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Coupling of Hydrodynamical, Biological, and Geochemical Processes in Streambeds

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Abstract

Recent interest in the effects of streambed and near-subsurface (benthic and hyporheic) processes on stream ecosystems has motivated study of the hydrodynamics of stream-subsurface interactions. Hydrodynamic transport places an important control on the delivery of reactive species such as contaminants and ecologically-relevant substances such as nutrients to the benthic and hyporheic zones. Conversely, biological processes such as biofilm growth and physicochemical processes such as colloid deposition can alter the transport environment within sedimentary systems. Multiple feedbacks between biological, chemical, and transport processes make these interfacial sedimentary environments very complex. Experimental results are presented to illustrate the feedbacks between hydrodynamic stream-subsurface exchange, biofilm development, and fine particle deposition. These studies demonstrate that a comprehensive interdisciplinary approach is required to assess even the most basic dynamic processes in these systems, such as the evolution of interfacial fluxes over time. We suggest that it is useful to consider these processes to be biophysicochemical in nature. That is, in such complex environmental systems, it is misleading to attempt to consider processes in isolation; rather, understanding of system dynamics can only come from an integrated approach that considers feedbacks among and between biological, physical, and chemical processes.

Keywords: stream-groundwater interactions, hyporheic zone, benthic zone, stream ecology

1. Introduction

Classical analysis of open channel flow assumes that there is no flux across channel boundaries and a no-slip condition just at the stream-subsurface interface.

However, natural streams and rivers normally have permeable sediment beds, which can admit a considerable pore water flow. From the hydrodynamic perspective, coupling between stream and pore water flows causes momentum transfer across the stream-subsurface interface and the development of a slip velocity at the channel boundary (Beavers and Joseph 1967, Ruff and Gelhar 1972). Detailed analysis indicates that these flow interactions can readily induce local fluxes across the stream-subsurface interface due to several distinct mechanisms, including turbulent interactions and induced advective pore water flows (Packman and Bencala 2000). These hydrodynamic processes carry solutes and suspended sediments into and out of the subsurface and help establish sedimentary biogeochemical conditions (Boudreau and Jorgensen 2001, Jones and Mulholland 2002). Even when the exchange flows are of minor importance to larger-scale stream hydrodynamics, they provide critical coupling of the stream and subsurface systems and thus affect the transport of reactive substances in watersheds.

The importance of exchanges between the stream and the streambed has been increasingly recognized over the last 20 years. Major functional components of the streambed include the water/sediment interface, termed the *benthic zone*, and the subsurface region where stream and ground waters mix near the stream channel, known as the *hyporheic zone* (*sensu* Orghidan 1959). Conceptually, the hyporheic zone can be regarded as a subsystem within the larger stream-aquifer continuum, with dynamic boundaries defined in terms of differences in physical, chemical, or biological properties from either the stream or bulk groundwater systems (Triska et al. 1989). The hyporheic zone is frequently subject to large gradients in physical (light, velocity), chemical (redox conditions) and biological (species composition, production) properties regulated by the interplay of ground and stream waters. In the context of the stream ecosystem, the hyporheic zone is considered an ecotone (Gibert et al. 1990), which inherently represents a region of transition for ecologically relevant environmental variables such as light, solutes, and particles.

The conditions of the benthic and hyporheic zones are both dominated by their sedimentary characteristics. First, the high resistance incurred by flow through a porous medium presents an essential control on the hydrodynamics of the streambed, and all resulting fluxes (Packman and Salehin 2003). Second, sediments provide a large and relatively stable surface area for both chemical reactions and microbial colonization. As a result, the streambed harbours considerable microbial biomass in the form of biofilms, which are collections of bacteria, algae, fungi and their associated exopolysaccharides (EPS) attached to interfacial substrates (e.g. Geesey et al. 1978, Lock et al. 1984). Biofilms greatly affect streambed processes, including both hydrodynamic exchange and the fate of bioreactive compounds, particles, and pathogens. Hence, the hyporheic zone can in some sense be considered as a bioreactor, which processes material delivered to it from either the stream or groundwater system.

