Extracellular polymeric substances induced cell-surface interactions facilitate bacteria transport in saturated porous media

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ABSTRACT

Bacteria often respond to dynamic soil environment through the secretion of extracellular polymeric substances (EPS). The EPS modifies cell surface properties and soil pore-scale hydration status, which in turn, influences bacteria transport in soil. However, the effect of soil particle size and EPS-mediated surface properties on bacterial transport in the soil is not well understood. In this study, the simultaneous impacts of EPS and collector size on *Escherichia coli* (*E. coli*) transport and deposition in a sand column were investigated. *E. coli* transport experiments were carried out under steady-state flow in saturated columns packed with quartz sand with different size ranges, including 0.300–0.425 mm (sand-I), 0.212–0.300 mm (sand-II), 0.106–0.150 mm (sand-III) and 0.075–0.106 mm (sand-IV). Bacterial retention increased with decreasing sand collector size, suggesting that straining played an important role in fine-textured media. Both experiment and simulation results showed a clear drop in the retention rate of the bacterial population with the presence of additional EPS (200 mg L^{-1}) (EPS+). The inhibited retention of cells in sand columns under EPS+ scenario was likely attributed to enhanced bacteria hydrophilicity and electrostatic repulsion between cells and sand particles as well as reduced straining. Calculations of the extended Derjaguin-Landau-Verwey-Overbeek (XDLVO) interactions energies revealed that high repulsive energy barrier existed between bacterial cells and sand particles in EPS+ environment, primarily due to high repulsive electrostatic force and Lewis acid-base force, as well as low attractive Lifshitz-van der Waals force, which retarded bacterial population deposition. Steric stabilization of EPS would also prevent the approaching of cells close to the quartz surface and thereby hinder cell attachment. This study was the first to show that EPS reduced bacterial straining in saturated porous media. These findings provide new insight into the functional effects of extrinsic EPS on bacterial transport behavior in the saturated soil environment, e.g., aquifers.

1. Introduction

Potential bacterial contamination in groundwater has challenged the safety of drinking water supply and poses high risks to public health. *Escherichia coli* (*E. coli*) is commonly considered as an indicator of pathogen presence for evaluating groundwater contamination (Chen and Walker, 2012; Syngouna and Chrysikopoulos, 2011). It was reported that such waterborne bacteria could cause severe gastrointestinal diseases in humans that may result in acute failures such as bloody diarrhea and hemolytic uremic syndrome (Dean-Nystrom et al., 2003; Kaper and Karmali, 2008). Accordingly, a systematical investigation concerning deposition and transport of the pathogen within soil-water

system should be carried out to assess and mitigate the potential risk.

Abiotic factors, including soil structural properties and water availability, are known to impact bacterial transport rate in soil. Bacterial cells may modify their immediate environment through the presence of extracellular polymeric substances (EPS) to alter water availability and chemical properties of soil particle surfaces. Numerous literatures have demonstrated that EPS and other macromolecules modify physico-chemical properties of the bacterial surface (e.g., hydrophobicity and surface charge), and thus alter their adhesion rate to solid particles (Han et al., 2013; Johanson et al., 2012; Kim et al., 2009; Zhao et al., 2014). Such modification of the cell surface has been shown to impact bacterial transport rate in porous media (Table 1). Previous studies showed that

extracellular macromolecules can either enhance (Feriancikova et al., 2013; Kuznar and Elimelech, 2005; Kim et al., 2009, 2010; Yang et al., 2012) or hinder (Johanson et al., 2012; Liu et al., 2007; Long et al., 2009; Tong et al., 2010) the attachment of bacteria onto abiotic surfaces under saturated conditions.

