

EVALUATING THE EFFECTS OF CULVERT DESIGNS ON ECOSYSTEM PROCESSES IN  
NORTHERN WISCONSIN STREAMSJ. C. OLSON<sup>a,b</sup>, A. M. MARCARELLI<sup>a\*</sup> , A. L. TIMM<sup>c</sup>, S. L. EGGERT<sup>d</sup> AND R. K. KOLKA<sup>d</sup><sup>a</sup> Department of Biological Sciences, Michigan Technological University, Houghton, Michigan USA<sup>b</sup> Department of Civil and Environmental Engineering, Wayne State University, Detroit, Michigan USA<sup>c</sup> Northern Research Station, USDA Forest Service, Baltimore, Maryland USA<sup>d</sup> Northern Research Station, USDA Forest Service, Grand Rapids, Minnesota USA

## ABSTRACT

Culvert replacements are commonly undertaken to restore aquatic organism passage and stream hydrologic and geomorphic conditions, but their effects on ecosystem processes are rarely quantified. The objective of this study was to investigate the effects of two culvert replacement designs on stream ecosystem processes. The stream simulation design, where culverts accommodate bankfull width and streambeds are re-constructed through the culvert, was compared with the bankfull and backwater design, where streambeds were left to fill naturally, as well as to non-replaced culverts. We predicted that stream simulation culverts would best preserve water velocity and coarse particulate organic matter (CPOM) retention within the culvert relative to upstream reaches, and that both replaced culvert styles would exhibit rates closer to upstream reaches than non-replaced culverts. In addition, we predicted that ecosystem processes (CPOM retention, transient storage and nutrient uptake) would be similar in reaches upstream and downstream of both replaced culvert styles, because both designs are constructed to maintain stream slopes and bankfull widths through the structure. We found that stream simulation design better maintained CPOM retention through culverts compared with non-replaced and bankfull and backwater design culverts, but observed no differences in ecosystem processes between reaches located upstream or downstream of replaced culverts. Although the stream simulation design requires additional streambed construction relative to the bankfull and backwater design, this step may lead to additional improvement if maintaining ecological conditions through the culvert is an important restoration goal. Copyright © 2017 John Wiley & Sons, Ltd.

KEY WORDS: culvert replacement; stream simulation design; bankfull and backwater design; restoration; monitoring; nutrient uptake; transient storage; coarse particulate organic matter

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## INTRODUCTION

In the Great Lakes region, 64% of dams and road crossings are impassable or partially passable to aquatic organisms, with 74% of road crossings classified as barriers in some watersheds (Diebel *et al.*, 2014; Januchowski-Hartley *et al.*, 2013). Road crossings and culverts can fragment populations by acting as barriers to the movement of aquatic organisms, primarily by altering the physical structure of stream channels and causing deviations from natural flow conditions that affect organisms differentially depending on their life histories and swimming ability (Blakely *et al.*, 2006; Bouska and Paukert, 2010; Warren and Pardew, 1998). Culverts can also alter geomorphic characteristics within, upstream and downstream of the structures. Culverts that obstruct natural flow conditions can retain fine sediments during high discharge events, increase accumulation

of fine sediments downstream or upstream of culverts (Bouska *et al.*, 2010; Lachance *et al.*, 2008; Wellman *et al.*, 2000) and influence the organic matter content of sediments upstream of culverts (Lachance *et al.*, 2008). For example, some box-type culverts in Kansas have deeper mean bankfull depths and smaller width-to-depth ratios compared with natural stream channels, and riffle spacing is closer in stream reaches downstream of these culverts relative to those upstream (Bouska *et al.*, 2010). These effects can transmit beyond the reaches immediately adjacent to the culverts. For example, Lachance *et al.* (2008) found that sediment accumulation was elevated for up to 1.4 km downstream of culverts. Consequently, culvert replacement is a widespread focus of restoration activity around the USA (Gillespie *et al.*, 2014; Januchowski-Hartley *et al.*, 2013; Price *et al.*, 2010).

The US Department of Agriculture, Forest Service (USFS) has implemented culvert replacement projects to alleviate the negative effects to physical processes and stream biota caused by poorly designed or undersized culverts (SSWG, 2008). The USFS's preferred approach for culvert

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replacement on all fish-bearing streams is the stream simulation design, which is designed to mimic the natural stream dimensions and streambed with goals of improving aquatic organism passage, geomorphic continuity and flood resiliency (Cenderelli *et al.*, 2011; Gillespie *et al.*, 2014; SSWG, 2008). Key components of the stream simulation design are considering the alignment of the stream and culvert relative to the road, maintaining a consistent streambed slope through the culvert, creating a culvert that is equal or greater than bankfull width to maintain the cross-sectional shape of the stream and recreating a streambed that matches the size and arrangement of bed material naturally found in adjacent or nearby reference stream reaches (Cenderelli *et al.*, 2011). Although they can cost 20–30% more to install than other replacement designs, stream simulation culverts have sufficient capacity to pass water and debris for a 100- to 500-year flood, thereby increasing their expected lifespan and decreasing maintenance costs to almost zero (Barnard *et al.*, 2015; Cenderelli *et al.*, 2011; Gillespie *et al.*, 2014). In the upper Great Lakes region, an alternative replacement style called the bankfull and backwater design (hereafter referred to as the bankfull design) has been implemented in some low-gradient locations (Dale Higgins, personal communication, 2015). In this style, the culvert design follows most principles of the stream simulation design such as maintaining streambed slope and including the bankfull channel, but rather than rebuilding the streambed, substrates within the culvert are allowed to fill via natural stream flows.

Similar to most stream restoration efforts, studies that evaluate the ecological effects of culvert replacements by pre-replacement and/or post-replacement and long-term monitoring are rare. Roni *et al.* (2008) surveyed 345 studies that reported the physical and biological effectiveness of stream rehabilitation projects, and only five described culvert replacement projects, all of which reported that previously inaccessible stream reaches upstream of culverts were readily recolonized by fish after replacement. Moreover, ecosystem processes have been more widely integrated in post-restoration monitoring over the past decade because these processes integrate across the responses of individual organisms and therefore may offer valuable insights that are missed by only monitoring the biota. Examples of ecosystem processes that have been applied for monitoring the effect of stream restorations include retention of coarse particulate organic matter (CPOM; organic particles larger than 1 mm including woody and non-woody debris; Lepori *et al.*, 2005; Rosi-Marshall *et al.*, 2006), transient storage characteristics (Becker *et al.*, 2013; Bukaveckas, 2007) and nutrient uptake (Hoellein *et al.*, 2012). Because culverts alter the physical and biological structure of streams within as well as upstream and downstream of the culvert structures, it is possible that ecosystem processes may be useful indicators of their effects, but they

have rarely been considered in studies of culvert effects or responses following culvert restoration or replacement.

