

ECOSYSTEM ENGINEERING AT THE STREAMBED:  
HOW NET-SPINNING CADDISFLIES INFLUENCE  
SUBSTRATE FLOW DYNAMICS

by

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A thesis submitted in partial fulfillment  
of the requirements for the degree

of

Master of Science

in

Biological Sciences

MONTANA STATE UNIVERSITY  
Bozeman, Montana

January 2020

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DEDICATION

For Katie.

## ACKNOWLEDGEMENTS

I would first like to thank my advisors and committee members, Dr. Lindsey Albertson and Dr. Geoffrey Poole for dedicating their time to ensuring success during my tenure at Montana State University. They created a collaborative atmosphere that was truly fun to be a part of and I feel fortunate to have been placed among their highly talented students. Additionally, I'd like to thank my third committee member Dr. Wyatt Cross for thoughtful edits that helped me produce this work. And of course, the folks working in these respective labs have spent considerable time assisting me in conceptualizing many of the ideas found within this thesis, and I can't overstate how grateful I am for their encouragement along the way.

I would also like to acknowledge the Teton Conservation District, and especially Carlin Girard for providing me an opportunity I view as the stepping stone that got me into a graduate program at Montana State University. Thanks for helping me develop a career in water resources.

And most importantly, thanks to my loving family for supporting me from day one. Mom, Dad, Matt, Maggie, Grammy, Grampa and Nan...I couldn't have gotten here without you and for that, I'm forever grateful.

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CHAPTER ONE

ECOSYSTEM ENGINEERING AT THE STREAMBED:  
HOW NET-SPINNING CADDISFLIES INFLUENCE  
SUBSTRATE FLOW DYNAMICS

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Manuscript Information

Michael J. MacDonald, Lindsey K. Albertson, Geoffrey C. Poole

*Ecohydrology*

Status of Manuscript:

Prepared for submission to a peer-reviewed journal

Officially submitted to a peer-reviewed journal

Accepted by a peer-reviewed journal

Published in a peer-reviewed journal

John Wiley & Sons Ltd.

## ABSTRACT

The streambed is an ecotone between surface waters and underlying hyporheic systems. Identifying the controls on advective flow through this ecotone is critical to understanding the movement of energy and matter in streams. Hydropsychids (net-spinning caddisflies) are aquatic macroinvertebrate ecosystem engineers that influence streambed cohesion, yet evidence of direct influence on hydrologic processes is lacking. Utilizing a novel downward flow permeameter, we demonstrate how net-spinning caddisfly colonization of the streambed interstia at moderate but common densities ( $2,000 \text{ m}^{-2}$ ) can reduce the vertical hydraulic conductivity ( $K_V$ ) by up to 55% in coarse sand and gravels (median diameter = 12.91 mm). Sediment columns incubated in artificial stream water occupied by caddisflies showed greater reductions in  $K_V$  relative to those without caddisflies. Additionally, organic matter content within sediment columns showed that occupation by caddisflies resulted in nearly two-fold increases in organic matter AFDM. Our research shows that the ubiquitous and numerous net-spinning caddisflies are likely to modulate the exchange of channel and hyporheic water by constructing nets in open pore spaces, increasing flow resistance, and decreasing flow velocities, as well as stimulating organic matter deposition with potential consequences for biofilm growth. These results suggest that caddisfly induced reductions to flow may influence transfer processes occurring at the streambed ecotone, altering biogeochemical processes in streams.

## 1 | Introduction

The movement of water, energy, and matter can be fundamentally altered at ecohydrological interfaces, which are the transition zones between ecosystems where dynamic and multi-scale biophysical factors act to control transfer dynamics (Krause et al., 2017). Ecohydrological interfaces are sites where important ecosystem functions and services occur such as maintaining water quality and biodiversity and regulating temperature (Arrigoni et al., 2008). In gravel-bedded rivers, the streambed is the ecohydrological interface that separates but links high flow channel ecosystems with relatively slower flow hyporheic ecosystems (Poole et al., 2008). At the streambed, spatial gradients in physical, chemical, and biological properties are large, creating hotspots for biogeochemical processing (Santschi, Höhener, Benoit, & Buchholtz-ten Brink, 1990). Identifying the factors that alter the permeability of this interface by promoting or inhibiting between-system transfers are critical to understanding the physical and biological states of adjacent stream and hyporheic ecosystems (Palmer, 1997).

A dynamic suite of physical mechanisms control the flux of water, energy and matter through the streambed. Water is transported across the streambed interface via hydrologic exchange (the continuous, bidirectional exchange of water between the stream channel and the streambed (Stanford & Ward, 1988)) which delivers organic matter, nutrients and electron acceptors and donors to subsurface biota (Mermillod-Blondin & Rosenberg, 2006). This exchange drives important in-stream processes such as nitrogen spiraling, and metabolism of organic carbon and alters temperature regimes and microbial

community structure (Battin, Besemer, Bengtsson, Romani, & Packmann, 2016; Hester, Doyle, & Poole, 2009; Rutherford & Hynes, 1987; Valett, Morrice, Dahm, & Campana, 1996). Hydrologic exchange is controlled by gradients in hydraulic head (pressure) at the streambed interface (Boano et al., 2014) which promotes the advective flow of water from areas of high pressure to areas of low pressure. However, rates of hydrologic exchange are constrained by the streambed hydraulic conductivity, a physical property which dictates the ease at which water moves through a porous medium (Darcy, 1856). Hydraulic conductivity is largely determined by the physical characteristics of sediments (e.g. grain size, grain size distribution, pore connectivity (Brunke & Gonser, 1997; Freeze & Cherry, 1979)). Together, hydrologic exchange and sediment hydraulic conductivity control the delivery of metabolic constituents to organisms living within the streambed. While the broad-scale physical factors that mediate streambed hydraulic conductivity and hydrologic exchange have been well studied (Boulton, Datry, Kasahara, Mutz, & Stanford, 2010), the tightly coupled biological and physical mechanisms operating at smaller scales has received less attention (Battin, Kaplan, Denis Newbold, & Hansen, 2003). Understudied feedbacks between small scale biological and physical processes that act to control water flow through the streambed deserve increased attention considering the importance of the streambed in driving key ecosystem functions.

Organisms inhabiting streams that modify the physical template of the streambed and influence patterns of resource delivery to others are ecosystem engineers (Jones, Lawton, & Shachak, 1994). Organisms can regulate water fluxes and associated resource delivery to subsurface biota by controlling either gradients in hydraulic head or the

hydraulic conductivity of the streambed. For example, biologically engineered structures like lamprey nests or macrophyte beds create gradients in hydraulic head which drive hydrologic exchange through sediments (White, 1990; White & Hendricks, 2000). Alternatively, engineers can act to increase or decrease the hydraulic conductivity of sediments through bioturbation or biological clogging, which in turn constrains rates of hydrologic exchange across the streambed (Mendoza-Lera & Mutz, 2013; Mermillod-Blondin, 2011; Nogaro et al., 2009; Palmer, 1997). Boulton et al. (2002), suggested that in systems dominated by advective flow, like gravel bedded rivers, organisms could act as “modulators” of water fluxes whereby aquatic ecosystem engineers would play critical roles in regulating subsurface biogeochemical processes by altering the transport of water, organic matter and additional metabolites across the streambed. Continued research on organisms that modify the permeability of the streambed interface, and thus transfer processes between the stream channel and hyporheic zones, is important for building our understanding of energy and matter transport in rivers.

