the micro- and macrofauna (Merritt and Cummins 1996). Also, they exploit a variety of habitats. Corbet (1999) defines four niches that correlate with morphological and behavioral characteristics. *Burrowers* dig in the sediment and often have strong tibial extensions for burrowing or a longer abdomen that acts as a respiratory siphon; *claspers* have an elongate abdomen and cling tightly to surfaces; *hiders* have a flattened abdomen that they often cover with detritus; and *sprawlers* use their long legs to support the body in detritus or aquatic vegetation (Corbet 1999).

Although many odonates are broadly tolerant to most chemical parameters (Roback and Westfall 1967), odonate abundance and diversity is affected by a variety of chemical, physical, and biological

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factors. For instance, low pH, low dissolved oxygen, and solutes such as chloride and nitrite limit the distribution of some species and may change the relative abundance of tolerant and intolerant species (Cannings and Cannings 1987, Carchini and Rota 1985, Corbet 1999, Roback and Westfall 1967, Romero 1988, Watson et al. 1982). Physical factors such as substrate type can influence oviposition site selection, foraging efficiency, and predator avoidance (Corbet 1999). Predation can reduce larval survivorship (Crowder and Cooper 1982, Martin et al. 1991) and change the composition of these assemblages (Morin 1984). The integrity of the terrestrial environment is also critical; logging can reduce odonate diversity in forest streams (Sahlén 1999). Anthropogenic changes to a landscape can affect all three classes of factors through the direct input of toxins, changes in erosion, channelization, and deposition patterns, and indirect effects mediated through trophic webs (Beavan et al. 2001). As such, the abundance and diversity of odonates should reflect the cumulative impact of humans on stream habitats (Clark and Samways 1996, Corbet 1999).

The western piedmont of South Carolina is an ideal place to examine the effect of land use patterns on odonate assemblages. The Enoree River is a primary river basin in this region and drains a variety of habitats. The southern half of the watershed is a mixture of forested and agricultural land and includes parts of Sumter National Forest. The northern third of the watershed is more urbanized, and includes the Greenville-Spartanburg metropolitan area. Over the last 20 years, the human population of the Greenville-Spartanburg metroplex has increased by 50%, the acreage of impervious surfaces has doubled, and the amount of farmland converted to development has increased by 400% (Spartanburg County Planning Commission 2000). In 1995, in the midst of this growth period, 53.7% of this watershed was forested, 25.6% was cultivated/grassland, and 10.0% was urbanized (Lahlou et al. 1995). Since 1995, conversion of agricultural land to residential and corporate complexes has continued unabated in the Greenville-Spartanburg corridor. As such, the urban area has grown larger and the difference in land use patterns between the northern and southern ends of the watershed are more pronounced.

In 1999-2000, the multidisciplinary *River Basins Research Initiative* of Furman University conducted a chemical and biological inventory of the Enoree River and selected tributaries to describe the impact of suburban development on water quality. In this paper, variation in the structure of odonate assemblages among these watersheds is described and related to anthropogenic effects.

METHODS

The Enoree River Basin is an 1193 km^2 sixth-order watershed in the piedmont of South Carolina, USA, with 170 km of perennial streams (Fig. 1). Odonates were sampled at a total of 127 sites in May-July 1999 (63 sites) and May-July 2000 (64 sites) in the Enoree River and nine of its tributaries (Fig. 1).

Sampling sites were selected by locating bridge crossings and streams with road access on USGS topographic maps. When possible, sampling was conducted upstream from bridge crossings to reduce runoff effects. Typically, a reach of 50-100m was sampled, purposefully selecting as many habitats (pool, riffle, run) as possible. At each site, odonates were collected by electrofishing with a Smith-Root$^{@}$ Backpack Electrofisher. Electrofishing provides accurate estimates of population size and diversity (Taylor et al. 2001). Sampling was standardized by electrofishing for a total of 8 minutes at each site. The substrate was kicked vigorously during the shocking period to dislodge organisms. Immobilized invertebrates were collected downstream from the Electrofisher with a seine (1.5m x 3.3m x 3.0mm) and dip nets. Each site was sampled once for animals. All specimens were sorted, counted, and preserved; odonate larvae were preserved in 75% EtOH and identified to species using the taxonomic keys of Huggins and Brigham (1982), Merritt and Cummins (1996), Needham et al. (2000), and Westfall and May (1996).