The overall goal of this study was to evaluate the effects of stream simulation and bankfull culvert designs on ecosystem processes in northern Wisconsin streams. For this study, we considered two different comparisons for how culverts may affect ecosystem processes. First, hydrologic and geomorphic conditions within culverts due to different designs (non-replaced, stream simulation and bankfull) may alter ecosystem processes within the culverts. We hypothesized that CPOM retention and water velocity measured within stream simulation culverts, where streambeds were rebuilt, would be most similar to those measured in upstream reaches, while they would be less similar in bankfull culverts and least similar in non-replaced culverts. Second, culverts may alter ecosystem processes in upstream and downstream reaches by altering hydrologic or geomorphic conditions through the culvert, and these effects may transmit over tens to hundreds of metres (Lachance *et al.*, 2008). We hypothesized that ecosystem processes measured at reach scales (CPOM retention, transient storage and nutrient uptake) would be similar upstream and downstream of both stream simulation and bankfull design culverts, as both designs accommodate a range of flows and do not constrict the bankfull channel.

## MATERIALS AND METHODS

### *Study sites and design*

Study sites were located in northern Wisconsin on the Chequamegon-Nicolet National Forest (Table I, Figure 1). The streams were located in northern mesic forests with sugar maple (*Acer saccharum*), eastern hemlock (*Tsuga canadensis*) and yellow birch (*Betula alleghaniensis*) established on predominately loamy or silty soils. Riparian vegetation was dominated by speckled alder (*Alnus incana*). The streams in the Washburn District flow into rivers that reach Lake Superior, the Medford District streams are located in the headwaters of the Mississippi River drainage and streams in the Eagle River District flow into rivers that reach Lake Michigan. Sites in the Eagle River District were largely located within the Pine and Popple watersheds, where prior analyses have shown that mean connectivity for stream reaches is 58% due to road crossings and dams that act as barriers to fish movement (Diebel *et al.*, 2014). The hydrologic regime of these streams is typical of those in the upper Midwestern USA, with a spring snowmelt peak, followed by a flashy storm-driven pattern in summer and fall and baseflow conditions during the winter (e.g. USGS monitoring station 04063700—Popple River near Fence, WI; <http://waterdata.usgs.gov/usa/nwis/>).

Table 1. Location, culvert characteristics and physical characteristics of the 15 study streams in 2013

Stream	District	Latitude	Longitude	Culvert type	Culvert length (m)	Discharge (L s <sup>-1</sup> )	Width (m)	Depth (m)
Preemption	Washburn	46.32818	-91.08728	Stream simulation	17	61	2.2	0.14
Whiskey	Washburn	46.30185	-90.91581	Bankfull and backwater	19	26	1.6	0.12
Joseph's	Medford	45.18215	-90.66065	Stream simulation	33	73	3.3	0.12
John's	Medford	45.18702	-90.91581	Bankfull and backwater	20	83	2.6	0.10
Popple tributary	Eagle River	45.79112	-88.68354	Stream simulation	18	447	5.4	0.24
Popple tributary	Eagle River	45.78059	-88.69206	Bankfull and backwater	10	392	4.3	0.29
Armstrong	Eagle River	45.64093	-88.44647	Stream simulation	27	191	5.8	0.40
Armstrong	Eagle River	45.65825	-88.47915	Non-replaced	33	87	3.6	0.34
Chuck's	Eagle River	45.96819	-88.67518	Non-replaced	25	18	1.5	0.34
Coldwater	Eagle River	45.83197	-88.69624	Bankfull and backwater	10	50	2.0	0.12
Duck	Eagle River	45.98114	-88.65333	Stream simulation	44	15	1.4	0.09
Gasparado	Eagle River	45.96789	-88.74136	Non-replaced	25	39	2.1	0.18
Kingstone	Eagle River	45.84748	-88.74287	Non-replaced	13	75	4.2	0.31
LillyPad	Eagle River	45.93664	-88.77200	Bankfull and backwater	12	24	2.9	0.19
Wisconsin	Eagle River	45.97665	-88.60285	Bankfull and backwater	15	45	1.8	0.23

Discharge measurements were collected on the same day or within one day of measuring CPOM retention, and width and depth reported here were measured on the discharge transect. All study streams were included in the upstream-downstream comparison, while the first six streams were the paired streams included in the culvert type comparison.

In the 'culvert-type comparison', we sought to determine whether ecosystem processes within replaced culverts were different from those within non-replaced culverts relative

to conditions in upstream reaches. We selected 15 culverts to include in this study (five stream simulation, six bankfull and four non-replaced culverts; Table I; Figure 1). Non-

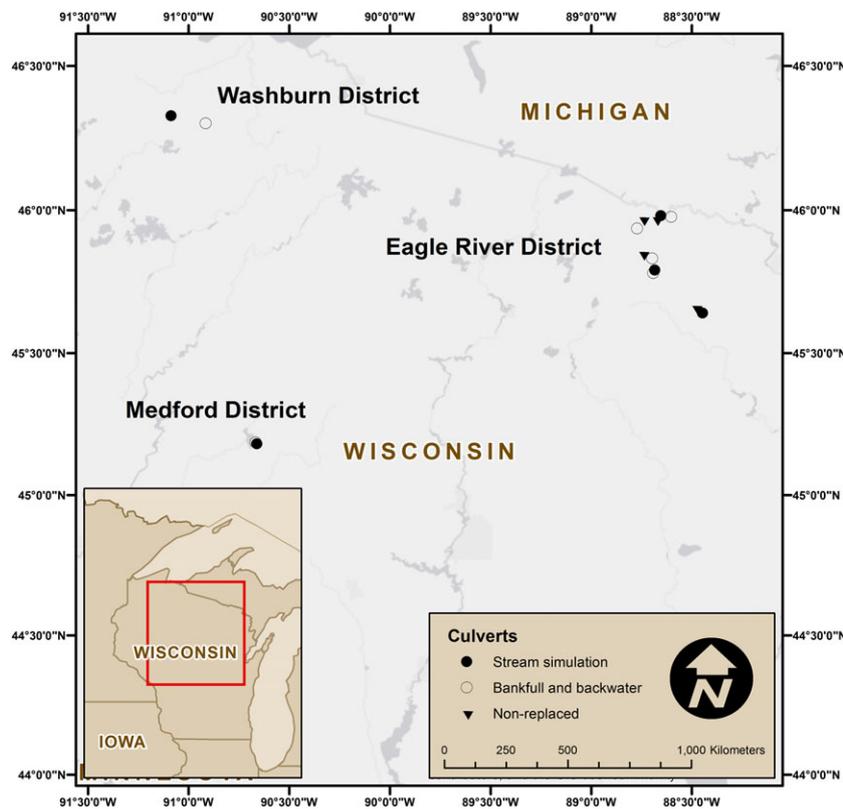


Figure 1. Location of study sites in northern Wisconsin. Two stream sites (one each stream simulation and bankfull and backwater design culverts) were located in the Washburn and Medford districts (points overlapping in Medford), while 11 sites (four non-replaced, three stream simulation and four bankfull and backwater culverts) were located in the Eagle River district. See Table I for stream names within each region, precise location information for each stream site and culvert characteristics. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

replaced culverts were defined as any culverts that were at least 20 years old and did not have upstream pond or wetland formation that would prevent reach-scale measurement of ecosystem processes. We selected four culverts that met these criteria for this study: two were concrete pipes and two were large corrugated culverts. Upstream reaches were established upstream of any obvious hydrologic or geomorphic alterations from the culvert. For this comparison, we focused on processes that could be measured within culverts: CPOM retention as a measure of how key organic matter energy sources are retained in a reach, which is necessary for incorporation into food webs (Wallace *et al.*, 1997), and water velocity as an indicator of overall hydrologic conditions.