One such ecosystem engineer is the net-spinning caddisfly (Trichoptera: Hydropsychidae; hereafter caddisflies), a ubiquitous and abundant family of insects that inhabit benthic and shallow hyporheic sediments in the streambed. They are widely distributed on six continents, and their densities range from hundreds to thousands per square meter but can reach numbers greater than  $10^3 \text{ m}^{-2}$  in some riffle habitats (Miller, 1984). At the streambed, caddisflies construct silk nets and retreat structures (Figure 1) on the tops, bottoms, and inside the pore spaces of sediments to capture algae, fine organic particles, and small invertebrates for food (Statzner, Arens, Champagne, Morel,

& Herouin, 1999; Wallace & Merritt, 1980). Early research on inter and intraspecific variation in silk net architectures has provided important insight into how caddisflies partition food resources (Wallace, 1975); however, more recent research has established the nets strong influence on physical processes. For example, their silk net structures can change sediment transport regimes by increasing the shear stress required for incipient sediment motion and enhance local invertebrate density and biomass by creating low flow refugia (Albertson, Sklar, Pontau, Dow, & Cardinale, 2014; Cardinale, Gelmann, & Palmer, 2004; Nakano, Yamamoto, & Okino, 2005; Statzner et al., 1999; Tumolo, Albertson, Cross, Daniels, & Sklar, 2019). Additionally, caddisfly silk structures have been shown to reduce the conductance of water pipes at hydro-power plants, lowering plant efficiency by 10-20% (Tsuda & Hiro, 1955) and reduce the horizontal hydraulic conductivity of simulated sediments by 70% (Juras, Albertson, Cahoon, & Johnson, 2018). Based on these examples of caddisflies engineering their environment, we question how caddisfly silk structures influence streambed transfer processes. We suggest that caddisfly nets play a role in altering sediment vertical hydraulic conductivity ( $K_v$  ( $\text{cm s}^{-1}$ )) given that silk structures often occupy pore spaces (Cardinale et al., 2004, Tumolo et al., in prep). Caddisfly engineered changes to the streambed could thus alter rates of hydrologic exchange and coupled fluxes of metabolites across the streambed.



**Figure 1.** A net-spinning caddisfly (*Arctopsyche grandis*) with its silk net built in the interstitial space between gravels of 20mm diameter.

Here, we present an experiment designed to determine whether caddisflies alter the vertical hydraulic conductivity in gravel sediments and potentially act as modulators of hydrologic exchange in advection dominated streambeds. We hypothesized that caddisfly silk structures influence  $K_v$  of the streambed by clogging interstitial spaces, and our experimental results highlight how caddisflies act as a biological modulator of streambed interface exchange processes, extending our knowledge of small-scale controls on the flow of energy and matter in streams.

## 2 | Methods

We built a constant downward-flow permeameter (Figure 2, Figure 3) to measure  $K_V$  of vertically oriented sediment columns. We used the permeameter to document temporal changes in sediment  $K_V$  under five experimental treatments: 1) “control”, 2) “ASW” (artificial stream water), 3) “algae”, 4) “caddis only” and 5) “algae plus caddis”. See section ‘2.2 | Treatments’ for specific details.

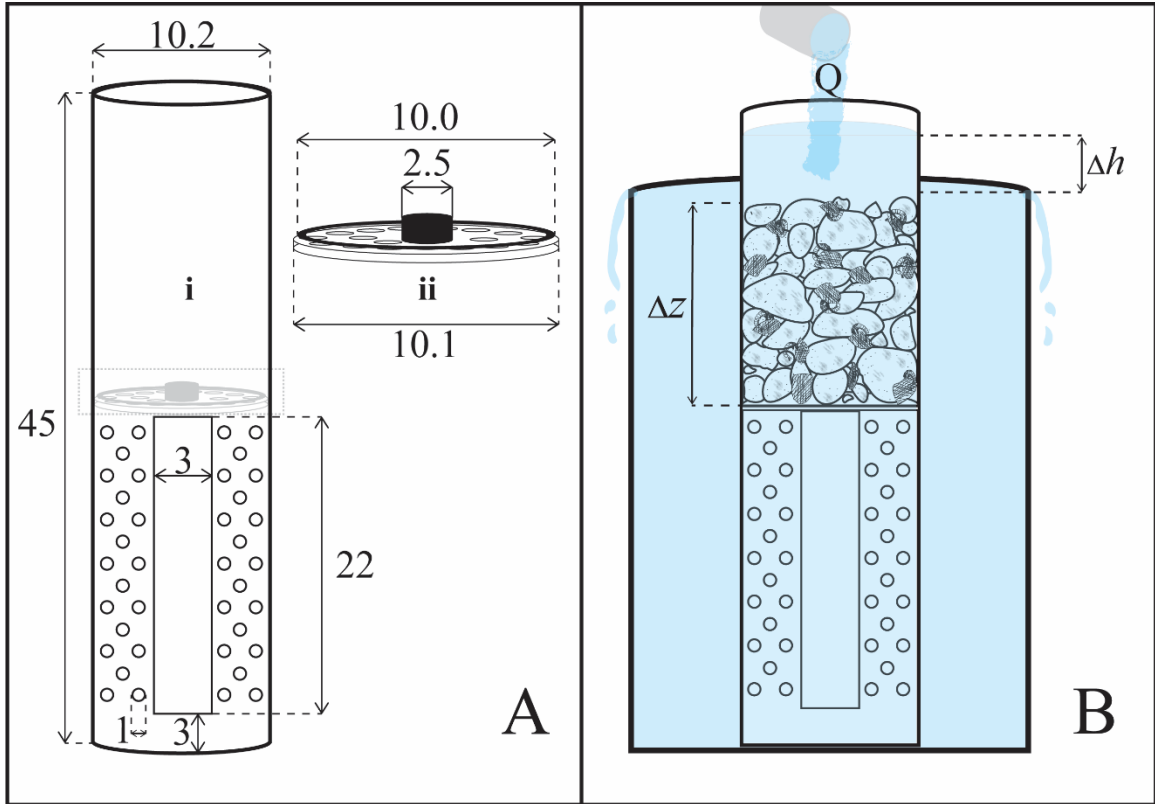
### 2.1 | Permeameter

#### 2.1.1 | Sediment columns

The permeameter consisted of four sediment columns, each 10 cm in depth, housed within a 45 cm long segment of 10.2 cm inside-diameter polyvinyl chloride (PVC) pipe (permeameter pipe), oriented vertically. Sediments ( $D_{50} = 12.91 \text{ mm} \pm 0.08 \text{ mm}$  (Table 1, Figure A1)) for all experimental trials were collected from a local stream and were supported within the upper half of the permeameter pipe by a 10.1 cm diameter PVC shower drain installed 20 cm below the top of the pipe. We left the permeameter pipe unperforated from the shower drain to the top of the pipe. Below the shower drain, no sediments occupied the permeameter pipe, which we perforated sufficiently to ensure that any water flow rate that would reasonably be expected through sediments above the shower drain could move unimpeded, horizontally, through the perforated pipe walls. Specifically, we cut four rectangular openings (width = 3 cm, height = 22 cm), evenly spaced around the circumference of the pipe and drilled 20 one cm diameter holes through the PVC wall between each rectangular opening. To deter the caddisflies (added to the sediment columns experimentally, see “Treatments” below) from dispersing from



