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ECOSYSTEM CONSEQUENCES OF CONTRASTING FLOW REGIMES IN AN URBAN EFFECTS STREAM MESOCOSM STUDY[1]

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ABSTRACT: A stream mesocosm experiment was conducted to study the ecosystem-wide effects of two replicated flow hydrograph treatments programmed in an attempt to compare a simulated predevelopment condition to the theoretical changes that new development brings, while accounting for engineering design criteria for urban stormwater management. Accordingly, the treatments (three replicates each) differed in base flow between events and in the rise to, fall from, and duration of peak flow during simulated storm hydrographs, which were triggered by real rain events occurring outside over a 96-day period from summer to fall, 2005. Incident irradiance, initial substrate quality, and water quality were similar between treatments. Sampling was designed to study the interactions among the treatment flow dynamics, sediment transport processes, streambed nutrients, and biotic structure and function. What appeared most important to the overall structure and function of the mesocosm ecosystems beyond those changes resulting from natural seasonality were (1) the initial mass of fines that infiltrated into the gravel bed, which had a persistent effect on nitrogen biogeochemistry and (2) the subsequent fine sediment accumulation rate, which was unexpectedly similar between treatments, and affected the structure of the macroinvertebrate community equally as the experiment progressed. Invertebrate taxa preferring soft beds dominated when the gravel was comprised of 5-10% fines. The dominant invertebrate algal grazer had vacated the channels when fines exceeded 15%, but this effect could not be separated from what appeared to be a seasonal decline in insect densities over the course of the study. Neither hydrograph treatment allowed for scour or other potential for flushing of fines. This demonstrated the potential importance of interactions between hydrology and fine sediment loading dynamics on stream ecosystems in the absence of flows that would act to mobilize gravel beds.

(KEY TERMS: urbanization; stormwater management; sediment transport; aquatic ecology; biogeochemistry; rivers/streams; mesocosms.)

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INTRODUCTION

Humans are becoming increasingly urbanized, with over 80% of new population growth in the United States expected to occur in urban and suburban environments (Bullard, 2000), and the spatial extent of urbanization is increasing much faster than the urban population (Cohen, 2003). The resulting urban and suburban sprawl leads to an increase in the area occupied by impervious surfaces (pavement, roof tops, compacted soils, etc.), which effectively lowers the rainwater infiltration capacity of the landscape (Booth and Jackson, 1997). The decrease in infiltration alone produces marked changes to the flow regime of natural channels draining urban watersheds both during and in between storm events (USEPA, 2002). The hydrological alterations for small urban streams have been characterized relative to their predevelopment condition as having reduced base flows (Simmons and Reynolds, 1982; Finkenbine *et al.*, 2000), increased peak flows during storms (Dunne and Leopold, 1978; Roesner, 1999), and generally flashier storm hydrographs (Roy *et al.*, 2005a; Walsh *et al.*, 2005).

Many aspects of the hydrological alteration resulting from urban land use have been linked to components of the biotic structure and, more recently, ecosystem function of small streams (Baer and Pringle, 2000; Suren, 2000; Paul and Meyer, 2001; Roy *et al.*, 2005a; Walsh *et al.*, 2005). Effects of urban stream hydrology on stream macroinvertebrates have been the most widely studied (Jones and Clark, 1987; Walsh *et al.*, 2001; Stepenuck *et al.*, 2002; Wang and Lyons, 2003); however, observed impacts on fish assemblages (Roy *et al.*, 2005a), and algal and periphyton biomass and dynamics (Sonneman *et al.*, 2001; Taylor *et al.*, 2004; Carr *et al.*, 2005) have also received attention. Ecologists have increased investigations on the effects of urbanization, and the resulting hydrological alteration, on a number of measures of stream ecosystem function, including nutrient spiraling, leaf litter breakdown, and organic matter processing (Palmer *et al.*, 2002; Meyer *et al.*, 2005; Miller and Boulton, 2005; Chadwick *et al.*, 2006).

The quantity, quality, and timing of sediment delivery from hillslopes is affected as a result of urban land use changes (Nietch *et al.*, 2005), as is channel incision and instream erosion, generally, by the resultant altered hydrology (Booth, 1990; Trimble, 1997). Increases in sediment transport associated with longer peak flow durations leads to increases in invertebrate drift and decreases in invertebrate densities and diversity, as well as decreases in periphyton biomass from sloughing (Quinn and Hickey, 1990; Bond and Downes, 2003; Suren and Jowett, 2006). Fine sedimentation within gravel substrates from excess loading is associated with lower invertebrate benthic densities as many species require beds devoid of fines for feeding, reproduction, or refugia (Bond and Downes, 2003; Kaller and Hartman, 2004; Roy *et al.*, 2005b).

Ecological consequences of the interactions between stream hydrology and sediment transport processes have been studied from the perspective of flow variability (Poff and Allan, 1995; Lytle and Poff, 2004; Poff *et al.*, 2006), bed stability (Lisle, 1989; Kaufmann *et al.*, 1999), and habitat heterogeneity (Kenworthy and Wilcock, 2001; Cardinale *et al.*, 2002; Hoffman *et al.*, 2006) as drivers of the structure of the biotic community. However, attempts to link these instream dynamics to watershed management prescriptions that would be applied at the landscape scale to abate hydrological and sediment alterations have lacked mechanistic understanding (Palmer *et al.*, 2002).

The requirement to understand the linkages between the forms and processes of urban landscapes and stream ecology well enough to prescribe cost-effective management strategies across multiple spatial scales with any degree of confidence represents a significant challenge (Nilsson *et al.*, 2003; Roy *et al.*, 2008). Although strong empirical models allow stream health predictions from land use configurations at broad scales (Strayer *et al.*, 2003) and from impervious surface coverage in smaller urban watersheds (Schueler, 1994; Arnold and Gibbons, 1996) that have been invaluable to identifying sources and degrees of biological impairment, their utility breaks down when specific management strategies are to be applied locally. Watershed managers in urbanizing areas need specific criteria to guide the design of urban landscapes that is predictive of ecology.

As a model of the type of design criteria in reference, engineering practices for urban areas have been in effect for some time that are geared toward controlling large peak flows and sediment loadings in receiving channels. These aspects posed the greatest risk to human safety and property (Ward and Trimble, 2004). As such, these practices tend to be only effective for large storms (McCuen and Moglen, 1988; Claytor and Schueler, 1996; McRae, 1997), are often not applied at the desired watershed scale (Pitt and Voorhees, 2003; Nietch *et al.*, 2005), and were not originally designed with the goal of ecological protection (Roesner *et al.*, 2001; Walsh, 2004). For example, a peak flow control goal for small urbanizing catchments has translated to the guiding principle in urban drainage design to detain the excess rainfall-runoff created by impervious surfaces within built structures, typically referred to as detention basin best management practices (BMPs), and release it more slowly to receiving channels at rates not to exceed a specific predevelopment flow condition (Booth and Jackson, 1997; Maxted and Shaver, 1997; Nehrke and Roesner, 2004). This amounts to "shaving" the peak of the postdevelopment runoff hydrograph to the same peak magnitude predicted to occur in the predevelopment condition. Because the total volume of stormwater associated flow in urban watersheds is higher than in similar undeveloped ones, the result is a hydrograph that has a longer duration peak flow rate. Although it differs among municipalities, the design criteria for flow control will specify a specific size of storm event that must be controlled by the BMP (e.g., rain event with recurrence of 1, 2, or 10 years). Simple models are used by engineers to design the structures for peak flow control, and in some instances, for channel erosion protection (McRae, 1993; Bledsoe and Watson, 2000) and sediment removal (Pitt and Voorhees, 2003).

A correctly applied flow control strategy should not generate more frequent channel-eroding flows in the postdevelopment condition (Bledsoe and Watson, 2000), and some think could be engineered to release detained runoff at prescribed intervals more amenable to ecological protection (Roesner *et al.*, 2001; Pitt and Voorhees, 2003). However, without specific criteria to guide new designs there is little incentive for municipalities to promote such considerations.

To help elucidate mechanistic linkages, in this study, we control and/or measure the governing hydrologic and sediment transport properties potentially affecting habitat quality in stream mesocosms. Simultaneously, we assess chemical and biological changes in naturally colonized communities in which the flow regimes are controlled. Two hydrograph treatments were established based on theoretical models that simulated, respectively, the shape characteristic of a predevelopment condition and of a detention management strategy applied at the watershed scale for small (less than two years) storms. It was recognized from the start that the experimental conditions may not exactly reflect any real field situation, but the results proved insightful to the mechanistic understanding of how managed flow regimes, sediment transport processes, and biology may interact to characterize small stream ecosystems in urban developments.

THE EXPERIMENTAL STREAM FACILITY

This study was conducted at the USEPAs Experimental Stream Facility (ESF), in Milford, Ohio, from July 25 to October 24, 2005. The ESF was built by the Proctor and Gamble Corporation to test the response of stream mesocosms to a continuous chemical dose while simultaneously allowing for natural environmental variability to sustain and/or influence the structure and function of the experimental systems (Belanger, 2003).

Each mesocosm inside the ESF consists of a 12 m long ultra high molecular weight polyethylene lined flume, with the following five subsections: (1) a 126 l head tank; (2) an upstream 4.3 m long by 0.3 m wide channel section containing 47 rows and 3 columns of unglazed ceramic tiles, providing a standardized substrate for periphyton analysis; (3) a 1.0 m tapered transitional zone; (4) a 4.3 m long by 0.54 m wide channel section with 15 rows and 3 columns of polypropylene trays filled with river gravel; and (5) a 222 l tail tank.

Each mesocosm was equipped with a conductivity meter (inductive, electrodeless; Foxboro Model 871EC-AB; The Foxboro Company, Foxboro, Massachusetts a part of Invensys, Plano, Texas), dissolved oxygen (DO) meter (TBI-Bailey model TB235; TBI-Bailey, Reno, Nevada), pH meter (differential electrode: TBI-Bailey model 551), and temperature probe (Rosemount Series 78S) mounted in the tail tank near an overflow weir. Water quality meters were cleaned and calibrated at weekly intervals during the experiment following manufacturer guidelines.