Field-based investigations of stream geomorphology, hydraulics, chemistry, and ecology have provided observations of the larger-scale controls on stream functioning and insight into the functional relevance of the benthic and hyporheic zones (Newbold et al. 1981, Bencala and Walters 1983, Grimm and Fisher 1984, Triska et al. 1989, Peterson et al. 2001, Hall et al. 2002). However, the complexity of the natural system and difficulties in making field measurements with good spatial and temporal resolution have hindered detailed investigation of the underlying processes (Harvey and Wagner 2000). As yet, we do not know much about the underlying mechanisms, such as small-scale hydrodynamics, solute and particle dynamics, or biofilm functions that drive streambed and particularly hyporheic processes at micro-scales. Clearly these processes are highly interrelated, both due to coupling at the micro-scale and because larger elements of the system, such as overall stream geomorphology, considerably constrain micro-scale processes.

We characterize these processes influenced by a combination of physical transport, chemical reactions, and biological action as *biophysicochemical processes*, and argue that complex environmental systems such as streambeds need to be considered from this interdisciplinary perspective due to the high degree of coupling between the various underlying processes. Herein, we examine major controls on solute and particle transport in streambeds, specifically considering physical transport, fine sediment deposition, and biofilms, as illustrated in Fig. 1. These processes will be discussed independently and then illustrative examples will demonstrate that transport in natural streambeds is often controlled by the coupling of all of these processes, so that considering any of them independently provides only a limited and misleading view of the functioning of the natural system.

2. Overview of Hydrodynamic Interactions with Permeable Streambeds

While open channel flows are normally analyzed by considering the channel boundaries to be impermeable, natural streams generally have permeable boundaries due to the underlying alluvial sediments. Indeed, it is well known that streams are supported by groundwater input at low flow conditions, and that large-scale interaction of surface- and ground-water flow systems often produces periodic gaining and losing stream reaches. It is less appreciated that stream flow over a porous streambed also produces local exchange across the stream channel boundaries due to a variety of fundamental hydrodynamic mechanisms (Bencala and Walters 1983, Harvey and Wagner 2000, Packman and Bencala 2000). Interaction of stream flow with the channel topography (bedforms) will generally induce advective flows in porous streambeds (Thibodeaux and Boyle 1987, Harvey and Bencala 1993, Elliott and Brooks 1997ab). In addition, turbulent coupling of stream and subsurface flows can also be important in coarser sediments, such as gravels (Zhou and Mendoza 1993, Fries and Trowbridge 2003).

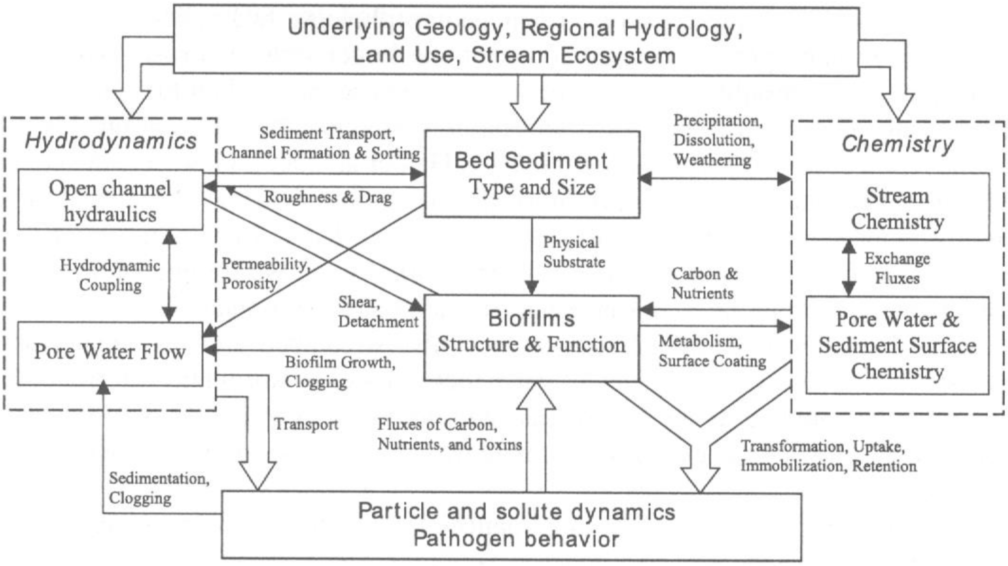

Fig. 1. Schematic diagram of couplings between hydrodynamic transport processes, aquatic and sedimentary chemistry, and streambed biofilms. Geology and hydrodynamics set the physical environment, but this is subject to biological modification. Microbial processes depend on fluxes of carbon and nutrients, but tend to control sedimentary chemical conditions