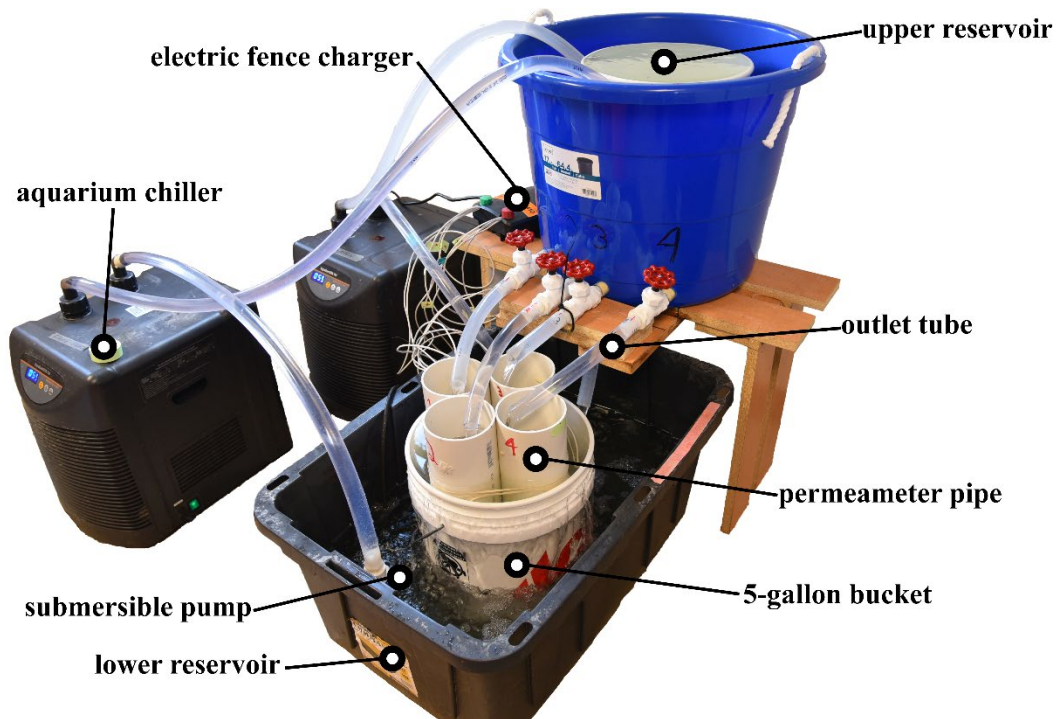
the sediment column through the shower drain, we created an electrical field across the bottom of the sediment column (Brown, Norris, Maher, & Thomas, 2000; C. M. Pringle & Blake, 1994; Utz, Cooper, Gido, & Stewart, 2017) (electric exclusion device, Figure 2A). We installed a copper ring (anode, 10 cm diameter) that spanned the diameter of the permeameter pipe just above the shower drain. At the center of the shower drain, we installed a copper pipe (cathode, 2.5 cm diameter) cut to approximately 3.5 cm in length. We attached insulated 12-gauge copper wire to the anode and cathode with electrical tape and connected both to a 0.3-joule electric fence energizer (Gallagher® M30) via the wires. The electric fence energizer delivered a pulsed direct current once per second to deter caddisflies from approaching and passing through the shower drain (Utz et al., 2017). This approach contained the caddisflies in the sediment columns and, unlike a fine mesh that would contain the caddisflies, ensured that water movement through the sediment was unaffected by the containment device itself.



**Figure 2.** (A) Schematic of the dimensions of the permeameter pipe (i) and the electric exclusion device (ii). Anode and cathode represented by outer black ring and inner black pipe respectively). All measurements are in cm. (B) Permeameter pipe submerged in 5-gallon bucket showing the sediment column and measurements for  $Q$  ( $\text{cm}^{-3} \text{s}^{-1}$ ),  $\Delta h$  (cm), and  $\Delta z$  (cm).

### 2.1.2 | Permeameter Assembly

Our experiment required that the permeameter (Figure 3) delivered an equal flow of artificial stream water (or mild bleach solution, in the case of the control) to each of the four experimental sediment columns inside the permeameter pipes. To ensure equal flows across each sediment column, our permeameter contained a constant hydraulic head (continuously overflowing) upper reservoir. Under the force of gravity, four outlet tubes fed water from the upper reservoir into the empty space in the pipe above each of the sediment columns. Outlet tubes were fitted with PVC screw gate stop-valves to make micro-adjustments to equalize  $Q$  ( $\text{cm}^3 \text{ s}^{-1}$ ) between the four sediment columns. Constant hydraulic head at the bottom of each sediment column was established by standing the pipes in a five-gallon bucket; with the rim of the bucket even with the top of the sediments. Water that flowed through the sediment columns filled and poured over the rim of the bucket (Figure 2B). Overflowing water from the upper reservoir and five-gallon bucket were captured in a lower reservoir and recirculated back to the upper reservoir via two submersible pumps (Danner Mfg.® Model 9.5 B). During recirculation, water passed through two  $\frac{1}{4}$  horsepower aquarium chillers (AquaEuroUSA® MC-1/4HP) maintaining water temperature at  $13.3^\circ\text{C}$  to create a suitable temperature for caddisfly larvae and to maintain constant water viscosity (Freeze & Cherry, 1979; Hauer & Stanford, 1982). In sum, the reservoirs, sediment columns, and five-gallon bucket contained 76 L of ASW (or dilute bleach solution in the control).



**Figure 3.** The fully assembled permeameter.

## 2.2 | Treatments

We applied five experimental treatments to the sediment columns by varying the abiotic and biotic starting conditions based on our *a priori* hypotheses. The five treatments were: (1) control, in which the permeameter was operated with tap water, to which 250 ml of bleach was added daily; (2) ASW which contained distilled water with added anions and cations per Bastviken et al. (2004) (3) algae, which contained ASW along with an initial 30 ml of concentrated algal subsidy (Carolina Biological Supply Company®, Algae: Food for Freshwater Invertebrates); (4) caddis only, which contained ASW and sediment columns were inoculated with caddisfly larvae at a density of  $\sim 2,000$   $m^{-2}$  and (5) algae plus caddis, which combined the algae and caddis only treatment. The

control treatment ruled out temporal changes in  $K_V$  via physical changes to the sediment column (e.g., gravel settling (Koltermann & Gorelick, 1995)). The ASW treatment allowed us to measure changes in  $K_V$  due to biological growth from residual biofilms living on sediments. The algae treatment acted as a biological control and established the effects that a combination of motile and sessile algae (*Scenedesmus spp.*, *Selenastrum capricornutum*, *Ankistrodesmus spp.*, *Chlorella spp.*) have on  $K_V$  in sediment columns. The caddis only treatment quantified the direct influence of caddisfly activity and construction of silk nets and retreats on  $K_V$  over time. Finally, the algae plus caddis treatment allowed us to measure a hypothesized combined influence of caddisflies and an algae subsidy on sediment column.

We developed specific predictions for both physical changes to sediment  $K_V$  and organic matter deposition within the sediment columns for each treatment. We predicted that sediment  $K_V$  in the control treatment would remain stable over time, while sediment  $K_V$  in the four treatments permitting biological activity would decrease over time. Additionally, we predicted that we would see a larger reduction in sediment  $K_V$  in the algae plus caddis treatment compared to both the ASW and algae treatments. Lastly, we expected to see larger effects on sediment  $K_V$  in the algae and caddis treatment compared to the caddis only treatment. For organic matter deposition, we predicted organic matter content would increase in non-control treatments from ASW, to algae, to caddis only, to algae plus caddis as decreased  $K_V$  would increase rates of deposition in the sediments.

## 2.3 | Samples and Data Collection

### 2.3.1 | Measuring $K_V$

We determined  $K_V$  ( $\text{cm s}^{-1}$ ) of each sediment column in each trial using Darcy's Law (Darcy, 1856):

$$K_V = \frac{Q}{A \cdot \Delta h / \Delta z},$$

where  $Q$  ( $\text{cm}^3 \text{s}^{-1}$ ) is the volumetric flow rate through the sediment column,  $A$  ( $\text{cm}^2$ ) is the area of the sediment column perpendicular to flow,  $\Delta h$  (cm) is the difference in hydraulic head above and below the sediment column, and  $\Delta z$  (cm) is the depth of the sediment column (parallel to flow). VHG (unitless) is represented by  $\Delta h / \Delta z$ .