Flow to each mesocosm was regulated via a diaphragm valve controlled by a linear actuator (A300 Poscon Electric Actuator; Poscon, West Conshohocken, Pennsylvania), which was wired to a Foxboro magnetic flow meter (Model 801H-WCT) that operated under programmable logic via a transmitter (Foxboro Model 8000-TC). A continuous-reading, online turbidity meter (Monitek Model 210; Monitek, Hayward, California), using the nephelometric method of measurement, was positioned at the ESFs river water monitoring station and recorded turbidity influent to all of the mesocosms. The data output from the turbidity meter was calibrated with weekly suspended sediment concentration (SSC) data obtained from grab samples (ASTM, 2004).

Full spectrum lighting was provided by 30 high intensity discharge 1,000 W lights. Day-night cycles were automatically adjusted to the Southwestern Ohio locale. Light levels were continuously monitored with quantum sensors (LiCor, Lincoln, Nebraska), and by design, simulated daily integrated irradiance at $\sim$12% of that recorded by an additional sensor positioned on a meteorological station outside the facility in an open area. The meteorological station also recorded rainfall. Data produced by the continuously monitored parameters (water quality, flow, light, and inside and outside climate conditions) were acquired at 5 min intervals and were processed by a supervisory control and data acquisition system running under the Camile (Argonaut Technologies, Inc., Redwood City, California) software program.

EXPERIMENTAL DESIGN

The primary objective of this experiment was to study the ecosystem consequences of two contrasting streamflow hydrographs: one would reflect that of a theoretical condition in a stream draining a developed watershed with detention structures for stormwater management, and the other would be shaped in relevance to simulate the theoretical predevelopment land use condition. The intent was to use the experimental conditions to add insight toward developing mechanistic relationships in support of developing engineering design criteria for managing stormwater runoff in terms of hydrograph dynamics and stream ecosystem endpoints.

The approach was to control flow regime while keeping other factors regulating ecology relatively constant. With the indoor mesocosms at the ESF, light intensity and initial stream substrate can be equalized across replicated units. Background water quality is also equal among units with respect to biological colonization potential and physiochemistry, but changes over time with variable climate conditions affecting the source water. Source water used for this ESF experiment was drawn from the East Fork of the Little Miami River (EFLMR). The river at the point of intake to the ESF is draining a large, mixed-use watershed. Water quality, in general, has relatively high turbidity and nutrient levels compared with a characteristically less impacted system (OEPA, 1995). Given this background condition, what would be considered "pristine" or "unimpacted" with respect to water quality could not be simulated. Therefore, the word "predevelopment" in terms of the experimental design should only be associated with the flow hydrograph shape, not water quality.

Another conceptually conflicting aspect of this ESF setup is that it allows for a relatively narrow range of surface water flow through the mesocosm gravel sections, ~38-197 l/min. This is because within the mesocosm setting, order of magnitude changes in flow rates are very difficult to achieve while still maintaining precision in flow control, integrity of biological seed material, and manageable sizes of individual units for sampling and replication. Recognizing the fact that pending the size of the drainage and the intensity of the rain event, among other variables, streamflow in natural channels may vary by several orders of magnitude, while the ESF could only produce factor of five changes in flow, we had to decide if the ESF limitations on flow rates would make the results irrelevant to real systems.

Based on measurements of current velocity made near the bed of gravel sections in both ESF mesocosms and riffle/run sections of nearby natural small stream channels, we determined that the range of flows provided by the ESF setup produced comparable hydraulic properties and boundary shear stresses reflective of field conditions measured under base and storm flows for small rain events. ESF peak flow rates, however, could not produce scour in the mesocosms. We reasoned that a stable riffle section in a real stream, by definition, would not experience transport during smaller rainfall/runoff events. Ecological consequences could be observed over a range of flows that would likely affect fine sediment deposition and resuspension but not induce transport (scour) in the larger particle sizes comprising the bed material placed at the outset. Therefore, we recognized that the experimental conditions may not be reflective of any real system in particular, without the ability to simulate scouring storm flows or reproduce "pristine" water quality.

TREATMENT HYDROGRAPHS

To ensure that mesocosm flows were changing under natural storm-flow water quality conditions, rainfall was compared with EFLMR flow data obtained from a historic USGS gauging station (#03247500) located 2.4 km upstream of the ESF water intake. This comparison allowed us to determine the amount of rainfall resulting in a significant increase in flow in the EFLMR (>0.0015 cm/min) and the lag time between rainfall and increased flow (2.5 h).

The relative differences between flow hydrographs were structured after taking into consideration (1) measurements of current velocity (ADP 2-D probe; Sontek, San Diego, California) in relatively impacted and unimpacted small stream reaches at nearby field sites, (2) a model of the downstream flow hydrograph response for a predevelopment *vs*. postdevelopment detention-based management condition provided in the literature, and (3) the constraints posed by the ESF setup discussed above.

First, measurements of current velocity in riffle sections made during base-flow conditions in natural streams draining subwatersheds of different degrees of urban development within the parent (EFLMR) watershed returned values that ranged between 1.5 and 20 cm/s, but generally differed by ~10 cm/s.

This was used as a target for velocity differences between experimental treatments under base flow. The lowest ESF base flow was set to keep gravel in the mesocosms totally and continuously submerged. Gravel sections were sloped to maximize near-bed velocities at the highest discharge.

Second, a discussion of the effects of detention-based management practices on downstream hydrographs presented by Pitt and Voorhees (2003), was used to develop the contrasting flow hydrograph dynamics; i.e., slopes for the rising and falling limbs and peak flow durations. The relative differences shown in Pitt and Voorhees (2003) between these conditions were based at the watershed scale, the target for new BMP design criteria, and represented conditions more reflective of those that are observed at field sites associated with the ESF research; namely, a hydrograph produced at the downstream-most reach of a subwatershed that may be receiving runoff from upstream hillslope and instream detention structures (Bennett, 2006). The slopes of the flow hydrograph meant to represent the predevelopment condition were programmed to rise and recede faster than those reflecting postdevelopment with detention, and in accordance with the relative differences between base and peak flow, divided by the time change that was reported in Pitt and Voorhees (2003).

Finally, the peak flow conditions of each hydrograph were based primarily on the fact that the highest flow achievable in the ESF was 197 l/min. This became the set point for the peak flow for the intended managed, postdevelopment hydrograph. The peak flow for the predevelopment hydrograph was set slightly lower as a reflection of output from previously modeled conditions for our field sites (Bennett, 2006). Considering that the flow hydrograph settings were meant to represent theoretical conditions, and the "unnatural" characteristics posed by the ESF setup discussed previously, so as not to be a misnomer, we refer to the two different flow hydrographs imposed as treatments on the mesocosms hereafter as higher base flow/shorter duration peak flow (HBSD) and lower base flow/longer duration peak flow (LBLD).

Six mesocosms within the ESF were randomly assigned to one of the two treatments. The three assigned to the HBSD treatment were set at a base flow of 94.6 l/min. Three others were assigned to the LBLD treatment and were set at a base flow of 37.9 l/min. Following a lag period of 2.5 h once a rain event was "sensed" by the outside rain gauge, flow rates for HBSD were programmed to increase from base flow to storm flow at a rate of 4.8 l/min every 5 min for 1.5 h, were set to a peak flow target (181.7 l/min) for 3 h, and were then decreased to base flow at a rate of 1.5 l/min every 5 min until it returned there in 5 h. In contrast, flow rates for the

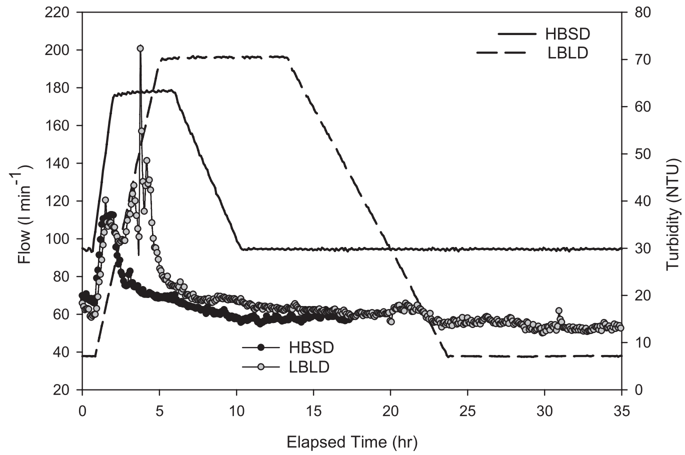

FIGURE 1. Experimental Treatments. Flow hydrographs for each treatment were programmed differently in accordance with theoretical predevelopment (HBSD) and postdevelopment with BMPs (LBLD) hydrographs. Turbidity data served as surrogate for differential effects of treatments on fine sediment resuspension. Turbidity data are in the absence of a rain event trigger to qualify the effects of changing flow alone on channel suspended sediment transport.

LBLD were increased at a 5 min ramp interval of 3.2 l/min for 4 h, were held at peak flow (189.3 l/min) for 8 h, with a decrease to base flow at a rate of 1.3 l/min every 5 min for 10 h (Figure 1). The storm-flow hydrographs had durations of 9.5 and 22 h for the HBSD and LBLD treatments, respectively.

Given these hydrograph differences, approximately two times more water was discharged during a simulated storm event for the LBLD hydrograph compared with the HBSD, 203,781 *vs*. 95,719 l, respectively. Volumetric discharge approaches unity for the two treatments after 33 h. In reality, without a seeping underlying aquifer, base-flow recession should then occur until the next rain event. This, however, was not accounted for in the flow programming, so that the frequency of rainfall triggers from the parent watershed affected the relative volumes of water integrated by the flow conditions over the course of the experiment. The similarities and differences in hydrology and hydraulic properties by the experimental conditions are depicted in Figure 1 and Tables 1 and 2.

METHODS

Mesocosm Preparation

Prior to the experiment, 45 polypropylene trays ($317\ cm^2$ area $\times$ 6.2 cm height) were positioned to

TABLE 1. Simulated Hydrologic Conditions for the Experimental Period.