One possible explanation for these contrary observations was the different methods used for the removal of EPS (Table 1), typically including proteinase treatment (Kim et al., 2009, 2010), cation exchange resin (Liu et al., 2007; Tong et al., 2010) and bacterial mutant strains with different EPS secretion capabilities (Feriancikova et al., 2013; Johanson et al., 2012). Furthermore, various bacterial species selected can also lead to different transport and deposition in packed sand columns (Bai et al., 2016; Johanson et al., 2014). For example, by comparing wild bacterial strain with its mutant, Johanson et al. (2012) found that EPS positively affected *Escherichia coli* transport, while negative influence of EPS on *Enterococcus faecium* transport was reported by Feriancikova et al. (2013). More important, EPS are susceptible to many factors that govern bacterial metabolism, of which composition and amount are thereby continuously dynamic (Flemming and Wingender, 2010; Mcswain et al., 2005; More et al., 2014). Consequently, precise control of EPS (e.g., concentration and composition) within transport column in laboratory environment poses a challenge to subsequent research. In addition, studies revealed that the modification capacity of EPS on bacterial surface properties was rather concentration dependent, and variations in presented external EPS concentration would eventually lead to different or even opposite consequences on bacterial surface characteristics (Hua et al., 2003; Kaczorek and Olszanowski, 2011; Lin et al., 2017; Ma et al., 2018; Carstens et al., 2021).

To stabilize the amount and composition of EPS in column experiment, artificial EPS solution was applied in this study, mimicking extrinsic source EPS in natural environments such as soil or sludge that are common for numerous studies (Yang et al., 2012; Jimenez-Sanchez et al., 2015; Madumathi, 2017; He et al., 2019). It was reported that dissolved organic matters would inhibit bacterial cell attachment onto surfaces and thus facilitate transport. In addition, the enhancement of EPS on bacterial transport was conditional. For example, Jimenez-Sanchez et al. (2015) found that EPS may facilitate bacteria transport at concentration level of ~130 mg L^{-1}, yet fairly weakened (even none) impacts at lower level of ~16 mg L^{-1}. It highlights that the dosage of organic matters, as well as EPS concentration, are important ingredients impacting bacterial transport.

Bacterial cells presented in an EPS-rich environment would likely exhibit different motility behaviors as compared with those in bulk (or EPS-scarce) media, largely due to EPS-mediated alternation in bacterial cell surface properties. All the transport experiments were conducted at 4 °C in ice chest to avoid bacterial growth and EPS secretion (Tourna et al., 2010). In addition, pore (or collector) size of porous media can influence physicochemical filtration, bio-colloid retention, and other cell-particle interactions, and thereby manipulates bacterial cell transport. The underlying mechanisms are yet poorly understood (Gargiulo et al., 2007; Syngouna and Chrysikopoulos, 2011; Bai et al., 2016). Therefore, the objective of this study was to investigate the joint effects of EPS and collector size on the transport and deposition processes of *E. coli* population in sand columns. The XDLVO calculation was employed to explain how EPS affected energy barrier between a bacterium and quartz sand surface in transport behavior. Bacterial transport was quantitatively simulated by HYDRUS-1D model, to examine dominant mechanism of bacterial transport under the combined effect of EPS and collector size. This study was the first to show that EPS reduced straining. These findings provide new insight into the functional effects of extrinsic EPS on bacterial transport behavior in the saturated soil environment, e.g., aquifers.

2. Material and methods

2.1. Porous media and background solution

Four sizes of quartz sands were applied for the sand column transport experiments, with diameter range of (I) 0.300–0.425 mm (d_{50} = 0.355 mm), (II) 0.212–0.300 mm (d_{50} = 0.265 mm), (III) 0.106–0.150 mm (d_{50} = 0.130 mm), and (IV) 0.075–0.106 mm (d_{50} = 0.095 mm) (Table 2). Quartz sands were thoroughly cleaned to ensure the removal of organic and metal impurities, according to Litton and Olson (Litton and Olson, 1993). Prior to wet-packing column, cleaned sands were sterilized in an autoclave at 121 °C for 30 min. Proteins and polysaccharides were two dominant components of EPS (70–95%) (Flemming and Wingender, 2010; More et al., 2014), commonly considered to represent EPS contents in numerous studies (Haznedaroglu et al., 2008; Nouha et al., 2018; Zhao et al., 2015; Zhu et al., 2015). Specifically, typical contents in EPS matrix of the two components range

Table 1

A review of the effect of EPS or extracellular macromolecules on bacterial transport and deposition in the past decade.