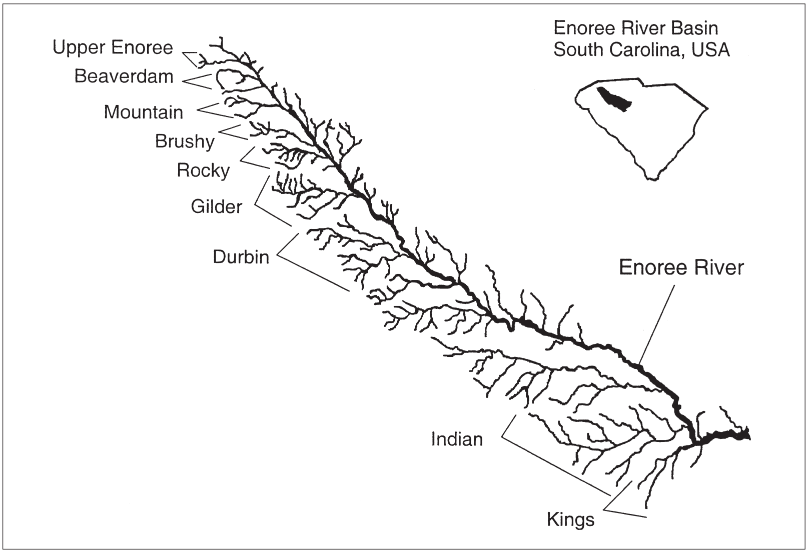

Figure 1. The Enoree River and the nine tributaries sampled in this study, and the location of the Enoree River basin in South Carolina.

The structure of these assemblages was described three ways. First, the total number of odonates, species richness, and Simpson's diversity ($D = 1/\Sigma(p_i^2)$) were computed at each site. Mean values for these variables in the main channel of the Enoree River and the nine tributaries were compared with one-way ANOVA and Tukey's multiple comparison tests (SPSS 1998). Abundance data were transformed before analysis ($\log_{10}(x + 1)$, Sokal and Rohlf 1995).

Abundance, richness, and diversity are useful descriptors, but they fail to describe compositional patterns such as associations among species and differences in relative abundance. Pair-wise Chi-square tests of independence were used to describe patterns of association among species. However, as there were 33 species collected (the number of pair-wise contrasts = $(N^2 - N)/2 = 528$), and because most of the contrasts involving rare species would be invalid (with expected values < 5), these analyses were arbitrarily limited to the eight most abundant species that together comprised 95% of the larvae collected. These species were: *Boyeria vinosa* (Say), *Cordulegaster maculata* Selys, *Gomphus cavillaris* Needham, *Hagenius brevistylus* Selys, *Macromia illinoiensis* Walsh, *Ophiogomphus mainensis* Packard, *Progomphus obscurus* (Rambur), and *Stylurus scudderi* (Selys). All 127 sites were scored for the presence or absence of each species, and pair-wise Chi-square tests of independence were conducted (continuity corrections for 2 x 2 tables and a Bonferroni correction for multiple contrasts were performed, SPSS 1998).

Differences in the composition of these assemblages among watersheds were described by analyzing changes in species' relative abundances. Because changes in relative abundance are largely determined by the abundances of the most common species, these analyses were limited to the five most abundant species that each accounted for $>$ 5% of all larvae collected: *B. vinosa*, *C. maculata*, *M. illinoiensis*, *O. mainensis,* and *P. obscurus*. The relative abundance (percentage of total odonates collected) of each species was determined at each site, and means for the 10 streams were compared with MANOVA, one-way ANOVA, and Tukey's multiple comparison tests (percentage data were arcsin square-root transformed, Sokal and Rohlf 1995).