Treatment	HBSD	LBLD
Mean flow (l/min ± 1 SD)	101 ± 21	62 ± 52
Coefficient of variation in mean daily flow (%)	9	30
Richards-Baker flashiness index	0.1	0.5
Total discharge (m^3)	13,227	8,117
Duration between rain-induced events (days)		
Min	0.8	
Mean	4.4	
Maximum	16.5	

Notes: HBSD, higher base flow/shorter duration; LBLD, lower base flow/longer duration.

comprise the gravel section of each mesocosm. A sampler for assessing intergravel water (aka pore water) chemistry was placed in the bottom of each tray. The samplers were constructed from 30 ml scintillation vials filled with deionized water, and covered with 63 μm mesh Nitex netting fastened in place by open-top, plastic screw caps with a 1.4 cm diameter opening. Preliminary measurements established that solute equilibration occurred within the samplers in a matter of hours.

Trays were then filled with washed river gravel with a median particle diameter (D_{50}) of 20 mm. Gravel particle size distribution was determined from 100 pieces chosen randomly and measured with calipers along the intermediate axis following Wolman (1954). The gravel sizes chosen approximated the median substrate sizes observed in nearby small stream sites and fell within the ranges cited for gravel-bed streams (i.e., 4-60 mm) (Bunte and Abt, 2001). The initial weight of each tray was recorded.

Hydrology and Hydraulics

Experimental hydrology was characterized from flow and rain data collected continuously at 5-min intervals throughout the experiment. Flow variability was assessed with a coefficient of variation for mean daily flow in the manner of Poff (1996) and with the Richards-Baker flashiness index (Baker *et al.*, 2004) for comparison between treatments. Hydraulic properties for the mesocosm gravel sections were characterized for both base-flow and storm-flow conditions for each treatment. Measurements of near-bed velocity were made at the approximate center of each gravel-filled tray and at a fixed depth of ~1.3 cm above the gravel surface with a micro-current meter (Schiltknecht, Zurich, Switzerland). Measurements were made on replicate mesocosms set at the same flow rate to test for differences. The slope of the gravel section was set at 4.3%, which was determined ahead of time to achieve a maximum range of current velocities given the influent flow changes that were programmed to occur. For comparison to riffle properties of real streams, Froude, Reynolds, and Boundary Reynolds numbers were calculated according to Jowett (1993). Boundary shear stress was calculated according to Whiting and Dietrich (1990). Particle diameters used in the hydraulic calculations were based on measurements described above. Equations and constants used therein can be found in Table 2.

Tray Removal and Initial Processing

Four gravel trays were randomly selected from each mesocosm on five dates during the experiment (August 8, August 22, September 12, October 10, and

TABLE 2. Hydrograph and Hydraulic Properties of Mesocosm Gravel Sections by Treatment.

	Base Flow		Storm Flow	
Hydrograph and Hydraulic Properties	HBSD	LBLD	HBSD	LBLD
Mean flow (l/min ± 1 SD)	95 ± 2	38 ± 1	175 ± 10	190 ± 12.3
Flow duration (% of time at flow condition for study)	90	79	10	21
Mean depth in gravel section (mm ± 1 SD)	29 ± 8	25 ± 8	35 ± 4	
Mean near-bed velocity (cm/s ± 1 SD)	26.1 ± 6.7	16.7 ± 7.1	40.0 ± 5.0	
Mean Froude number $[V/(g\ d)^{-2}]$	0.49	0.33	0.68	
Mean Reynolds number $(V\ d/v)$	7,520	4,230	14,057	
Mean boundary Reynolds number $(V\ D_{50}/v)$	5,254	3,351	8,048	
Mean boundary shear stress[1] $\{\rho\ (V\ k)^2\ [\ln(10\ z/D_{84})]^{-2}$ (dynes/cm^2)$\}$	25.4	12.6	45.8	

Notes: d, depth; D_{50}, gravel diameter – 50% finer (20.1 mm); D_{84}, gravel diameter – 84% finer (23.7 mm); g, acceleration due to gravity (9.81 m s^{-2}); HBSD, higher base flow/shorter duration; k, von Karman's constant (0.40); LBLD, lower base flow/longer duration; p, fluid density; SD, standard deviation; v, kinematic viscosity; V, velocity; z, depth of velocity measurement (d – 1 cm)..

[1]After Whiting and Dietrich (1990).

October 24) to measure fraction-specific sediment, intergravel nutrients, periphyton, and invertebrate parameters. Of the four trays, two each were sampled for sediment size fractions and biota (periphyton and invertebrates). Intergravel nutrients were sampled in all four trays. Although newly filled trays were added to the channels immediately following tray removal, random sampling took place without replacement.

Size-specific sediment fractions were obtained immediately after removal by wet sieving the contents of two of the four trays through three 12″ diameter sieves (2 mm, 250 μm, and 63 μm mesh sizes). Fine sediments <63 μm were collected in a large plastic bucket. The resultant slurry volume was weighed, subsampled under homogenization, the weight of the subsample was recorded, and then it was filtered onto 1.2-μm pore size glass fiber filters (Whatman GF/A).

Samples for measuring periphyton parameters were collected from six randomly selected pieces of gravel from the surface of two trays per channel that were not sampled for sediments. The periphyton was removed from the gravel by scrubbing with a toothbrush and then rinsed into a collection tray. The resultant slurry was diluted to a known volume, and separate aliquots were filtered for subsequent ash-free dry mass (AFDM), chlorophyll-*a* (Chl-*a*), and elemental [carbon (C) and nitrogen (N)] analysis onto precombusted glass fiber filters (Whatman GF/A – AFDM and Chl-*a* and Whatman GF/C – periphyton CN). Subsamples for Chl-*a* determination were placed on ice immediately after filtering, transferred to a −20°C freezer within an hour of sample collection, and stored until analysis. Gravel surface area for periphyton responses was calculated by wrapping dried gravel with aluminum foil, then comparing those foil weights to foil weights of known areas (Aloi, 1990).

The remaining tray contents were wet sieved through a 2 mm and 250 μm mesh sieve, in series. Contents retained in the 250 μm mesh sieve were evenly divided into two subsamples using a Folsom plankton splitter (Wildlife Supply Company, Buffalo, New York). One subsample was preserved in 75% ethanol for subsequent benthic invertebrate analysis, while a second subsample was dried, weighed, and saved for benthic organic matter analysis.

During each sampling event, water column samples were collected from the head tank and tail tank of each mesocosm in clean glass vials. Contents of the extracted intergravel samplers and water column vials were split and filtered through 0.7 μm filters (Whatman GF/F), to divide between total and dissolved nutrient fractions, stored on ice, and returned to the laboratory for nutrient chemistry analysis within 24 h of collection.

Laboratory Analysis

Sediment size fractions were dried at 105°C for 24 h and weighed to determine dry weights. A weighed subsample for each fraction was ashed at 550°C for 1 h and then reweighed. The difference between the dried and ashed weight was the loss on ignition (LOI), expressed as a percentage of the dry weight.

Periphyton AFDM was determined by drying subsamples at 75°C for 48 h, measuring dry weight, ashing dried samples at 500°C for 2 h, and then reweighing ashed samples (Wetzel and Likens, 2000). Periphyton Chl-*a* was measured fluorometrically following 90% acetone extraction without acidification (Arar and Collins, 1992). Periphyton C and N was determined by drying subsamples at 75°C for 48 h, measuring dry weight, then determining carbon and nitrogen levels on an Exeter EA-440 Elemental Analyzer (Exeter, North Chelmsford, Massachusetts).

Preserved invertebrate samples collected from gravel trays were sorted, enumerated, and identified in the laboratory using dissecting microscopes. Invertebrate taxa were sorted to family level, with the exceptions of Annelids and Ostracods (class), Copepods (subclass), Cladocereans (suborder), and Collembola (order). Fifteen percent of all processed samples were shipped to an outside laboratory for quality control purposes, following established quality assurance quality control procedures (Moulton *et al.*, 2000).

Analysis of surface and intergravel water samples for total and total dissolved phosphorus (TP and TDP, respectively) consisted of an acid persulfate wet oxidation method followed by automated colorimetric analysis for othrophosphate (Prokopy, 1992). Total and total dissolved nitrogen (TN and TDN, respectively) were analyzed by making adjustments to an alkaline oxidative persulfate method (APHA, 2001) followed by automated colorimetric analysis for nitrate (Wendt, 1995). Dissolved reactive phosphorus (DRP), nitrite + nitrate nitrogen ($NO_{2\text{-}3}$), and ammonium nitrogen (NH_4^+) were analyzed simultaneously with automated colorimetry by adjusting single analyte methods (Wendt, 1995; Sardina, 2000; Smith, 2001, respectively). All samples for nutrients were run on a Lachat Instruments QuickChem 8000 Flow Injection Autoanalyzer (Loveland, Colorado).

Data Analysis

Prior to statistical analysis, values for all responses collected from gravel trays within a mesocosm, on a particular date, were averaged, so that the mesocosm was the unit of analysis. Effects of treatment on (1) fine sediment and %LOI; (2) intergravel nutrients;

(3) periphyton Chl-*a*, AFDM, and molar C/N; and (4) the invertebrate endpoints total, mollusk, insect, chironomid, and ephemeroptera densities across the five sampling dates were analyzed with repeated measures analysis of variance (ANOVA), with three replicates per treatment. Repeated measures ANOVA analysis was performed on the model Response = Treatment + Time + Treatment: Time with the following degrees of freedom: $\text{Treatment}_{1,4}$, $\text{Time}_{4,16}$, and $\text{Treatment:Time}_{4,16}$. The significance of individual responses is provided in statistics reported in the appropriate figure captions. Error bars represent 1 SD of the mean value. Tests for comparing slopes and intercepts (Wuensch, 2007) between treatments were performed on the fine sediment accumulation to further define this specific effect.

Relationships for selected invertebrate taxa were evaluated using analysis of covariance (ANCOVA), with treatment as the independent categorical variable and Chl-*a* or fine sediment concentration as the continuous covariate, and the individual gravel tray as the unit of analysis. Prior to all analyses, continuous dependent variables (i.e., fine sediment and Chl-*a* concentrations) were natural log (ln) transformed, or (ln + 1) transformed for invertebrate benthic densities, and proportional dependent variables (i.e., % LOI) were arcsin square root transformed to meet the parametric assumptions of the ANOVA and ANCOVA models. Finally, dependent variables that were ratios (i.e., periphyton C/N) were not transformed.