In the 'upstream–downstream comparison', we quantified ecosystem processes upstream and downstream of replaced culverts. We selected three pairs of stream simulation and bankfull culverts based on proximity to each other and similarity in stream width and depth. All streams were also included in the culvert-type comparison (Table I). For this comparison, we measured three ecosystem processes: CPOM retention as in the culvert-type comparison; transient storage, or the temporary delay in downstream movement of water in areas outside of the main channel as a measure of surface–subsurface exchange capacity (Runkel, 1998, 2002); and ammonium uptake as a metric of biotic and abiotic nutrient retention (Webster and Valett, 2006). We could not quantify these last two processes for the within-culvert comparison because culvert lengths were too short ( $21.1 \text{ m} \pm 9.8 \text{ SD}$ ; Table I) to apply the measurements techniques (typical required reach length = 50–400 m based on discharge). Non-replaced culverts were not included in the upstream–downstream comparison because of logistical and funding constraints.

#### Field and lab methods

*Coarse particulate organic matter retention.* Coarse particulate organic matter retention using leaf analogues was measured for the culvert-type comparison in August 2013 and the upstream–downstream comparison in May/June 2013. CPOM retention was measured by conducting short-term releases of equilateral triangles (sides ~4 cm long) made of computer paper as leaf analogues. A known number of leaf analogues (100–200) were released at the top of a reach for each CPOM release. Upstream and downstream reach lengths were defined as approximately 10 times the wetted width downstream of the release location (15–100 m), while culvert reaches were defined by the upstream and downstream ends of the culvert. A block seine was stretched across the stream at the bottom of the reach and/or the mouth of the culvert to catch the paper leaf analogues still in transport and

deployed for about 1 h after release or until paper transport ceased (Lamberti and Gregory, 2006). The analogues that were captured in the seine at the end of the reach were counted. In addition, the reach was divided into 5- to 10-m intervals and searched for retained leaf analogues. The location of retained analogues and the object that retained them were recorded. Because not all retained analogues could be found within a reach, the number of leaf analogues in transport at each interval ( $P_d$ ) was estimated proportionally based on the ratio of the number of analogues found at a given stream distance over the total number of analogues found. We then estimated the instantaneous retention rate ( $k$ ) by fitting an exponential decay function as described in Lamberti and Gregory (2006).

Generally, researchers compare between reaches and streams using instantaneous retention rates. However, discharge was different between sites and sometimes between reaches on the same stream if CPOM releases could not be completed on the same day due to weather or time limitations. Higher discharge can result in longer transport distances that may inaccurately appear to be lower CPOM retention if not accounted for. Therefore, we normalized retention for discharge by calculating deposition velocity ( $V_{dep}$ ,  $\text{L T}^{-1}$ ), *sensu* Webster *et al.* (1999):

$$V_{dep} = \frac{u \cdot h}{1/k} \quad (1)$$

where  $u$  is average water velocity ( $\text{L T}^{-1}$ ) and  $h$  is average depth (L).

*Water velocity and transient storage.* Field measurements to estimate water velocity and transient storage dynamics were completed in August 2013 for the culvert-type comparison and in May/June 2013 for the upstream–downstream comparison. We conducted salt releases within culverts and in all upstream and downstream reaches by deploying one YSI 6920 V2 multiparameter sonde equipped with a 6560 conductivity/temperature probe ~20 m downstream of the location of the salt release and a second similar sonde at the downstream edge of the reach. The length of the reach was determined to target a travel time of ~45 min unless being conducted through a culvert, in which case the sondes were deployed within a few metres of the upstream and downstream ends of the culvert. 1–1.5 kg of sodium chloride per  $100 \text{ L sec}^{-1}$  of discharge was dissolved in a bucket of stream water, and this solution was then released while sondes recorded conductivity at 5 s and 1 min intervals for the upstream and downstream sonde, respectively. The upstream sonde was given shorter intervals because the salt mass moves through in a shorter length of time as it has not dispersed yet at the upstream

edge of the reach. Breakthrough conductivity curves, created by the moving salt mass, were used to calculate travel times based on the time between peak concentration of upstream and downstream conductivity probes. Travel times were then used to calculate average water velocities throughout the reach as travel time divided by reach length.

The conductivity curves collected in reaches upstream and downstream of culverts were used to model transient storage characteristics using the one-dimensional transport with inflow and storage (OTIS) model and its modified automated parameter estimation version (OTIS-P) (Runkel, 1998). This model describes the physical processes that affect salt concentrations such as advection (downstream transport of a solute), dispersion (spreading of a solute mass via diffusion and velocity variations due to shear stress) and transient storage (for detailed explanation of the model and equations, see Runkel, 1998). For this study, we were particularly interested in the parameters  $D$  (dispersion coefficient,  $L^2 T^{-1}$ ),  $A$  (main channel cross-sectional area,  $L^2$ ),  $A_s$  (storage zone cross-sectional area,  $L^2$ ) and  $\alpha$  (storage zone exchange coefficient,  $T^{-1}$ ). These parameters help to describe how flow paths may change between stream reaches by describing the storage zone, the main channel and interactions between both. To facilitate comparisons in transient storage between reaches, we also derived the ratio of storage zone cross sectional area to channel cross sectional area ( $A_s/A$ ), storage zone residence time ( $T_{sto}$ , T; Thackston and Schnelle, 1970) and hydraulic retention factor ( $R_h$ ,  $TL^{-2}$ ; Morrice *et al.*, 1997), where the last two metrics are indicative of the amount of time an average salt molecule spends in storage. When completing the hydrologic modelling, we discovered gaps in logging caused by wipers on the sonde sensors that caused the upstream sondes to sometimes miss the leading edge and peak of the conductivity curve, which passed very quickly. This resulted in upstream curves at some sites with different areas than the downstream curves from the same release, which violated a central assumption of OTIS and resulted in no model solution. Therefore, we instead simulated the upstream curve as a 5-s (near instantaneous) conductivity peak at the point of release, where the height of the upstream curve was determined by dividing the area of the downstream curve by 5 s. The upstream curves were simulated for all study sites to insure comparability of the estimates across all sites.

