Modulation of near-bed hydrodynamics by freshwater mussels in an experimental channel
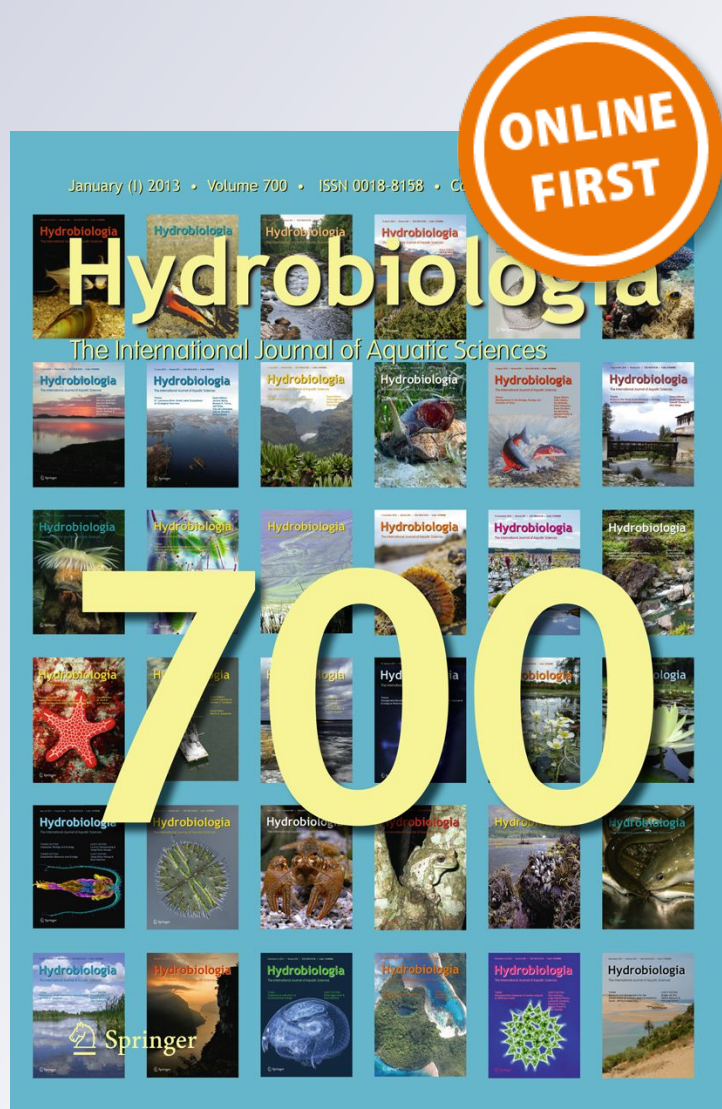
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Modulation of near-bed hydrodynamics by freshwater mussels in an experimental channel

Brandon J. Sansom · Joseph F. Atkinson · Sean J. Bennett

Abstract Freshwater mussels are important ecosystem engineers, and recent studies have illustrated their many ecological contributions, but little is known about the interaction between mussels and their surrounding flow environment at the organism scale. In the present experimental campaign, we examine the hydraulic interactions between mussels and open-channel flow. We quantify how a mussel-covered bed alters bed roughness and near-bed turbulent flow, determine the filter behavior and capacity of live *Lampsilis siliquoidea*, and design a model mussel to simulate live mussel filtering to examine the impact of the biologically mediated activity of filter feeding on near-bed turbulent flow. In comparison to a gravel bed, a mussel-covered bed increased shear velocity by 28% and bed roughness by nearly 300%, and significantly reduced near-bed flow velocity. The filter velocity in *L. siliquoidea* varied within and between individuals, and ranged from 0.4 to 20 cm/s. The excurrent flow of the model mussel accurately simulated excurrent flow observed in live mussels and, when subjected to various boundary conditions, altered water velocity and turbulent kinetic energy downstream. The ability to describe and quantify these hydrodynamic interactions provides new insight into how mussels modulate near-bed flow and mixing processes, which can contribute to future conservation efforts.

Keywords Unionidae · Ecosystem engineer · Experimental models · Organism-flow interactions · Near-bed turbulent flow · Biologically mediated activity

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Introduction

The structure and function of aquatic ecosystems are largely controlled by interactions of biological, physical, and chemical processes across multiple scales (Statzner et al., 1988; Hart & Finelli, 1999; Boudreau & Jorgensen, 2001; Statzner, 2008; Nikora, 2010). Developments in aquatic ecology have encompassed many research foci (e.g., eco-hydrology, eco-hydraulics, and eco-geomorphology), and significant progress is being made at the interfaces of these disciplines (see Nikora, 2010). Statzner & Borchardt (1994) predicted that incorporating fluid dynamics with ecosystem studies would advance ecological

theory faster than past and current research approaches. Progress has been slow, and stream ecologists still lack an understanding of how organisms have evolved and adapted to exploit natural flow conditions (Statzner, 2008).

An intriguing component of ecological interactions within river systems is the active modification of the environment by specific biological agents for an evolutionary advantage, competitive exclusion, or symbiosis. Ecosystem engineers are organisms that change the availability of resources to other species through physical modifications of biotic or abiotic components (Jones et al., 1994). Moore (2006) recognized that freshwater species can markedly affect rivers through habitat creation, bioturbation, bed stabilization, and the processing of particulate matter. Salmonids directly modify substrate texture and topography through redd construction and spawning activity, strongly affecting nutrient dynamics, bed stability, and bedload transport (Gende et al., 2002; Janetski et al., 2009; Hassan et al., 2011). Beaver dams in streams alter slope, flow, sediment transport, nutrient dynamics, riparian zone structure, composition, and diversity (Naiman et al., 1988; Pollock et al., 2014). Macroinvertebrates like net-spinning caddisflies (*Hydropsyche* spp.) can increase the stability of benthic substrate and food availability while providing localized refugia for other species (Cardinale et al., 2004; Nakano et al., 2005). Riparian vegetation also can affect the form, function, and dynamics of fluvial systems and landscape evolution (Gurnell, 2014).

Freshwater mussels (Bivalvia: Unionidae) are another group of ecosystem engineers (Gutierrez et al., 2003). Mussels can account for 50 to 90% of the benthic biomass (Strayer et al., 1994) and provide biogenic habitat for benthic organisms (Vaughn et al., 2008). The burrowing behavior of mussels disturbs substrate, provides niche partitioning between mussel species, increases dissolved oxygen concentration, redistributes nutrients, and enhances primary productivity (Vaughn & Hakenkamp, 2001; Lohrer et al., 2004; Allen & Vaughn, 2009). Mussels are powerful filter feeders that link the water column to the benthos by excreting nutrients that fertilize algae (Howard & Cuffey, 2006; Spooner et al., 2012; Atkinson et al., 2013), which promotes secondary production (Allen et al., 2012; Atkinson et al., 2014). The cumulative filtration of relatively high-density mussel beds may actually equal the stream's flow rate (Strayer et al., 1994; Vaughn & Hakenkamp, 2001) and can measurably increase water clarity (Haag, 2012).