Community-level invertebrate changes in response to physical and chemical variables were subjected to ordination analysis using nonmetric multidimensional scaling (nMDS) analysis applying the Bray-Curtis distance coefficient. Environmental (physical and chemical) variables were relativized prior to the analysis so that each data point represented the number of standard deviations from the mean for that variable (Brazner and Beals, 1997). Relativization serves to weigh each environmental variable equally, so that variables with large numbers are not disproportionately weighted (McCune and Grace, 2002). The nMDS ordination was produced using multiple runs and following the stress and stability criteria described in detail by McCune and Grace (2002).

RESULTS

Experimental Hydrology and Water Quality

Twenty-one outside rain events triggered a flow increase in the mesocosms during the experimental period. Two events occurred before the first sampling date, and six more took place by the second sampling event. Before the third sampling date, four more events happened; one just after sampling, and then three triggered flow change when the climate system that produced hurricane Katrina passed through the Ohio Valley near the 35th day of the study. This system produced the largest outside rain event of the study and had the greatest affect on influent water quality. Afterwards, there was a 16-day lull in precipitation. Six more events with a broader recurrence interval (six days, on average) than previously in the study occurred before sampling on the 77th day, and were followed by a 12-day dry period, until three additional events triggered flow change within the last four days of the study. On average an event trigger occurred every 4.4 days. Expected rainfall frequency for the Southwestern Ohio locale would be closer to 3.3 days (MRCC, 2000). Although a little over two times the water was passed by the LBLD hydrograph during a simulated storm event, the longer outside rain recurrence meant that the differences in base flow dominated the total discharge between treatments, with the HBSD treatment passing 1.6 times the water volume than that of the LBLD treatment (Table 1). Event triggers would have had to occur every 1.4 days for the treatment-specific discharges to be equal. The coefficient of variation of the mean daily flows was higher in the LBLD treatment, but compared with data collected from long-term flow records by Poff (1996), it was several factors lower than those observed for perennial flashy streams. The Richards-Baker flashiness index is perhaps more appropriate for a comparison to real streams with short-term flow records, and the differences here would span the range observed for streams draining small to midsized watersheds in the Midwest (up to 500 km^2) (Baker *et al.*, 2004). In both measurements, the magnitude of the change between base flow and storm flow for the LBLD relative to HBSD characterizes this treatment as flashier.

Mean base flow and peak flows for each treatment were on target with those programmed, speaking to the precision of the flow control system (Table 2). The flow programming produced measurements of water depth and near-bed velocity in the gravel sections that differed between treatments during base flow as expected. During the peak flows of simulated storm events, however, there was not a significant difference in these parameters even though the LBLD treatment had higher mean storm flow. As such, the pooled data are reported for the hydraulic properties of the gravel section during storm-flow conditions (Table 2). Dimensionless Froude and Reynolds numbers quantified flow conditions as subcritical and turbulent, respectively, and were within the ranges reported for riffle habitats of natural small streams (Jowett, 1993; Lamouroux and Jowett, 2005; Schweizer *et al.*, 2007). Estimates of boundary shear stress varied by a factor of 2 and 3 as flow conditions changed from base flow to storm flow in the HBSD and LBLD treatments, respectively (Table 2). The estimated changes in shear stress during storm events were similar to values found to induce invertebrate drift in a natural system (Gibbins *et al.*, 2007), but were not great enough to disrupt the gravel, which was expected.

The shear stress changes did appear to be great enough to resuspend settled solids. This was evident by the changes in turbidity that were measured in response to the flow hydrograph treatments under nonstorm-flow water quality conditions. These data were collected post experiment by placing a turbidity meter in the mesocosm tail tanks to observe the effects of the flow change programming alone on sediment transport potential. The contrasting treatment hydrographs produced significant differences in the turbidity response (Figure 1). The hydrodynamics produced by the LBLD flow change algorithm resulted in changes in turbidity that suggested a higher magnitude and longer duration of sediment resuspension compared with that produced by the HBSD algorithm. In both treatments, the elevated turbidity generated by sediment resuspension was most pronounced when flows were accelerating.

Table 3 describes general water quality characteristics influent to the mesocosms during the experiment. Values for water temperature, DO, conductivity, and pH were similar for all mesocosms, regardless of treatment, and did not differ between mesocosm inflow and outflow. Therefore, water quality changes were driven by the processes affecting the source water supply, and the data provided in Table 3 are for the water influent to all mesocosms, not segregated by treatment. Water temperature declined from mean daily highs of 27.6°C at the beginning to 12.3°C by the end of the study. DO ascribed to a natural daily cycle, and pH showed

TABLE 3. General Water Quality Statistics for Influent to All Mesocosms During the Experimental Period.

Variable	Min	Mean ± 1 SD	Max
Water temperature (°C)	12.2	24.6 ± 4.4	33.3
Conductivity (μS/cm)	188.0	389 ± 33	553.0
pH	7.3	7.8 ± 0.2	8.5
Dissolved oxygen (mg/l)	4.5	7.7 ± 1.1	12.1
Turbidity (NTU)	45	101 ± 56	506

Notes: There were no significant differences between experimental treatments or the water quality recorded by the sensors in the mesocosm tail tanks and the influent monitoring station.
NTU, nephelometric turbidity unit.

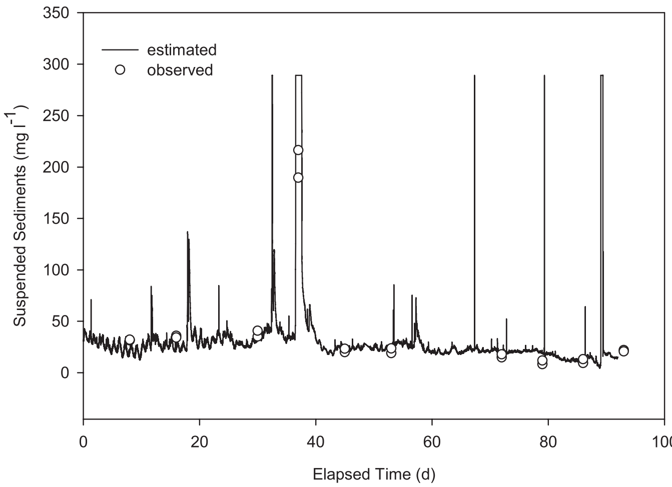

FIGURE 2. Estimated Suspended Sediment Concentrations. SSC was predicted from influent turbidity data using the equation SSC = 0.6388 × Turbidity − 34.511 (r^2 = 0.97) obtained from analysis of weekly grab samples of the ESF influent river water and regressing with turbidity recorded at the time of sampling.

similar diel fluctuations in tune with DO. Conductivity decreased during storm events, with the magnitude of the decrease related to the amount of rainfall. Rainfall-runoff from the hurricane Katrina climate system resulted in a significant decrease in conductivity and a breakdown in the diel cycles for both DO and pH between days 37 and 43.

Suspended sediment concentration-calibrated with turbidity averaged 31 mg/l and the baseline declined slightly over the course of the study (Figure 2). On six separate occasions, the concentration rose above 50 mg/l for longer than a day, with an eight-day period of elevated concentration associated with the events produced by the hurricane Katrina climate system. Estimates of suspended solids loaded to the mesocosms were made using the discharge data, and equated to 435 and 307 kg for the HBSD and LBLD treatments, respectively.

Streambed Sedimentology

Over 85% of the sediments deposited in the sampled gravel trays were <63 μm. Based on the repeated measures ANOVA tests, there was more fine sediment found in the HBSD treatment (Figure 3a), while sediment %LOI, a measure of the organic content of fine sediments, was higher in the LBLD treatment (Figure 3b). Over the course of the study, fine sediment accumulated and sediment %LOI decreased to an asymptote after sampling on day 49. There was a step up in the rate of fine sediment accumulation between the second and third sampling events that

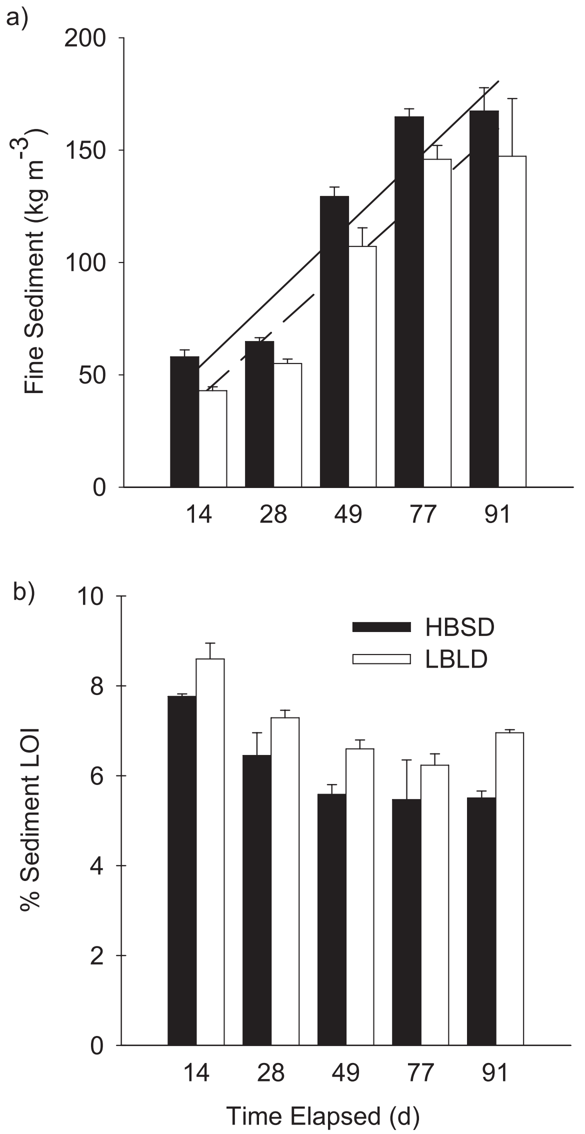

FIGURE 3. Fine Sediments in Mesocosm Gravel Section; p-scores for responses in ANOVA models were (a) Fine Sediment (Treatment, $p < 0.01$; Time, $p < 0.001$; and Treatment:Time, n.s.). (b) Fine Sediment %LOI (Treatment, $p < 0.01$; Time, $p < 0.001$; and Treatment:Time, n.s.).