**Nutrient uptake.** Ammonium uptake velocities ( $V_f$ ) were estimated upstream and downstream of each culvert using whole-stream nutrient injections in June 2013. Ammonium uptake was measured using standard nutrient spiralling techniques (Stream Solute Workshop, 1990; Webster and Valett, 2006). A solution of Rhodamine WT (conservative tracer), ammonium chloride and stream water was continuously released at the top of the reach using a fluid

metering pump. The pump dripped the solution at  $\sim 100 \text{ mL min}^{-1}$ , and the concentration in the solution was adjusted accordingly with discharge so that concentrations of ammonium were elevated by  $\sim 10 \mu\text{g N L}^{-1}$  above the background concentration in the stream. Reach lengths were adjusted to achieve  $\sim 45$  min of travel time when possible (50–400 m depending on discharge). Prior to initiating the nutrient release, water samples were collected from seven sampling stations downstream of the pump and analysed for background concentrations of  $\text{NH}_4\text{-N}$ . Water was sampled again at all sampling stations once the conservative tracer concentrations reached a plateau (no change in rhodamine WT concentrations over  $\sim 5$  min) at the furthest downstream station. Rhodamine WT concentrations were analysed using a Turner Aquafluor handheld fluorometer.  $\text{NH}_4\text{-N}$  concentrations were determined following Taylor *et al.* (2007) using the light sensitive orthophthaldialdehyde (OPA) method. Ammonium and Rhodamine WT samples were processed within 6 h of collection in the field. We then calculated the overall uptake coefficient ( $k_c$ ) and uptake length, or the average distance travelled by a solute before it is removed from solution ( $S_w$ , L), following standard equations described in Webster and Valett (2006). Because  $S_w$  is influenced by changes in stream discharge as well as biotic uptake (Webster and Valett, 2006), we also calculated  $V_f$  ( $LT^{-1}$ ), which is an estimate of the velocity at which a nutrient atom travels to immobilization in the stream and is more appropriate for comparisons across streams with different discharges:

$$V_f = \frac{u * h}{S_w} \quad (2)$$

where  $u$  is average water velocity ( $LT^{-1}$ ) and  $h$  is average depth (L).

#### Statistical analyses

Both the culvert-type and the upstream–downstream comparisons were analysed using two-way analysis of variance (ANOVA). For the culvert-type comparison, fixed factors were reach (upstream and through culvert) and culvert type (stream simulation, bankfull and non-replaced), with stream as a random factor. The response variables compared were CPOM  $V_{dep}$  and water velocity. For the upstream–downstream comparison, fixed factors were reach (upstream and downstream) and culvert type (stream simulation and bankfull), with stream as a random factor. The response variables compared were CPOM  $V_{dep}$ , transient storage parameters ( $D$ ,  $A_s$ ,  $\alpha$ ,  $A_s/A$ ,  $T_{sto}$ ,  $R_h$ ) and ammonium  $V_f$ . To meet ANOVA assumptions of normality we log transformed water velocity, CPOM  $V_{dep}$ ,  $D$ ,  $A_s$ ,  $A_s/A$ ,  $T_{sto}$  and  $R_h$  before

analyses;  $\alpha$  and ammonium  $V_f$  did not require transformation. Alpha values were set at 0.05 for all two-way ANOVAs. When two-way ANOVAs revealed significant interactions between reach and culvert type, we conducted post hoc *t*-tests to evaluate differences between study reaches within each culvert type; for these tests, all alpha values were Bonferroni corrected. All statistics were completed using R statistical software (R Core Team, 2013).

## RESULTS

### Culvert-type comparison

For the culvert-type comparison, we expected that CPOM retention and water velocities would be most similar between upstream and through reaches for stream simulation culverts, less similar for bankfull culverts and least similar for non-replaced culverts. For upstream reaches of all culvert types, 43–53% of released leaf analogues were retained in the study reach, and wood and rocks were the objects that most commonly retained leaf analogues (Figure 2). We found that CPOM  $V_{dep}$  decreased, and therefore CPOM retention increased, in all culvert types relative to upstream reaches, and the interaction effect between reach and culvert design was significant using a two-way ANOVA (Table II). CPOM  $V_{dep}$  decreased the least in stream simulation culverts

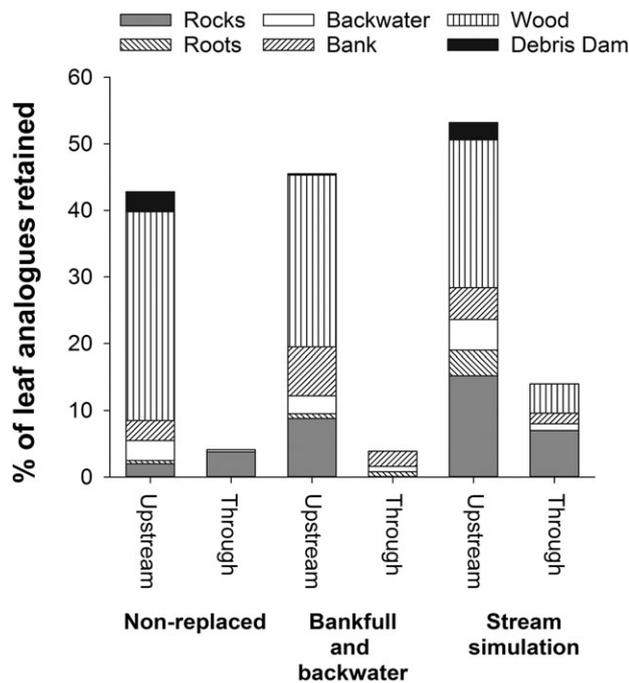


Figure 2. Per cent of leaf analogues retained by different substrates in the upstream and through culvert reaches in the culvert-type comparison. Analogues not retained on these substrates were transported through and recovered at the downstream end of the reach

(74.0%) and was not significantly different between the upstream and within-culvert reaches (post hoc *t*-test  $t_{1,8} = 1.73$ ,  $p = 0.12$ ). In contrast, CPOM retention significantly decreased 98% through bankfull (post hoc *t*-test  $t_{1,10} = 5.68$ ,  $p = 0.0002$ ) and 99.5% through non-replaced (post hoc *t*-test  $t_{1,4} = 4.82$ ,  $p = 0.0085$ ) culverts (Figure 3). Within culverts, rocks were the most common substrate retaining leaf analogues in non-replaced (3.8%) and stream simulation culverts (7.0%), while the bank was the most common feature retaining leaf analogues in bankfull culverts (2.3%). Wood also was a key retentive feature in stream simulation culverts, increasing the overall retention of leaf analogues to 14% in these culverts relative to ca. 4% in non-replaced and bankfull culverts (Figure 2). Contrary to our hypothesis, we found that stream water velocity decreased 33.8% through bankfull culverts compared with upstream reaches, but increased 16.7% and 66.1% through non-replaced and stream simulation culverts, respectively. The interaction effect for reach and culvert design was statistically significant (Figure 3, Table II), but post hoc *t*-tests revealed no significant differences between upstream and through reaches for any culvert type (non-replaced  $t_{1,6} = 0.53$ ,  $p = 0.62$ ; bankfull  $t_{1,10} = 1.34$ ,  $p = 0.21$ ; stream simulation  $t_{1,8} = 1.61$ ,  $p = 0.15$ ).

