Contents lists available at ScienceDirect





journal homepage: www.elsevier.com/locate/ecoleng



Incorporating macroinvertebrate biological structures into gravel-bedded stream fluid dynamics using 3D CFD modelling



Mark Juras^a, Lindsey K. Albertson^{b,*}, Joel Cahoon^a, Erick Johnson^c

^a Department of Civil Engineering, 205 Cobleigh Hall, Montana State University, Bozeman 59717, USA

^b Department of Ecology, 310 Lewis Hall, Montana State University, Bozeman 59717, USA

^c Department of Mechanical & Industrial Engineering, 220 Roberts Hall, Montana State University, Bozeman 59717, USA

ABSTRACT

ARTICLE INFO

Keywords: Ecohydraulics

Ecohydrology

Hvdropsychidae

Sediment motion

Silk-producing insects

Stream morphodynamics

In gravel-bedded streams and rivers, silk nets of hydropsychid caddisfly larvae (Trichoptera:Hydropsychidae) can increase the critical shear stress, τ_c^* , required for sediment particle motion, reduce bedload flux, and provide a low flow refuge for other organisms. However, there is still a limited understanding of the mechanisms that regulate how biological silk structures might influence near-bed fluid dynamics. Part of the challenge in identifying both the per capita and population level influences of caddisfly silk nets lies in the difficulty of modelling such fine-scale and detailed architecture of the structures. Here, we use a 3D computational fluid dynamics (CFD) model to evaluate the impact of silk nets on shear stress and pore space velocity by varying silk net aerial density within a modelled gravel bedded stream where the silk nets are simulated as small rigid bodies of realistic distribution, geometry, and orientation. The model revealed that silk net densities of 330 and 735 nets/ m^2 reduce the average shear stresses by an average 6.0% and 11.6%, respectively, over a range of inflow velocities. Silk nets also result in near-bed flows close to 0 m/s by reducing velocity by up to 60%. Our research sheds light on the important influence of small but numerous aquatic animals on water flow paths and highlights the significance of adding biological complexity into water flow models in lotic ecosystems to improve erosion models that may be used in river channel and riparian habitat design.

1. Introduction

To model freshwater ecological habitats, a growing body of research has emphasized the need for both biological and physical sciences to inform and complement one another (Allen et al., 2014). Stream ecosystems provide an ideal habitat to investigate interactions between biology and physical dynamics because stream hydraulics are fundamentally intertwined with aquatic communities and ecosystem function. For decades, ecologists and geomorphologists have separately tried to identify how fluid dynamics influence biological organisms in lotic ecosystems. However, attention has recently turned to the reciprocal relationships between organisms and their physical environment, highlighting the need for better interdisciplinary modelling approaches to more accurately capture the interplay and feedbacks between the two systems (Dietrich and Perron, 2006). For example, flow velocity can influence distribution of biofilm, macroinvertebrates, and vegetation and these organisms can, in turn, influence flow characteristics through production of structures or behaviours (Statzner et al., 1988, Arnon et al., 2009, Aseada et al., 2010, Albertson et al., 2014a). Recent advances at the interface of stream ecology and

geomorphology emphasize the remarkable effect that organisms themselves have on physical properties of the system, including meander patterns and bank stability (Pollen and Simon, 2005, Braudrick et al., 2009).

Movement of sediment in rivers is an important driver of channel formation, channel maintenance, and ecosystem function (Leopold et al., 1964, Resh et al., 1988). A variety of factors control sediment movement, retention, and texture, including sediment supply, grain protrusion, and grain friction angle (Buffington and Montgomery, 1999, Church, 2006). Further, critical shear stress measured at the initiation of movement of riverbed sediments is known to vary by a factor of two for a given grain size and does not follow theoretical predictions related to bed slope, with several physical processes such as local flow velocity and turbulence hypothesized to drive this variability (Buffington and Montgomery, 1997, Lamb et al., 2008). Some have also suggested that the variation in observed measurements may be explained by the unaccounted-for influence of plants and animals that act as ecosystem engineers (Jones, 2012; Rice et al., 2012). Ecological engineering is widespread and especially prevalent by small but numerous invertebrates (Albertson and Allen, 2015; Romero et al., 2015). Applied

* Corresponding author.

E-mail address: lindsey.albertson@montana.edu (L.K. Albertson).

https://doi.org/10.1016/j.ecoleng.2018.05.011

Received 14 November 2017; Received in revised form 1 April 2018; Accepted 7 May 2018 0925-8574/@ 2018 Elsevier B.V. All rights reserved.

river restoration problems are increasingly focused on the importance of sediment transport dynamics as well as the presence of ecosystem engineers in structuring the hydrological and geomorphological processes that are so critical to river channel maintenance and ecosystem function (Trush et al., 2000, Pollock et al., 2014), but the links between ecosystem engineers and sediment transport modelling dynamics remain understudied.

Here, we use net-spinning hydropsychid caddisfly larvae (Trichoptera:Hydropsychidae) to model how aquatic organisms affect water flow dynamics in their surrounding stream habitat. Hydropsychid caddisflies are filter-feeders that produce silk net structures to capture food particles flowing downstream (Wiggins, 1977). Hydropsychids and their structures play a substantial role in the ecosystem by providing a source of food for fish (Wallace and Webster, 1996, Williams and Williams, 1998), shelter for other organisms living in the benthos (Nakano et al., 2005, Tumolo et al., in review), and a mechanical stabilizer between gravel bed particles (Statzner, Arens, Champagne, Morel, & Herouin, 1999; Johnson et al., 2009, Albertson et al., 2014a). The Shields stress, τ^* , is a non-dimensional number relating the stresses on a particle from a flow and the mass of the particle, where exceeding some critical Shields stress, τ_c^* , results in mobilization of the particle. Experiments have shown that two common hydropsychids, Arctopsyche californica and Ceratopsyche oslari, can increase the critical Shields stress required for sediment particle motion by up to 40-70% for 10-22 mm diameter gravels by binding bed particles together with their silk, thereby resisting downstream movement and stabilizing the streambed (Albertson et al., 2014a). Simulation models of Shields stress that include the binding forces of caddisfly silk on the resultant stress have been developed (Albertson et al., 2014b), but the physical structure itself has not yet been incorporated into modelling techniques.