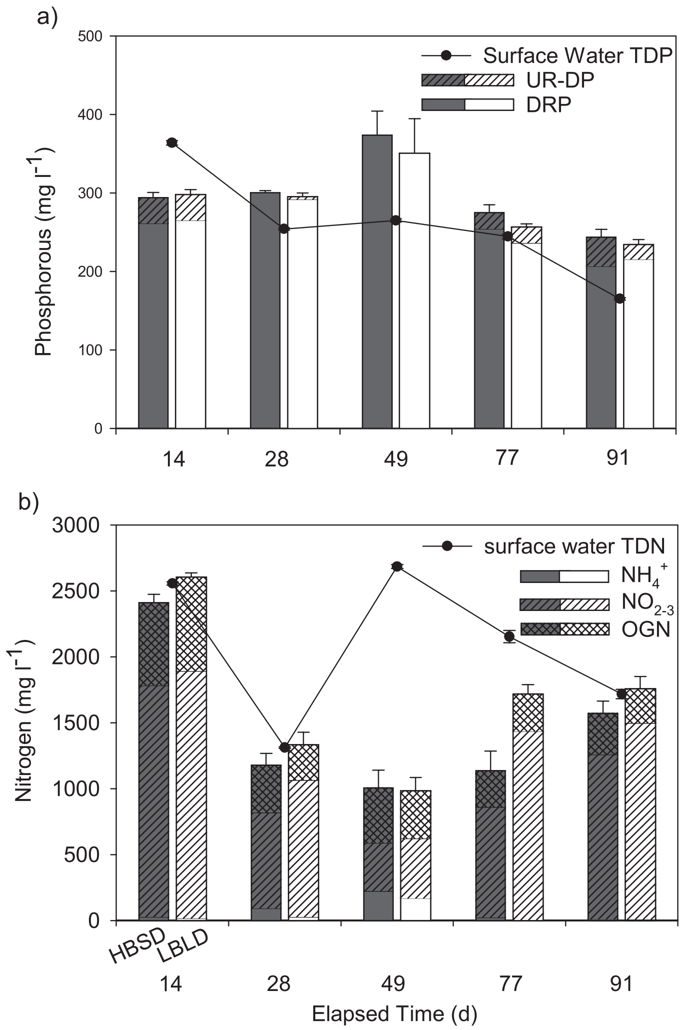

FIGURE 4. Intergravel Nutrients. (a) Phosphorus species in intergravel water. "UR-DP" is unknown reactive dissolved phosphorus; UR-DP = TDP − DRP. (b) Nitrogen species in intergravel water. OGN is dissolved organic nitrogen; OGN = TDN − ($NO_{2\text{-}3}$ + NH_4); p-scores for select ANOVA responses are as follows: intergravel DRP (Treatment, n.s.; Time, $p < 0.001$; and Treatment:Time, n.s.). $NO_{2\text{-}3}$ (Treatment, n.s.; Time, $p < 0.001$; and Treatment:Time, n.s.). NH_4^+ (Treatment, $p < 0.01$; Time, $p < 0.001$; and Treatment:Time, n.s.). Surface water nutrients and intergravel TDP and TDN on any given sampling day were similar between treatments.

coincided with the hurricane Katrina climate system and concomitant high sediment load entering at the ESF intake (Figure 2). Separate linear regressions were applied to the trends in fine sediment accumulation. Comparison tests for the slopes ($t = 0.08$, $df_{n1 + n2\text{-}4} = 56$, $p = 0.94$), and intercepts ($t = 1.87$, $df_{n1 + n2\text{-}4} = 56$, $p = 0.06$) suggested that fines accumulated at the same rate but differed by the amounts that were deposited early in the experiment, by the first sampling date. While the estimated total flux of suspended solids to the HBSD mesocosms was 128 kg higher than that delivered to the LBLD treatment (see previous paragraph), the percentage of the total flux that deposited in the gravel section was slightly higher in the LBLD treatment; 4% of total deposited compared with 3% in the HBSD treatment.

Nutrient Biogeochemistry

The mean inorganic nutrient concentrations influent to all mesocosms generally decreased during the experiment (Figures 4a and 4b). Concentrations of intergravel nutrients changed through time, with the pattern of the change dependent on the nutrient species. Concentrations of intergravel $NO_{2\text{-}3}$ decreased and then increased, while concentrations of DRP and NH_4^+ were opposite of this trend. Furthermore, intergravel $NO_{2\text{-}3}$ concentrations were higher in the LBLD treatment, while intergravel NH_4^+ concentrations tended higher in HBSD treatment (Figure 4b). The trends for TP/TDP and TN/TDN were generally reflective of their DRP and $NO_{2\text{-}3}$ inorganic counterparts, respectively.

Periphyton

Periphyton parameters did not differ significantly between treatments. Chl-*a* decreased and then increased across the five sampling dates (Figure 5a). Periphyton AFDM remained similar across the first three sampling dates, and then increased during the last two sampling dates (Figure 5b). Periphyton molar C/N decreased between days 14 and 49, and then increased (Figure 5c). Overall, periphyton C/N was higher in the HBSD treatment. The ratio of periphyton Chl-*a* to AFDM (data not shown) decreased dramatically between days 14 and 28, and then a slight upward trend was observed for the remainder of the study.

Macroinvertebrates

Thirty-nine invertebrate taxa were collected from the gravel trays during the five sampling dates, including both larval and adult elmid beetles (Table A1). Benthic densities of most invertebrate taxa changed across sampling dates, with the majority of insect taxa decreasing, and oligochaete and mollusk taxa increasing. Cladocera were the most numerically dominant taxa during the first two sampling dates, and then rapidly declined during the last three sampling dates. The ESF experiences seasonally high cladocera densities resulting from water releases from Harsha Lake, a drinking source water reservoir 17.2 km upstream. Because their abundances were similar between treatments and they are more associated with pelagic environments, cladocera densities were excluded from subsequent invertebrate analyses.

Total insect densities declined in all mesocosms for the study period, driven largely by declines in chironomid (Figure 6) and philopotamid caddis fly (Table A1) densities across the five sampling dates. In contrast, mayfly (order Ephemeroptera) densities increased between days 14 and 49, then decreased on days 77 and 91, and were higher in the HBSD mesocosms (Figure 6). While the abundances of insects decreased over the experiment, mollusk and

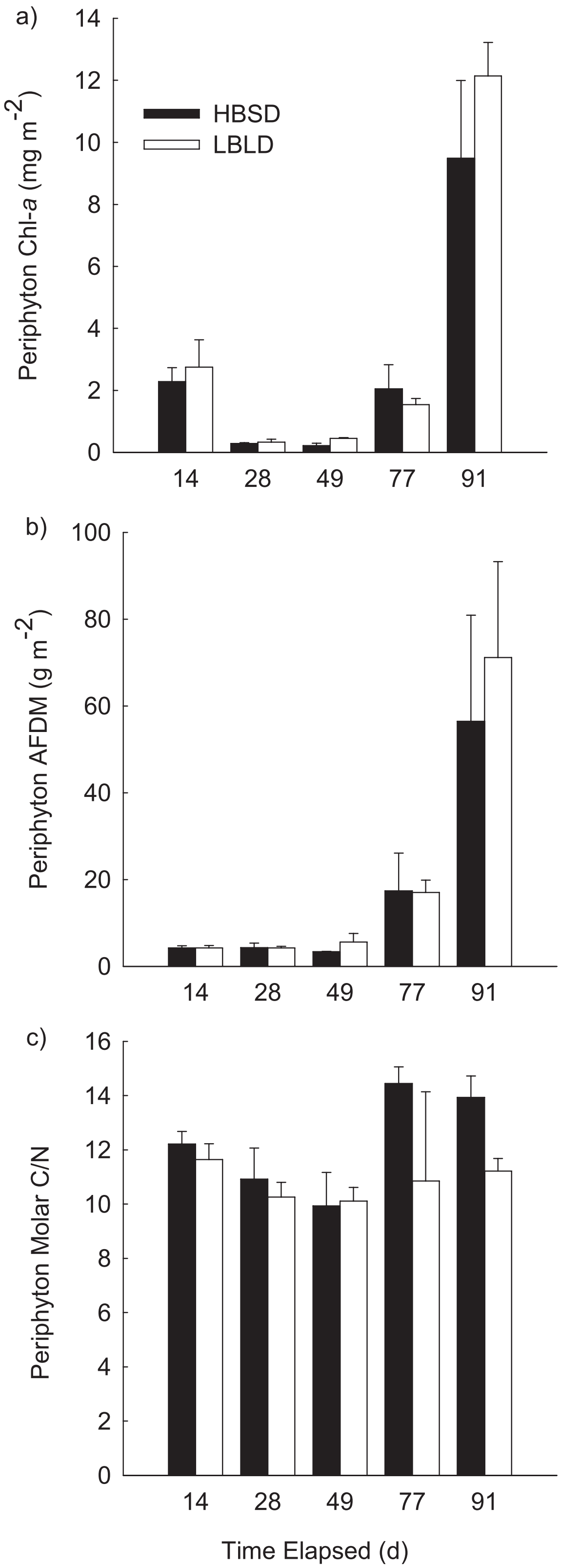

FIGURE 5. Periphyton Responses; *p*-scores for Responses in ANOVA Models Were: (a) Chl-*a* (Treatment, n.s.; Time, $p < 0.001$; and Treatment:Time, n.s.); (b) Ash-Free Dry Mass (AFDM) (Treatment, n.s.; Time, $p < 0.001$; and Treatment:Time, n.s.); and (c) Molar C/N Ratio (Treatment, $p < 0.05$; Time, $p < 0.01$; and Treatment:Time, n.s.).