RESULTS

In total, 7569 odonates were collected from 33 species (Table 1). The mean abundance, species richness, and Simpson's diversity of odonates captured/site in nine tributaries and the main channel of the Enoree River were compared with one-way ANOVA tests (abundance was $\log_{10}(x + 1)$ transformed before analysis, Sokal and Rohlf 1995). All three measures varied significantly among these drainages (abundance: F = 3.37, df = 9, 117, p = 0.001; species richness: F = 4.76, df = 9, 117, p = 0.0001; Simpson's diversity: F = 2.71, df = 9, 117, p = 0.007). Odonate abundance in Durbin Creek and Kings Creek were significantly greater than in Brushy and Rocky Creek (Tukey's multiple comparison tests, p = 0.05; Fig. 2). Kings and Durbin Creek also had the highest species richness values, significantly higher than at Brushy Creek, Rocky Creek, and the Upper Enoree (Tukey's multiple comparison tests, p = 0.05; Fig. 2). Brushy, Rocky, and the Upper Enoree also had the lowest Simpson's diversity values of the 10 streams; mean Simpson's diversity in Brushy Creek was significantly lower than in Beaverdam Creek and the main channel of the Enoree River (Tukey's multiple comparison tests, p = 0.05; Fig. 2).

Patterns of co-occurrence were described for the eight most abundant species using Chi-squared tests of independence (with the appropriate continuity correction for 2 x 2 tables and a Bonferroni correction for multiple comparisons, SPSS 1998). There were very strong positive associations among these species (Fig. 3). *Ophiogomphus mainensis* anchored one node and was usually found with *C. maculata*, *B. vinosa*, and *H. brevistylus* (Fig. 3). *Hagenius brevistylus* was also found in strong association with *M. illinoiensis* and *P. obscurus*, which seemed to represent another axis in this assemblage. *Progomphus obscurus* was also associated with *Gomphus cavillaris* and *S. scudderi* (Fig. 3).

Table 1. The number of individuals of each odonate species collected in the Enoree River basin, SC, in the summers of 1999 and 2000.

Suborder Zygoptera ("Damselflies")	
Family: Calopterygidae	
Calopteryx dimidiata Burmeister	3
C. maculata (Beauvois)	24
Hetaerina titia (Drury)	1
Family: Coenagrionidae	
Argia fumipennis (Burmeister)	9
A. sedula (Hagen)	13
Argia sp.	6
Suborder Anisoptera ("Dragonflies")	
Family: Aeshnidae	
Aeshna umbrosa Walker	6
Boyeria grafiana Williamson	1
B. vinosa (Say)	482
Family: Gomphidae	
Dromogomphus spinosus Selys	41
Gomphus abbreviatus Hagen	7
G. cavillaris Needham	284
G. dilitatus Rambur	2
G. lividus Selys	1
G. parvidens Currie	62
G. vastus Walsh	1
Hagenius brevistylus Selys	204
Lanthus parvulus Selys	1
Ophiogomphus mainensis Packard	1228
Progomphus obscurus Rambur	3730
Stylogomphus albistylus (Hagen)	103
Stylurus amnicola (Walsh)	1
S. ivae (Williamson)	5
S. notatus (Rambur)	26
S. scudderi (Selys)	196
S. spiniceps (Walsh)	1
Family: Cordulegastridae	
Cordulegaster erronea Hagen	14
C. maculata Selys	708
Family: Libellulidae	
Didymops transversa (Say)	3
Macromia illinoiensis Walsh	398
Pantala flavescens (Fabricius)	1
Somatochlora provocans Calvert	6