We measured  $Q$  into each sediment column in the permeameter pipes by placing a 1 L Erlenmeyer flask under each outlet tube of the constant-head upper reservoir (inlet to the permeameter pipe; Figure 2B), recorded the time between the placement and removal of the flask, then divided the volume of water captured ( $\text{cm}^3$ ) by the time (seconds). We calculated  $Q$  six times per sediment column in each treatment ( $n = 3$  at the start and  $n = 3$  at the end of each experimental trial), then averaged these six  $Q$  values to derive  $K_V$  for the given sediment column and treatment level (Table 1).  $Q$  was assumed constant during the experiment because water was delivered to sediment columns via a gravity-fed system, supported by the fact that the mean difference in  $Q$  prior to and following each experiment between each sediment column was 2.3% (SD = 1.9%).

**Table 1.** Caddisfly densities, median grain size, and volumetric flow rate across treatments (means  $\pm$  SDs).

Treatment	#Caddis (m <sup>-2</sup> )	Substrate D50 (mm)	Q (cm <sup>3</sup> s <sup>-1</sup> )
Control	-	12.91 $\pm$ 0.08	115.05 $\pm$ 1.75
ASW	-	12.77 $\pm$ 0.12	114.24 $\pm$ 1.37
Algae	-	13.03 $\pm$ 0.04	115.18 $\pm$ 2.53
Caddis Only	2418 $\pm$ 338	12.88 $\pm$ 0.12	116.36 $\pm$ 2.34
Algae & Caddis	2754 $\pm$ 308	12.83 $\pm$ 0.14	116.29 $\pm$ 1.82

We derived VHG by dividing the difference in head pressure parallel to flow across the sediment column ( $\Delta h$ ), by the thickness of the sediment column ( $\Delta z = 10$  cm).

We calculated  $\Delta h$  as:

$$\Delta h = h_{top} - h_{bot} ,$$

where  $h_{top}$  was the head (water surface elevation) of the water perched on top of the sediments inside the permeameter pipe and  $h_{bot}$  was the head of the water at the bottom of the sediments, measured in the bucket containing the permeameter pipe (Figure 2B).

Head measurements for each column were collected both inside ( $h_{top}$ ) and outside ( $h_{bot}$ ) of each pipe using digital calipers (Neiko 01407A) to determine the distance between the water surface and an arbitrary datum marked on each pipe (Figure A2). Daily,  $\Delta h$  was calculated as the mean of  $n = 3$  replicated measurements collected at approximately the same hour of each day ( $\pm 120$  minutes).  $K_V$  measurements spanned 8-11 days depending on the treatment with a shortened duration for the control treatment (8 days) and a missed day of measurement (day-10) for the algae treatment.

We de-gassed each sediment column before measuring VHG because vertical water flow can trap gas bubbles in sediment pores (Beckwith & Baird, 2001; Cuthbert et

al., 2010). Without disturbing the permeameter pipes, we redirected the outlet flow from the upper reservoir for 90 seconds to halt vertical flow through the sediment columns, which allowed any trapped gas to escape. Downward flow was then returned to the sediment columns, and after a 30-second re-equilibration, we collected measurements of  $\Delta h$ .

### 2.3.2 | Measuring Caddisflies and Organic Matter AFDM

At the termination of an experimental trial, we extracted caddisflies (living, dead, and body parts) from the sediment columns of the caddis and algae plus caddis treatments and counted living caddisflies. We then converted the raw number of caddisflies in a sediment column to an areal density commonly used to assess stream invertebrate numbers (#caddis  $m^{-2}$ ; Table 1).

Additionally, we estimated total organic matter ash-free dry mass (AFDM<sub>tot</sub> (mg sediment column<sup>-1</sup>)) for all treatments (after caddisfly extraction in the caddis and algae plus caddis treatments) at the termination of an experimental trial by adapting a method for epiphytic and epipsammic algae sampling (Hauer & Lamberti, 2007). We collected an organic matter slurry from each sediment column by vigorously shaking sediments for 90 seconds in a 4 L polyethylene bottle filled with 0.9 L of distilled water, and scrubbing the permeameter pipe wall using a stiff brush. We sieved the slurry twice; first through a 1 mm sieve to remove sediments, then through a 63  $\mu m$  sieve to collect “coarse” organic matter, which we dried at 60°C and ashed at 500°C (AFDM<sub>course</sub>). We then filtered a 50 ml subsample from the slurry that passed through the 63  $\mu m$  sieve (“fine” organic matter) through a pre-ashed 0.45  $\mu m$  glass fiber filter, dried, and ashed the subsample, and



multiplied the subsampled ashed fraction by a correction coefficient to estimate  $AFDM_{\text{fine}}$ .  $AFDM_{\text{tot}}$  was estimated by summing  $AFDM_{\text{course}}$  and  $AFDM_{\text{fine}}$ .

Because we could not extract caddisfly nets before sampling epilithic biofilm, we adjusted  $AFDM_{\text{tot}}$  to account for caddisfly silk production within the sediments by subtracting the dry mass of silk that could reasonably be expected to have been collected in the biofilm slurry. We allowed caddisflies to colonize sediments (identical to those used in the permeameter experiment) in a laboratory mini-flume (1.2m long  $\times$  0.15m wide  $\times$  0.20m deep) filled with tap water for 3 days and successfully collected 16 nets from the sediments. The nets were pooled, dried at 60°C, ashed at 500°C, and weighed ( $AFDM_{\text{pooled}}$ ). We then estimated the AFDM of a single net ( $AFDM_{\text{net}}$  (mg)) by dividing the  $AFDM_{\text{pooled}}$  by 16. Under the assumption that some caddisflies abandoned nets, we calculated adjusted AFDM ( $AFDM_{\text{adj}}$  (mg sediment column<sup>-1</sup>)) for each sediment column in each trial as:

$$AFDM_{\text{adj}} = AFDM_{\text{total}} - AFDM_{\text{net}} * 2C$$

where  $C$  was the number of living caddisflies in the sediment column, and 2 was the assumed number of nets built accounting for abandonment (Georgian & Thorp, 1992). While the adjustments for caddisfly net production were minute, we believe  $AFDM_{\text{adj}}$  (hereafter organic matter AFDM) provides a stronger estimate of sediment organic matter content by adjusting AFDM estimates for the potential presence of caddisfly silk.

## 2.4 | Statistical Analysis

All statistical analyses were performed in the R statistical computing environment, version 3.4.3 (R Core Team, 2017). Variation in  $K_V$  across treatments were compared

using a linear mixed-effects model with treatment (factor) and day (continuous) as fixed effects and sediment column as a random grouping factor to account for the non-independence of repeated daily measures of  $K_V$ . The model was fit using the nlme package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017). We tested for differences in the rate change of sediment  $K_V$  among treatments by comparing model slope coefficients. Comparisons were relative to the baseline slope coefficient in the model which could be changed accordingly to acquire specific contrasts testing previously mentioned *a priori* predictions. Our first tests compared  $K_V$  in the control treatment to each other treatment. To test additional predictions, we set the caddis plus algae treatment as the baseline slope in the linear mixed-effects model and tested comparisons accordingly.

A two-sample unpaired Wilcoxon rank-sum test was used to test for differences in caddisfly density among the two independent treatments that were inoculated with caddisflies. This allowed us to assess whether median caddisfly densities differed between the two treatments, thus potentially contributing to differences in estimates of sediment column  $K_V$ .