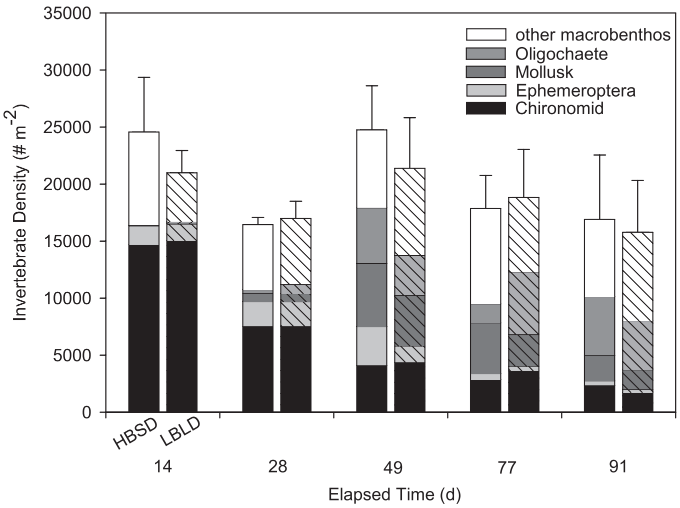

FIGURE 6. Selected Invertebrate Responses; p-scores for Each Response in ANOVA Models Were: Total Density (Treatment, n.s.; Time, $p < 0.05$; and Treatment:Time, n.s.); Oligochaete Density (Treatment, n.s.; Time, $p < 0.05$; and Treatment:Time, n.s.); Mollusk Density (Treatment, n.s.; Time, $p < 0.001$; and Treatment:Time, n.s.); Insect Density, Data Not Shown (Treatment, n.s.; Time, $p < 0.001$; and Treatment:Time, n.s.); Chironomid Density (Treatment, n.s.; Time, $p < 0.001$; and Treatment:Time, n.s.); Ephemeroptera Density (Treatment, $p < 0.05$; Time, $p < 0.001$; and Treatment:Time, n.s.). Data show the relative abundances of insects decreased, while those of mollusks and oligochaetes increased. See Table A1 for information on "other" invertebrates.

oligochaete benthic densities increased, and were higher on the final three sampling dates compared with the first two sampling dates, regardless of treatment (Figure 6).

Analysis of covariance models were used to test the significance of interactions among fine sediments, Chl-a, select invertebrate taxa, and treatment. Total insect benthic densities were negatively correlated to Chl-a concentrations, with Ephemeroptera showing a strong negative relationship ($r^2 = 0.56$), and the slopes of the relationships were similar between treatments (Figure 7a). Total insect benthic densities were also negatively correlated with fine sediment levels, with similar slopes between treatments, as well. The relationship between Ephemeroptera benthic densities and fine sediment concentrations was hump-shaped, showing an increase and then decrease with increasing fine sediment levels (Figure 7b). In contrast, both oligochaete and mollusk benthic densities were positively correlated with fine sediment levels. For oligochaetes, the y-intercept was lower, and the slope of the correlation between benthic densities and fine sediments was steeper in HBSD verses LBLD mesocosms (Figure 7c), while for mollusks, the correlation between benthic densities and fine sediment levels was similar regardless of treatment. Concerns about multicollinearity precluded interpretation

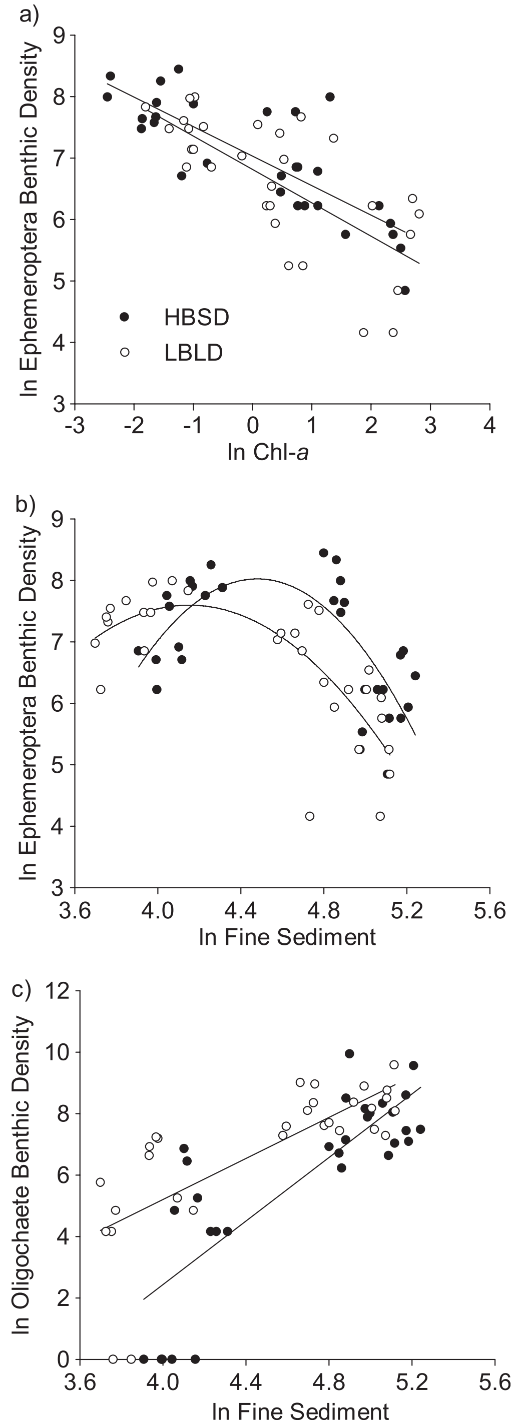

FIGURE 7. Relationships Between Fine Sediments, Chl-a, and Selected Invertebrate Taxa. ANCOVA statistics were based on the model [y = Treatment + x + Treatment:x]. ANCOVA statistics for (c) based on the model [y = Treatment + x + $x2$ + Treatment:x]. ANCOVA results were: (a) Response, Ephemeroptera, Intercept, $p < 0.001$; Treatment, n.s.; Chlorophyll-a, $p < 0.001$; Treatment:Chl-a, n.s.; df = 3,55; adjusted $r^2 = 0.56$; (b) Response, Ephemeroptera, Intercept, $p < 0.001$; Treatment, $p < 0.05$; Fine Sediment, $p < 0.001$; Fine Sediment^2, $p < 0.001$; Treatment:Fine Sediment, $p < 0.01$; df = 4,55; adjusted $r^2 = 0.49$; and (c) Response, Oligochaete, Intercept, $p < 0.001$; Treatment, $p < 0.001$; Fine Sediment, $p < 0.001$; Treatment:Fine Sediment, $p < 0.05$; df = 3,56; adjusted $r^2 = 0.61$.

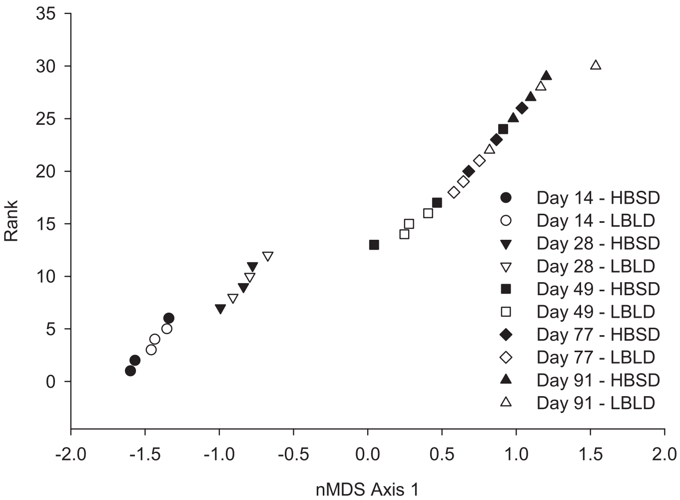

FIGURE 8. One Dimensional (1-D) nMDS Ordination Plot Based on Community-Level Changes in Benthic Invertebrate Densities During the Experimental Period. The r^2 of the regressions between ordination scores and ln transformed fine sediment concentrations and surface water temperatures were 0.88 and 0.76, respectively, suggesting that fine sediment accumulation and seasonal changes, rather than hydrological treatment, were the primary determinants of benthic invertebrate community structure.

of controlling variables on chironomid densities, as fine sediment levels were positively autocorrelated with time and chironomid densities declined steadily over the course of the study.

The majority of the community-level invertebrate variance could be explained by a one dimensional (1-D) nMDS ordination axis (Figure 8). The stress of the final 1-D model was 12.4, and the final instability was 0.0, indicating acceptable levels of each (McCune and Grace, 2002). The r^2 of the correlation between the 1-D ordination values and log-transformed fine sediment concentrations was 0.88, and the r^2 of the correlation between the 1-D ordination values and surface water temperature was 0.76, suggesting that invertebrate communities were most strongly affected by fine sediment accumulation and seasonality. The single axis explained 0.91 of the variability in invertebrate community structure.

DISCUSSION

Achieving experimental control over flow hydrographs in a natural setting is very difficult. Instead one might try to seek out paired watersheds within relative proximity that reflected the desired land use conditions. However, to meet the objectives put forth in this study watersheds would need to be identified that contained detention structure(s) that had been appropriately scaled to meet the theoretical watershed-scale design criteria. Given that current trends in BMP implementation do not tend to follow a prescribed watershed approach (USEPA, 1994, 2005) this proves to be a difficult specification to meet.

Similarly, there are many ecologically relevant factors that change in accordance with altered hydrology that act to confound interpretation in natural settings. For example, SSC is often in excess in urban watersheds (Nietch *et al.*, 2005) either resulting from active and legacy soil disturbances from the development phase (Wolman, 1967; Bartley and Rutherford, 2005) or instream erosion from higher and/or longer duration peak flows postdevelopment (Trimble, 1997). Furthermore, hydrological alteration often coincides with changes in riparian canopy cover, which can affect incident light levels and water temperature (USEPA, 2007). The myriad direct and indirect interacting variables occurring under natural conditions as watersheds urbanize make it difficult to achieve the level of mechanistic understanding required to develop new design criteria for management practices.