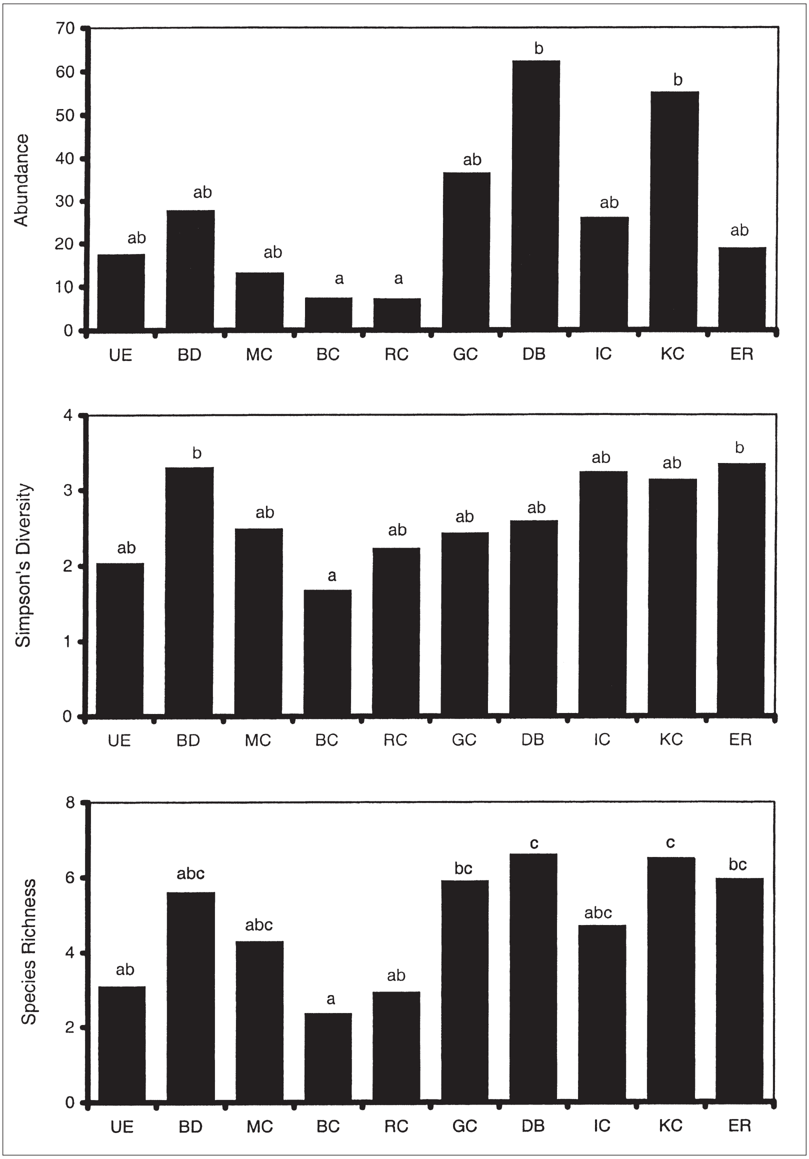

Figure 2. Mean abundance, species richness, and Simpson's diversity values for odonate communities ten streams in the Enoree River basin, SC. Means are calculated on samples collected at 8-17 sites within each stream. The streams vary significantly for these variables (ANOVA, see text). Means with the same letter are not significantly different from one another (Tukey multiple comparison test, p = 0.05). Streams are ordered, left to right, from the headwaters of the Enoree downstream: Upper Enoree (UE), Beaverdam Creek (BD), Mountain Creek (MC), Brushy Creek (BC), Rocky Creek (RC), Gilder Creek (GC), Durbin Creek (DB), Indian Creek (IC), Kings Creek (KC), and the main channel of the Enoree River (ER).

The five most abundant species, *P. obscurus*, *B. vinosa*, *M. illinoiensis*, *C. maculata*, and *O. mainensis*, each accounted for > 5% of the individual odonate larvae collected. The composition of this core group of species varied significantly among the drainages (MANOVA Wilk's Lambda = 0.253, F = 3.005, df = 54, 524, p < 0.0001). In particular, there were significant differences in the relative abundances of *O. mainensis* (one-way ANOVA: F = 6.55, df = 9, 117, p = 0.0001) and *C. maculata* (one-way ANOVA: F = 9.11, df = 9, 117, p = 0.0001). Brushy, Rocky, Upper Enoree, and the main channel of the Enoree River had significantly lower relative abundances of *O. mainensis* than Durbin and Kings Creeks (Tukey's mean comparison tests, p = 0.05, Fig. 4). Rocky Creek, Gilder Creek, and the main channel of the Enoree had significantly lower relative abundances of *C. maculata* than Beaverdam Creek, Kings Creek, and the Upper Enoree (Tukey's mean comparison tests, p = 0.05, Fig. 4).