The challenges associated with describing how these ecogeomorphological relationships operate in lotic ecosystems include visualization (Hesselink et al., 1994), in-situ measurements (Liao et al., 2015), and lack of appropriate numerical models. Aquatic habitats characterized by complex flow patterns generated by irregular channel topography and submerged obstructions are well-suited for three-dimensional computational fluid dynamics (hereafter 3D CFD) modelling (Shen and Diplas, 2008), and recent studies have utilized CFD to quantify the flow effects of living organisms ranging from biofilms to large marine vertebrates (Liu et al., 1996, Shorter et al., 2013, Horn and Lackner, 2014). To better understand how biological stabilizing effects of aquatic insect silk might occur, we test how different densities of caddisfly silk nets affect flow in a gravel-bedded stream using 3D CFD modelling. We hypothesize that caddisfly silk nets increase bed stability by mechanically binding grains together and reducing shear at the bed via an increase in drag and resulting reduction of interstitial velocity. We also predict that near-bed velocity and shear stress, τ , acting on the gravel bed particles will decline as the density of silk nets increases. Our findings demonstrate how numerical tools can aid in the understanding of complex ecological dynamics in lotic systems, providing a unique link between ecology and hydraulic river modelling and design.

2. Materials and methods

2.1. Study organism

Hydropsychidae is a family of aquatic insects consisting of netspinning caddisflies. Hydropsychids are common worldwide, often comprising an important group within the benthic macroinvertebrate community (Wiggins, 1977, Mackay and Wiggins, 1979). Their life history consists of an aquatic egg, larval, and pupal stage followed by a short-lived terrestrial adult stage. A typical stream may support a community of several species of coexisting hydropsychid larvae that have silk nets each composed of 10 s–100 s of silk threads woven together into unique architectures and sizes (Fig. 1; Loudon and Alstad, 1992, Harding, 1997). The silk net that a caddisfly produces serves as a



Fig. 1. A caddisfly silk net built between two bed particles (Albertson et al. 2014b).

retreat for the larva and a filter feeding structure that catches food particles. Benthic densities of hydropsychids in nature can range from 100 s to over 10,000/m² and are regulated by various environmental factors such as water temperature, food availability, and water flow (Miller, 1984, Albertson et al., 2018). We selected three different but relatively conservative aerial densities of silk nets (0, 330, and 735 nets/m²) to investigate the influence of silk on shear stress and flow velocity. These densities roughly match the number of nets that were observed from photographs of a previous caddisfly microcosm study (Fig. 2).

2.2. Three-dimensional solid geometry

A hydropsychid caddisfly silk net (Fig. 1) acts as a support structure that resists motion of the gravel particles, potentially by reducing the velocity of the water flowing over and around them (Albertson et al., 2014a,b). Here, we investigate the mechanistic effect that the nets have on the fluid dynamics and shear stress (Pa), τ , around the gravel bed. The model geometry seeks to mimic a natural, gravel-bedded habitat by accurately representing the two principal components of this study, the gravel bed itself and caddisfly silk nets.

2.2.1. Gravel bed

The gravel bed is the main geometry of the system, dictating the water flow over and through it and providing a prop for the



Fig. 2. Gravel bed photo used to generate objects for the CFD model including individual gravels and silk nets. Note, white labels do not correspond to silk net locations.

construction of the caddisfly silk nets. To determine the position of particles to inform the model construction, a representative gravel bed was created in a laboratory microcosm (10.0 m long \times 0.4 m wide \times 0.2 m deep), consisting of gravels with median grain sizes of 40–45 mm. The particles were asymmetrical, sub-angular to rounded, and arranged in a singular layer that has a variety of horizontal pore spaces between individual particles (Fig. 2). Grain size was selected to be in the range that hydropsychids have been shown to increase critical shear stress (Albertson et al., 2014b). Hydropsychids were introduced to the microcosms and allowed to build silk nets for five days, after which time photographs were used to document placement of individual gravels and silk nets.

Detailed photos of the rocks in the experiment were imported into AutoCAD (Autodesk, Inc.) and scaled to a size that produced a median rock diameter of 40 mm. These photos provided a base image for generating 3D virtual rocks by tracing a 3D mesh object on top of each rock, defining a rock height dimension with a mean of 40 mm and varying from 25 to 55 mm, and smoothing the mesh using AutoCAD. The mesh objects were then converted to 3D solid objects. Finally, in order to more closely match a natural streambed, a solid block was created underneath the middle-portion of the rocks, in essence partially submerging the rocks in sand. The final computer-aided design (CAD) gravel bed spans a 600 mm \times 325 mm area.

2.2.2. Incorporating silk nets into the model

A detailed parameterization of silk nets includes describing structures with a given thread tensile strength, silk thread diameter, width and length between individual threads, and total mesh area (Loudon and Alstad 1992). Incorporating this level of detail into the model is computationally cost prohibitive. Therefore, we chose to represent the silk nets as 1 mm thick, rigid solid walls (Fig. 3). While caddisflies typically tend their nets and remove food particles regularly to maintain some baseline level of porosity in the silk structure, nets can be clogged under certain conditions such as those experienced during high suspended sediment loads (Runde and Hellenthal 2000) We assume that the solid sheets simulate a poorly-tended silk net and provide an upper limit to the reduction in shear stress for the gravel bed that silk nets might have.

When generating the silk nets, we strove to match realistic silk net densities in the range of 100 s-1000 s of hydropsychids/m² that have been measured in natural streams (Albertson et al., 2018). We used the photographs to position the silk nets within the modelled gravel bed with an identical net orientation and location within the microcosm gravels where the caddisflies colonized and built silk structures. We sketched silk nets directly into the AutoCAD gravel bed (Fig. 3) in the same position and with approximately the same net area as observed in the microcosms. Employing this method, the widths of the silk nets varied from 3 to 10 mm and lengths varied from 5 to 15 mm to span pore spaces between adjacent gravel particles. We then positioned the



Fig. 3. Top view of the CAD generated gravel bed with the silk nets within the gravel matrix colored. Blue nets represent a density of $330/m^2$, and blue and red nets combined represent a density of 735 nets/m^2 .

silk nets into an elevation that varied from 1 to 5 mm above the sand surface based on its location in the photograph. Finally, the silk net sheets were rotated so that the underside of the sheets faced toward the direction of incoming flow, at roughly 45°. We chose this orientation as a conservative representation of how the silk might protrude into water flow since silk net architecture, location, and orientation on substrate is highly plastic depending on microhabitat physical characteristics (Plague and McArthur 2003), and a 45° orientation allows the silk to interact with but not completely block the flow. Using this technique, 70 nets (blue sheets in Fig. 3) were placed in the modelled gravel bed, or equivalently 330 nets/m^2 . Caddisflies are territorial animals and they typically spread themselves out in a spatial arrangement so that there is one silk net per pore space (Cardinale et al., 2002). To further investigate how variation in silk net density might influence their impact on near-bed flow, an additional 86 nets (red sheets in Fig. 3) were added to the system at not more than one per empty pore space and totalling 156 nets over the same area, or equivalently 735 nets/m². In addition, we included the zero silk net scenario, 0 nets/m², for comparison.