Bedforms develop on loose sediment beds due to the interaction of the stream flow with bed sediment transport and the bed topography (Vanoni 1975, Raudkivi 1998). Bedforms are normally considered as boundary roughness elements owing to their importance in producing the form drag component of flow resistance in streams. Flow-boundary interactions induce an advective pore water flow by a similar mechanism: stream flow over the bedform topography produces a variation in the dynamic head or pressure over the bedform, which in turn induces an advective flow through the underlying porous medium (Elliott and Brooks 1997ab). In fact, the same forces that cause bedforms to present a resistance to stream flow drive the subsurface pore water flow. As a result, stream flow induces local advective subsurface flows under every bedform, obstacle, or other topographical feature on the streambed surface (Huettel and Gust 1992, Harvey and Bencala 1993, Hutchinson and Webster 1998).

Bedform-induced advective flows occur whenever the streambed is permeable, and the magnitude of induced advective flows depends on the hydraulic conductivity and porosity of the sediments. The induced flows can be calculated from first principles by applying the dynamic head distribution at the bed surface as a boundary condition, solving Laplace's Equation to obtain the subsurface head distribution, and then applying Darcy's Law to determine the subsurface velocity field (Ruff and Gelhar 1973, Elliott and Brooks 1997a). When the bed sediment becomes coarser, the induced advective flows increase in velocity and non-Darcy inertial effects become important. Turbulent momentum transfer to the subsurface directly couples the stream and subsurface flows, which produces a slip velocity at the bed surface and induces a general subsurface flow (Beavers and Joseph 1967, Zhou and Mendoza 1993). The turbulent exchange process induces a significant flow only in coarse sediments, such as gravels, while bedform-induced advective flows often dominate exchange in sandy sediments (Packman and Bencala 2000).

These processes obviously establish connectivity between stream and pore waters, and this connectivity is critical to the functioning of the hyporheic ecosystems and plays an important role in determining the transport and fate of contaminants in streams. The following sections will examine the role of hydrodynamic transport in transferring fine particles from the stream to the bed and encouraging hyporheic microbial growth, and conversely the effects of these processes on the hydrodynamic connectivity of streams and streambeds.

3. Overview of Relationships between Water Fluxes and Particle Deposition

The deposition of particles from a turbulent stream to surfaces on and within streambed sediments involves an array of disparate processes that fall within several different disciplinary traditions. Sedimentation theory, in its simplest form, views particle deposition as gravitational transfer to the bed from a fully mixed water column. Suspended particle deposition is viewed as a constant rate of transfer to the bed per unit time given by v_s/d, where v_s is the quiescent fall velocity and d is the depth of the water column. Thus, v_s is analogous to a mass transfer coefficient for particle removal. In addition, the removal of particles from suspension can often be described as a first-order removal process with an empirical deposition velocity, v_{dep}. Thus the simplest prediction of sedimentation theory is that the removal rate is equivalent to the Stokes settling velocity of the transported particles, i.e., $v_{dep} = v_s$. Such agreement has been observed in flumes (Einstein 1968, Reynolds et al. 1990), and in some streams (Miller and Georgian 1992, Wanner and Pusch 2000), but a growing literature fails to confirm its general applicability to natural streams. It appears, rather, that the deposition of fine particles in natural streams and rivers is little influenced by fall velocity, and remains within a relatively narrow range ($10^{-1} - 10^{0}$ mm/s), even as fall velocities range from $\sim 10^{-4}$ (for bacteria), to $\sim 10^{1}$ (for particles $> 100 - 250\ \mu$m) (Hall et al. 1996, Thomas et al. 2001, Paul and Hall 2002, Georgian et al. 2003). Thus, small particles deposit much more rapidly than their fall velocity would suggest, whereas larger particles deposit more slowly.

These apparent discrepancies are not surprising when additional mechanisms of particle removal are considered (Boogerd et al. 2001). The rich literature on sediment transport, with origins in the 19th century and basis in hydrodynamic theory, provides a more mechanistic perspective that emphasizes the interplay of gravitational settling, vertical mixing, and boundary shear stresses. This theory includes the classical solutions for the vertical distribution of particles in a turbulent water column, as specified by the Rouse number (which involves the ratio of the settling velocity, v_s, to the shear velocity, u^*), and the Shields critical shear for particle mobilization (Rouse 1937, Vanoni 1975). Sediment transport theory, however, focuses on bulk transport (i.e., on suspended and bed loads), rather than on quantifying exchange fluxes (deposition and resuspension) under steady flow conditions.