### Upstream–downstream comparison

We hypothesized that CPOM retention, transient storage characteristics and ammonium uptake would be similar upstream and downstream of both stream simulation and bankfull culverts because both designs accommodate the bankfull stream width. We found that CPOM  $V_{dep}$  decreased from upstream to downstream of stream simulation culverts, while the opposite pattern was observed for bankfull culverts, and the interaction effect for reach and culvert design was statistically significant (Figure 4, Table II). However, post hoc *t*-tests revealed no significant differences between upstream and downstream reaches for either culvert type (bankfull  $t_{1,4} = 1.54$ ,  $p = 0.20$ ; stream simulation  $t_{1,4} = 1.49$ ,  $p = 0.21$ ). For transient storage, estimates of  $D$ ,  $A$ ,  $A_s$  and  $\alpha$  and derived estimates of  $T_{sto}$ ,  $R_h$  and  $A_s/A$  determined using OTIS-P were similar between upstream and downstream reaches (Table III). Only  $D$  (dispersion) was determined to be statistically different between reaches and culvert types, with an observed increase of 48% from upstream to downstream of stream simulation and a decrease of 78% from upstream to downstream of bankfull culverts (Tables II and III), but post hoc tests revealed no significant differences between upstream and downstream reaches for either culvert type (bankfull  $t_{1,4} = 1.22$ ,  $p = 0.29$ ; stream simulation  $t_{1,4} = 1.18$ ,  $p = 0.30$ ). For ammonium uptake,  $V_f$  ranged from 0.02 to 0.14  $\text{mm s}^{-1}$  (Table IV) and was not different either between culvert types or between upstream and downstream study reaches (Table II).

Table 2. Two-way ANOVA results for all response variables for the culvert-type and upstream–downstream comparisons

Metric	Reach		Culvert type		Reach × culvert type	
	$F_{df}$	$P$ -value	$F_{df}$	$P$ -value	$F_{df}$	$P$ -value
<b>Culvert-type comparison</b>						
CPOM deposition velocity $V_{dep}$	<b>65.0</b> <sub>1,11</sub>	<b>&lt;0.001</b>	<b>5.9</b> <sub>2,11</sub>	<b>0.02</b>	<b>9.7</b> <sub>2,11</sub>	<b>0.004</b>
Water velocity	0.1	0.74	<b>4.7</b> <sub>2,12</sub>	<b>0.03</b>	<b>4.5</b> <sub>2,12</sub>	<b>0.03</b>
<b>Upstream–downstream comparison</b>						
CPOM deposition velocity $V_{dep}$	0.0	0.99	0.5	0.53	<b>11.1</b> <sub>1,4</sub>	<b>0.03</b>
Dispersion coefficient $D$	2.4	0.19	1.6	0.27	<b>10.0</b> <sub>1,4</sub>	<b>0.03</b>
Storage zone cross-sectional area $A_s$	2.1	0.22	0.0	0.88	2.8	0.17
Storage zone exchange coefficient $\alpha$	3.4	0.14	2.2	0.21	3.7	0.13
Ratio of storage zone to main channel cross-sectional area $A_s/A$	3.5	0.13	0.2	0.69	3.7	0.13
Storage zone residence time $T_{sto}$	1.3	0.31	0.0	0.93	2.4	0.20
Hydraulic retention factor $R_h$	1.2	0.33	1.2	0.33	6.3	0.07
Ammonium uptake velocity $V_f$	21.9	0.13	1.9	0.40	11.1	0.18

CPOM, coarse particulate organic matter.

DISCUSSION

Both culvert replacement and habitat improvement projects are common stream restoration activities in the USA

(Januchowski-Hartley *et al.*, 2013; Roni *et al.*, 2008). Stream simulation culverts combine both strategies by trying to improve longitudinal stream connectivity as well as

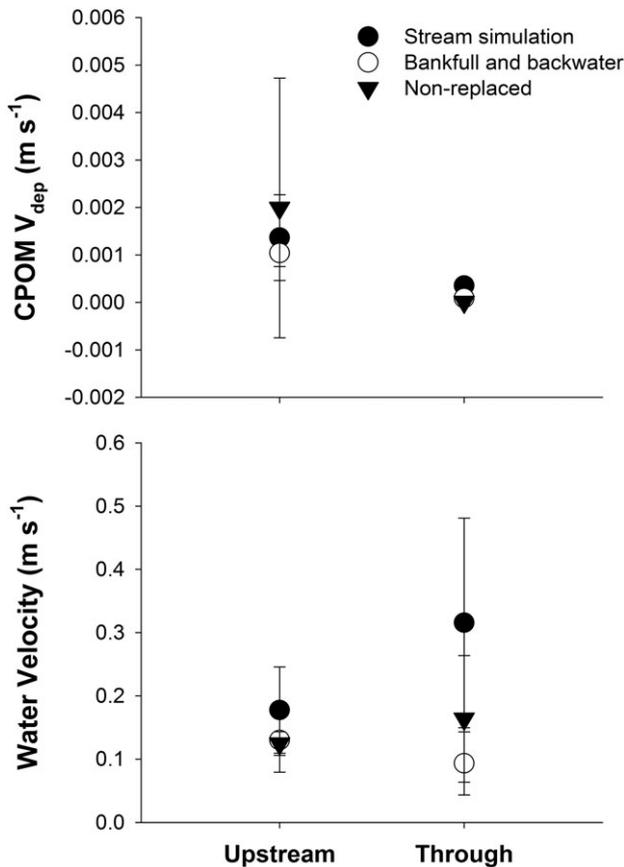


Figure 3. Coarse particulate organic matter (CPOM) deposition velocity ( $V_{dep}$ ) (top) and water velocity measured for the culvert-design comparison. Error bars  $\pm 1$  SE,  $n = 5$  for stream simulation,  $n = 6$  for bankfull and backwater and  $n = 4$  for non-replaced

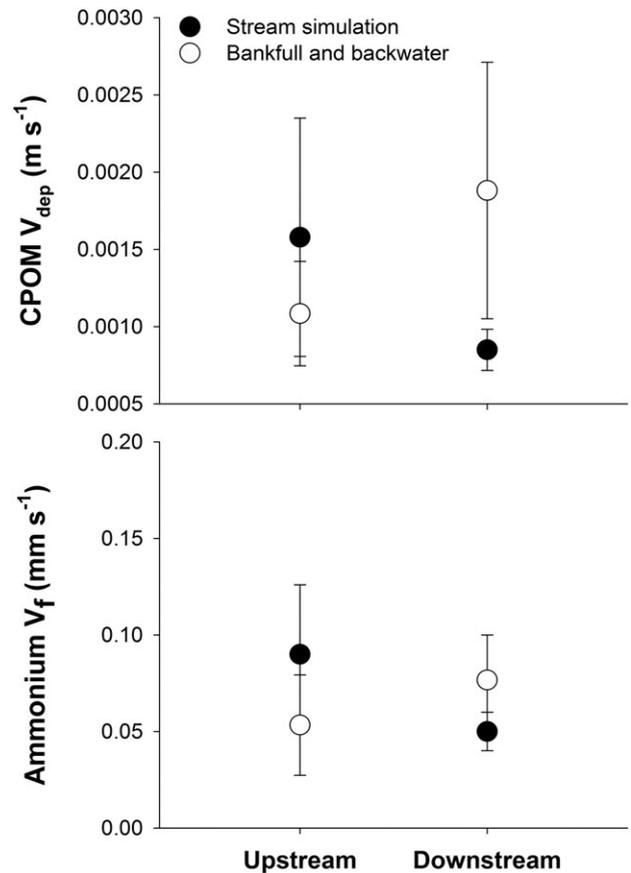


Figure 4. Coarse particulate organic matter (CPOM) deposition velocity ( $V_{dep}$ ) (top) and ammonium uptake velocity ( $V_f$ ) for the upstream–downstream comparison. Error bars  $\pm 1$  SE,  $n = 2$  for  $V_f$  stream simulation downstream and  $n = 3$  for all other means