2.3. CFD model

A commercial package, STAR-CCM+, was used to solve for the flow velocity, shear stress, and any subsequent changes caused by the silk nets. The model simulates the water flowing within the microcosm, and the water surface is free to adjust to the pressure field.

2.3.1. Governing equations

CFD modelling is the general term for solving the Navier-Stokes equations, the equations of motion developed specifically for fluid flow. In the modelling process, the general equations are typically modified for a specific fluid and solution domain (Anderson, 1995). We restrict our discussion here to compressible, Newtonian fluids, and we refer the reader to contemporary fluid mechanics texts for derivations and details (White, 2006). In our problem, water is assumed to be incompressible, a standard assumption for open-channel flow driven by gravity. This assumption makes the fluid density constant and results in the divergence of the flow being equal to zero (the time rate of change of the volume per unit volume of a moving fluid element is constant). For negligible density changes this is an appropriate approximation and simplifies the equations further, speeding up the simulation calculation. However, the air above the water surface is kept compressible and governed by the ideal gas law. Both fluids are assumed to be Newtonian, a standard assumption for both air and water, where the shear stress is linearly related to the time rate of strain. We assume no-slip conditions between the fluid and confining solids. That is, the velocity of the fluid flow at the point of contact with the any solid boundary is equal to the velocity of the solid, in this case zero. The reduced Navier-Stokes equations representing unsteady, three-dimensional, compressible flow that result are those typical to fluid mechanics texts:

$$\frac{\partial \rho V}{\partial t} + \boldsymbol{V} \cdot \nabla \rho \boldsymbol{V} = -\nabla p + \rho \boldsymbol{f} + \mu \nabla^2 \boldsymbol{V}$$

$$\frac{\partial \rho}{\partial t} + \nabla \cdot \rho \boldsymbol{V} = 0$$

where ρ is the fluid density, *t* is time, *V* is the directional velocity vector, *p* is the pressure, *f* is the directional body force vector, and includes gravity, and μ is the fluid dynamic viscosity. An additional governing equation is introduced to account for the change in temperature required for the ideal gas approximation of air:

$$\left(\frac{\partial\rho e}{\partial t} + \boldsymbol{V}\cdot\nabla\rho e\right) = -\nabla\cdot\boldsymbol{q} - p\nabla\cdot\boldsymbol{V}$$

where e is the total internal energy, and q is the conductive heat flux.

Averaging the equations further simplifies the system of equations into what are commonly referred to as the Reynolds-averaged NavierStokes (RANS) equations by removing velocity fluctuations from the majority of the system. However, the internal shear stresses become dependent upon the averaged fluctuations and related to the viscosity by correlations in turbulent regions. Without solving for the velocity fluctuations directly other equations can be used to determine the shear stresses. This approach introduces new variables and requires additional equations to "close" the system of equations. The realizable k- ε turbulence model is chosen because it is an industry standard for the gravity-induced, open-channel flow, where k is the turbulent kinetic energy and ε is the turbulent dissipation.

To account for both water and air in the model simultaneously the volume-of-fluid method is used to track the free surface between the two fluids. The volume fraction of both the water and air are tracked throughout the domain and weighted averages of certain variables, like density, are then used at the free surface. The Navier-Stokes equations are solved as usual. From the solution of the velocity and pressure fields, quantities such as the shear stress can be calculated.

2.3.2. Simulation domain

Mirroring the experimental microcosm, a rectangular box 1.885 m long \times 0.323 wide \times 0.4 \times deep with zero slope was created to simulate the water and air moving over the gravel bed and nets. The 0.6 m long target section where caddisflies colonized gravels was located in the middle of the box, allowing the water a suitable distance upstream of the gravel bed to develop a boundary layer and stable water surface before passing over the gravel-bedded section. While this boundary layer becomes disrupted as it enters the gravel region and will impact the velocity and shear stress fields, it is the best representation of the experimental environment. The complex geometry of the entire volume was split into a large number of smaller finite volume elements. To improve accuracy, small elements were used in the vicinity of complex solids; however, as the number of elements increases the simulation takes longer to run and requires more computational storage. The mesh around the rock particles and silk nets had a base size of 2 mm with a surface growth rate of 1.1, which reduced the volume change of adjacent elements and minimized the effect of numerical diffusion on the results. The maximum element size grew to approximately 20 mm near the inlets and outlets. Under these parameters, about 500,000 individual polyhedral elements comprise the entire domain. A mesh independence study was performed to ensure the element size was not unduly influencing the results.

2.3.3. Simulation conditions

Due to the nature of a changing free-surface, the simulation was solved as an implicit unsteady problem. Implicit models are attractive because they allow larger time steps and tend to be numerically stable but require more computational resources than explicit solutions due to the iterative nature of the solution at each time step (Zikanov, 2010). While implicit solutions place limited requirements on the time step, accuracy is increased as the time step is reduced. A time step of 0.025 s was chosen to balance accuracy and solution time. To analyse the impact of the caddisfly silk nets on the gravel particle shear stress, we progressed the model until a quasi-equilibrium state of those stresses was achieved. The equilibrium condition required that the asymptote of the shear stress of the gravel bed not vary by more than 2% of the total shear stress over 1 s. Generally, this occurred after approximately 7.5 s of model time.

The boundary conditions were chosen in such a way as to best represent previous microcosm lab experiments, which were in turn designed to represent natural occurrences of the flow regime within a lotic system. Four bulk flow velocities of 1.136, 0.568, 0.426, and 0.284 m/s were prescribed at the inlet cross section resulting in a Froude number of less than 0.805, indicating subcritical flow. We used four velocities to assess how variable flow conditions my modulate the impact that the caddisfly silk has, and all velocities are consistent with observations in microcosm experiments and for natural streams where caddisflies are



Fig. 4. System boundary conditions, where u at the inlet represents one of the four velocities simulated and the modelled gravel bed is located beneath the flow arrow.

known to colonize the benthic habitat. Though caddisflies occupy both subcritical and supercritical flow regimes in natural runs and riffles, subcritical flow in lotic settings is far more common in the systems where caddisflies are abundant (Mackay and Wiggins, 1979). The downstream boundary condition was specified as having hydrostatic pressure with a depth of 0.203 m. We used no-slip solid boundaries for the vertical sidewalls, flat portion of the bottom, gravel bed, and silk nets. The top boundary was specified as having constant ambient pressure, simulating an open atmosphere condition where air is free to flow in and out of the system (Fig. 4).

Initial conditions are required for transient simulations and should be reasonably representative of the system being modelled. For highly complex systems a steady-state solution can be used to provide an appropriate starting point for an unsteady simulation. We specified hydrostatic pressure distribution throughout the entire length and width of the domain to a height of 0.203 m from the bed. Everything below this depth was specified as water with a velocity equal to the inlet. The remainder of the domain was specified as air, with a 0 m/s velocity.