The approach then may turn to trying to simulate field conditions in a controlled laboratory setting as was attempted here. The conditions simulated in this mesocosm study it could be argued were akin to comparing a segment of riffle/run habitat in two real streams, both fed by water with the same water quality while differing in flow regime, which was designed to mimic hydrograph shapes observed for predevelopment (HBSD) and postdevelopment with detention BMPs (LBLD). The influent water quality conditions, though fluctuating, held SSC in excess throughout the study. Mesocosm flow rates changed in tune with outside storm conditions to affect fine sediment deposition and resuspension dynamics (Figures 1 and 3), but did not allow for transport of the gravel size fraction (no scour). Furthermore, the potential supply of sediment to the mesocosms through the ESF water delivery system was limited to particles within the size range of fine gravel (ca. ≤6 mm) and smaller; large particle sizes could not be passed through the intake screens or kept in suspension by the delivery system. Admittedly, the combination of sediment supply and hydrology that occurred experimentally was unique in practice, but the conditions controlled for could not be easily produced in the field setting. The ability to precisely regulate flow using the ESF setup allowed for focus on how prescribed variation in lower flows along with measured trends in sedimentology interacted to influence the ecological structure and function of riffle/run habitat.

It was hypothesized that the HBSD treatment, with distinctly higher base-flow velocities and shorter duration of elevated sediment loading that came with the simulated storm flow would produce instream conditions in favor of less fine sediment deposition. In turn, we were interested in testing for effects on nutrient biogeochemistry, periphtyon biomass, and the macroinvertebrate community, which we expected to be characterized by more desirable taxa associated with lower levels of fine sediments (i.e., Ephemeroptera, Plecoptera, and/or Tricoptera [EPT] insect orders) (USEPA, 1996). Contrary to expectations, greater fine sediment was observed in the gravel of the HBSD treatment, and no differences between treatments were found for periphyton. The macroinvertebrate community as a whole did not differ between treatments, though Ephemeroptera densities were higher overall in the HBSD treatment. What appeared most important to the overall structure and function of the mesocosm ecosystems outside of those changes resulting from natural seasonality were (1) the initial mass of fines that infiltrated into the gravel bed, which had a persistent effect on nutrient biogeochemistry and (2) the subsequent fine sediment accumulation rate, which affected the structure of the macroinvertebrae community as the experiment progressed. In the remainder of this discussion a mechanism is proposed for the observed ecosystem effects and finally, the implication these results may have for watershed management are briefly considered.

Fine Sediment Mechanisms

The key observation for the study was the higher fine sediment mass in the HBSD treatment, which was established early on (Figure 3a). With similar SSC influent to both treatments, but differing base flows between them, by the first sampling event, it was estimated that 1.5 times more sediment had been delivered to HBSD compared with LBLD. This could be used to suggest a higher deposition potential. Alternatively, turbidity produced by the flow control algorithms alone (in the absence of storm-flow conditions in the EFLMR) suggested a lower potential and shorter duration for sediment resuspension in HBSD treatment when a storm event was triggered (Figure 1). Therefore, relatively higher sediment loading and less resuspension may favor higher deposition rates in HBSD.

On the other hand, the higher near-bed current velocities of HBSD (Table 2) coupled with the predominantly fine sediment size (85%, <63 μm) may counter the effect of the greater sediment loading by decreasing settling potential relative to LBLD. This appeared to be the case, because even though the total flux of sediment was higher in the HBSD treatment, the percentage of the total flux that deposited in the gravel section was slightly higher in the LBLD treatment. This is consistent with the assumption that higher settling potential produced by the lower base flow of LBLD favored deposition, comparatively. Furthermore, the significantly higher %LOI of the fine fraction in the LBLD treatment (Figure 3b) might be considered a reflection of increased settling rate of lighter organic material, also afforded by the slower base-flow velocities (Kozerski, 2003). But when the LOI fraction is converted to organic matter concentrations (mass per bed volume) by multiplying by fine sediment density, the differences between treatments with respect to organic content are nullified. The difference in %LOI between treatments appeared to be a function of fine particle packing density, and not differences in settling potential.

Collectively, the sediment and flow data suggested that a mechanism directing differences in the degree of fine sediment infiltration and packing into the originally clean intergravel space was at play. A specific stream sediment transport model could not be readily located from the literature that might be used to simulate the observed phenomenon. Although the subject appears to have been broached from the standpoint of fine sediment infiltrating salmon spawning beds (Lisle, 1989), how matrix packing density affects bed motion thresholds (Dancey *et al.*, 2002), how vertical bed packing relates to effective porosity, which correlates with invertebrate habitat quality (Gayraud and Philippe, 2003), and among others, most sediment transport work as it applies to ecology has been addressed from the standpoint of bed stability as a function of initial bed composition and critical shear stress (Whiting and Dietrich, 1990; Buffington and Montgomery, 1997; Whiting *et al.*, 1999; Bledsoe and Watson, 2000; Kaufmann *et al.*, 2008).

The mechanism we propose for the elevated fine sediment density in the mesocosm gravel experiencing the higher base-flow regime is that of fine sediment advection into the gravel void space as the result of downward deflecting flow vectors emanating from the gravel itself. The tendency is to think of objects sitting in a turbulent flow field as generating reverse currents (e.g., eddies) of low flow velocity (or high settling velocity) in a predominantly backward direction. The deflections, however, are multidirectional, including downward when there is underlying void spaces for water to enter. At the scale of the intergravel space, individual pieces of gravel suspended within the homogenous gravel matrix deflect fine sediment-laden flow downward to places of minimal velocity. Water may continue to exchange within these spaces (hyporheic flow) but cohesive sediment particles are more likely trapped. The downward deflective force may act akin to an actuated rod "packing" fine sediment into the void space. The packing density then depends on the time integrated downward driving force for bed infiltration, generated by average current velocities near the bed, and the fine sediment concentration of the flow stream. As the packed layer of fines increases in depth, filling-in the void space, it transgresses into a more active layer of deposition and resuspension governed by the settling mechanics of particles suspended in a fluid (e.g., Stoke's Law) (Hsü, 2004). The data suggested that the difference in packing occurred early in the experiment, within the first 14 days. Subsequently, the stair-step nature observed for fine sediment accumulation rate (Figure 3a) tracked the timing of simulated storm events and the associated influent SSC (Figure 2), but was similar between treatments (similar slopes and different intercepts) (Figure 3a). To override the positive trend in fine sediment accumulation during the study it appeared that shear velocities would need to reach the motion threshold for gravel. Once the gravel begins to move, finer particles packed around it would be exposed to transportable currents, acting to flush fines from the bed, in the manner described by Wilcock (1998, 2004).

Sediment and Nutrient Biogeochemistry

The sediment transport factors controlling the difference in fine sediment packing in the gravel appeared important to nitrogen biogeochemistry. Biogeochemical mechanisms affecting the distribution and concentrations of nitrogen species relate directly to the role streams play in nitrogen sequestration and removal (Peterson *et al.*, 2001; Grimm *et al.*, 2005). The LBLD treatment showed consistently lower NH_4^+ and higher $NO_{2\text{-}3}$ intergravel concentrations across all sampling dates (Figure 4b). This was assumed to be due to differences in bed/water column oxygen exchange (Dahm *et al.*, 1998) that was probably greater in the LBLD gravel sections as a result of less fine sediment packing. For phosphorus, there was no difference between treatments. Although we are not able to infer differences in nutrient turnover rates from this data, we can say that the difference between treatments affected the mechanisms regulating the concentrations for nitrogen species in the gravel, and that this difference appeared to be controlled more by the extent of fine sediment packing in the gravel space than velocity differences near the bed.

Temporal dynamics for both nitrogen and phosphorus species in the intergravel were pronounced during the study, and were generally disconnected from the nutrient trends in surface water (Figure 4). However, it was difficult to determine the controlling factors for the specific trends. For example, NH_4^+ and DRP represent bioavailable nutrient forms, and if limiting to algal growth, their trends may be inversely related to algal biomass. Indeed, this was the case for DRP ($p = 0.018$, $r^2 = 0.52$), which is often limiting in freshwater systems (Dodds, 2003), but not NH_4^+. With respect to NH_4^+, as it covaried with $NO_{2\text{-}3}$ and sediments (density and accumulation rate), we suggest that the temporal trend was a function of exchange rates between the gravel and water column, which would have been regulated by the frequency of storm flow-induced changes in near-bed sediment transport conditions of the active layer (i.e., resuspension and deposition). The ramp upward in sediment accumulation associated with the hurricane Katrina system (starting on the 35th day) coincided with drastic shifts in both intergravel N and P concentrations between the sampling events on days 28 and 49.

Biota Effects

Periphyton metrics appeared to relate to insect densities rather than surface water nutrients, flow regime, or sedimentology. This was despite the fact that natural stream periphyton communities can be extremely susceptible to flow related disturbances, particularly after thick periphyton mats have accumulated, and the resource limited periphyton at the bottom of the mats begin to senesce and become more loosely attached (Hill and Boston, 1991). Many stream periphyton communities are characterized by cycles of colonization, growth, sloughing, and recolonization (Power, 1992). The observed decrease, then increase in periphyton Chl-*a* was reminiscent of a cycle (Figure 5a), but appeared unrelated to differences in flow regimes as it was consistent between treatments. Furthermore, the relatively high periphyton C/N ratios across all sampling dates in this study (10.5-12.5), compared with typical stream periphyton communities (~8.5) (Kahlert, 1998) are suggestive of the retention of senescent material within the periphyton mats, which is consistent with the absence of scouring flows.

Periphyton Chl-*a* was inversely correlated with mayfly benthic densities (Figure 7a), suggesting that these grazers represented a top down control mechanism for the algal community (Rosemond, 1993; Nisbet *et al.*, 1997; Wellnitz and Poff, 2006). As the density of these grazers decreased between the sampling events on days 49 and 77 periphyton Chl-*a* increased. During this timeframe the periphyton community shifted from one dominated by single celled diatoms to a less edible filamentous diatom and green algae-dominated community, consistent with previous observations of periphyton communities following grazer removal (Scrimgeour *et al.*, 1991; Biggs *et al.*, 1998).

Benthic invertebrate densities, in general, were similar between treatments despite the higher discharge, and, therefore, higher delivery rate of invertebrates to the HBSD treatment. This supported the supposition that instream factors, such as habitat quality and food availability, were more important for structuring the communities than immigration potential. Invertebrate community patterns over the study appeared to be influenced by both habitat quality and seasonality, with the relative importance of each varying by taxa.