Flow dynamics are largely important for mussel distribution and abundance. Strayer (1999) found that mussel beds tend to occupy areas of the streambed identified as flow refuges, or those areas of the streambed where shear stresses were below a given threshold value. This concept has since sparked interest in examining how hydraulic variables (Hardison & Layzer, 2001; Howard & Cuffey, 2003; Allen & Vaughn, 2010), channel geomorphology (Gangloff & Feminella, 2007), and substrate composition (Allen & Vaughn, 2010; Strayer, 1999, 2008) contribute to the abundance, diversity, density, and distribution of mussel populations.

Despite general understanding of the ecological contributions of mussels and how flow dynamics are influential to mussel distribution throughout streams, little is known about the physical interactions between mussels and turbulent flow at an organism-level scale, how such interactions impact both static and dynamic boundary conditions, and how these interactions may contribute to the evolutionary success of a given species. Mussels interact with the environment actively through filter feeding, which represents a mass and momentum flux that can alter the near-bed flow field. Filtering rates can range from 0.5 to 1 l/h (Kryger & Riisgård, 1988; Vaughn et al., 2008) with estimates as high as 4.6 (McMahon & Bogan, 2001) to 8.6 l/h (Price & Schiebe, 1978). The rate at which mussels filter and their impact on ecosystem and hydrodynamic processes are influenced by species, animal size, population density, and environmental conditions (Vaughn et al., 2008). Furthermore, methods to obtain filtration rates have led to unreliable information (McLatchie, 1992; Riisgård, 2001), and few studies have provided in-depth analyses of the hydrodynamic properties of unionid filter processes.

Mussels also interact with the flow passively by increasing surface bed roughness (see Vaughn & Hakenkamp, 2001). Constantinescu et al. (2013) demonstrated that flow past a cluster of mussels exhibited large areas of flow separation and extremely complex turbulence downstream of the cluster. The extent to which mussels influence physical roughness is dependent upon burrowing activity. Season (Amyot & Downing, 1997; Watters et al., 2001), reproductive cycle (Amyot & Downing, 1998), substrate (Lewis & Riebel, 1984), and species composition (Allen &

Vaughn, 2009) all influence the frequency and extent to which mussels burrow. When alive or spent mussel shells protrude from the sediment, flow disruption will occur and affect near-bed hydrodynamics.

Much knowledge remains to be discovered concerning the interaction between individual mussels and flow. The aim of this paper is to investigate how mussels influence turbulent flow and mixing processes within stream ecosystems via active and passive interactions. Our main objectives are (1) to examine how a moderate density of mussels contributes to bed roughness and impacts near-bed velocity, (2) to characterize the filtering behavior of live *Lampsilis siliquoidea*, a common mussel in western New York, and (3) to examine how a model mussel that incorporates the biologically mediated activity of filter feeding influences the near-mussel turbulent flow field under various boundary conditions. By examining such interactions, we hope to provide new insight into the success of freshwater mussels and their conservation.

Methods

Hydraulic flume setup

All experiments were performed in a recirculating hydraulic flume filled with a gravel bed ($D_{50} = 0.01$ m) that was 0.2 m deep. The flume is 10.7 m long, 0.5 m wide, and was filled with water to a depth of 0.25 m. A 2-m-long section of the flume, located 6 m downstream of the head box and 2.7 m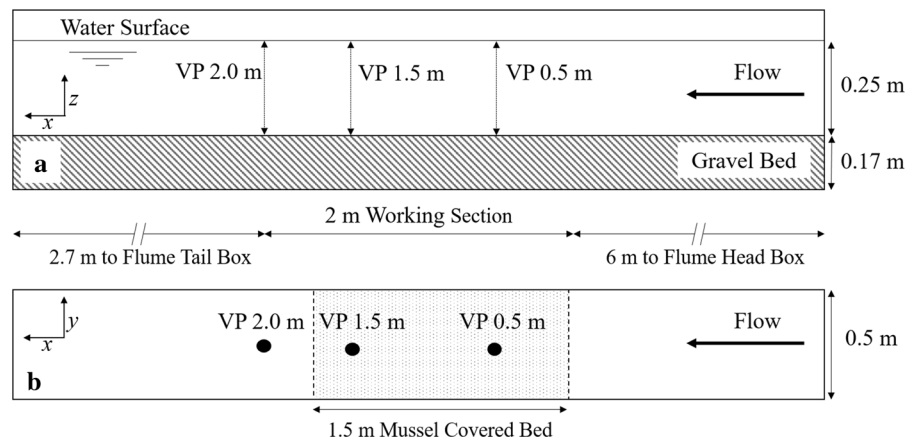 upstream of the tail box, was designated as the experimental area for all experiments (Fig. 1). The location of the experimental area was chosen to allow for flow to be fully developed and to negate any exit effects. Uniform, steady flow in the test section was established by adjusting the slope of the flume.

Flow over a mussel-covered bed

To test the first objective, we performed experiments in two phases to compare flow over a gravel bed to flow over the same gravel bed populated by mussels. To isolate the influence of mussels acting as roughness features on the streambed from the biological activity of mussels, no filtering processes were considered for these experiments. We measured flow with an Acoustic Doppler Velocimeter (ADV) Vectrino Profiler (Nortek, Boston, MA). The ADV Vectrino Profiler collects high-frequency, 3-dimensional velocity data at a user-defined resolution. For this study, we determined the optimal resolution (i.e., data with the highest correlation and minimum variation in instantaneous velocity) to be 2 mm cells from a range of 4 to 6 cm from the ADV probe. All velocity data were collected at 80 Hz for 60 s, with a nominal velocity range of ±6 mm/s. Vertical velocity profiles were obtained at various locations along the centerline of the flume. Quality control was performed at each depth increment by validating the bottom check feature and verifying that the correlation parameter and signal-to-noise ratio remained within pre-determined ranges for high-quality data (above 90% and 20–25 dB, respectively).