3. Results

3.1. Shear stresses

As expected, increasing silk net density resulted in a substantial reduction in the averaged shear stress in the flow direction. The values for the downstream (x) and vertical (z) directions are detailed in Table 1. While increasing flow velocity showed a marked increase in the downstream shear stress for the scenario with 0 nets/m², the presence of nets consistently reduced τ_x and more nets always resulted in smaller shear stresses. The change in the average τ_x from 0 to 330 nets/m² and 0 to 735 nets/m² was a 6.0% and 11.6% decrease, respectively (Table 1). The shear stresses in the cross-stream direction were small and demonstrated a bias toward one side that was likely a result of the gravel bed geometry. Stresses in the vertical direction were also small compared to those in the direction of flow. The three smallest inflow velocities had an averaged upward shear on the gravel bed that appears to want to force the gravel into the stream. In some instances, the presence of nets further increased these forces. However, the upward

Table 1

Average shear stress (Pa) magnitudes in the τ_x (downstream) and τ_z (vertical) directions for the entire microcosm gravel bed under different inflow velocities. Percent change from the 0 nets/m² scenario is shown in parentheses, with a positive value indicating a reduction and a negative value indicating an increase.

Shear stress	Inlet Velocities	et Velocities (m/s)			
	0.284	0.426	0.568	1.136	
τ _{x-0}	0.156	0.324	0.565	2.092	
τ_{x-330}	0.148 (5.0%)	0.305 (6.0%)	0.539 (4.6%)	1.918 (8.3%)	
τ_{x-735}	0.142 (8.8%)	0.287 (11.4%)	0.493 (12.7%)	1.809 (13.5%)	
τ_{z-0}	0.004	0.007	0.008	-0.022	
τ_{z-330}	0.004 (0.0%)	0.007	0.008	-0.018	
		(-4.6%)	(-6.3%)	(17.2%)	
τ_{z-735}	0.004	0.006 (3.1%)	0.008	-0.016	
	(10.3%)		(-6.3%)	(29.9%)	



Fig. 5. Shear stress magnitudes for the (top) 0 nets/m² and (bottom) 735 nets/m² at an inlet velocity of 0.568 m/s, (left) show the centreline shear stress along the entire length of the bed while (right) show an overhead contour of the gravel bed and the smooth microcosm directly upstream and downstream. Flow is from left to right.

vertical stresses were predominately a result of a large upward shear force at the transition from the flat channel into the gravel section. The majority of the bed experienced downward shear stresses and these showed no strong trends with the addition of silk nets.

The shear stress magnitude was generally higher on the tops of the rock particles due to flow acceleration as water moved around the obstructions and decreased in the pore spaces (Fig. 5). While the majority of the bed experienced relatively small shear stresses, maximum stresses on individual particles had the potential to be an order of magnitude larger. The maximum shear stress observed was 29.5 Pa and occurred in the 1.135 m/s flow with 735 nets/m². However, larger pore spaces could also attract channel water, creating localized regions of acceleration and higher stresses. A clear change in total shear stress was observed as the flow moved into the gravel bed from the smooth channel section upstream (Fig. 5). Large shear stresses were observed uniformly across the first layer of gravel but rapidly transitioned into the turbulent regime expected. The shear stress downstream of the bed became steady again, though at a slightly reduced magnitude. Similar profiles were observed for all flow conditions. While localized stresses may be elevated in scenarios with nets, the average stress was consistently reduced (Table 1). Averaged τ_x for 5 cm sections along the length of the gravel bed are shown in Fig. 6. A jump in stress at the front of the gravel bed was observed but became relatively steady for all but the fastest velocity. The variance in τ_x through the gravel bed, for an inflow velocity of 0.568 m/s, is shown in Fig. 7 and calculated over a 2 s period. This particular velocity produced the largest variance in τ_x across the gravel bed for the 735 nets/m², which otherwise demonstrated no significant bias based on net density. It is unclear at present why this particular velocity deviated so significantly. The variance decreased with increasing velocity.

The potential for mobilization of sediment beds of different grain sizes under various flow conditions can be characterized by the nondimensional Shields stress, as given by,

$$\tau^* = \frac{\tau}{(\rho_s - \rho)gD}$$

where, ρ_s (2600 kg/m³) and ρ (1000 kg/m³) are the densities of the sediment and fluid, respectively, *g* is gravity, and *D* is the particle diameter (Shields, 1936). The critical Shields stress, τ_c^* , is then an allowable limit to the shear acting on the rock particles before they begin to move (Wiberg and Smith, 1987). Relationships exist to determine τ_c^* from a particle Reynolds number, given as $Re_* = u_*\rho D/\mu$ and the

friction velocity $u_* = \sqrt{\tau/\rho}$ (Shields, 1936, Wiberg and Smith, 1987, Dey, 1999). A minimum $Re_* \approx 500$ was calculated from the average shear rates in Fig. 6 and occurs at an inlet velocity of 0.284 m/s. This calculation results in $\tau_c^* \approx 0.04$ for a particle to mobilize. All other flow velocities result in larger particle Reynolds numbers and the critical Shields stress relationships tend to asymptote to approximately 0.045–0.06 at these Reynolds numbers. While the largest average shear stress ($\tau_{x-0} = 3.31Pa$) at 1.136 m/s results in $\tau^* = 0.0053$ well below the critical Shields stress, the maximum of $\tau_{x-735} = 29.5Pa$ results in $\tau^* = 0.047$, which is within the range of motion. Thus the majority of the gravel beds would not move under these flow conditions, though a few of these 40 mm particles could begin to travel under the 1.136 m/s flow. Additionally, as τ_c^* is proportional to the shear stress, the inclusion of silk nets in the pore space between particles could further reduce the prospect of bed mobilization.

3.2. Pore space velocity and water surface level

Evaluating the water flow field helps to explain the decrease in average shear stress values. Introducing nets within the gravel bed slowed the water moving through the bed. Pore space velocity was evaluated on the XY plane 20 mm from the bed, approximately in the middle of the gravel depth, and quantified the velocity by taking a time average sample of the velocity magnitude, u, v, and w components over 400 points on this plane (Table 2). The average change across different inlet velocities in the x-component of velocity from 0 to 330 nets/m² and 0 to 735 nets/m² was a 40.5 and 60.1% decrease, respectively. A consistent decrease in pore-velocity in the flow direction was observed across the range of inlet velocities as the number of nets was increased. However, the vertical velocity tended to increase in the presence of nets, relative to the bed without nets. These velocities remained small, but approached 50% of those in the flow direction and should not be ignored in terms of the flow environment of the hydropsychids. That said, these larger vertical velocities in portions of the pores did not translate into significantly larger vertical shear stresses. The average cross-stream velocity was negligible as it was limited by pore space size and in general by the constrained nature of the channel walls.