More recently, the classical model for turbulent mixing in the water column has been augmented by stochastic diffusion theory, which describes the motion of an individual particle and determines its probability of reaching the streambed in a given time or distance (Denny and Shibata 1989, McNair et al. 1997, McNair 2000, McNair and Newbold 2001). This work has shown that, under conditions typically found in marine and lotic environments, turbulent mixing can be expected to deliver particles to the bed with far greater frequency than could quiescent particle settling or microbial locomotion. Thus gravitational settling in the stream may play only a minor role in overall particle removal. In addition, discrepancies between theoretical analysis and empirical observations suggest that only a small number of particles that reach the streambed are actually retained there.

The exchange of water with porous streambeds, as discussed above, also provides a pathway for transfer of particles from the water column to the hyporheic zone. Fine particles can readily be carried into porous streambeds composed of sediments of sand size or larger, and then deposit due to a combination of gravitational settling and attachment to bed sediment surfaces (Einstein 1968, Packman et al. 2000ab, Fries and Trowbridge, 2003). This also indicates that the problem of particle deposition becomes a matter of retention, which in turn suggests that surface properties of both the transported particles and the bed sediment play a critical role in overall particle capture. This point is demonstrated most clearly by the deposition of sub-micron colloids in sand streambeds. Such fine particles will not settle because they are small enough to be kept in suspension indefinitely simply due to Brownian motion. Thus their deposition can only be explained by hydrodynamically driven stream-subsurface exchange followed by immobilization due to interactions with the bed sediment. Detailed analysis of the fundamental physical and chemical processes that control this behaviour allows quantitative prediction of the overall fine particle deposition (Ren and Packman 2002).

While hyporheic exchange fluxes are clearly important for fine particle immobilization, accumulation of these fine particles in the subsurface also presents a feedback on pore water transport. Significant accumulation of fine particles in pore spaces reduces both the porosity and permeability of the porous medium. Einstein (1968) observed that particle deposition in flumes diminished as interstices filled. This process has been observed to be important in streams, and has significant implications for stream ecology (Brunke 1999). Minshall et al. (2000)

observed a significant correlation between the deposition of fine particulate organic carbon and the volume of the hyporheic zone in Idaho streams.

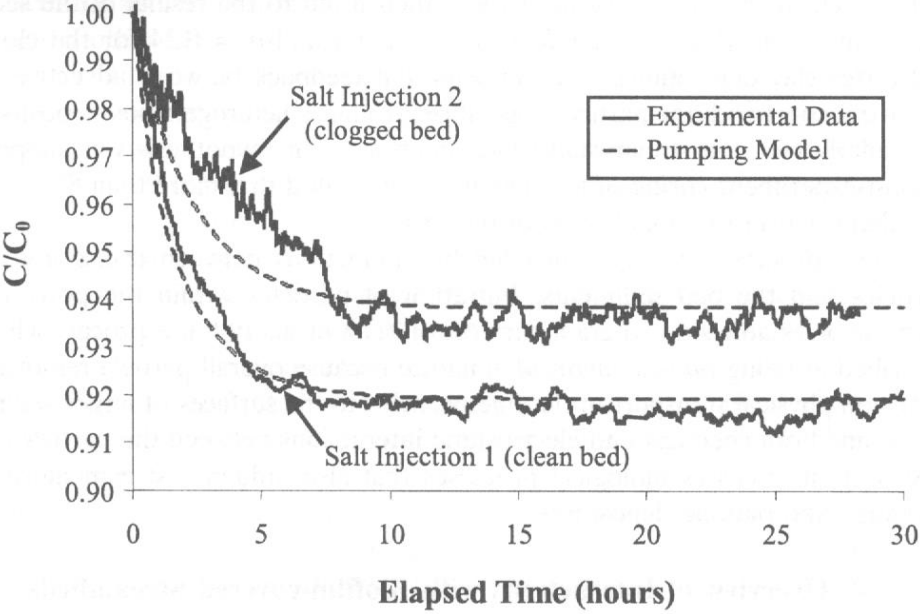

Fig. 2. Comparison of solute exchange with a sand bed with and without accumulated clay. Reprinted from (Packman and MacKay 2003)