We used a one-way ANOVA to compare differences in organic matter AFDM at the end of a trial between treatment levels. Values of organic matter AFDM were log-transformed to meet the standard assumptions of ANOVA models. Post-hoc comparisons of log-transformed mean organic matter AFDM among treatments were compared with a Tukey's Honest Significant Difference (HSD) test using the glht package (Hothorn,

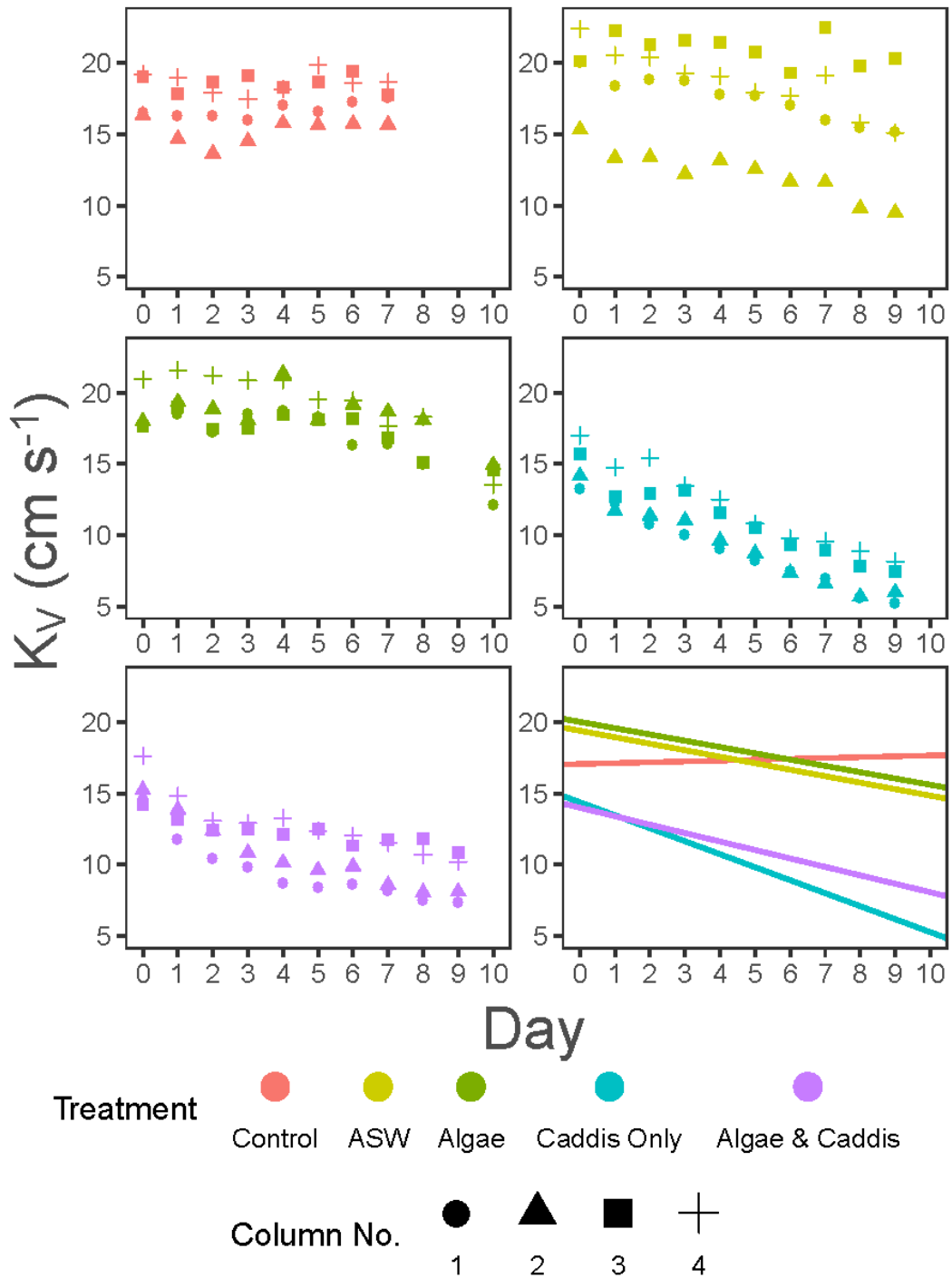
Bretz, & Westfall, 2008). We back-transformed estimates and reported them as differences in median organic AFDM between treatments with 95% confidence intervals.

### 3 | Results

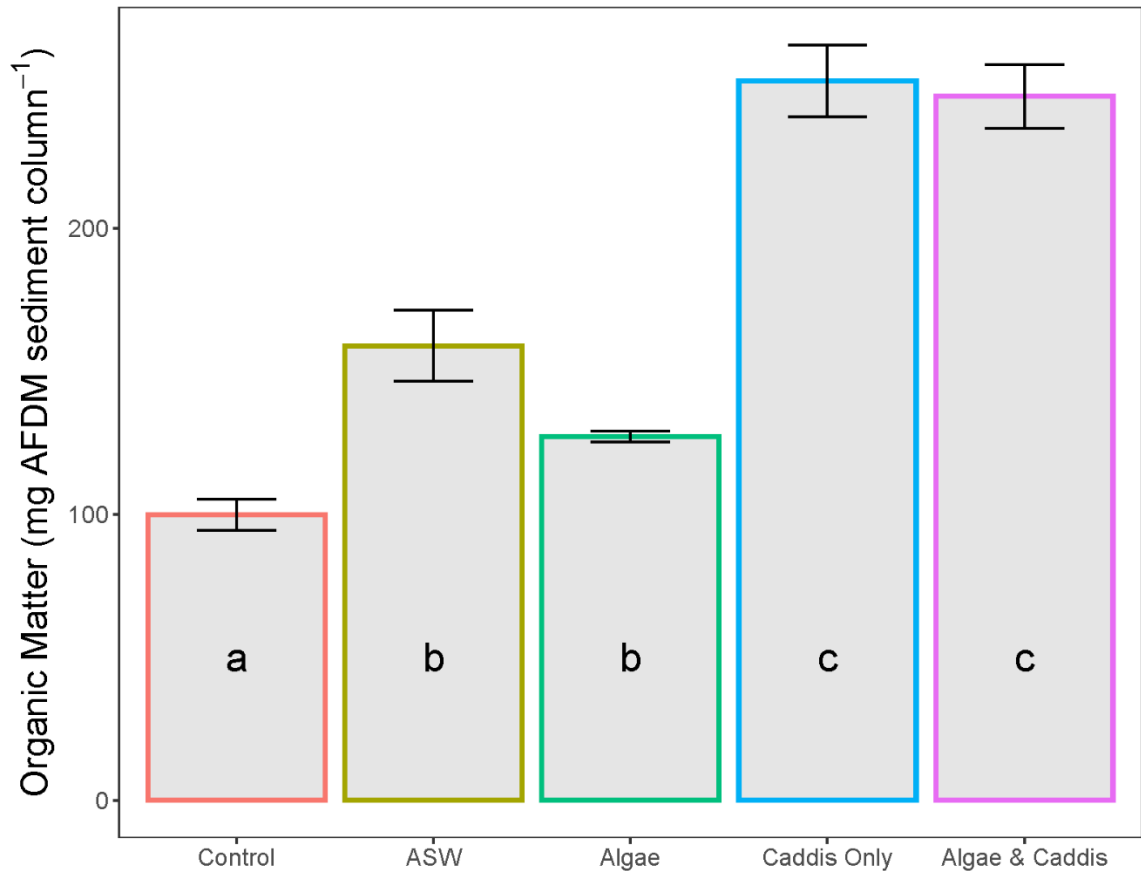
#### 3.1 | Variation in $K_V$ and Caddisfly Density