Mayflies exhibit a strong habitat preference for hard, unembedded, substrate (Kiffney and Bull, 2000). We speculate the sediment accumulation represented a strong controlling factor for these invertebrates, as their numbers increased through day 49, and then decreased in the two sampling events thereafter, as fine sediment levels continued to increase. A previous study observed declines in EPT taxa when benthic sediments increase above a particular threshold level, ~1% (Kaller and Hartman, 2004). If the abrupt decline in Ephemeroptera densities observed between days 49 and 77 were indeed a function of fine sediment levels and not a seasonal effect, then this corresponded to 15% fines. Current velocity preference, also a part of habitat quality (Vieira *et al.*, 2006), emerged as an additional control factor, as the only significant treatment difference observed within the invertebrate community was a higher overall Ephemeroptera density in HBSD mesocosms, including a large difference on day 49 (ANOVA, $F_{1,4} = 27.0$, $p < 0.01$) that was driven largely by differences in Baetidae mayfly densities (Table A1). The near-bed velocities (Table 2) produced at base flow for the HBSD treatment would have been more desirable compared with those found in the LBLD for baetids (Halwas *et al.*, 2005; Hoffman *et al.*, 2006; Vieira *et al.*, 2006). Finally, the change in season from summer to fall may have had a role to play in the decline in Ephemeroptera densities after day 49. However, if this was a dominant controlling factor, then a steady-declining trend with temperature over the study would have been expected, as was observed for Chironomidae (Figure 6).

The declining trend for chironomids occurred even though the majority of chironomid taxa are generalist collector gatherers, and are typically more tolerant to a wide range of habitat quality (Johnson *et al.*, 2003). In addition, many chironomids use filamentous algae for food, shelter, or both (Wootton and Power, 1993), yet chironomid densities did not increase when periphyton Chl-*a* increased 10-fold in the mesocosms. These observations suggest that the decline in chironomid densities was primarily related to seasonal change.

In general, as fine sediments accumulated in the mesocosms, the insect dominated community that initially colonized the channels was replaced by a mollusk and oligochaete dominated community. Benthic densities of oligochaetes and mollusks, which generally prefer soft sediments and, in the case of oligochaetes, consume organic matter deposited within sediments, increased with increasing fine sediments (Figure 7c).

From an ecosystem perspective, although the habitat quality of the HBSD treatment may have been favored initially by taxa within the order Ephemeroptera, treatment effects were minimal, and by the middle of the experiment fine sediment accumulation and the temperature changes occurring with the seasonal shift had acted to replace the insect dominated macroinvertebrate community that maintained periphyton at a relatively low level through grazing, to one dominated by mollusk and oligochaete taxa, which are often associated with high levels of fine sediment. The community-level nMDS analysis (Figure 8) reinforced these notions.

Watershed Management Implications

To guide the development of better watershed management practices the question becomes, how can the interactions between expected hydrologic alteration and sediment transport dynamics be accounted for to protect ecosystem structure and function in design criteria? The range of contrasting flow conditions simulated in this mesocosm study falls within the lower end of the natural flow spectrum for small streams. Much of the work that has contributed to our understanding of how urban hydrologic alterations affect stream ecosystems has focused on the increased frequency and duration of channel-eroding peak flows. Sediment transport formulas focus on thresholds of incipient motion for median or higher bed particle diameters. It has been suggested that stormwater management structures could be engineered to discharge excess water at rates not to exceed these thresholds, thereby being more protective of channel geomorphology, and as corollary, ecology (Finkenbine *et al.*, 2000; Bledsoe and Watson, 2001; Roesner *et al.*, 2001; Pitt and Voorhees, 2003). The results from this study suggest that it may also be necessary to pay consideration to the base-flow condition and lower-end peak flows (i.e., those produced by small storms), especially if fine suspended solids are in excess in the supply. This is not an uncommon case for urban areas especially where active construction is taking place (Pitt *et al.*, 2007). To put the relative importance of both the low end flows and scouring peak flows into perspective, especially under conditions of excess SSC, the full range and exceedence frequency of motion thresholds for bed-load transport would need to be simulated for natural streambeds (e.g., Torizzo and Pitlick, 2004), along with mechanisms that account for the dynamics of fine SSC in the supply.

The importance of fine sediment flushing from gravel beds has been considered from a fish spawning habitat perspective (Lisle, 1989; Ryan, 1991; Kaufmann *et al.*, 1999). At the microhabitat scale, a particle within the gravel size range may only have to move a short distance (e.g., one roll) to expose finer particles packed around it to full transport velocities, thereby preserving habitat quality of the bed while not removing it entirely. Sediment transport models that can account for both coarse and fine sediment fractions, both in the bed and in the supply, and that facilitate the study of flow thresholds for the initial movement of gravel compared with the total transport thereof could play an important role in linking habitat quality to the design of better management practices. For example, the partial sediment transport models under development by Wilcock and others (Wilcock, 1998; Haschenburger and Wilcock, 2003) may be a key to effective flow control designs.

CONCLUSIONS

Differences in base-flow velocity between two contrasting hydrograph treatments appeared to control the relative density of fine sediment packing that occurred in an initially clean gravel bed. A suggested mechanism for the density difference required a mechanism for differential advection of fines into the bed matrix, which is separate from the more typical Stokes'-type settling velocity for sediment deposition. Once the depth of the packed sediment layer transgressed into an active deposition and resuspension layer the rates of change from base flow to storm flow and the magnitude and duration of storm flow studied were of no consequence to subsequent fine sediment accumulation. Near-bed velocities never generated enough shear to move coarse gravel, and this appeared requisite for flushing accumulating fines as long as high suspended sediments persisted in the base-flow condition. The initial differences observed for fine sediment packing density between treatments affected the distribution of nitrogen species in the bed, presumably via an affect on oxygen exchange necessary for the conversion of ammonia to nitrate. No substantial consequences of the contrasting flow regimes could be discerned for biotic structure and function. Regardless of treatment, fines accumulated in the absence of scouring/sediment flushing flows and the invertebrate community trended toward one dominated by taxa preferring softer beds. For better urban watershed management, flow control designs may need to consider the lower end of the natural flow range when excess fine sediment loading is expected; a partial transport model for gravel beds may be key. This mesocosm study helped to better define the mechanisms controlling fine sediment accumulation in clean gravel beds under contrasting flow regime dynamics, and in the absence of flows that would force gravel into transport.

APPENDIX

TABLE A1. Benthic Densities (# individuals/m^2) of Macroinvertebrate Taxa Colonizing Gravel Trays.

	Aug 8, 2005		Aug 22, 2005		Sep 12, 2005		Oct 10, 2005		Oct 24, 2005	
Taxon	HBSD	LBLD	HBSD	LBLD	HBSD	LBLD	HBSD	LBLD	HBSD	LBLD
Non-Insects										
Hydrozoa	11	0	0	11	32	63	11	0	0	74
Nematoda	42	32	42	116	63	315	546	850	420	1,050
Nemertia	0	0	0	0	168	84	672	609	567	294
Turbellaria	0	0	11	21	724	787	1,785	1,491	1,606	787
Clitella (oligocheata)	11	95	336	798	4,871	3,506	1,890	5,490	5,175	4,314
Mollusca										
Corbicula	53	11	483	283	1,207	640	1,197	420	840	682
Ancylidae	0	0	32	158	4,209	3,443	1,995	1,554	1,029	682
Physidae	11	116	137	283	126	367	63	283	0	53
Planorbidae	0	0	0	0	0	0	0	11	0	0
Lymnaidae	0	0	0	0	0	0	0	32	11	0
Crustacea										
Cladocera	41,276	47,868	84,650	98,255	3,496	12,083	210	409	63	84
Copepoda	1,764	1,144	2,152	1,449	367	252	116	137	95	74

TABLE A1. (Continued)

Taxon	Aug 8, 2005		Aug 22, 2005		Sep 12, 2005		Oct 10, 2005		Oct 24, 2005	
	HBSD	LBLD	HBSD	LBLD	HBSD	LBLD	HBSD	LBLD	HBSD	LBLD
Amphipoda	0	0	0	0	0	11	21	0	0	11
Ostracoda	1,302	724	1,858	2,068	1,659	2,026	682	1,008	567	1,249
Non-Insect Arthropods										
Thyasidae	21	0	0	0	11	0	0	0	0	11
Collembola	0	0	0	11	21	21	0	11	42	11
Insects										
Coleoptera										
Elmidae-larvae	168	147	556	399	3,643	2,131	2,184	1,113	2,624	3,160
Elmidae-adult	32	21	0	0	11	0	21	11	32	42
Hydrophilidae	0	0	0	0	11	0	11	0	0	0
Psephenidae	0	0	0	0	21	0	11	0	11	0
Diptera										
Ceratopogonidae	21	11	11	74	32	84	53	74	74	95
Chironomidae	14,686	15,043	7,537	7,537	4,115	4,388	2,719	3,611	2,341	1,732
Simuliidae	63	84	0	11	0	0	0	0	0	0
Tipulidae	0	0	32	0	0	21	11	11	11	11
Ephemeroptera										
Baetidae	1,281	1,092	1,522	913	1,543	441	32	32	11	0
Caenidae	74	84	189	472	63	32	0	0	0	0
Heptageniidae	147	84	231	388	651	367	84	116	105	42
Isonychiidae	0	0	11	11	21	0	0	0	11	11
Tricorythidae	147	199	210	304	682	535	399	262	283	210
Odonata										
Coenagrionidae	0	32	21	11	11	11	0	11	11	21
Plecoptera										
Unknown Plecoptera	0	0	21	42	0	0	0	0	0	21
Perlidae	11	0	0	0	53	32	53	32	21	11
Perlodidae	0	0	0	0	0	0	0	0	11	0
Tricoptera										
Brachycentridae	0	11	0	0	0	0	0	0	0	0
Hydropsychidae	325	179	42	63	53	74	0	11	21	42
Hydroptilidae	0	53	42	32	0	11	0	0	95	42
Leptoceridae	0	21	32	11	32	11	0	0	0	0
Philopotamidae	4,367	1,764	766	1,407	367	1,669	336	661	158	462
Polycentropodidae	21	53	11	21	0	21	0	0	0	0
Rhyacophilidae	11	0	11	0	0	0	0	0	53	0

Notes: HBSD, higher base flow/shorter duration; LBLD, lower base flow/longer duration.
Densities were averaged across three replicate mesocosms for particular taxa on each of the five sampling dates in 2005.

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