Velocity profiles in depth over the gravel bed are shown in Figs. 8 and 9 with 0 nets/m² and 735 nets/m². The upstream profile was relatively uniform, but collapsed and began to accelerate once it interacted with the gravel bed. The velocity profile downstream of the gravel bed, and again over a smooth channel, retained the elevated



Fig. 6. Shear stress, τ_x , along the length of the gravel bed for all four velocity and caddisfly silk net density conditions.

disturbance caused by the bed. The depth variation in velocity through the gravel pore space is also shown in Fig. 8 and zoomed into the region of the gravel particles in the lower half of the profile. While different flow paths were preferred in certain locations, it was unclear if the nets were directly responsible for the chosen paths or if they only introduced a perturbance that the gravel particles then redirected. The rigid nature of the nets in these simulations likely forced some velocity closer to the bed than may be observed in nature. Of particular note is how the introduction of silk nets delayed the re-energization of the velocity profile near the bed. A similar profile with and without nets is observed at the start of the bed (12.5% into the bed). However, in the case of 735 nets/ m^2 , higher velocity gradients are observed in the vicinity of the bed, whereas a more gradual profile develops without nets. This may imply that while smaller overall shear stresses exist in the presence of nets, large velocity gradients exist immediately outside of the bed. As with the shear stresses, similar trends were observed across the range of inlet velocities. The gravel bed arrangement that resulted from placing the each particle by hand in the microcosm did vary across the width of the flume, potentially also influencing these preferential flow paths, but shear stress averaged across the flume width revealed relatively consistent patterns along the length of the gravel bed regardless of the

Table 2

Average velocities (m/s) within the bed in the U_x (downstream) and U_z (vertical) directions under different inflow velocities. Percent change from the 0 nets/m² scenario is shown in parentheses, with a positive value indicating a reduction and a negative value indicating an increase.

Average velocity	Inlet velocities (m/s)				
	0.284	0.426	0.568	1.136	
U _{x-0}	0.0282	0.0453	0.0633	0.1582	
U _{x-330}	0.0164	0.0267	0.0367	0.0994 (31.2%)	
	(41.8%)	(41.1%)	(42.0%)		
U _{x-735}	0.0085	0.0180	0.0263	0.0765 (51.6%)	
	(69.9%)	(60.3%)	(58.5%)		
U _{z-0}	0.0048	0.0067	0.0085	0.0017	
U _{z-330}	0.0061	0.0099	0.0155	0.0187	
	(-27.1%)	(-47.8%)	(-82.4%)	(-100.0%)	
U _{z-735}	0.0040	0.0078	0.0098	0.0197	
	(16.7%)	(-16.4%)	(-15.3%)	(-1058.8%)	

inflow velocity conditions.

Additionally, because the volume-of-fluid method was used, we observed a rise in the water surface before flowing over the model



Shear stress at 0.57 m/s

Fig. 7. The 2-s variance in shear stress in the flow direction at an inlet flow velocity of 0.568 m/s. The median is represented by a point, the 25th and 75th percentiles within the boxes, and the minimum and maximum by the tails.



Fig. 8. Normalized velocity profiles over the gravel bed at different centerline locations along the downstream bed distance for the (left) 0 nets/m² and (right) 735 nets/m² cases at an inlet velocity of 0.568 m/s. The (top) full velocity profile in the water column is (bottom) zoomed to show the local change in the vicinity of the gravel bed.

section containing the gravel bed. This rise resulted from a pressure increase due to the presence of the gravel bed and subsequent acceleration of flow over the bed before relaxing and being forced to the prescribed pressure outlet condition. Due to the mesh resolution and relatively small volume change required for flow over the gravel bed, all three silk net density scenarios, 0, 330, and 735 nets/m², had negligibly different changes in the water surface level across the various inlet velocities.

4. Discussion

The CFD model revealed a strong, negative relationship between hydropsychid caddisfly silk net density and velocity measured in the pore spaces between rock particles. The presence of silk nets blocked the pore space flow paths, likely routing flow out of the gravel bed and into the channel. Because the pore space velocity decreased, we also found that the shear stress experienced on the gravel bed decreased. By directly incorporating biological structures into a physical fluid dynamics model, we have identified how aquatic insects commonly found in streams across the world may influence near-bed water flow.

Our findings support previous experiments showing that caddisfly silk can affect stream bed gravels by, for example, significantly increasing the threshold of motion for sediments in the range of 6-45 mm diameter compared to controls without caddisfly silk structures present (Statzner et al., 1999, Cardinale et al., 2004, Albertson et al., 2014b). The modelling presented here further explores the mechanisms that potentially regulate this stabilizing effect. First, the simulated silk nets alter shear stress experienced by grains at the gravel bed surface. Our study revealed that simulated silk nets accounted for a 6.0 to 11.6% decrease in average shear stress (Pa), over the entire gravel bed and upwards of a 20% decrease in local shear stresses acting on the gravel particles depending on the silk net density. Second, the remaining reduction in sediment motion that has been observed in previous experiments may be due to the structural stabilization occurring when a silk net is built between two or more particles. For example, Hydropsyche siltalai silk threads carry a tensile stress of 221 ± 22 MPa (Brown et al., 2004) and the threads act as anchors from one gravel particle to another, thereby increasing the critical shields stress required for incipient sediment motion (Johnson et al., 2009). Third, the local velocity fields are drastically impacted by the presence of nets,



Fig. 9. Velocity profiles through the gravel bed thresholded between 0 and 0.3 m/s with an inlet velocity of 0.568 m/s for the scenario of a) and b) 0 nets/m² and scenario of c) and d) 735 nets/m².

primarily through a reduction in downstream velocity.

The influence of caddisfly silk nets on transport processes may have substantial impacts on stream benthic communities through reduced sediment movement, reduced near-bed and interstitial flow, and regulation of disturbance regimes. It is widely recognized that physical processes can control the function, structure, diversity, and productivity of freshwater ecosystems (Resh et al., 1988; Bond and Downes, 2003), and with changing flow regimes being experienced world-wide, there is a growing interest in understanding how organisms living in streams cope with flow conditions (Nilsson and Svedmark, 2002, Wang et al., 2017). Some evidence suggests that caddisfly silk structures provide a low flow refuge for other macroinvertebrates (Nakano et al., 2005; Tumolo et al., in review), and thus provide an energetically advantageous colonization location. Other silk-producing insects such as blackfly larvae have been shown to increase colonization rate and shift community composition of primary producers (Hammock and Bogan, 2014). Because interest has recently turned to the reciprocal relationships between the physical and ecological components of freshwater ecosystems, a better understanding of the ways these caddisfly silk structures influence other organisms and ecosystem processes via a direct control on the size and timing of physical disturbances, near-bed flows, and motion of sediments will help elucidate some of the factors driving the distribution and abundance of benthic communities. If hydropsychid caddisflies are altering flow paths within natural gravelbedded streams, future work might address how changes to flow due to the presence or absence of hydropsychids influences other macroinvertebrate and biofilm community composition, macroinvertebrate density, and feeding relationships among trophic levels.