Treated method	Bacterial strain	Effect of EPS/extracellular macromolecules on bacteria					
		MATH[a]	Surface charge[b]	Cell size	A[c]	$\Delta G_{h_0}^{AB}$[d]	Transport
Proteinase	*Escherichia coli*	Increase	Increase	NS	ND	ND	Facilitate[g]
Proteinase	*Escherichia coli*	Increase	Increase	NS	ND	ND	Facilitate[h]
Cation exchange resin	*Escherichia coli*	ND[e]	NS[f]	NS	ND	ND	Inhibit[i]
Cation exchange resin	*Pseudomonas sp*	ND	NS	NS	ND	ND	Inhibit[i]
Cation exchange resin	*Rhodococcus sp*	ND	NS	NS	ND	ND	Inhibit[i]
Cation exchange resin	*Bacillus subtilis*	ND	NS	NS	ND	ND	Inhibit[i]
10% cultured nutrient in background solution	*Escherichia coli*	ND	Increase	Increase	ND	ND	Facilitate[j]
	Bacillus subtilis	ND	Increase	Increase	ND	ND	Facilitate[j]
Wild bacterial strain and its mutant with different EPS secretion	*Escherichia coli*	ND	NS	NS	Decrease	Decrease	Facilitate[k]
	Enterococcus faecium	Increase	NS	NS	Decrease	Decrease	Inhibit[l]

[a] Microbial adhesion to hydrocarbon test.
[b] Measured as zeta potential or electrophoretic mobility.
[c] Hamaker constant.
[d] Hydrophobicity interaction free energies per unit area.
[e] Not determined.
[f] Not significant.
[g] Kim et al. (2009).
[h] Kim et al. (2010).
[i] Tong et al. (2010).
[j] Han et al. (2013).
[k] Feriancikova et al. (2013).
[l] Johanson et al. (2012).

Table 2
Experimental conditions for bacteria transport and mass balance for column transport experiments.

Sand	Particle size (mm)	EPS	Darcy velocity (cm min^{-1})	Bulk density (g cm^{-3})	Porosity (%)	$R_{effluent}$ (%)	R_{column} (%)	R_{total} (%)	K_d (h^{-1})
I	0.300–0.425	–	0.182	1.492	43.7	59.9 a	23.4 a	83.4 a	0.23 a
		+	0.181	1.486	43.9	63.7 a	19.6 b	83.3 a	0.22 a
II	0.212–0.300	–	0.186	1.518	42.8	55.0 b	26.2 a	81.2 b	0.40 a
		+	0.185	1.507	43.1	63.1 a	23.8 b	86.9 a	0.17 b
III	0.106–0.150	–	0.197	1.582	40.3	49.5 b	31.3 a	80.8 b	0.56 a
		+	0.198	1.584	40.2	59.5 a	26.5 b	86.0 a	0.37 b
IV	0.075–0.106	–	0.200	1.597	39.7	44.7 b	36.9 a	81.7 b	0.81 a
		+	0.201	1.602	39.5	57.3 a	30.3 b	87.7 a	0.55 b

$R_{effluent}$ and R_{column} are the mass percentage of bacteria recovery from effluent and column; $R_{effluent} + R_{column} = R_{total}$. K_d is deposition rate coefficient. Different letters indicate significant difference between EPS+ and EPS- bacteria in the same sand media (LSD-test, n = 3, p ≤ 0.05).