The dynamics of this process are not well understood, but laboratory examination of the underlying processes suggests that fine particle deposition should be almost irreversible under low flow conditions, so that fine particles will accumulate in the streambed until a high-flow event scours the bed (Packman et al. 2000ab). Feedback between advective delivery of fine sediments to the bed and particle deposition also implies that accumulation will preferentially occur in regions of high influx, and can alter pore water flows (Packman and MacKay 2003). This behaviour was examined in laboratory experiments where solute exchange between a stream and sand bed was examined under differing states of clay accumulation in the streambed. An initial salt injection was performed with a clean sand bed, suspended clay was added to the stream and allowed to deposit in the bed, and then a second salt injection was performed after all the clay had deposited in the bed. Fig. 2 shows that clay deposition greatly reduced solute penetration in the bed over the timescale of the experiments. Application of the fundamentally based pore water pumping model (Packman et al. 2000a) indicates that clay deposition greatly decreased the effective bulk permeability and porosity of the streambed, despite the fact that clay accumulation represented less than 0.25% of the bed sediment by mass. The properties of the sand were measured independently, notably hydraulic conductivity $K = 10.8$ cm/min and porosity $\theta = 0.38$, and application of the model with these values yielded a good prediction of exchange with the clean sand bed. The model was then fitted to the results of the second solute injection, which yielded $K = 1.25$ cm/min and $\theta = 0.24$ for the clogged bed (after clay deposition). This suggests that feedback between advective pore water transport and fine particle deposition produces heterogeneous deposits that particularly clog the stream-subsurface interface. This hypothesis was supported by post-experiment coring of the bed, which indicated that more than 85% of the clay deposited in the upper 4 cm of the bed.

These processes are all controlled by interactions between transported fine particles and the bed sediments. Filtration of particles within the porous medium involves adhesion to grain surfaces (Logan et al. 1995), a process which is described as being *physicochemical* in nature because overall particle removal depends on physical transport of the fine particles to the surfaces of larger sediment grains and both chemical and electrostatic interactions between the particles. The next section discusses biological processes that also influence stream-subsurface exchange and particle deposition.

4. Overview of Interactions with Biofilm-covered Streambeds

Despite the importance of benthic and hyporheic biofilms, we do not currently have a clear understanding of their structural properties, the importance of these in controlling ecological processes, and the impact of feedbacks between biofilm growth and hydrodynamic processes. In early engineering studies, biofilms were generally considered as planar and rather homogeneous systems with mass transfer largely governed by diffusion (Grady et al. 1999). Novel microscopic and microelectrode technologies have changed this perception, and biofilms are now recognized as 3D systems with internal channel networks that admit advective transport (e.g. Costerton et al. 1995). Microbial biofilms in streams and rivers are complex ecological communities that are cross-trophic and multi-phylic in nature and their community structure depends on flow and their location within the streambed (Lock et al. 1984, Battin et al. 2003). To illustrate some of the couplings between hydrodynamics and biofilms, we combine knowledge from laboratory model biofilms with the few available studies conducted directly in environmental systems.

Fluid flow exerts a force on biofilms and also controls mass transfer of oxygen, nutrients, and other biologically important solutes (e.g., Stoodley et al 2000). Therefore, hydrodynamic processes shape biofilm structure and function. Pure bacterial biofilms behave like elastic and viscoelastic solids with fluid shear causing short-term structural deformation and influencing mass transfer within the biofilm (Stoodley et al. 1999). It is also well known that the flow regime in streams affects biofilm structure by processes such as shear-induced detachment of entire biomass clusters (Blenkinsopp and Lock 1994, Battin et al. 2003). Furthermore, the hydrodynamic exchange between surface and interstitial waters can control the microbial activity of streambed biofilms (Battin 2000).

On the other hand, biofilms can also affect hydrodynamic processes. The accumulation of bacterial biomass, production of extracellular polymeric substances (EPS), deposition of iron hydroxides or manganese, and microbial production of methane can induce clogging of porous media (Baveye et al. 1998). Battin and Sengschmitt (1999) presented the first evidence of microbial participation in the clogging of a large riverbed. Furthermore, biofilms can cause pressure drop in pipelines, and Godillot et al. (2001) demonstrated that biofilm growth in a laboratory flume increased the boundary roughness. Solute retention in the benthic and hyporheic zones has become a focal point in stream ecology since it constitutes a physical template for biogeochemical and ecological processes (Jones and Mulholland 2000). As illustrated below in Section 5, our experimental work reveals that there can also be significant transient storage of solutes within benthic and hyporheic biofilms.