DISCUSSION

In general, the odonate assemblages of the Enoree River basin were dominated by a group of eight common species. In eight of the ten streams studied, the assemblages were numerically dominated by burrowing species, either *P. obscurus* or *C. maculata*. This is consistent with the predominance of sandy substrates throughout these streams (Worthen et al. 2001a). However, odonates that fill other ecological

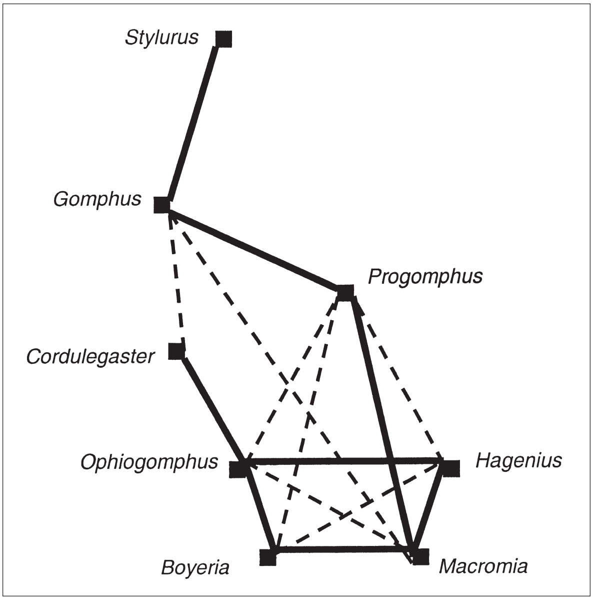

Figure 3. A network depicting statistically significant associations (Chi-square tests of independence) among the eight most abundant odonate species in our survey. All associations are positive. Only those associations significant after a 2 x 2 contingency correction and a Bonferroni correction for multiple comparisons have been included (solid line, $p < 0.0001$; dashed line, $p < 0.001$). See text for full species names.

niches were also abundant, and niche parameters (as defined in Corbet 1999) seem to impose some substructure on these assemblages. For instance, the hider *O. mainensis* was associated most closely with the shallow burrower *C. maculata*, the hider *H. brevistylus*, and the clasper *B. vinosa*. The sprawler *M. illinoiensis* formed strong associations with the deep burrower *P. obscurus*, the clinger *B. vinosa*, and the hider *H. brevistylus*. The deep burrower *P. obscurus* was linked with the shallow burrower *G. cavillaris,* which was also linked to another deep burrower *S. scudderi*. As such, species were most strongly associated with species that occupy different niches. The only contradiction to this trend was the strong association between the hiders *O. mainensis* and *H. brevistylus*.

These non-random associations are superficially consistent with predictions of classical niche theory; interspecific competition in equilibrial systems should result in resource partitioning and niche complementarity (Ben-Moshe et al. 2001, MacArthur and Levins 1967). Odonate assemblages are stable over time (Johnson and Crowley 1989), density-dependent mortality can be significant (Van Buskirk 1993), and interspecific competition can be locally important (Mahato and Johnson 1991, Pierce et al. 1985). So, it is possible that competition for food or predator-free space structures these assemblages. However, the patterns in this study are very coarse (pres-