For both phases of the experiment, the flume was set up as described above and the flow velocity in the

Fig. 1 Schematic drawing showing the side view (**a**) of the experimental set up for flow over a gravel bed. The aerial view (**b**) indicates the location of the randomly placed mussel shells to create a mussel-covered bed. Vertical velocity profiles were taken at VP 0.5, 1.5, and 2.0 m downstream the leading edge of the working section

flume was kept constant at 0.38 m/s (Fig. 1). In the first phase, we examined flow over the gravel bed only (hereafter referred to as the control trial). Vertical velocity profiles were collected with the ADV profiler at 0.5, 1.5, and 2 m downstream from the upstream end of the experimental area (Fig. 1a). In the second phase, we examined flow over a gravel bed populated by mussels (hereafter referred to as the mussel trial). *Lampsilis siliquoidea* shells with fully intact valve pairs were collected from local streams in western New York (Buffalo River, Ellicott Creek, and Tonawanda Creek). Shells were filled with sand to represent the mass of a live mussel and glued shut with epoxy resin. A grid consisting of repeating 10×10 cm^2 units was assigned to the experimental area, and a random number generator was used to place the mussel shells in the upstream 1.5 m section of the experimental area of the flume at a density of 10 mussels per m^2, representative of moderate densities for western New York (L. Burlakova, pers. comm.). Mussels were kept a minimum of 5 cm away from the flume walls to minimize sidewall effects, and all mussels were aligned with their valves parallel to the flow and burrowed into the gravel so that 5 cm of the shell was exposed (Fig. 2). Vertical velocity profiles were repeated at the same locations as the control trial, corresponding to locations 0.5 and 1.5 m downstream of the leading edge of the mussel-covered bed, and 0.5 m downstream of the trailing edge of the mussel-covered bed, respectively (Fig. 1b).

Velocity data were exported to MATLAB, despiked to remove noise associated with the velocity

Fig. 2 Image of *Lampsilis siliquoidea* shells randomly placed in the experimental area of the flume to create a moderate density (10 mussel per m^2) mussel-covered bed

data following methods in Goring & Nikora (2002). Streamwise velocity in the *x*-direction was time averaged per 2 mm cell, and space averaged between the three point locations for each phase. Linear regression analysis was performed between mean downstream velocity U and height above the bed z_b to compare for differences between velocity profiles in the mussel and control trials. Additionally, bed roughness height was calculated and compared between the mussel and control trials, based on the Karman-Prandtl law of the wall. The law of the wall is a well-known fluid dynamics theory that states that the mean velocity U of a turbulent flow at a height z_b above the boundary is proportional to the logarithm of the distance from that point to the boundary (von Karmen, 1931), defined as

$$\frac{U}{u_*} = \frac{1}{\kappa} \ln\left(\frac{z_b}{z_0}\right), \qquad (1)$$

where u_* is shear velocity; κ is von Karman's coefficient (0.41); and z_0 is the virtual origin of the velocity profile. Equivalent bed roughness height k_s was calculated using the well-known relation (Bridge & Bennett, 1992; Bennett et al., 1998)

$$k_s = 30.2 z_o. \qquad (2)$$

Live mussel filtering behavior

Live *Lampsilis siliquoidea* were collected from Tonawanda Creek, NY, and housed in a laboratory at the University at Buffalo. Particle image velocimetry (PIV) was used to analyze the flow field around the incurrent and excurrent apertures, while ADV was used to determine the mean sustained filtering velocity of the excurrent aperture.

An individual mussel was selected and placed in a 10 gallon tank with sediment obtained from Tonawanda Creek and allowed to acclimate for a minimum of 12 h. After the mussel was acclimated, the filtering activity was recorded with PIV and ADV at separate times. Immediately before data collection, a syringe was used to inject a solution of seed particles into the water just above the mussel. The PIV system was used to measure the two-dimensional velocity field focusing on the plane passing the centerline of the mussel (Fig. 4). The single camera captured up to 500 images in memory for each collection period (~ 6 s).

Because of laser warm-up time, variation in particle density, and other experimental issues, about 300 to 350 images were considered valid for each collection period. The sampling rate of the camera was set to 80 Hz, and three collection periods for each mussel were captured for averaging. For each collection period, the exposure time for the camera and the time between laser pulses were set so that particles moved no more than 25% within each frame. An adaptive cross-correlation was performed on all collected image pairs at 16×16 pixel grid size. Processed data were exported and analyzed using user-defined codes in MATLAB and R. Two-dimensional vector maps were created to represent the time-averaged velocity magnitude U_{uw} represented as

$$U_{uw} = \sqrt{u^2 + w^2}, \tag{3}$$

where u and w are time-averaged velocity in the x (downstream)- and z (vertical)-directions, respectively.

The ADV probe was positioned to record velocity ∼0.5 cm above the excurrent aperture. All ADV data were collected at 80 Hz with a nominal velocity range of ± 3 mm/s. Data were collected for a minimum of 2 h to determine the frequency of mussel filtering. Velocity data were despiked to remove noise associated with the velocity data following methods in Goring & Nikora (2002), and a mean sustained filtering velocity U_{uvw} was determined by analyzing the periods of filtering activity within the time series, defined as

$$U_{uvw} = \sqrt{u^2 + v^2 + w^2}, \tag{4}$$

where v is the time-averaged velocity in the y (cross-stream)-direction.

Biologically mediated activity

To test the third objective, we designed a model mussel using spent valves of *Lampsilis siliquoidea*, a continuous duty pump (Iwaki Walchem, 1/250 HP, magnetic drive), PVC tubing, and modeling clay. A pair of PVC tubes (3.5 mm ID) was glued to the internal surface of one valve to match the approximate locations of the incurrent and excurrent apertures (Fig. 3a). A small portion of the anterior end of the shell was cut away to allow for the PVC tubes to pass into the shell when both valves were glued together.

Modeling clay was placed around the PVC tubing to match the size of the aperture openings based on field and laboratory observations (Fig. 3b, c).

The same flume and setup described above were used in this experiment. The model mussel was placed into the experimental area of the flume buried in the gravel along the flume centerline until 5 cm of the shell was exposed (Fig. 4a). The PVC tubes were buried underneath the gravel bed and exited over the downstream end of the flume wall where they were connected to the recirculating pump (Fig. 4b).

Based on the live mussel results (see below), the recirculating pump connected to the model mussel was calibrated to an excurrent filter velocity of 8 cm/s. Although we observed sustained filter velocities as high as 20 cm/s in live mussels, the majority of mussels we observed filtered at less than 8 cm/s (see results below). The excurrent velocity of 8 cm/s flow velocity is equal to a volumetric flow rate of 2.7 l/h, well within the range of reported filtration rates in unionids (0.5 to 8.6 l/h; Price & Schiebe, 1978; Kryger & Riisgård, 1988; O'Riordan et al., 1995; McMahon & Bogan, 2001; Pusch et al., 2001; Vaughn et al., 2008) and what we observed in our study with live *L. siliquoidea*.

Three different experimental setups were conducted to assess the hydrodynamic impact on mussel filtration. In the first experiment (A), only the effect of mussel filtration was examined. The recirculating pump to the model mussel was turned on so that the excurrent filter was 8 cm/s, but there was no current in the flume. In the second experiment (B), flow around a non-filtering mussel was examined. The same model mussel was used, but the filter pump was turned off and the flume flow velocities were 4, 8, and 16 cm/s. In the third experiment (C), the influence of mussel filtration was examined within a flow field. Again, the model mussel filtration was set to an excurrent velocity of 8 cm/s, while the approach flow velocity consisted of 4, 8, and 16 cm/s, which resulted in approach flow-to-mussel filtration velocity ratios of 1:2, 1:1, and 2:1, respectively.