Microbial biofilms affect particle transport dynamics in several ways. First, microbially induced changes in bed roughness and pore water hydrodynamics alter bulk particle transport. In addition, the proliferation of benthic biofilms at the streambed surface often produces filamentous “streamers” composed of algae, bacteria, and EPS that protrude into the main stream flow and can capture suspended particles. Oscillation of these streamers under turbulent flow conditions enhances the scavenging of particles from the stream. Microorganisms also alter the chemical environment of the streambed and thus affect physicochemical interactions between fine particles, mobile microbes such as pathogens, and bed sediments. In particular, biofilm EPS has considerable affinity for inorganic particles, colloidal organic matter, and pathogens, and thus biofilm growth tends to increase overall particle deposition onto bed sediments. We thus propose that transfer of particles to streambed surfaces is strongly mediated by biofilms, and that particle deposition in biofilms represents an important feedback process that plays a critical role in determining the characteristics of natural streambeds. We believe that stream-subsurface exchange, fine particle deposition in streambeds, and hyporheic biofilm growth truly represent a set of coupled biophysicochemical processes. These concepts will now be illustrated with observations of stream-subsurface exchange and suspended sediment deposition in biofilm-covered and biofilm-free streambeds.

5. Results: Coupled System Dynamics

Coupling between hydrodynamic transport, fine particle deposition, and biofilm growth will be illustrated using results obtained from flume experiments. Laboratory flumes have been used extensively over the last 50 years for the study of open channel flows and sediment transport (Vanoni 1975), and they have also proven to be very useful for the examination of hydrodynamic stream-subsurface exchange processes (Elliott and Brooks 1997b). With suitable control of stream chemical conditions, these systems have also allowed detailed investigation of the dynamics of reactive transport processes and physicochemical fine particle deposition in streambeds (Packman et al. 2000b, Huettel et al. 1998, Ren and Packman 2002). However, it is extremely difficult to reproduce natural biological and ecological processes in the laboratory. As a result, we have used stream-side flumes to examine coupling of physical, chemical, and biological processes in streambeds. Like laboratory flumes, stream-side flumes provide a controlled open channel flow over a sediment bed, but stream-side flumes also utilize natural stream water, are exposed to natural environmental conditions such as sunlight, and receive natural biological inputs. Consequently these systems are colonized by indigenous microbes from the stream. Experimental results presented here were obtained from four stream-side flumes, 0.3 m wide and 29 m long, at the Stroud Water Research Center in Avondale, Pennsylvania, USA, with water supplied from White Clay Creek.

We monitored the growth of microbial biofilms under two different flow regimes in these stream-side flumes and investigated the effects of biofilm growth on solute transport. Two flumes were set at a slope of 0.002, with a flow of 1.1 L/s and velocity of 0.09 m/s. The other two were set at a slope of 0.024 with a flow of 4.0 L/s and velocity of 0.22 m/s. Each flume had a mixed-size gravel bed approximately 3 cm deep. Bed sediments were completely dry and biofilm-free before the start of the experiments, and developed natural biofilms in the flumes. Periodic injections of a dissolved sodium chloride tracer were used to assess solute transport with different biofilm growth conditions. Solute transport dynamics were analyzed using the Transient Storage Model (Bencala and Walters 1983), which considers solute advection and dispersion in the stream flow, as well as exchange with the streambed.

Results from this flume experiment are presented in Figures 3 and 4. As indicated by the development of chlorophyll *a*, microbial biomass increased steadily after a short lag phase, and then subsequently decreased due to biofilm detachment and grazing by invertebrates. Streambed biofilms were found to have a higher average mass under the slower stream flow condition. This indicates the role of stream hydrodynamics in controlling the extent of microbial growth on the streambed sediments. Biofilm growth also influenced solute transport and retention in the flume. Fig. 3 compares solute transport under conditions where no biofilms were present and where biofilms had extensively colonized the streambed sediments. These results are from the experiment with the lower velocity. The presence of biofilms clearly influenced solute transport, with the solute breakthrough curve showing considerably more solute retention (tailing) when biofilms were present. This effect is described by the Transient Storage Model in terms of an area for solute storage (A_s) and an exchange coefficient (α) (see Bencala and Walters 1983, or Packman and Bencala 2000 for a description of the model). The flume experiments demonstrated that the extent of transient solute storage, characterized as the relative areas of the storage zone and the stream ($A_s : A$), closely followed the observed pattern of microbial growth under both flow conditions, as shown in Fig. 4.