from 40% to 95% for polysaccharides and from 1% to 60% for proteins, respectively (Flemming and Wingender, 2010; More et al., 2014). Although natural EPS often contain different kinds of proteins and polysaccharides, the functional groups that affect bacterial surface properties and attachment behavior are rather similar (Zhu et al., 2015; Xia et al., 2016). Therefore, simplified protein and polysaccharide are employed to quantify the effects of EPS on bacterial transport characteristics in porous media. Studies have shown the EPS concentration in numerous environmental systems varies widely. For example, researches reflected high value of 0.8–27.7 g L^{-1} maximum bacterial EPS production in fermentation systems (Zheng et al., 2008; Buthelezi et al., 2010; Patil et al., 2011; Li et al., 2013), which led to a common EPS dosage range of 1–5000 mg L^{-1} for kaolin flocculation activity (Li and Yang, 2007; Xiong et al., 2010; Subramanian et al., 2010; Patil et al., 2011). Meanwhile, optimum EPS concentration of 1–500 mg L^{-1} were found for sludge dewatering and flocculation (Li and Yang, 2007; Patil et al., 2011; Mabinya et al., 2012; Zhao et al., 2013). Redmile-Gordon et al. (2014) found that soil EPS content, typically the total polysaccharides and proteins may up to 169–16010 mg kg^{-1}-soil and 43–1269 mg kg^{-1}-soil, respectively. In addition, one parallel study has been conducted on the effect of EPS content on bacteria transport under five EPS concentrations of 0 mg L^{-1}, 50 mg L^{-1}, 200 mg L^{-1}, 1000 mg L^{-1} and 5000 mg L^{-1}. Specifically, no statistical difference (slightly higher numerical value) was observed between concentrations of 0 and 50 mg L^{-1}. While EPS concentrations of 200 and 1000 mg L^{-1} facilitate (in certain levels) bacteria transport, further increase of EPS concentration to 5000 mg L^{-1} resulted in a fairly inhibited bacteria transport. Accordingly, an artificial EPS concentration of 200 mg L^{-1} (consisting of 80 mg L^{-1} bovine serum protein and 120 mg L^{-1} dextran, pH value of around 7) was employed to quantify the effect of EPS on bacterial transport characteristics in porous media. Bacterium-free NaCl solution (IS = 150 mM) was selected as the background electrolyte. Bacterial culture suspended in the above-mentioned bacterium-free NaCl solution was served as negative control (EPS-).

2.2. Strains and culture conditions

E. coli ATCC 25922 strain, obtained from Kechuanghuida Co., Ltd. (Beijing, China), was applied as a model bacterium in this study. Bacterial culture was harvested by centrifugation (Herexi H/T18MM, Hunan, China) at 3420×g for 10 min at an exponential growth phase (3.5 h at 37 °C with shaking at 200 rpm) in a Luria Broth medium (1.0 g NaCl, 1.0 g Tryptic Casein and 0.5 g bacto-yeast extract in 100.0 mL DI water). The harvested cells were washed twice with NaCl solution (150 mM) by centrifugation. The cell pellets were then re-suspended in EPS+ or EPS- solution (~1.0 ×10^8 cells mL^{-1}) for experiments.

2.3. Surface properties of bacteria and quartz sand

The length and width of bacteria (n ≥ 50) were measured by ImageJ software, expressed as equivalent radii of $\sqrt{Length \times Width/\pi}$. Bacterial surface hydrophobicity was determined by the microbial adhesion to

hydrocarbon (MATH) test (Parent and Velegol, 2004). Briefly, one milliliter of n-dodecane was mixed with four milliliters of bacterial suspension, and the mixture was then vortexed (Lab Dancer, IKA, Germany) at a full speed for 2 min followed by 45 min of sedimentation to allow sufficient phase separation. The OD$_{600}$ of water phase before and after settling was determined by a spectrophotometer (AOE A590, Shanghai, China). The hydrophobicity of bacteria was quantified as the percentage of total cells partitioned into the hydrocarbon phase. Zeta potential of bacteria and quartz sand was determined using a Zetasizer (Nano ZS90, Malvern, UK). All the measurements were repeated four times for each treatment and the average values of 10 runs were calculated for each assay.