Table 3. Means ( $\pm$ SE,  $n=3$ ) and effect sizes (mean % change) for transient storage metrics derived from OTIS modelling as part of the upstream–downstream comparison

Metric	Stream simulation			Bankfull and backwater		
	Upstream	Downstream	Mean % change	Upstream	Downstream	Mean % change
Dispersion coefficient $D$ ( $\text{m}^2 \text{s}^{-1}$ )	$0.29 \pm 0.06$	$0.44 \pm 0.10$	47.69	$0.47 \pm 0.30$	$0.13 \pm 0.02$	–78.44
Storage zone cross-sectional area $A_s$ ( $\text{m}^2$ )	$0.14 \pm 0.09$	$0.19 \pm 0.16$	44.07	$0.11 \pm 0.06$	$0.21 \pm 0.11$	57.67
Storage zone exchange coefficient $\alpha$ ( $\text{s}^{-1}$ )	$0.0012 \pm 0.0003$	$0.0011 \pm 0.0005$	–3.34	$0.0010 \pm 0.0007$	$0.0031 \pm 0.0008$	215.02
Ratio of storage zone to main channel cross-sectional area $A_s/A$	$0.15 \pm 0.03$	$0.16 \pm 0.06$	8.53	$0.13 \pm 0.05$	$0.22 \pm 0.01$	81.90
Storage zone residence time $T_{sto}$ (s)	$139 \pm 21$	$186 \pm 65$	33.32	$587 \pm 448$	$79 \pm 22$	–85.17
Hydraulic retention factor $R_h$ ( $\text{s m}^{-1}$ )	$0.68 \pm 0.09$	$0.57 \pm 0.14$	–15.22	$0.93 \pm 0.46$	$0.90 \pm 0.02$	49.37

restoring natural substrates and stream dimensions through culverts (Gillespie *et al.*, 2014; SSWG, 2008). Our results suggest that rebuilding the streambed, as is performed in stream simulation culverts, may support more natural rates of one ecosystem process (CPOM retention) in the short reaches within culverts compared with bankfull and non-replaced culverts. In addition, we observed little difference in CPOM retention, transient storage and nutrient uptake upstream and downstream of stream simulation and bankfull culverts. This suggests that these two culvert designs, which both are designed to mimic the slope and bankfull width of reference stream channels (Cenderelli *et al.*, 2011), did not

have transmitting effects that alter the ecosystem processes we monitored in this study, as is sometimes observed for undersized or poorly designed culverts (e.g. Lachance *et al.*, 2008).

#### *Ecosystem processes within replaced and non-replaced culverts*

We found that CPOM retention and water velocity were significantly different among culvert designs and between reaches upstream of and through culverts. Contrary to our hypothesis, we found that non-replaced culverts were most

Table 4. Nutrient uptake parameters measured as part of the upstream–downstream comparison

Stream	Culvert type	Reach	Discharge ( $\text{L s}^{-1}$ )	Width (m)	Depth (m)	Background ammonium ( $\mu\text{g N L}^{-1}$ )	Enrichment factor	Uptake length $S_w$ (m)	Uptake velocity $V_f$ ( $\text{mm s}^{-1}$ )	$P$ -value
Preemption	Stream simulation	Down	72.9	2.0	0.19	13.2	1.5	1014	0.04	0.47
Preemption	Stream simulation	Up	54.0	1.7	0.18	22.1	1.2	292	0.11	0.21
Whiskey	Bankfull and backwater	Down	14.9	1.4	0.09	19.5	1.4	78	0.12	0.10
Whiskey	Bankfull and backwater	Up	12.3	1.4	0.09	23.3	1.2	580	0.01	0.55
Joseph's	Stream simulation	Down	3.0	1.7	0.05	14.4	1.0	ND	ND	ND
Joseph's	Stream simulation	Up	3.0	1.7	0.05	43.0	1.1	71	0.02	0.04
John's	Bankfull and backwater	Down	5.7	2.0	0.10	16.0	1.3	68	0.04	0.05
John's	Bankfull and backwater	Up	4.1	1.2	0.06	19.8	1.2	83	0.05	0.05
Popple	Stream simulation	Down	255.9	5.0	0.16	10.5	2.0	807	0.06	0.13
Popple	Stream simulation	Up	228.5	5.0	0.15	12.8	2.1	305	0.14	0.01
Popple	Bankfull and backwater	Down	196.8	4.8	0.19	12.1	1.9	594	0.07	0.08
Popple	Bankfull and backwater	Up	196.8	4.8	0.19	8.0	2.4	418	0.10	0.06

ND indicates no data because plateau concentrations were not elevated enough above background to achieve a decreasing relationship between ammonium concentration and distance from release. Enrichment factor is the plateau ammonium concentration divided by the background concentration.  $P$ -values reported here were for the regression applied to the nutrient uptake data collected in each reach. In the reach column, 'down' indicates the study reach downstream of the culvert, and 'up' indicates the study reach upstream of the culvert.

similar in water velocity between upstream and downstream reaches and that water velocity increased through stream simulation culverts. This may be because the stream simulation culverts included in our study were rebuilt to mimic conditions found in riffles, which have naturally faster flow than average water velocities across longer stream reaches that include both pools and riffles. We found that CPOM  $V_{dep}$  decreased through all culvert types relative to upstream reaches. However, the decrease in  $V_{dep}$  was least through stream simulation culverts and most through non-replaced culverts, likely due to the reconstructed streambed that retained leaf analogues on rocks and woody debris in the stream simulation culverts. Leaf analogue retention on rock substrates in non-replaced culverts appeared similar to that in stream simulation culverts (Figure 2), but in reality was driven by a few rocks at the exit of one culvert and was not a general feature of non-replaced culverts in our study.

Our results agree with evidence from other studies suggesting that CPOM retention may be particularly sensitive to restoration efforts focused on physical habitat. Several studies have shown that restoration projects where wood structures were added to streams to create pool habitats also increased CPOM retention at the habitat and reach scales (Entekin *et al.*, 2008; Rosi-Marshall *et al.*, 2006). Furthermore, Lepori *et al.* (2005) found that streams restored from channelization by widening channels and adding large boulders had increased CPOM retention. An increase in CPOM retention could influence the distribution of CPOM standing stocks and subsequently distribution of invertebrates dependent on CPOM as a food source. Other research in our study streams has identified that invertebrate biomass within culverts is greater in stream simulation compared with bankfull culverts (S. Eggert, USFS, unpublished), which could be related to CPOM retention and availability.