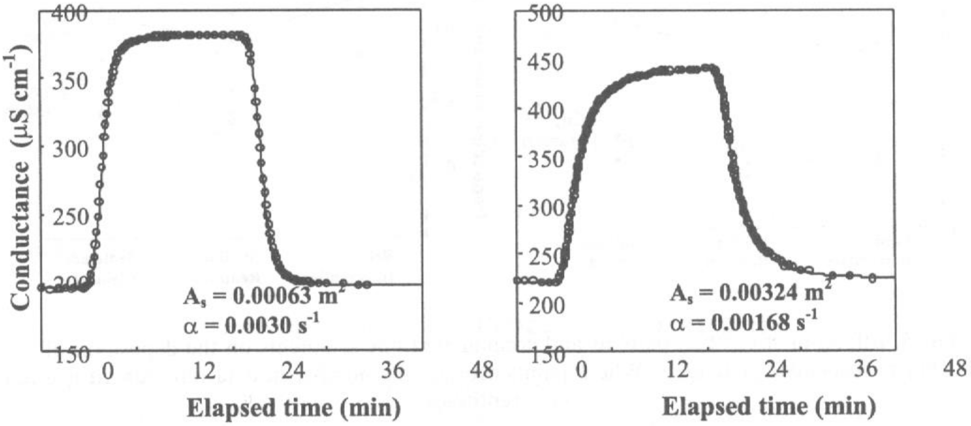

Fig. 3. Observed solute breakthrough curves in flume experiments with growing biofilms. Left panel: no biofilms present (day 0 of experiment). Right panel: extensive biofilms present (day 18)

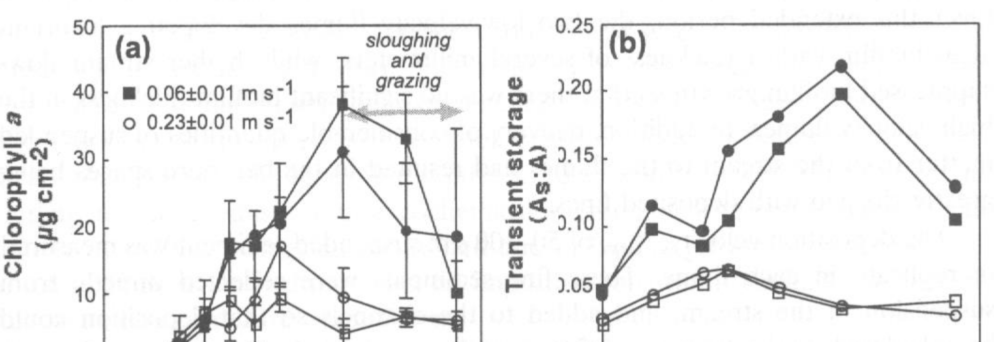

Fig. 4. Effect of streambed biofilm growth on transient storage of solutes during transport through flumes

We suggest two mechanisms for this linkage between microbial processes and stream hydrodynamics. (i) Biofilms have a complex three-dimensional structure, including internal channel networks. This void system allows solute uptake and storage within biofilms. (ii) Biofilms also have heterogeneous surface structures, which include filamentous streamers. Flow through these structures creates eddies and alters the velocity profile of the stream, which also increases transient storage of solutes.

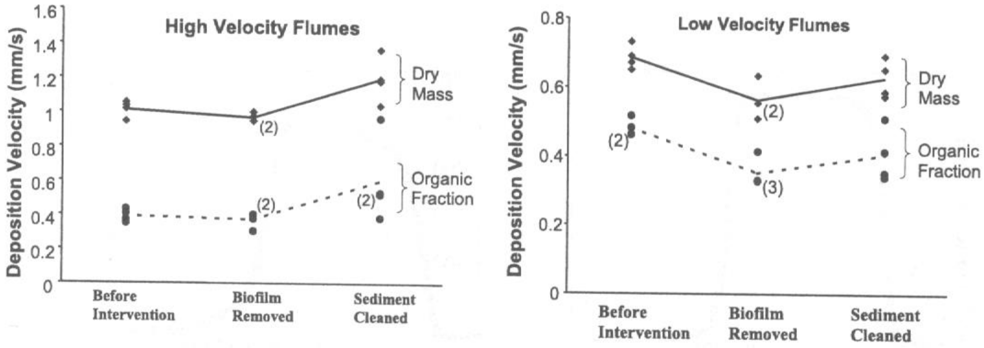

Fig. 5. Effects of streambed biofilms and accumulated fine sediments on the deposition of 50–100 μm suspended sediments. Where points overlap, the number of data represented is given in parentheses