Biological inocula significantly reduced the movement of water through the pore spaces of the sediment columns (Figure 4). We found strong evidence of an interaction effect between day and treatment (Type III F-test,  $F_{4,167} = 30.74$ ,  $p < 0.0001$ ) which indicated that temporal changes in sediment  $K_V$  depended on the treatment. In the control treatment (bleach solution), sediment  $K_V$  increased slightly at a rate of  $0.06 \text{ cm s}^{-1}\text{day}^{-1}$  but remained statistically stable ( $t_{167} = 0.81$ ,  $p = 0.4171$ ), affirming that changes in sediment  $K_V$  observed in subsequent treatments were due to biological effects rather than physical changes to the sediment columns like settling. The rate of decrease in sediment  $K_V$  for the ASW treatment was  $0.52 \text{ cm s}^{-1}\text{day}^{-1}$  greater than the control treatment ( $t_{167} = -5.69$ ,  $p < 0.0001$ ) and helped establish a baseline for the effect of residual sediment organic matter growth on  $K_V$  in sediment columns. The rate of decrease in sediment  $K_V$  for the algae treatment was  $0.50 \text{ cm s}^{-1}\text{day}^{-1}$  greater than the control treatment ( $t_{167} = -5.64$ ,  $p < 0.0001$ ). This result helped establish a baseline for additional algal effects on sediment  $K_V$  in the absence of caddisflies. For the caddis only treatment we saw the largest effect on the rate of decrease which was  $0.97 \text{ cm s}^{-1}\text{day}^{-1}$  greater than the control treatment ( $t_{167} = -10.72$ ,  $p < 0.0001$ ). We found the algae plus caddis treatment imparted an additional  $-0.65 \text{ cm s}^{-1}\text{day}^{-1}$  change in sediment  $K_V$  relative to the control treatment ( $t_{167} = -7.20$ ,  $p$

<0.0001). Caddisfly density was similar between the two treatments with caddisflies present (Wilcoxon rank-sum test,  $W = 12$ ,  $p = 0.3094$ ). Contrary to our prediction, the rate of decrease in sediment  $K_V$  for the caddis only treatment was  $0.32 \text{ cm s}^{-1}\text{day}^{-1}$  greater ( $t_{167} = -4.28$ ,  $p < 0.0001$ ) than the algae plus caddis treatment. When caddisflies and algae colonized the sediment columns, the additional rate of change in  $K_V$  was  $0.14 \text{ cm s}^{-1}\text{day}^{-1}$  greater than the ASW treatment ( $t_{167} = 1.85$ ,  $p = 0.0665$ ) and  $0.15 \text{ cm s}^{-1}\text{day}^{-1}$  greater than the algae treatment ( $t_{167} = 2.09$ ,  $p = 0.0383$ ).



**Figure 4.** (A-E) Changes in  $K_V$  over time. Colors represent treatments ( $n = 5$ ), and shapes represent replicate sediment columns ( $n = 4$ ). (F) Estimated slopes for changes in  $K_V$  over time derived from linear mixed effects model.



**Figure 5.** Organic matter (mean AFDM  $\pm$  SE) collected from sediment columns across treatments ( $n = 5$ ). Reported values are adjusted to account for the silk production and thus represent organic matter content. Means sharing a letter are not significantly different at  $\alpha = 0.05$  (Tukey's HSD).

### 3.2 | Variation in Biofilm AFDM

There was strong evidence that organic matter AFDM varied between the five treatments ( $F_{4,15} = 61.38$ ,  $p < 0.0001$ ) and that caddisflies promoted accrual of organic matter in the sediments (Figure 5). Estimated median organic matter AFDM in sediment columns receiving the algae plus caddis treatment was 55.70 mg higher (95% CI [24.18, 95.24]) than the ASW treatment (Tukey's HSD,  $p = 0.0002$ ), and 92.98 mg higher (95% CI [53.90, 141.96]) than the algae treatment (Tukey's HSD,  $p < 0.0001$ ). Additionally,

estimated median organic matter AFDM in sediment columns with the caddis only treatment was 59.06 mg higher (95% CI [26.85, 99.44]) than the ASW treatment (Tukey's HSD,  $p = .0001$ ), and 97.14 mg higher (95% CI [57.22, 147.19]) than the algae treatment (Tukey's HSD,  $p < 0.0001$ ). We did not detect differences in median organic matter AFDM between the two treatments with caddisflies present (Tukey's HSD,  $p = 0.9982$ ).

## 4 | Discussion

To our knowledge, no studies have experimentally investigated invertebrate mediated controls on hydrologic exchange in gravel dominated sediments, subsequent biological responses, and implications for gravel-bedded rivers. Links between invertebrates and geomorphic processes like sediment transport are well established; however, how invertebrates influence hydrology remains largely unknown. While invertebrates per capita effects may be small, considering their ubiquity and density at the streambed interface in gravel-bedded rivers (Boulton, 2000; Kasahara & Wondzell, 2003) coupled with the expectation that hydrologic exchange will strongly influence ecosystem processes here (Fellows, Valett, & Dahm, 2001) we hope our experiment can shed light on overlooked controls of hydrologic processes. Many organisms influence characteristics of their environment however ecosystem engineers have a disproportionately large influence on abiotic dynamics which can be demonstrated when engineers are experimentally excluded or introduced (Nogaro et al., 2009). Using a novel downward-flow permeameter, we demonstrate that net-spinning caddisflies reduce the

vertical hydraulic conductivity and hydrologic exchange across coarse sand and gravel sediments by producing silk structures in pore spaces that impede the flow of water. Caddisflies at moderate and common densities found in streams ( $2,000 \text{ m}^{-2}$ ) reduced sediment  $K_V$  more rapidly well recognized clogging mechanisms like algae or supposed organic matter deposition or biofilm growth (Battin & Sengschmitt, 1999; Ibisch, Seydell, & Borchardt, 2009; Su, Jasperse, & Constantz, 2008). Additionally, we found that organic matter AFDM was higher in sediments colonized by caddisflies relative to those without caddisflies, suggesting that the caddisflies stimulated organic matter growth and or deposition.

#### 4.1 | $K_V$ Changes and Implications

Patterns in sediment column  $K_V$  varied according to the treatment administered however the largest reductions were seen with caddisfly additions. We saw similar effects on  $K_V$  in both the Algae and ASW treatments (non-caddis treatments permitting biological growth) which suggests that organic matter growth or deposition in the sediment matrix acts to reduce hydraulic conductivity. Our largest reductions in hydraulic conductivity however were seen in the caddis only treatment ( $0.97 \text{ cm s}^{-1} \text{ day}^{-1}$ ), and the caddis plus algae treatment ( $0.65 \text{ cm s}^{-1} \text{ day}^{-1}$ ) which were larger in comparison to the ASW treatment ( $0.52 \text{ cm s}^{-1} \text{ day}^{-1}$ ) and the algae treatment ( $0.50 \text{ cm s}^{-1} \text{ day}^{-1}$ ). A previous study found 70% reductions in horizontal hydraulic conductivity ( $K_H$ ) when simulated caddisfly nets spanned pore spaces, although results were based on caddisfly densities of  $735 \text{ m}^{-2}$  (Juras et al., 2018). Given caddisfly modulated changes to sediment column  $K_V$  in our experiments we expect they could influence exchange rates across and residence time



distributions of water within the streambed, both well-studied drivers of subsurface biogeochemical processing (Findlay, 1995; Valett et al., 1996). In gravel-bedded rivers with rapid hydrologic exchange and short residence time distributions, biofilm uptake kinetics can ultimately constrain biofilm assimilation of metabolites (Battin & Sengschmitt, 1999; Boano et al., 2014; Hall, Bernhardt, & Likens, 2002). Therefore if silk structures reduce pore flow velocities and lengthen water residence times, we posit the effect would increase opportunities for biogeochemical transformations by extending the contact time between solute rich surface water and the solute hungry biofilms (Battin et al., 2003; Hall et al., 2002; Harvey & Wagner, 2000).