Our results are consistent with previous research showing that insects can be strong ecosystem engineers that alter the physical properties and near-bed conditions of freshwater channel and riparian habitats, even given their small body sizes compared to other aquatic animals such as fish and crustaceans (Albertson and Allen, 2015). The stabilizing effect of organisms in streams is significantly under studied compared to organisms that bioturbate or destabilize physical properties of streams, as well (Albertson and Allen, 2015). For example, biofilms are known to produce extracellular substances that can bind particles together but the spatial and temporal scales at which this effect operates are relatively unknown (Gradbowski et al., 2011, Vignaga et al., 2013). Silk-producing chironomid midges are common worldwide and have also been shown to regulate sediment transport and suspension dynamics, thereby influencing benthic communities (Edwards, 1962, Webbert et al., 2017). Along with biofilms, silk-producing insects provide a model organism that links biological activity with sediment stability in lotic ecosystems.

The CFD model we developed provides a resource for evaluating small organism impact on near-bed flow dynamics, allowing us to pinpoint ecological and geomorphologic interactions, providing a link between the fields of ecology and physical sciences. A growing body of literature has emphasized the need for a better understanding of the links between ecology and geomorphology to make advances in both fields and to improve the burgeoning field of river restoration designs (Bernhardt et al., 2005; Palmer and Bernhardt, 2006). These efforts often focus on vegetation (Braudrick et al., 2009, Corenblit et al., 2009) but often ignore effects of animals, despite the fact that relatively wellrecognized animals such as beavers are gaining traction as a restoration tool (Naiman et al., 1998, Pollock et al., 2014) and that several studies have identified the importance to stream geomorphology of animals spanning a wide range of body sizes from large to small (Rice et al., 2012, Statzner, 2012). We propose that our results might enhance models of streams and riparian habitats by incorporating the effect of stream insects such as net-spinning caddisflies. For example, a new shear equation might be derived for a given grain size or discharge that includes caddisfly net density represented by a change in roughness parameter or x-flow velocity. Overall, these findings suggest that streams with higher caddisfly densities have reduced shear stresses acting on gravels so that the initiation of sediment motion and stream erosion may be altered.

4.1. Future considerations

Our CFD modelling approach allows us to ask novel questions that advance our understanding of the role of these dominant and widespread macroinvertebrates on freshwater ecosystems. However, our CFD modelling approach has certain limitations. We suggest that future work might address the ecological conditions (caddisfly density, caddisfly species identity, silk net architectural plasticity, etc.) under which these biological forces are strongest to better predict when and where the biological structures will influence physical properties of stream ecosystems. Incorporating the complex net structure composed of individual silk threads was difficult. Our CFD software was unable to recognize even a simplified version of a rectangular silk net represented with individual threads as a valid 3D body. Future studies should seek to increase the complexity of the silk net structure, improving on the solid sheet assumption, for example, considering a solid porous sheet utilizing Darcian flow (Kou and Tan, 2010), or considering a flexible, elastic material. Adding flexibility to the silk structure might highlight the importance of species' or individual's net architectures and velocity preferences such that more flexible, balloon-like silk structures reduce shear more so than stiff, vertical structures (Wiggins, 1977). Additionally, developing a finite volume mesh around detailed silk net structures on even a microcosm size scale would require immense computational power. Future analysis should include a mesh independency study. That is, the mesh size, type, and number of total finite volume elements ought to be varied in order to determine the threshold of obtaining an accurate and valid solution. Such a study could drastically reduce computational resource requirements, improving the viability of incorporating more complex silk net structures into the CFD model.

In addition, the solid body representing the gravels could be improved by including variation observed in nature. Natural gravelbedded streams have varying particle diameters, with a great variety of coarseness and shape, which our model did not incorporate (Lisle, 1995). Utilizing digital photogrammetry or laser scanning to generate the geometry of a natural gravel bed system may prove beneficial (Butler et al., 2002). Furthermore, the position of individual gravel particles could more accurately represent a natural habitat. For example, varying size particles ought to be placed in interacting layers, simulating porosity, instead of assuming a solid bed of sand submersing a portion of the gravel particles (Lane and Hardy, 2004). Also, the variation in silk net position within the layered particle bed may help clarify how the silk influences pore space velocity. It could be that rougher, textured gravel beds could dictate how silk nets influence shear stress, such that the overriding signal would be physical instead of biological, or that silk net density, spacing, or aggregations of nets become relatively more important. These improvements would provide more representative shear stress values on rock particles within a natural system.

Finally, a more complex computational model could enhance the results. We modelled the gravel bed particles and silk nets as rigid solid sheets, unable to move in the CFD system, at a constant inflow velocity. Additional modelling should incorporate changes in the flow velocity, and establish a relationship between flow velocity and shear stress, with and without caddisfly silk nets, up to the threshold of motion. In addition, efforts should be made to account for the mechanical stabilization between gravel particles caused by the silk net, incorporating that effect into the model. Mechanical and structural analysis software could illuminate the tensile strength capacity of the silk nets and their stabilizing effect on gravel particles. These explorations would elucidate the silk net and gravel particle interaction, even if a single silk net between two gravel particles was considered.

4.2. Conclusions

Our purpose was to quantify the effect of caddisfly silk nets on shear stresses experienced by gravel particles in near-bed flow. We verified that caddisfly silk nets simulated as rigid bodies decreased the average shear stress on gravel particles, and that shear stress decreased as silk net density increased. Given that caddisfly population densities in natural streams can reach 10,000/m², greatly exceeding the densities that we studied, our findings suggest that effects of caddisfly silk on near-bed fluid dynamics could be substantial. These results might improve sediment transport and erosion models used in river channel design and riparian habitat modelling and emphasize the need to more accurately incorporate biological complexity into physical process models in gravel-bedded systems using 3D CFD modelling.

Acknowledgements

The 3D CFD model output summary files are available from the authors upon request. Gratitude is due to K. Plymesser, who provided expertise during model development. We thank B. Tumolo for constructing and taking photographs of the gravel-bedded microcosm. Funding was provided for M. J. and L.K.A. by Montana State University and for L.K.A by the National Science Foundation (DEB 1556684).