The combined influences of biofilms and subsurface exchange on particle removal are evident in Fig. 5, which shows results from flume experiments conducted with and without both biofilms and accumulated fine sediments in the streambed. Prior to this experiment, the flumes had been running undisturbed for approximately nine months under the same flow conditions reported above. Over this extended period, the two low-velocity flumes developed a luxuriant algal biofilm with a thickness of several millimeters, while higher stream flows suppressed biofilm growth so that there was no significant biofilm thickness in the high-velocity flumes. In addition, delivery of considerable quantities of suspended matter from the stream to the flumes had resulted in the bed pore spaces being greatly clogged with deposited fines.

The deposition velocity, v_{dep}, of 50–100 μm suspended sediment was measured in replicate in each flume. These fine sediments were collected directly from suspension in the stream, and added to the channels so that deposition could be calculated as the fraction of fine particles retained during transport through the flumes. Following this initial measurement, biofilms were reduced in each flume by manually brushing rock surfaces to remove biofilms, and v_{dep} of the 50–100 μm suspended sediments was again measured. This biofilm removal step did not produce any significant disturbance of the underlying sediments. Finally, the sediments were manually cleaned by vigorous agitation and flushing in order to remove accumulated fines from the bed, and v_{dep} was measured a third time.

In both high- and low-velocity flumes, and for both total and organic fractions of the suspended sediment mass, the mean particle deposition velocity decreased after biofilms were removed. The effect was statistically significant ($P<0.05$, 2-way ANOVA, Tukey's test), however, only for the low velocity flumes, which had thicker biofilms. The subsequent removal of fine sediments from the gravel bed produced an increase in the mean v_{dep} in both high- and low-velocity flumes for both total and organic fractions, but in this case the effect was significant only for total v_{dep} in the high velocity flumes. The final v_{dep} was greater than the initial v_{dep} in the high velocity flumes, whereas the final v_{dep} was intermediate between the previous measurements in the low velocity flumes. These results demonstrate that both biofilms and stream-subsurface exchange influence particle removal, and suggest that their relative importance depends on the stream flow conditions and degree of biofilm development. It is difficult to separate the effects of physical and biological processes since stream flow affects both particle transport and biofilm growth.

6. Discussion: Challenges and Strategies

It is clear that many observed processes in streams result from the simultaneous operation of physical, chemical, and biological mechanisms. While different disciplinary traditions have made great progress in improving understanding of these mechanisms in isolation, synthesis of these processes in natural environmental systems remains a challenge. Streambeds, including the benthic and hyporheic zones, represent particularly complex environments because they include a region of transition from stream flow conditions to bulk subsurface conditions and thus feature sharp gradients in physical, chemical, and biological properties. A variety of hydrodynamic processes transport solutes and suspended particles between streams and streambeds. In turn, this transport drives pore water chemical processes and microbial growth, but experimental results show that biological growth also has a significant effect on pore water transport. Experimental results also indicate that fine particle deposition is influenced by a wide variety of processes, including advective transport, physicochemical interactions with bed sediments, and uptake by biofilms. Clogging of the bed due to biofilm growth and the accumulation of fines in the bed represent an important long-term feedback mechanism due to its effect on pore water flows.

We believe that such complex, interrelated processes cannot be addressed adequately when considered in terms of discrete operations of independent mechanisms. Instead, coupling between these processes must be considered explicitly, and bulk observations must be interpreted with an interdisciplinary view that integrates processes across scales. Thus we advocate the adoption of a process-oriented biophysicochemical approach to address the interplay of controlling system features such as geology, geomorphology, and hydrology, local-scale hydrodynamic transport processes that determine the fluxes of reactive constituents, aqueous and surface chemical reactions that transform and immobilize transported substances and also influence sediment composition over the long term, and the biological processes that mediate and often control a wide variety of natural conditions. Even when examining relatively simple processes, such as pore water fluxes in streambeds and the migration of fine sediments in streams, experiments that *consider* the possible feedbacks between biophysicochemical processes *clearly demonstrate that they occur*. As these investigations expand to include long-term dynamics of ecologically relevant solutes and particles, such an interdisciplinary approach will be required to unravel emergent behaviour of natural systems.

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