All experiments examining filtration employed PIV to measure flow around the model mussel (Fig. 4). The PIV system was set up similarly as explained above. To obtain enough data to compute turbulent statistics, 10–11 collection periods for each experiment were captured. An adaptive cross-correlation was performed on all collected image
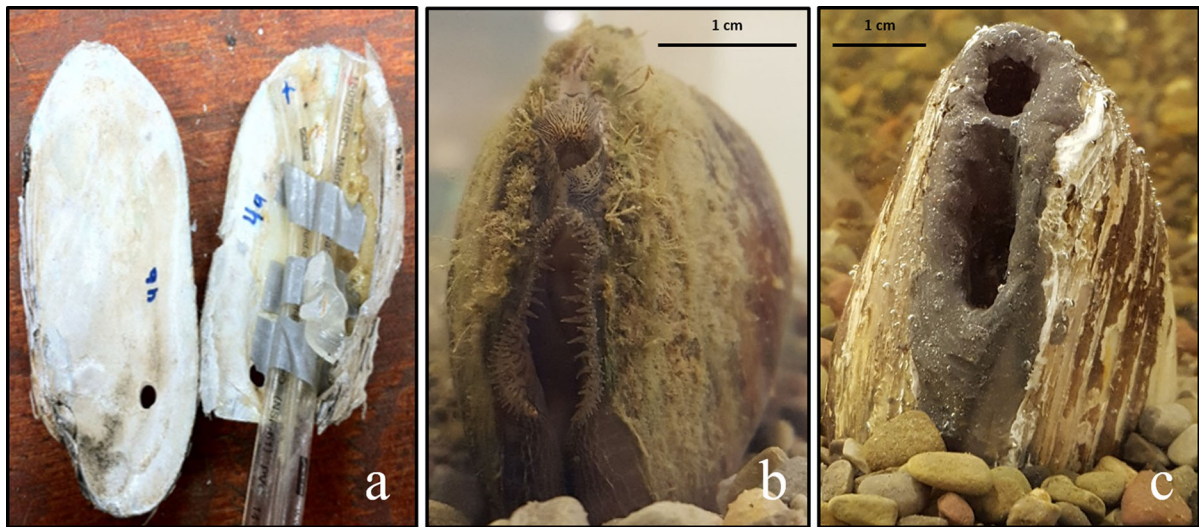
Fig. 3 PVC tubes connected to the inside of one valve prior to the modeling clay fitted to match the incurrent and excurrent apertures (**a**). Panel **b** shows an image of a live *Lampsilis* *siliquoidea* filtering with apertures open. The completed model mussel is shown in panel **c**
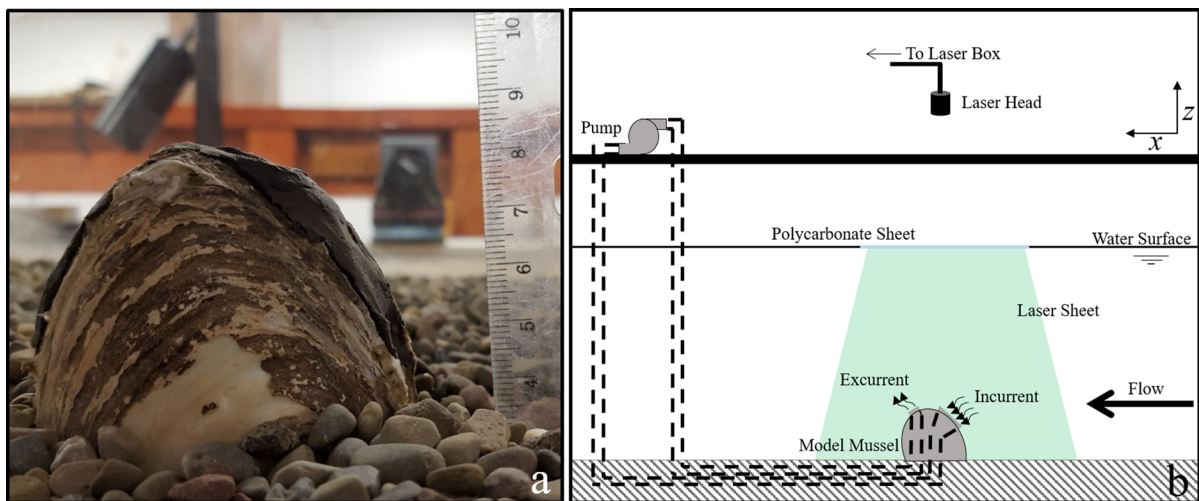

Fig. 4 Image showing the model *Lampsilis siliquoidea* mussel placed into the gravel bed (**a**). The schematic drawing (**b**) shows the experimental setup used to collect PIV data for flow around the model mussel

pairs at 16×16 pixel grid size. Processed data were exported and analyzed using user-defined codes in MATLAB and R, and two-dimensional vector maps were created to represent the mean velocity magnitude U_{uw}.

We provide a brief analysis of the velocity and turbulent kinetic energy (TKE, per unit mass) profiles upstream and downstream of the model mussel for filtering and non-filtering scenarios to investigate the hydrodynamic interactions between mussels and the near-bed turbulent flow. TKE is a measurement of the instantaneous velocity fluctuations over time and defined for two dimensions as

$$\text{TKE} = 0.5\left(\overline{u'^2} + \overline{w'^2}\right), \tag{5}$$

where u' is the velocity fluctuation in the x-direction and w' is the velocity fluctuations in the z-direction. PIV data were spatially averaged in the x-direction over a 1 cm distance immediately downstream of the

trailing edge of the model mussel and 1 cm immediately upstream of the leading edge of the model mussel to determine any potential impacts of either the incurrent or excurrent aperture. Velocity and TKE data were normalized by the mean velocity U (m/s) of the incident flow for each scenario.