#### *Ecosystem processes upstream and downstream of replaced culverts*

The main motivation for culvert replacements is that improperly designed culverts can act as semipermeable or complete barriers to aquatic organism movement (Bouska and Paukert, 2010; Warren and Pardew, 1998), and that sedimentation, erosion and flood risk can exceed natural levels because of hydrologic changes through culverts (Bouska *et al.*, 2010; Gillespie *et al.*, 2014; Wellman *et al.*, 2000). Sometimes, these issues within culverts can transmit upstream or downstream to change stream geomorphology or hydrology in ways that could influence ecosystem processes over many metres or kilometres (Lachance *et al.*, 2008). In our study, we found that CPOM retention, transient storage and nutrient uptake were all similar in reaches upstream and downstream of both stream

simulation and bankfull culverts, and all rates were within the range of other studies reporting these processes in restored and unrestored streams (e.g. Becker *et al.*, 2013; Hoellein *et al.*, 2012; Runkel, 2002). The lack of difference in rates of ecosystem processes observed upstream and downstream of culverts could be because both replacement culvert styles are designed to accommodate the full bankfull channel across a range of flow conditions (Gillespie *et al.*, 2014), and we observed consistent stream geomorphic characteristics (width, depth and discharge) between stream reaches upstream and downstream of the culverts included in this study (Tables I and IV). Similarly, Timm *et al.* (in press) report that bankfull widths were not significantly different upstream and downstream of the stream simulation and bankfull culverts included in our study, but that substrate particle sizes were significantly larger upstream than downstream of both styles of culverts. However, without similar upstream–downstream data prior to replacement or from non-replaced culverts in the region, it is impossible to attribute the difference observed in geomorphology or ecosystem processes to specific culvert characteristics.

An alternative possibility is that the ecosystem processes we measured in upstream and downstream reaches were not sensitive to culvert effects. Others have found that nutrient uptake and transient storage may or may not be sensitive to stream restoration. For example, Hoellein *et al.* (2012) found no significant differences in ammonium uptake on reaches that were restored for fish spawning habitat by increasing substrate size with the addition of gravel and boulders and building upstream sediment traps compared with unrestored reaches. However, other studies have found that manipulations of physical complexity such as adding coarse woody debris to streams can increase ammonium uptake (Roberts *et al.*, 2007). Studies evaluating transient storage characteristics after restorations of physical complexity, similar to stream simulation culverts, have also reported mixed results. Becker *et al.* (2013) evaluated the effects of natural channel design restoration, which involved creating physical structures with boulders in stream channels, and found restored reaches had 33% larger transient storage zones compared with unrestored reaches and a slight decrease in residence time in transient storage zones, although these differences were not statistically significant. Bukaveckas (2007) found that reaches restored from channelization by decreasing bankfull capacity and creating channel meanders, pools and riffles had higher transient storage ( $A_s/A$ ) compared with channelized reaches. Additionally, Hoellein *et al.* (2012) found that restored reaches with larger substrate sizes had increased transient storage ( $A_s/A$ ). In our study,  $D$  was the only metric found to have statistically significant differences between upstream and downstream reaches for any of the transient storage metrics.

However, because the variability in  $D$  was very high and the absolute change in the  $D$  values were small, we think this significant difference in  $D$  may be due to chance rather than a true difference between the study reaches.

#### *Limitations and broader implications*

It must be noted that culverts vary widely in terms of sizes and design specifics (e.g. length and spanning structure), even within our groups of stream simulation, bankfull and non-replaced culverts (Table I). Low replication limited our ability to quantify the full suite of potential variation within groups, particularly non-replaced culverts, where we sampled only two small concrete and two large corrugated culverts. Furthermore, culverts with hydrologic issues such as severe ponding at the inlet or outlet had to be excluded from this study because the three ecosystem processes we measured require predominant downstream water movement through advection, which is not the case in nearly lentic conditions. Measurements of ecosystem processes not requiring flowing water such as metabolism and nutrient uptake in benthic chambers would be viable options to evaluate process differences across the full breadth of culvert variability.

Our results add to a growing body of literature suggesting careful consideration is required to avoid mismatches between stream restoration activities and monitoring techniques (Hoellein *et al.*, 2012; Hopkins *et al.*, 2011). We found that CPOM retention was significantly different depending on culvert design, possibly because it was an ecosystem process that could be measured at the spatial scale of the restorations (through culverts). Considering elements of physical and biological structure as well as ecosystem processes may provide the most robust approach for monitoring. For example, Hopkins *et al.* (2011) found that macroinvertebrate assemblages were more responsive than some ecosystem processes (metabolism and decomposition) to hydrologic conditions in a western river, suggesting that restoration activities to restore hydrologic regimes in that river would be best served by focusing on macroinvertebrate community responses. However, Ogren and Huckins (2015) found that macroinvertebrate and fish communities were not sensitive to changes in stream habitat following three culvert replacements in the Big Manistee River watershed in Michigan, likely because of the overriding effects of habitat and water quality degradation occurring at larger scales within the study watersheds. Additionally, monitoring may occur too soon after restoration activities to allow the ecosystem to recover from the degradation (Palmer *et al.*, 2010). Monitoring in this study occurred 3–8 years following culvert replacement; however, Louhi *et al.* (2011) found that a response in macroinvertebrate diversity was not detectable after nearly 20 years of

monitoring streams restored for habitat heterogeneity in Finland. Together, our results and these other studies suggest that restoration practitioners must carefully consider the spatial and temporal scale of their monitoring activities as well as the overall goals of the restoration project when selecting metrics of ecosystem structure or function to use in post-monitoring programmes.

To evaluate the value of the replacement culvert designs in the current study, we follow the criteria from Palmer *et al.* (2005) based on both ecological and stakeholder success. In addition to the likely effects of improving fish movement and hydrologic conditions compared with improperly designed culverts, we found the ecosystem processes that we measured were similar upstream and downstream of both stream simulation and bankfull culverts, while stream simulation culverts had CPOM retention within the culvert closer to natural rates compared with bankfull and non-replaced culverts. Furthermore, these culverts may be viewed as a stakeholder success because of the economic benefit of reduced flood risk and damage, longer life expectancies without costly repairs (Gillespie *et al.*, 2014) and a perception that they are more aesthetically pleasing (Personal communication with adjacent landowners, J.M. Kraemer). An important question is whether the additional cost of rebuilding the streambed in the stream simulation design is worth the improvement in ecosystem processes we observed in these short stream reaches through culverts. If restoration activities are aimed at maintaining ecological conditions in reaches upstream and downstream of culverts, then the bankfull design, where the culverts are sized to accommodate the stream channel but the stream bottom is not rebuilt, may be adequate. On the other hand, if maintaining ecological conditions through the culvert is an important restoration goal, then the investment in the stream simulation design can lead to improvement in ecosystem processes.