A goniometer (contact angle system OCA, Dataphysics, Germany) was used to determine bacterial contact angles of three probe liquids according to Ong et al. (1999). Briefly, bacterial cells (suspended in EPS+ or EPS- solutions, ~10^8 cells mL^{-1}, 60 mL) were vacuum-suctioned onto a 0.2-μm cellulose acetate membrane for 60 min, creating a compacted bacterial lawn. Three separate filters were used for each treatment. Liquid droplets were applied at four different places for each filter.

2.4. Column configuration and transport experimental setup

Three plexiglass columns (4.0 cm in inner diameter and 15.0 cm in length) were wet-packed with cleaned quartz sand by mild knock and vibration to eliminate air entrapment. Then, each column was pre-equilibrated with ~10 pore volumes (PV) of bacterium-free NaCl solution by a peristaltic pump (Leadfliud BT101S, Baoding, China) at a flow rate of 1 mL min^{-1} (Table 2). After precondition, bacterial suspension of 6 PV (EPS+ or EPS-) was injected into each column, followed by bacterium-free NaCl solution. The effluent was collected using auto-collector and bacterial concentration was quantified by plate counting. The column experiments were carried out at 4 °C in ice chest to avoiding bacterial growth and EPS secretion (Tourna et al., 2010). Four parallel transport experiments were conducted according to the sand sizes. Triplicate were done for each condition.

2.5. Cell retention and deposition

Following each transport experiment, sand media were carefully excavated in 5.0 cm increments (3 layers), and then gently shaken with NaCl solution for 20 min to liberate reversibly absorbed cells. The bacterial concentration in supernatant was determined by plate counting. The percentage of deposited E. coli population in a sand column was calculated by the number of cells recovered divided by the number of entire cells injected. Table 2 presented the calculated effluent ($R_{effluent}$), sand (R_{column}), and the total ($R_{total} = R_{effluent} + R_{column}$) mass percentage of bacteria recovered from the experimental systems.

2.6. XDLVO calculations of bacterium-quartz sand interaction energy profiles

The XDLVO theory (Oss, 1993, 1995) was widely employed to quantify interaction energy within colloidal or bio-colloidal attachment (Johanson et al., 2014; Georgopoulou et al., 2020; Wang et al., 2021), considering the system as sphere-plate interactions. The total energy Φ_{total} between an *E. coli* cell and sand surface was a summary of Lifshitz-van der Waals (LW) interaction energy Φ_{LW}, repulsive electrostatic double layer (EDL) interaction energy Φ_{EDL}, and Lewis acid-base (AB) interaction energy Φ_{AB}, which were calculated according to Eqs. (1), (3) and (5), respectively.

$$\Phi_{LW} = -\frac{Aa_p}{6h} \tag{1}$$

$$A = 24\pi h_0^2 \left(\sqrt{\gamma_b^{LW}} - \sqrt{\gamma_w^{LW}} \right) \left(\sqrt{\gamma_s^{LW}} - \sqrt{\gamma_w^{LW}} \right) \tag{2}$$

where a_p represents equivalent radius of a bacterial cell, h represents the separation distance between a sand particle and bacterial cell, $h_0 = 0.157$ nm, A is Hamaker constant obtained by Eq. (2), γ_b^{LW}, γ_w^{LW} (21.8 mJ m^{-2}) and γ_s^{LW} (39.2 mJ m^{-2}) are LW interfacial tension parameter of bacteria, water and sand, respectively.

$$\Phi_{EDL} = \pi\varepsilon_0\varepsilon_r a_p \left\{ 2\Psi_p\Psi_c ln\left[\frac{1 + e^{-\kappa h}}{1 - e^{-\kappa h}} \right] + \left(\Psi_p^2 + \Psi_c^2 \right) ln\left(1 - e^{-2\kappa h} \right) \right\} \tag{3}$$

where Ψ_p and Ψ_c are the electric potentials of a bacterial cell and quartz sand, respectively, ε_0 and ε_r are the relative dielectric permittivity of water and permittivity under vacuum, e is the electron charge, $1/\kappa$ is Debye length and the value of κ can be determined by

$$\kappa = \sqrt{\frac{e^2 \sum n_{i0} z_i^2}{\varepsilon_0 \varepsilon_r kT}} \tag{4}$$

where k and T refer to the Boltzmann's constant and absolute temperature, n_{i0} and z_i are number concentration and valence of ion i in bulk solution, respectively.