Results

Flow over a mussel-covered bed

Near-bed velocity was significantly reduced in the presence of mussels compared to the control trial. The velocity profiles obtained in each scenario followed a logarithmic distribution of velocity as a function of depth consistent for open-channel flow (Fig. 5). This trend was opposite for the upper 0.15 m of the water column, thus indicating a significant interaction between the treatment (i.e., mussel vs. control trial) and depth (Fig. 5b; Interaction: $F = 266.15$, $P < 0.0001$). There was no measureable difference in water depth between the gravel bed and mussel bed scenarios. However, shear velocity u_* and bed roughness k_s were influenced by the addition of the mussel shells. For the gravel bed, $u_* = 0.029$ m/s and $k_s = 0.016$ m, which is similar to the median diameter of the gravel in the flume ($D_{50} = 0.01$ m). Adding the mussels to the gravel bed increased u_* to 0.037 m/s
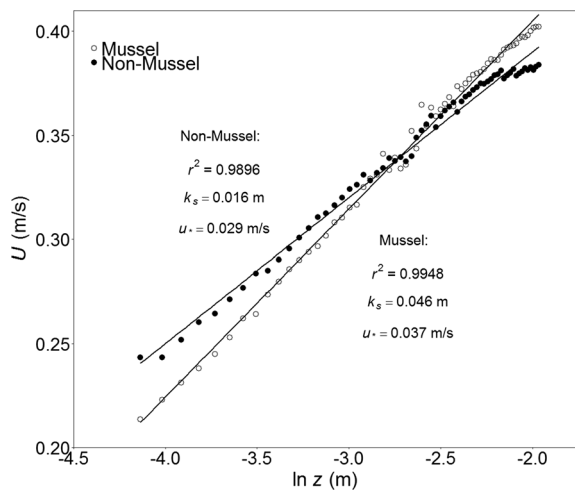
and increased k_s to 0.046 m, which was almost identical to the mean length of shell protrusion into the flow for all the mussels used in this study. In comparison to the gravel bed, a mussel-covered bed increased shear velocity by 28% and increased bed roughness by nearly 300%.

Live mussel filtering behavior

The filtering behavior of live mussels was highly variable between and within individual mussels. General observations were made to allow for design criteria of the model mussel. Mean sustained excurrent velocities recorded with the ADV ranged from 0.4 to 20 cm/s (Table 1). No obvious pattern in daily filter behavior was observed (Fig. 6a, c, d). When mussels were filtering, however, an oscillatory pattern was observed in which there was a consistent time between filtering and non-filtering behavior (Fig. 6b). Occasional excurrent burst velocities were observed in excess of 20 to 50 cm/s, but these were infrequent, not sustained, and not representative of normal filtering activity. PIV analysis showed that the excurrent flow had characteristics very similar to a circular jet exiting a nozzle (Rajaratnam, 1976). Little to no incurrent velocity was observed for any mussel at the incurrent aperture (Fig. 7a).
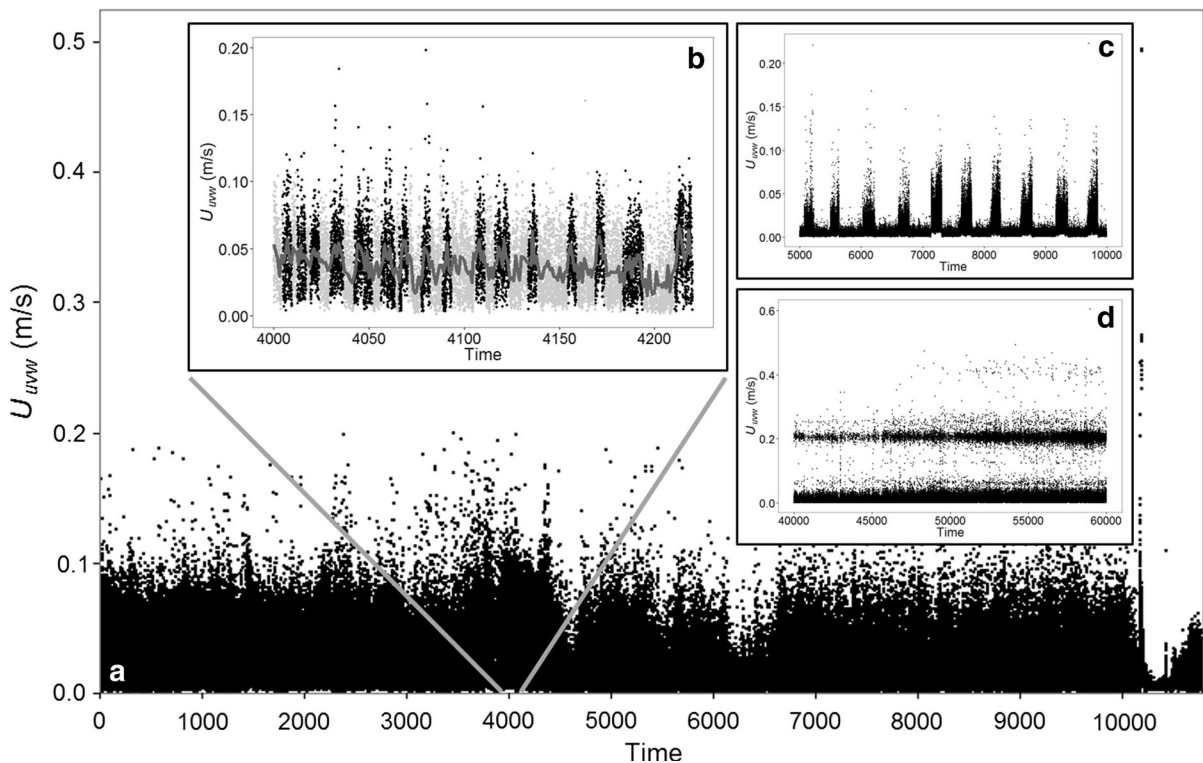
Biologically mediated activity

The filtering behavior of the model mussel was designed to mimic the flow pattern and velocity magnitude observed with the live mussels. The excurrent velocity in the model mussel was calibrated to have a maximum 8 cm/s velocity (Fig. 7b). This velocity was observed immediately after exiting the shell, followed by an expanding jet-like flow and slower velocity with distance away from the shell margin as the jet entrained the ambient water, very similar to the excurrent flow field with a live mussel. Velocity vectors smaller than 0.5 cm/s were removed from Fig. 7b, indicating little to no measureable incurrent velocity with the model mussel. When the pump controlling the filtering was engaged, hydrodynamic impacts (e.g., vortex formation and shedding) were observed immediately downstream of the excurrent aperture (Fig. 7c).

For each scenario with no mussel filtering, flow patterns appeared as expected. Flow accelerated over

Fig. 5 A linear regression between the ln(z) and mean velocity U showed that the mussel-covered bed had significantly lower near-bed velocity. The mussel-covered bed also increased shear velocity by 28% and increased bed roughness by nearly 300%

Table 1 Sustained excurrent filter velocities u_f for live *Lampsilis siliquoidea*. Sample effort and time filtering represent the time spent collecting data with the ADV and the actual time filtering was observed, respectively

Mussel	Mussel length (cm)	Sustained excurrent filter velocity (cm/s)	Sample effort (h)	Time filtering (h)
D4	8	5.2	24	8
D5	8.9	7.5	16	10
U1	8.4	NA	24	NA
U10	10.7	0.4	2	1
U11	10.4	NA	3	NA
U13	9.7	0.5	2	1.5
U14	10.2	1–20.5	4	3.5
U2	8.7	NA	26	NA
Total			101	24