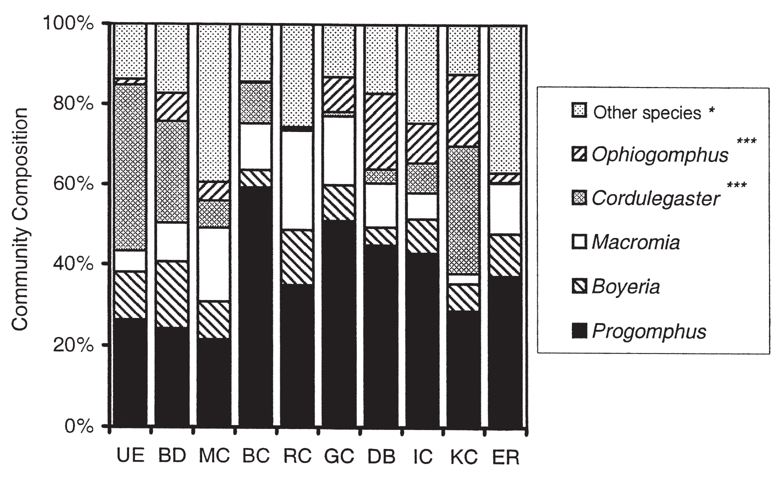

Figure 4. Relative abundances of the five most common odonate species, in each of the ten streams sampled in the Enoree River basin. Streams varied significantly in the composition of their communities (MANOVA, $p < 0.0001$). The relative abundance of *Ophiogomphus mainensis*, *Cordulegaster maculata*, and ‘other species’ also varied significantly among these ten streams (one-way ANOVA, * = $p < 0.05$, ** = $p < 0.0001$).

ence/absence data) and have been accumulated across 127 sites. Experiments are required to determine whether competition contributes to this pattern of microhabitat selection at single sites.

When the structure of these assemblages was compared across watersheds, the ten streams varied significantly in mean odonate abundance, species richness, Simpson's diversity, and the relative abundance of the five most abundant species. In general, Brushy Creek, Rocky Creek, and the Upper Enoree had assemblages with fewer odonates, lower richness, lower diversity, and an unusual paucity of *O. mainiensis* compared to other streams. These patterns may be the result of local anthropogenic factors. For instance, a waste containment pond at a metal refinishing plant ruptured above the headwaters of the Upper Enoree in 1985, spilling 75,700 liters of HCl, dissolved metals, and other contaminants into the water table (Hagins 1988). Twelve years after the spill, the site 0.3 km from the plant contained no macroinvertebrates or fish, and fish transplanted into these sites died within 24 hrs (Worthen et al. 2001b). Concentrations of Zn^{+2} and Cl^{-} at these sites were 100X and 20X higher, respectively, than at the site 7 km downstream (Worthen et al. 2001b). High concentrations of chloride and other toxins limit the distribution of some species and change community structure in other studies (Watson et al. 1982, Carchini and Rota 1985, Romero 1988, Corbet 1999). It seems likely that low odonate abundance and diversity in the Upper Enoree, and the shift in composition, are the result of this spill. *Cordulegaster maculata* may be more tolerant of these toxins than other species; it occurs just 0.7 km from the spill site whereas most other species were not present for another 2 km downstream (unpublished data).

In the Enoree River basin, the most intensive suburban development over the last decade has been in the Brushy Creek and Rocky Creek watersheds. As Greenville has grown east along Interstate 85 towards Spartanburg, these watersheds have had agricultural land converted to corporate parks and residential developments. However, the chemical signature of these impacts is not obvious against the natural variation in stream chemistry. For instance, the most significant difference in water chemistry among Enoree waterways is the high concentration of silica and bicarbonate in Kings Creek, Indian Creek, and the Enoree River (Worthen et al. 2001a). These differences are probably due to differences in the underlying geology of the lower portion of the Enoree basin (Andersen et al. 2001). As such, there is no single chemical parameter that distinguishes Brushy and Rocky Creeks from the other watersheds (Worthen 2001a). Rather, it may be that cumulative or interactive effects of several chemicals, or the physical changes resulting from development (increased discharge, increased sediment load, reduced shade, reduced habitat heterogeneity), are affecting dragonfly assemblages. In any event, these watersheds with extensive recent human disturbance have odonate assemblages with the lowest abundance, richness, and diversity. This pattern is consistent with other studies documenting the effects of urbanization on stream invertebrate communities (Beavan et al. 2001, Watson et al. 1982).

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