Besides larger effects on  $K_V$ , two important distinctions between biological treatments with caddisflies and without were that reductions in  $K_V$  occurred more rapidly when caddisflies were present in the sediment column and that the largest reductions in  $K_V$  occurred in the caddis only treatment. Given the rapid response in  $K_V$  to caddis colonized sediment columns, combined with the fact that caddisflies are early colonizers following disturbance in streams (Cardinale et al., 2004; Hemphill, 1988), we propose that caddisflies could influence streambed  $K_V$  soon after events like bed-altering floods and improve hydrologic conditions for early successional biofilm communities. Additionally, we expected the caddis plus algae treatment to show larger effects on sediment  $K_V$  than just caddisflies only, owing to the combined presence of two potential engineering groups in the caddis plus algae treatment. However, we found that the caddis only treatment showed the largest effects. Our experimental design was not nuanced enough to isolate the mechanism generating this result, however we hypothesize

caddisflies may change net architectures, net locations, or gross number of nets when denied algal resources to improve capture efficiencies during resource scarcity (Wallace, 1975). Further work should seek to investigate the specific mechanism that leads to variation in caddisfly induced Kv reductions across a gradient of resource availability.

#### 4.2 | Influences on Biofilm and Organic Matter

We observed increased organic matter accumulation in the two treatments that contained caddisflies and suggest that caddisfly effects could contribute to our understanding of processes that drive heterotrophic biofilm abundance, habitat selection, and diversity at the streambed, where heterotrophic processes can dominate metabolic regimes (Fellows et al., 2001; Pusch, 1996). Three non-mutually exclusive mechanisms could potentially account for empirical differences in organic matter AFDM and deserve further investigation. First, biodeposited caddisfly fecal pellets likely leach dissolved organic matter (DOM) into the hyporheic zone. Previous studies have demonstrated that bioavailable carbon can control biogeochemical activity in the streambed and the leeching of DOM from animal fecal pellets makes up a substantial proportion of available DOM for heterotrophic organisms (Jumars, Penry, Baross, Perry, & Frost, 1989; Reeder et al., 2018; Urban-Rich, 1999). Second, caddisfly nets directly increase the surface area available for heterotrophic biofilm colonization in the interstitia. Biofilms proliferate in ecosystems with high sediment-surface area to water-volume ratios (Battin et al., 2008) and pore spanning caddisfly nets must increase this ratio. Third, caddisfly nets likely diversify flow and create zones of flow stagnation within gravel sediments that otherwise would be characterized by fast hydrologic exchange rates. This added physical

complexity could lower hydrodynamic constraints on biofilm structures by reducing the chance of detachment and entrainment (Boano et al., 2014; Taherzadeh, Picioreanu, & Horn, 2012), or add physical and chemical heterogeneity to pore flow dynamics and redox conditions respectively, encouraging alternate metabolic pathways and increased biofilm diversity in bed sediments (Singer, Besemer, Schmitt-Kopplin, Hödl, & Battin, 2010). Our sampling methodology did not allow us to discriminate between biofilms growing on substrates and organic matter deposited within the sediment matrix in our experiment. However, considering that prior studies have shown biofilms influence exchange rates and subsurface residence times, we posit they contributed to the patterns in our data (Aubeneau, Hanrahan, Bolster, & Tank, 2016; Orr, Clark, Wilcock, Finlay, & Doyle, 2009). At the end of our experimental trials, we measured a nearly two-fold difference in organic matter AFDM in sediments colonized by caddisflies compared to sediments without caddisflies, and direct observations revealed that organic matter was noticeably thicker on silk surfaces compared to sediment surfaces. Taken together, these findings suggest that caddisflies stimulated biofilm growth in sediment column interstitial spaces.

### 4.3 | Limitations of Approach

Laboratory microcosms such as ours have been used extensively to isolate biological engineering effects in controlled environments, nevertheless, extrapolating results derived from these experiments to streams is difficult. While we present compelling findings, we also acknowledge inherent limitations in our approach that reduce our ability to make broad inferences across streams. Despite these limitations, however, we provide the first

empirically derived evidence that *Arctopsyche* and *Hydropsyche* caddisflies could regulate vertical hydrologic exchange across the streambed interface.

#### 4.3.1 | Acknowledgment of Pseudoreplication

Because of the continuous exchange and mixing of water through the chillers and sediment columns (hence a mixing of treatment conditions), the five treatments could not be operated at the same time; i.e. randomized block design with one treatment per column. Our experimental design necessitated that four replicates of a single treatment be run together during each trial resulting in replicates that are not spatially independent (Hurlbert, 1984). We encourage our readers not to interpret our inferences as strict causal statements, and rather must ultimately judge whether the divergence between treatment effects is considerable enough to prove the contrasts were a result of the treatment administered (Oksanen, 2004; Schank & Koehnle, 2009).

#### 4.3.2 | Spatial and Temporal Limitations

Our sediment columns were composed of course sands to medium gravels, while caddisflies can occupy habitats with substrates as large as cobbles and boulders (Hauer & Stanford, 1982). Obtaining measurable VHGs with larger sediments would require a permeameter capable of delivering high volumetric flow ( $Q$ ) through the sediment columns. Budgetary constraints and limited laboratory space prevented such a design. Additionally, our experiment contained just two genera (*Arctopsyche* and *Hydropsyche*) from the Hydropsychidae family during a short period of their life cycle, comprising a small fraction of the intra and interspecific variation of species found in streams. The Hydropsychidae family contains approximately 145 species in North America alone

(Wiggins, 1996), and a given stream might contain ~6-10 different species, each building silk structures with variation in capture-net mesh sizes and architectures. Thus, inter and intraspecific variations in capture-net mesh size and architecture could impart significant variation on flow pattern control, which could be explored in future experiments (Loudon & Alstad, 1992; Wallace, 1975). Finally, the temporal extent of our experiment spanned just 8-11 days, thus attempting to scale caddisfly effects on sediment  $K_V$  over longer time frames should be approached with caution.

#### 4.4 | An Ecosystem Engineering Frontier

Extensive research on ecosystem engineering has documented that organism modifications of habitats can control the availability of resources for others. The effects of engineers range from microalgae enhancing sea ice breakup in the Arctic, to pocket gophers altering soil development in North American prairies, to elephants affecting habitat structure in the African savanna (Buynitskiy, 1968; Huntly & Inouye, 1988; R. M. Pringle, 2008). In gravel-bedded rivers, organisms play a particularly important role in modifying hydrologic exchange across the streambed. For example, beavers construct dams creating hydraulic gradients that effect lateral and vertical hydrologic exchange through sediments, and salmonids increase hydrologic exchange by digging redds that drive oxygenated water towards incubating eggs (Janzen & Westbrook, 2011; Tonina & Buffington, 2009). However, recent studies have identified that invertebrates can play a greater role than larger organisms in regulating physical processes in streams (Albertson & Allen, 2015; Romero, Gonçalves-Souza, Vieira, & Koricheva, 2015), yet only a few have documented the role of invertebrates at the critical streambed ecotone. It stands to

reason that invertebrates' small per capita but large overall influence in the channel could extend to the hyporheic zone of gravel-bedded rivers, and this study is the first to document this potential influence. Given the importance of hydrologic exchange to ecosystem processes in gravel bedded, we hope our work can direct more attention towards ubiquitous and abundant invertebrate modulators of flow and the consequences of their engineering activities on exchange processes in rivers.

#### 4.5 | Conclusion

Our experiment demonstrates that caddisflies could regulate  $K_V$ , a critical constraint on vertical hydrologic exchange at the streambed ecotone, by constructing flow modulating nets in the sediment pore spaces. Ecotone boundary permeability has been highlighted as a fundamental control on exchange processes between adjacent ecosystems (Vervier, Gibert, Marmonier, & Dole-Olivier, 1992; Wiens, Crawford, & Gosz, 1985), and we shed light on an invertebrate mediated mechanism that directly reduces the permeability of the surface water-hyporheic zone interface that could influence local heterotrophic biofilm communities and alter metabolic processes in streams and rivers. A difficult but promising future direction will be investigating these laboratory, experimentally based effects in natural gravel-bedded rivers. As aquatic scientists continue to investigate exchange processes between and among ecosystems, we suggest developing synthetic concepts that integrate invertebrate constraints on physical processes could elucidate underappreciated drivers of biogeochemistry in rivers and extend our understanding of how energy and matter traverse rivers.