References

- Albertson, L.K., Allen, D.C., 2015. Meta-analysis: abundance, behaviour, and hydraulic energy shape biotic effects on sediment transport in streams. Ecology 96 (5), 1329–1339.
- Albertson, L.K., Cardinale, B.J., Sklar, L.S., 2014a. Species interactions generate nonadditive increases in sediment stability in laboratory streams. PLoS ONE 9, e103417.
- Albertson, L.K., Ouellet, V., Daniels, M.D., 2018. Impacts of riparian land use and stream temperature on timing of terrestrial and aquatic insect food availability for fish. J. Freshwater Ecol. 33, 195–210.
- Albertson, L.K., Sklar, L.S., Pontau, P., Dow, M., Cardinale, B.J., 2014b. A mechanistic model linking insect (Hydropsychidae) silk nets to incipient sediment motion in gravel-bedded streams. J. Geophys. Res. Earth Surface 119, 1833–1852.
- Allen, D.D., Cardinale, B.J., Wynn-Thompson, T., 2014. Towards a better integration of ecological principles into interdisciplinary ecogeoscience research. Bioscience 64, 444–454.
- Anderson, J.D., 1995. Computational Fluid dynamics, the Basics with Applications. McGraw-Hill, Inc.
- Arnon, S., Marx, L.P., Searcy, K.E., Packman, A.I., 2009. Effects on overlying velocity, particle size, and biofilm growth on stream-subsurface exchange of particles. Hydrol. Process. 24, 108–114.
- Asaeda, T., Rajapakse, L., Kanoh, M., 2010. Fine sediment retention as affected by annual shoot collapse: *Sparganium Erectum* as an ecosystem engineer in a lowland stream. River Res. Appl. 26, 1153–1169.
- Bernhardt, E.S., Palmer, M.A., Allan, J.D., Alexander, G., Barnas, K., Brooks, S., Carr, J., Clayton, S., Dahm, C., Follstad-shah, J., Galat, D., Gloss, S., Goodwin, P., Hart, D., Hassett, B., Jenkinson, R., Katz, S., Kondolf, G.M., Lake, P.S., Lave, R., Meyer, J.L., T. K. O'donnell, Pagano, L., Powell, B., Sudduth, E., 2005. Synthesizing U.S. river restoration efforts. Science 308, 636–637.
- Bond, N.R., Downes, B.J., 2003. The independent and interactive effects of fine sediment and flow on bethink invertebrate communities characteristic of small upland streams. Freshwater Biol. 48 (3), 455–465.
- Braudrick, C.A., Dietrich, W.E., Leverich, G.T., Sklar, L.S., 2009. Experimental evidence for the conditions necessary to sustain meandering in coarse-bedded rivers. Proceed. Natl. Acad. Sci. 106 (40), 16936–16941.
- Brown, S.A., Ruxton, G.D., 2004. Physical properties of *Hydropsyche Siltalai* (Trichoptera) net silk. J. North Am. Benthol. Soc. 23 (4), 771–779.
- Buffington, J.M., Montgomery, D.R., 1997. A systematic analysis of eight decades of incipient motion studies, with special reference to gravel-bedded rivers. Water Resour. Res. 33 (8), 1993–2029.
- Buffington, J.M., Montgomery, D.R., 1999. Effects of sediment supply on surface textures of gravel-bed rivers. Water Resour. Res. 35, 3523–3530.
- Butler, J.B., Lane, S.N., Chandler, J.H., Profiri, E., 2002. Through-water close range digital photogrammetry in flume and field environments. Photogramm. Rec. 17 (99), 419–439.
- Cardinale, B.J., Palmer, M.A., Collins, S.L., 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. Nature 415, 426–429.
- Cardinale, B.J., Gelmann, E.R., Palmer, M.A., 2004. Net spinning caddisflies as stream ecosystem engineers: the influence of *Hydropsyche* on benthic substrate stability. Funct. Ecol. 18, 381–387.
- Church, M., 2006. Bed material transport and the morphology of alluvial river channels. Ann. Rev. Earth Planet. Sci. 34, 325–354.
- Corenblit, D., Steiger, J., Gurnell, A.M., Tabacchi, E., Roques, L., 2009. Control of sediment dynamics by vegetation as a key function driving biogeomorphic succession

within fluvial corridors. Earth Surface Process. Landform. 34 (13), 1790–1810.