Fig. 6 An example 3-h time series of the excurrent velocity U_{uvw} of a live mussel (**a**). The time series is truncated to a 3-min section in panel b to show the oscillating behavior observed during active filtering. On panel **b**, *black dots* represent periods of active filtering, *gray dots* represent inactive filtering, and the *dark gray line* is the moving average (per second) of the filtering behavior. Panels **c** and **d** are examples of additional time series for different mussels to represent the various patterns observed in filter behavior

the leading edge of the mussel with an area of flow separation and deceleration immediately downstream of the mussel (Fig. 8a, c, e). When the filter was engaged, the excurrent flow was progressively deflected as the approach flow increased. For a 1:2 flow-to-mussel filtration velocity ratio, the excurrent plume impacts up to 25% of the flow field above the mussel for a distance of at least 10 cm downstream
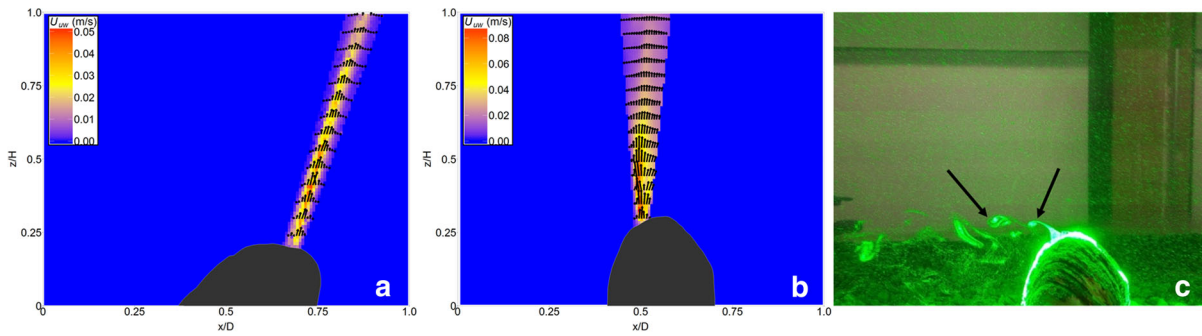
Fig. 7 A two-dimensional velocity vector map generated from PIV data showing the excurrent filter pattern of a live mussel (**a**). The model mussel was designed to have a similar excurrent filter pattern and a calibrated excurrent velocity of 8 cm/s (**b**). The hydrodynamic impacts as a result of filtering simulated by the model mussel are seen immediately downstream, as indicated by the two arrows (**c**)
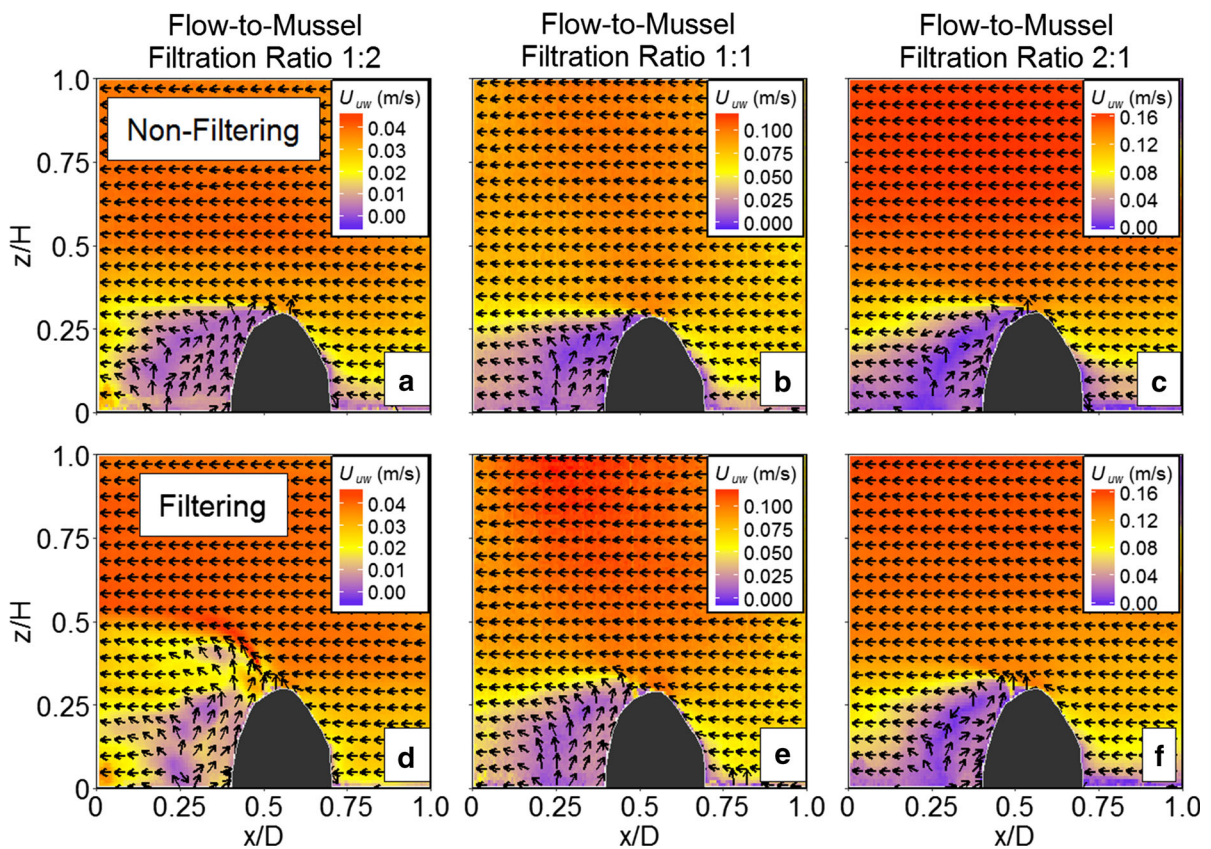

Fig. 8 Two-dimensional contour and vector maps showing mean velocity U_{uw} over the non-filtering model mussel (*top panel*) and over the filtering model mussel (*bottom panel*). Flow is in the negative *x*-direction. Flow-to-mussel filtration velocity ratio of 1:2 is represented in panels **a** and **d**, 1:1 in panels **b** and **e**, and 2:1 in panels **c** and **f**

(Fig. 8b). At a 1:1 ratio, the excurrent filter has a weakened impact region of ~ 1 cm above the mussel for a distance of ~ 5 cm downstream (Fig. 8d). At a flow ratio of 2:1, any impacts of the excurrent filter on the flow field are negligible except for the point of discharge from the shell (Fig. 8f).