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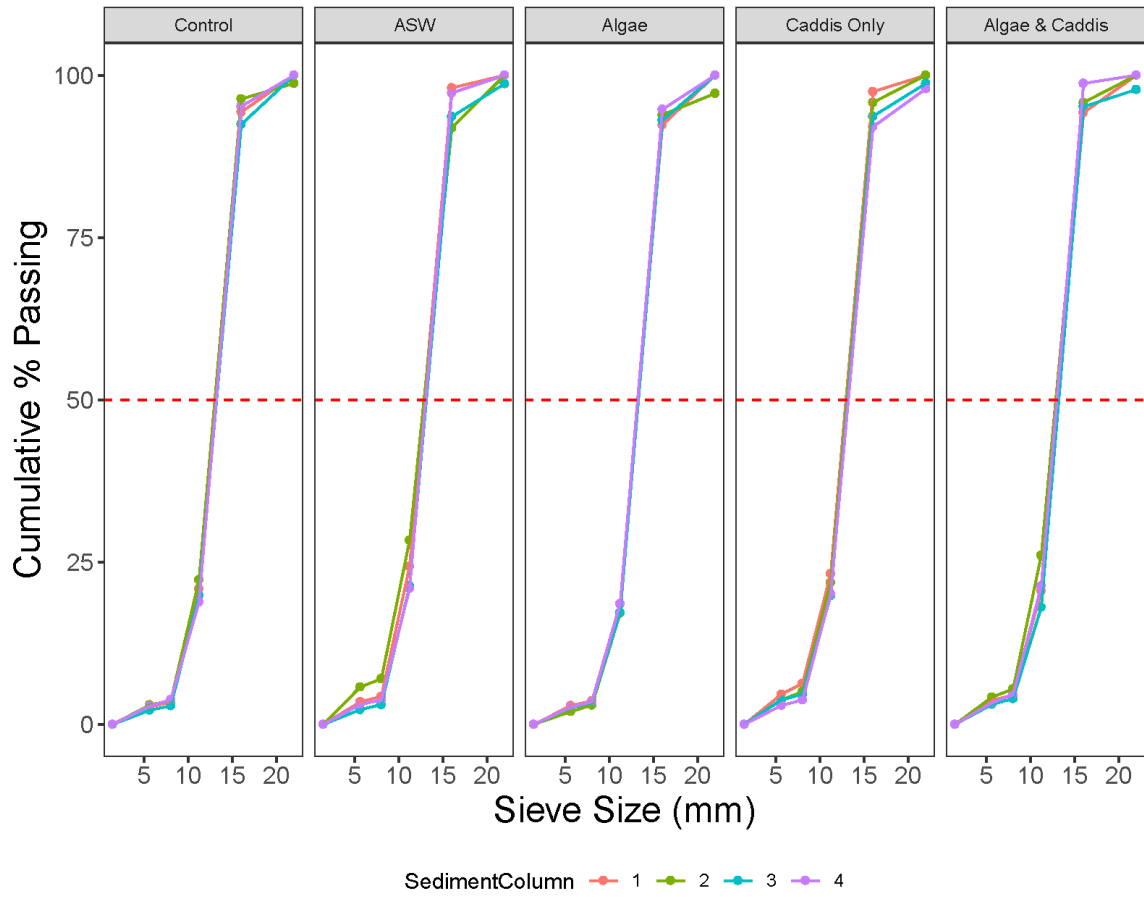
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APPENDICES

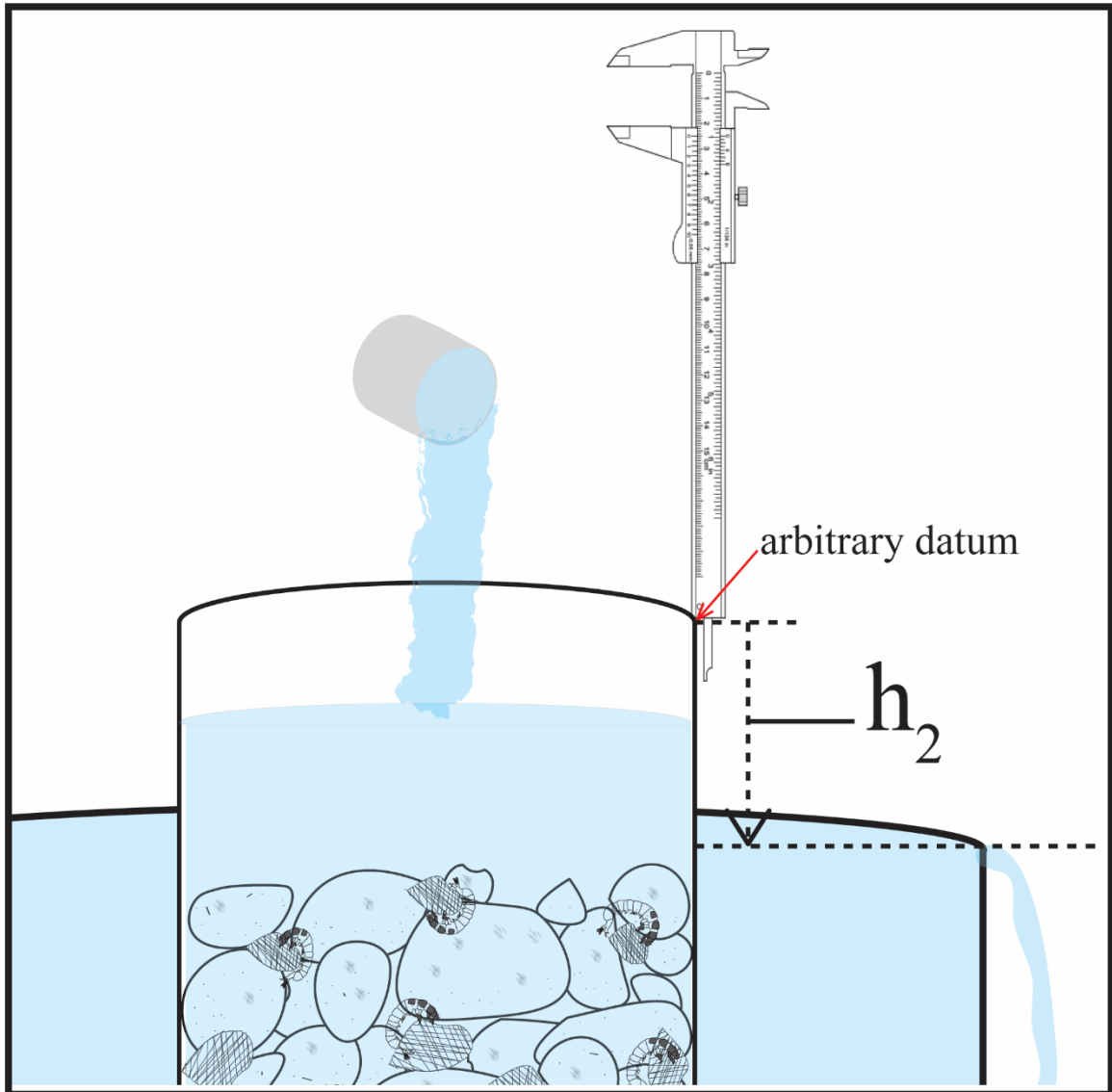


APPENDIX A

SUPPLEMENTARY FIGURES



**Figure A1.** Grain size analysis gradation curves across treatments. Hashed red line indicates D<sub>50</sub>.



**Figure A2.** Example of protocol for measuring  $h_2$  (hydraulic head at bottom of sediment column) from an arbitrary consistent datum marked on the upper edge of the permeameter pipe to the water surface in the 5-gallon bucket.