- Dey, S., 1999. Sediment threshold. Appl. Mathemat. Model. 23 (5), 399-417.
- Dietrich, W., Perron, J., 2006. The search for a topographic signature of life. Nature 439, 411–418.
- Edwards, R.W., 1962. Some effects of plants and animals on the conditions in fresh-water streams with particular reference to their oxygen balance. Int. J. Air Water Pollut. 6, 505–520.
- Gradbowski, R.C., Droppo, I.G., Wharton, G., 2011. Erodibility of cohesive sediment: the importance of sediment properties. Earth Sci. Rev. 105, 101–120.
- Hammock, B.G., Bogan, M.T., 2014. Black fly larvae facilitate community recovery in a mountain stream. Freshwater Biol. 59 (10), 2162–2171.
- Harding, J.S., 1997. Strategies for coexistence in two species of New Zealand Hydropsychidae (Trichoptera). Hydrobiologia 350, 25–33.
- Hesselink, L., Post, F.H., van Wijk, J.J., 1994. Research issues in vector and tensor field visualization. IEEE Comput. Graph. Appl. 14 (2), 76–79.
- Horn, H., Lackner, S., 2014. Modeling of biofilm systems: A review. Adv. Biochem. Eng. Biotechnol. 146, 53–76.
- Johnson, M.F., Reid, I., Rice, S.P., Wood, P.J., 2009. Stabilization of fine gravels by netspinning caddisfly larvae. Earth Surf. Process. Landform. 34, 413–423.
- Jones, C.G., 2012. Ecosystem engineers and geomorphological signatures in landscapes. Geomorphology 157, 75–87.
- Kou, X.Y., Tan, S.T., 2010. A simple and effective geometric representation for irregular porous structure modelling. Comput.-Aid. Des. 42, 930–941.
- Lamb, M.P., Dietrich, W.E., Venditti, J.G., 2008. Is critical Shields stress for incipent sediment motion dependent on channel-bed slope? J. Geophys. Res. Earth Surf. 113, F02008.
- Lane, S.N., Hardy, R.J., 2004. Numerical modelling of flow processes over gravelly surfaces using structured grids and a numerical porosity treatment. Water Res. Res. 40, W01302.
- Leopold, L.B., Wolman, M.G., Miller, J.P., 1964. Fluvial Processes in Geomorphology. Dover Publications, New York, USA.
- Liao, Q., Wang, B., Wang, P.F., 2015. In situ measurements of sediment resuspension caused by propeller wash with an underwater particle image velocimetry and an acoustic Doppler velocimeter. Flow Measur. Instrument. 41, 1–9.
- Lisle, T.E., 1995. Particle size variations between bed load and med material in natural gravel bed channels. Water Resour. Res. 31 (4), 1107–1118.
- Liu, H., Wassersug, R.J., Kawachi, K., 1996. A computational fluid dynamics study of tadpole swimming, J. Exp. Biol. 199, P1245–1260.
- Loudon, C., Alstad, D.N., 1992. Architectural plasticity in net construction by individual caddisfly larvae (Trichoptera: Hydropsychidae). Can. J. Zool. 70 (6), 1166–1172.
- Mackay, R.J., Wiggins, G.B., 1979. Ecological diversity in Trichoptera. Ann. Rev. Entomol. 24, 185–208.
- Miller, J.C., 1984. Competition, predation, and catchnet differentiation among net-spinning caddisflies (Trichoptera). Oikos 43, 117–123.
- Naiman, R.J., Johnston, C.A., Kelley, J.C., 1998. Alteration of North American streams by beaver. BioScience 38 (11), 753–762.
- Nakano, D., Yamamoto, M., Okino, T., 2005. Ecosystem engineering by larvae of netspinning stream caddisflies creates a habitat on the upper surface of stones for mayfly nymphs with a low resistance to flows. Freshwater Biol. 50, 1492–1498.
- Nilsson, C., Svedmark, M., 2002. Basic principles and ecological consequences of changing water regimes: riparian plant communities. Environ. Manage. 30 (4), 468–480.
- Palmer, M.A., Bernhardt, E.S., 2006. Hydroecology and river restoration: ripe for research and synthesis. Water Resour. Res. 42, W03S07.
- Plague, G.R., McArthur, J.V., 2003. Phenotypic plasticity of larval retreat design in a netspinning caddisfly. Behav. Ecol. 14, 221–226.
- Pollen, N., Simon, A., 2005. Estimating the mechanical effects of riparian vegetation on stream bank stability using a fiber bundle model. Water Resour. Res. 41, W07025.
- Pollock, M.M., Beechie, T.J., Wheaton, J.M., Jordan, C.E., Bouwes, N., Weber, N., Volk, C., 2014. Using beaver dams to restore incised stream ecosystems. Bioscience 64 (4), 279–290.
- Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B., Wissmar, R.C., 1988. The role of disturbance in stream ecology. J. North Am. Benthol. Soc. 7 (4), 433–455.
- Rice, S., M. Johnson, I. Reid. 2012. Animals and the geomorphology of gravel-bed rivers.
 In: M. Church, P. Biron, A. Roy (eds.). Gravel-bed Rivers: Processes, Tools, Environments. Chichester, UK pp. 225–241.
- Romero, G.T., Goncalves-Souza, C. Vieira, Koricheva, J., 2015. Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. Biol. Rev. 90, 877–890.
- Runde, J.M., Hellenthal, R.A., 2000. Effects of suspended particles on net-tending behaviors for *Hydropsyche sparna* (Trichoptera: Hydropsychidae) and related species. Ann. Entomol. Soc. Am. 93, 678–683.
- Shen, Y., Diplas, P., 2008. Application of two- and three-dimensional computational fluid dynamics models to complex ecological stream flows. J. Hydrol. 348, 195–214.
- Shields, A. 1936. Anwendung der Ähnlichkeitsmechanik und der Turbulenzforschung auf die Geschiebebewegung; In: Mitteilungen der Preussischen Versuchsanstalt für Wasserbau und Schiffbau, Heft 26.
- Shorter, K.A., Murray, M.M., Johnson, M., Moore, M., Howle, L.E., 2013. Drag of suction cup tags on swimming animals: Modeling and measurement. Mar. Mamm. Sci. 30, 726–746.
- Statzner, B., 2012. Geomorphological implications of engineering bed sediments by lotic animals. Geomorphology 157, 49–65.
- Statzner, B., Arens, M.F., Champagne, J.Y., Morel, R., Herouin, E., 1999. Silk-producing stream insects and gravel erosion: Significant biological effects on critical shear stress. Water Resources Research 35, 3495–3506.
- Statzner, B., Gore, J.A., Resh, V.H., 1988. Hydraulic stream ecology: observed patterns

and potential applications. J. North Am. Benthol. Soc. 7, 307-360.

- Statzner, B., Arens, M.F., Champagne, J.Y., Morel, R., Herouin, E., 1999. Silk-producing stream insects and gravel erosion: significant biological effects on critical shear stress. Water Resour. Res. 35, 3495–3506.
- Trush, W., McBain, S., Leopold, L., 2000. Attributes of an alluvial river and their relation to water policy and management. Proceed. Natl. Acad. Sci. 97, 11858–11863.
- Tumolo, B. B., L. K. Albertson, W. F. Cross, M. D. Daniels, and L. S. Sklar. In review. Could what you leave behind count? Abandoned ecosystem engineering structures facilitate headwater stream community colonization.
- Vignaga, E., Sloan, D.M., Luo, X., Haynes, H., Pheonix, V.R., Sloan, W.T., 2013. Erosion of biofilm-bound fluvial sediments. Nat. Geosci. 6, 770–774.
- Wallace, J.B., Webster, J.R., 1996. The role of macroinvertebrates in stream ecosystem function. Ann. Rev. Entomol. 41, 115–139.
- Wang, X.Y., Yang, T., Wortmann, M., Shi, P.F., Hattermann, F., Lobanova, A., Aich, V., 2017. Analysis of multi-dimensional hydrological alterations under climate change

for four major river basins in different climate zones. Clim. Chan. 141 (3), 483-498.

- Webbert K. C., C. M. Herren, A. Einarsson, M. Bartrons, U. Hauptfleisch, A. R. Ives. 2017. Midge-stabilized sediment drives the composition of benthic cladoceran communities in Lake Mývatn, Iceland. Ecosphere 8, e01659.
- White, F.M., 2006. Viscous Fluid Flow, 3rd Ed. McGraw-Hill, New York, NY pp. 59–73. Wiberg, P.L., Smith, J.D., 1987. Calculations of the critical shear stress for motion of
- uniform and heterogeneous sediments. Water Resour. Res. 23, 1471–1480. Wiggins, G.B., 1977. Larvae of the North American caddisfly genera (Trichoptera). University of Toronto Press.
- Williams, D.D., Williams, N.E., 1998. Seasonal variation, export dynamics and consumption of freshwater invertebrates in an estuarine environment. Estuar. Cost. Shelf Sci. 46 (3), 393–410.
- Zikanov, O., 2010. Essential Computational Fluid Dynamics. John Wiley & Sons, Inc. 76-78, 108-119.