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## REFERENCES

- Barnard RJ, Yokers S, Nagygyor A, Quinn T. 2015. An evaluation of the stream simulation culvert design method in Washington state. *River Research and Applications* **31**: 1376–1387.
- Becker JF, Endreny TA, Robison JD. 2013. Natural channel design impacts on reach-scale transient storage. *Ecological Engineering* **57**: 380–392.
- Blakely TJ, Harding JS, McIntosh AR, Winterbourn MJ. 2006. Barriers to the recovery of aquatic insect communities in urban streams. *Freshwater Biology* **51**: 1634–1645.
- Bouska WW, Keane T, Paukert CP. 2010. The effects of road crossings on prairie stream habitat and function. *Journal of Freshwater Ecology* **25**: 499–506.
- Bouska WW, Paukert CP. 2010. Road crossing designs and their impact on fish assemblages of great plains streams. *Transactions of the American Fisheries Society* **139**: 214–222.
- Bukaveckas PA. 2007. Effects of channel restoration on water velocity, transient storage, and nutrient uptake in a channelized stream. *Environmental Science & Technology* **41**: 1570–1576.
- Cenderelli DA, Clarkin K, Gubernick RA, Weinhold M. 2011. Stream simulation for aquatic organism passage at road-stream crossings. *Transportation Research Record* **2203**: 36–45.
- Diebel MW, Fedora M, Cogswell S, O'Hanley JR. 2014. Effects of road crossings on habitat connectivity for stream-resident fish. *River Research and Applications* **31**: 1251–1261.
- Entrekin S, Tank JL, Rosi-Marshall EJ, Hoellein TJ, Lamberti GA. 2008. Responses in organic matter accumulation and processing to an experimental wood addition in three headwater streams. *Freshwater Biology* **53**: 1642–1657.
- Gillespie N, Unthank A, Campbell L, Anderson P, Gubernick R, Wienhold M, Cenderelli D, Austin B, McKinley D, Wells S, Rowan J, Orvis C, Hudy M, Bowden A, Singler A, Fretz E, Levine J, Kirn R. 2014. Flood effects on road-stream crossing infrastructure: Economic and ecological benefits of stream simulation designs. *Fisheries* **39**: 62–76.
- Hoellein TJ, Tank JL, Entrekin SA, Rosi-Marshall EJ, Stephen ML, Lamberti GA. 2012. Effects of benthic habitat restoration on nutrient uptake and ecosystem metabolism in three headwater streams. *River Research and Applications* **28**: 1451–1461.
- Hopkins JM, Marcarelli AM, Bechtold HA. 2011. Ecosystem structure and function are complementary measures of water quality in a polluted, spring-influenced river. *Water, Air, and Soil Pollution* **214**: 409–421.
- Januchowski-Hartley SR, McIntyre PB, Diebel M, Doran PJ, Infante DM, Joseph C, Allan JD. 2013. Restoring aquatic ecosystem connectivity requires expanding inventories of both dams and road crossings. *Frontiers in Ecology and the Environment* **11**: 211–217.
- Lachance S, Dube M, Dostie R, Berube P. 2008. Temporal and spatial quantification of fine-sediment accumulation downstream of culverts in brook trout habitat. *Transactions of the American Fisheries Society* **137**: 1826–1838.
- Lamberti GA, Gregory SV. 2006. CPOM transport, retention, and measurement. In *Methods in Stream Ecology*, 2nd edn. Academic Press: San Diego, California; 273–289.
- Lepori F, Palm D, Malmqvist B. 2005. Effects of stream restoration on ecosystem functioning: detritus retentiveness and decomposition. *Journal of Applied Ecology* **42**: 228–238.
- Louhi P, Mykra H, Paavola R, Huusko A, Vehanen T, Maki-Petays A, Moutka T. 2011. Twenty years of stream restoration in Finland: little response by benthic macroinvertebrate communities. *Ecological Applications* **21**: 1950–1961.
- Morrice JA, Valett HM, Dahm CN, Campana ME. 1997. Alluvial characteristics, groundwater-surface water exchange and hydrological retention in headwater streams. *Hydrological Processes* **11**: 253–267.
- Ogren SA, Huckins CJ. 2015. Culvert replacements: improvement of stream biotic integrity? *Restoration Ecology* **23**: 821–828.
- Palmer MA, Bernhardt ES, Allan JD, Lake PS, Alexander G, Brooks S, Carr J, Clayton S, Dahm CN, Shah JF, Galat DL, Loss SG, Goodwin P, Hart DD, Hassett B, Jenkinson R, Kondolf GM, Lave R, Meyer JL, O'Donnell TK, Pagano L, Sudduth E. 2005. Standards for ecologically successful river restoration. *Journal of Applied Ecology* **42**: 208–217.
- Palmer MA, Menninger HL, Bernhardt E. 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? *Freshwater Biology* **55**: 205–222.
- Price DM, Quinn T, Barnard RJ. 2010. Fish passage effectiveness of recently constructed road crossing culverts in the Puget Sound region of Washington State. *North American Journal of Fisheries Management* **30**: 1110–1125.
- R Core Team. 2013. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing: Vienna, Austria URL <http://www.R-project.org/>.
- Roberts BJ, Mulholland PJ, Houser AN. 2007. Effects of upland disturbance and instream restoration on hydrodynamics and ammonium uptake in headwater streams. *Journal of the North American Benthological Society* **26**: 38–53.
- Roni P, Hanson K, Beechie T. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. *North American Journal of Fisheries Management* **28**: 856–890.
- Rosi-Marshall EJ, Moerke AH, Lamberti GA. 2006. Ecological responses to trout habitat rehabilitation in a Northern Michigan stream. *Environmental Management* **38**: 99–107.
- Runkel RL. 1998. One dimensional transport with inflow and storage (OTIS): a solute transport model for streams and rivers. United States Geological Survey Water Resources Investigation Report 98-4018. (<http://co.water.usgs.gov/otis>).
- Runkel RL. 2002. A new metric for determining the importance of transient storage. *Journal of the North American Benthological Society* **21**: 529–543.
- SSWG. 2008. *Stream simulation: an ecological approach to providing passage for aquatic organisms at road-stream crossings*. Publication 0877-1801. San Dimas Technology and Development Center, U.S. Department of Agriculture, Forest Service: San Dimas, California [www.fs.fed.us/eng/pubs/pdf/StreamSimulation/index.shtml](http://www.fs.fed.us/eng/pubs/pdf/StreamSimulation/index.shtml).
- Stream Solute Workshop. 1990. Concepts and methods for assessing solute dynamics in stream ecosystems. *Journal of the North American Benthological Society* **9**: 95–119.
- Taylor BW, Keep CE, Hall RO, Koch BJ, Tronstad LM, Flecker AS, Ulseth AJ. 2007. Improving the fluorometric ammonium method: matrix effects, background fluorescence and standard additions. *Journal of the North American Benthological Society* **26**: 167–177.
- Thackston EL, Schnelle KB. 1970. Predicting the effects of dead zones on stream mixing. *Journal of Sanitary Engineering Division* **96**: 319–331.
- Timm A, Higgins D, Stanovick J, Kolka R, Eggert S. In press. Quantifying fish habitat associated with stream simulation design culverts in northern Wisconsin. *River Research and Applications*. DOI: 10.1002/tra.3117.
- Wallace JB, Eggert SL, Meyer JL, Webster JR. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* **277**: 102–104.
- Warren ML, Pardew MG. 1998. Road crossings as barriers to small-stream fish movement. *Transactions of the American Fisheries Society* **127**: 637–644.
- Webster JR, Valett MH. 2006. Solute dynamics. In *Methods in Stream Ecology*, 2nd edn. Academic Press: San Diego, California; 169–185.
- Webster JR, Benfield EF, Ehrman TP, Schaeffer MA, Tank JL, Hutchens JJ, D'Angelo DJ. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. *Freshwater Biology* **41**: 687–705.
- Wellman JC, Combs DL, Cook SB. 2000. Long-term impacts of bridge and culvert construction or replacement on fish communities and sediment characteristics of streams. *Journal of Freshwater Ecology* **15**: 317–328.