Vertical profiles for velocity and TKE were constructed to compare the effects of filter feeding

on the near-mussel flow field. For all flow scenarios, no major differences were observed in the upstream flow (in either velocity or TKE; Fig. 9). Additionally, all flow scenarios show a velocity deficit in the wake of the model mussel. For the 1:2 and 1:1 flow-to-mussel filtration velocity ratios, the filtering activity resulted in an increase in velocity at greater depths from the streambed than the non-filtering case (Fig. 9a, b). The 2:1 flow-to-mussel filtration velocity ratio had nearly identical velocity profiles except for the lower 25% of the flow, where the filtering activity resulted in a slightly higher velocity (Fig. 9c). Filtering had the greatest impact on TKE values in the 1:2 flow-to-mussel filtration velocity ratio. At this ratio, the maximum TKE value was greater during the filtering scenario, and the height above the bed at which the maximum value of TKE occurred was also greater (Fig. 9d). For the 1:1 and 2:1 flow-to-mussel filtration velocity ratios, the maximum TKE value and the height

of the maximum TKE value were similar between filtering and non-filtering mussels (Fig. 9e, f).

Discussion

In this study, we demonstrate that a mussel-covered bed significantly impacts bed roughness and affects near-bed turbulent flow velocity. Furthermore, we used the results of the live mussel behavior to successfully design a model mussel to simulate the filtering activity of freshwater mussels. Using this model, we characterize the interactions between mussel filter activity and near-bed hydrodynamics at an organism-level scale.

Flow over a mussel-covered bed

Our first objective examined how mussels passively contribute to streambed roughness and thereby impact
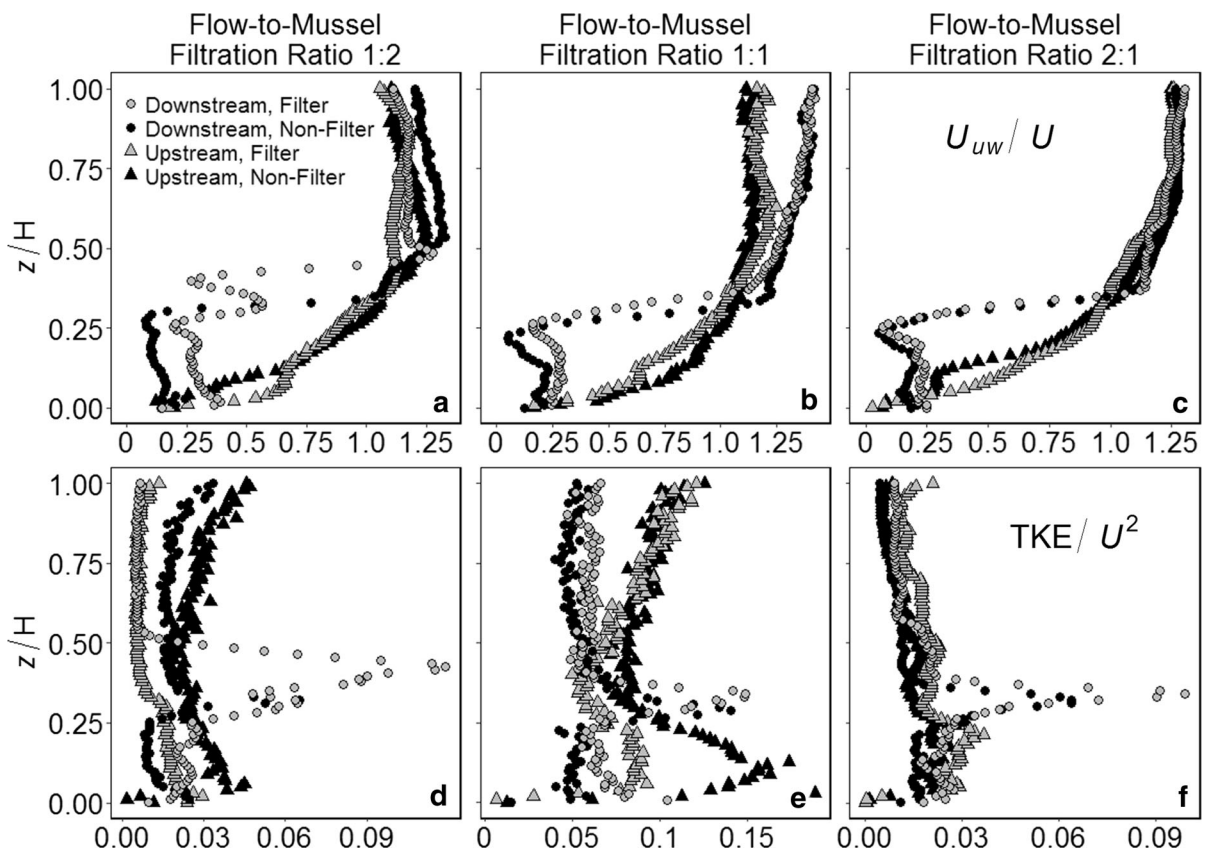

Fig. 9 Upstream (*triangles*) and downstream (*circles*) time and space averaged values for standardized velocity (*top panel*) and TKE (*bottom panel*) for the non-filtering model mussel (*black symbols*) and the filtering model mussel (*gray symbols*) at flow-to-mussel filtration ratios of 1:2 (**a**, **d**), 1:1, (**b**, **e**), and 2:1 (**c**, **f**)

near-bed flow. Many studies have shown that mussel shells provide an important ecological role (Beckett et al., 1996; Francoeur et al., 2002; Spooner & Vaughn, 2006; Vaughn & Spooner, 2006). Here, we demonstrate that mussel shells also contribute to a hydrodynamic signal. First, the addition of mussel shells at a moderate density increased shear velocity by 28% and streambed roughness by nearly 300%. Shear velocity controls mixing processes (e.g., diffusion and dispersion), near-bed flow velocity, and sediment transport processes in rivers (Bridge, 2003). The roughness coefficient calculated over the mussel-covered bed was nearly threefold larger than the gravel bed and scaled to the same height as the mussel shell length protruding from the gravel bed. The increased roughness over the mussel bed contributes to the second hydrodynamic signal we observed within the mussel-covered bed: the reduction of near-bed velocity. This occurred because the mussel shells protruded into the flow at a sufficient distance to influence the velocity profile and significantly increased near-bed flow resistance. Although we did not analyze the turbulence parameters, flow separation, or vortex formation and shedding in this experiment, we can draw on the conclusion of Constantinescu et al. (2013) and predict that the increased roughness provided by mussel shells leads to complex turbulent flow in and downstream of the mussel-covered bed. Furthermore, we can also state that as the height of mussel shell protrusion increases, vortex size, frequency, and turbulence intensity of the flow field should also increase (Bridge, 2003).

Live mussel filtering behavior

Our second objective characterized the filter behavior of live mussels. Live mussels exhibited no consistent patterns in filtering. The lack of diurnal or other filtering patterns has been observed among other unionids in a laboratory (Chen, 1998). When mussels were actively filtering, a distinct oscillatory pattern was observed in the excurrent velocity signature. Although this pattern has been described due to frequent and rapid shell closures (Barnes, 1962; Imlay, 1968), we observed the oscillatory pattern even while the shell remained opened, in which such behavior was likely driven by the cilia-generated current on the gill surface (Haag, 2012).

The magnitude of the excurrent velocity was largely variable between and within individual mussels and the mean sustained excurrent velocity spanned two orders of magnitude (0.4–20 cm/s). We observed that the flow pattern exiting the excurrent aperture resembled a circular jet, in which the highest velocity occurred along the centerline of the jet, and velocity reduced with distance away from the shell margin as it became entrained in the surrounding water. The incurrent velocity was difficult to measure because it was markedly smaller than the excurrent velocity, likely because the cross-sectional area of the incurrent aperture is two to three times larger than the cross-section area of the excurrent aperture.

While working with live mussels, we observed several variables that further suggest the importance of using a model specimen. First, any type of handling caused the live mussels to halt all filtering activity. Often times, it would take upwards of a few hours after handling before the mussel commenced filtering. This is consistent with Kryger & Riisgård (1988), who reported that filtration rates in disturbed bivalves are greatly reduced relative to non-disturbed bivalves.

Second, there are limitations with using PIV and ADV with live mussels. The PIV system used here collects high-frequency data over a short time (~ 6 s) for one collection period. Although some mussels exhibit feeding preferences (McCorkle et al., 1979; Englund & Heino, 1994), no clear diurnal or other pattern exists (Chen, 1998; Haag, 2012). Similarly, we did not observe a consistent pattern in the frequency of mussel filtration. Further, while using PIV, the plane at which measurements are being made must be precisely parallel to the laser sheet and ideally perpendicular to the camera. Live mussels often moved outside of this plane or their excurrent aperture was not exactly parallel to the measurement plane. Attempts to reposition the mussel resulted in reduced or no filter activity. Alternatively, attempts to reposition the laser or camera greatly increased the time needed to setup the PIV system. While using ADV, the movement of live mussels (e.g., burrowing, horizontal movement, or repositioning the excurrent aperture) also limited our ability to capture the sustained excurrent velocity. Finally, it is not known how the seeding particles used in PIV or ADV will affect the performance of mussel filtering. Seed particles are typically hollow glass spheres (~ 10–100 um) with a thin silver coating. Mussels typically feed on particles <20 μm in size

(Vaughn et al., 2008), and PIV or ADV seeding particles may be ingested and alter the filter performance of live mussels.

Given the limitations encountered using live mussels, we believe that a model specimen increases the efficacy of such experimental campaigns. For example, we attempted to measure the excurrent velocity of eight different mussels using ADV. The time of sampling for each mussel ranged from 2 to 24 h, for a total time effort of 101 h. During these 101 h, we were able to record data for only five mussels and observed only 24 h of total filtering, or ∼25% of our effort. Similarly, because PIV is capable of collecting data only over short-time periods, much time was spent waiting for live mussels to filter. Therefore, the ability to have a model specimen in which the timing, frequency, and magnitude of mussel filtering can be precisely controlled and that can be precisely located within an experimental setup will greatly enhance the efficiency of experimental campaigns.

Biologically mediated activity

Our third objective investigated how the biological activity of mussel filtering interacted with flow. Because of the difficulties we encountered using live mussels noted above, we designed our model mussel so that we could have precise control over the frequency and magnitude of mussel filtering and the location at which we collected data. Using PIV, we were able to confirm that our model mussel accurately simulated the flow pattern and magnitude of the excurrent flow. For example, the model mussel had a similar jet-like flow pattern exiting from the excurrent aperture compared to live mussels, and the model mussel was calibrated to have an excurrent velocity of 8 cm/s, well within the range of excurrent velocities observed with the live mussels. The oscillatory pattern we observed during periods of active filtration varied in time between filtering and length of filtering within and between mussels. Thus, for the scope of this project, we did not attempt to replicate the oscillatory pattern observed during active filtering. The oscillatory component is something we would need to explore in a future study before we replicate this in a model mussel.

To test the third objective, we examined four different flow-to-mussel filtration velocity ratios. With a 0:1 flow-to-mussel filtration velocity ratio, the excurrent behavior was similar to a circular jet (Rajaratnam, 1976; Witze & Dwyer, 1976). The highest velocity was observed close to the shell margin, the excurrent velocity plume expanded as distance from the shell increased, and the velocity decreased as it became entrained in the surrounding flow. Although this example provides an idealized condition to examine the specific hydrodynamic properties of the excurrent filter process, as similarly done for a marine mussel (Riisgård et al., 2011), freshwater mussels are unlikely to inhabit environments with a zero mean flow. Three flow-to-mussel filtration velocity ratios were chosen to demonstrate the interaction of filtration within an open-channel flow. Similar to other studies that have explored how jets behave in a cross flow (O'Riordan et al., 1993, 1995), the impact of filtration activity on the flow field was dampened as the approach flow increased. When the filtration velocity was greater than the approach flow, there was a strong downstream hydrodynamic signal as a result of the excurrent velocity. This signal is greatly reduced when the approach flow reaches the same magnitude or is greater than the filtration rate. Noticeable differences still remain, specifically within the velocity profiles immediately downstream of the model mussel. The TKE downstream of the model mussel was also impacted from the excurrent filter activity. For all non-filtering scenarios, TKE reached a maximum at approximately the same height above the gravel bed as the mussel protruded into the flow. This is expected as the mussel shell alone provides a barrier to flow, thus acting as a source for local turbulence. When the filter was engaged, maximum TKE not only increased, but also the height of the maximum TKE slightly increased, indicating that mussel filtering also displaces TKE into the surrounding flow.

Conservation implications

Ultimately, this study seeks to provide critical information for the preservation, conservation, and restoration of freshwater mussels. Understanding how mussels interact with flow is essential to inform management decisions and important ecological theory can be understood by examining specific details of the mussel–flow interaction (see Statzner & Borchardt, 1994). To date, freshwater mussel conservation efforts are largely focused around population

protection, critical habitat restoration, and reintroduction or population augmentation (Haag, 2012). Such efforts have been successful and remain necessary, but more diversified approaches would enhance our ability to better protect this species. The ability to describe and quantify the hydrodynamic interactions between mussels and flow, as presented in this study, offer a better understanding of how mussels contribute to the structure and function of stream ecosystems. For example, it is well understood that the filtering behavior of freshwater mussels greatly contributes to both primary and secondary production, and plays a critical role in the nutrient transport of stream ecosystems. Coupling this information with the hydrodynamics associated with individual mussels, such as TKE, will lead to a better understanding of nutrient availability and dispersal within streams. Local hydrodynamics can also be important in controlling additional processes including sediment transport, the interaction between flow and an individual mussel's filter behavior, and the stability of burrowed mussels. Further, these results can be used to inform future numerical models to investigate turbulent flow and sediment transport interactions in biologically conditioned boundary layers. Moving forward, we hypothesize that mussels are capable of exerting control over flow properties of a biologically conditioned boundary layer, such as mixing or turbulent processes, in ways that are advantageous to the long-term success of this species and possibly other organisms.

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