The AB forces Φ_{AB} were calculated using:

$$\Phi_{AB} = 2\pi a_p \lambda_w \Delta G_{h_0}^{AB} e^{\frac{h_0 - h}{\lambda_w}} \tag{5}$$

$$\Delta G_{h_0}^{AB} = 2\left[\sqrt{\gamma_w^+} \left(\sqrt{\gamma_b^-} + \sqrt{\gamma_s^-} - \sqrt{\gamma_w^-} \right) + \sqrt{\gamma_w^-} \left(\sqrt{\gamma_b^+} + \sqrt{\gamma_s^+} - \sqrt{\gamma_w^+} \right) - \sqrt{\gamma_b^- \gamma_s^+} - \sqrt{\gamma_b^+ \gamma_s^-} \right] \tag{6}$$

where λ is the characteristic decay length of AB interactions in water, $\Delta G_{h_0}^{AB}$ is hydrophobicity interaction free energies per unit area corresponding to h_0, γ^+ and γ^- are electron-accepting and electron-donating interfacial tension parameters. Other parameters values were taken from literatures (Oss, 1993, 1995), including $\gamma_w^+ = \gamma_w^- = 25.5$ mJ m^{-2}, $\gamma_s^+ = 1.4$ mJ m^{-2}, $\gamma_s^- = 47.8$ mJ m^{-2} and $\lambda = 0.6$ nm.

Bacterial surface tension parameters were calculated using:

$$\gamma_i^L (1 + \cos\theta) = 2\sqrt{\gamma_i^{LW}\gamma^{LW}} + 2\sqrt{\gamma_i^+\gamma^-} + 2\sqrt{\gamma_i^-\gamma^+} \tag{7}$$

where the subscript i represents three probe liquid selected, including water ($\gamma^L = 72.8$, $\gamma^{LW} = 21.8$, $\gamma^+ = \gamma^- = 25.5$ mJ m^{-2}), glycerol ($\gamma^L = 64.0$, $\gamma^{LW} = 34.0$, $\gamma^+ = 3.92$, $\gamma^- = 57.4$ mJ m^{-2}), and diiodomethane ($\gamma^L = 50.8$, $\gamma^{LW} = 50.8$, $\gamma^+ = \gamma^- = 0$ mJ m^{-2}).

2.7. Breakthrough curve simulations

Bacterial transport was simulated by applying a Hydrus-1D model (Simunek et al., 2005; Gharabaghi et al., 2015). The Eq. (8) described mass balance between aqueous and solid phase in two-site model:

$$\frac{\partial\theta C}{\partial t} + \rho\frac{\partial S_1}{\partial t} + \rho\frac{\partial S_2}{\partial t} = \frac{\partial}{\partial x}\left(\theta_m D\frac{\partial C}{\partial x} \right) - \frac{\partial qC}{\partial x} \tag{8}$$

where C is bacterial concentration; t is time; θ is water content; ρ is bulk density of sand column; D is dispersion coefficient; q is Darcy velocity; x is the distance.

Bacterial transport within background solution and both S_1 and S_2 sites are calculated as:

$$\rho\frac{\partial S}{\partial t} = \rho\frac{\partial(S_1 + S_2)}{\partial t} = \theta_m\psi_t k_{att}C - k_{det}\rho s_1 + \theta_m k_{str}\psi_x C \tag{9}$$

where k_{att}, k_{det} and k_{str} are the attachment coefficient rate, detachment coefficient rate and straining coefficient rate, respectively; ψ_t and ψ_x are time- and depth-dependent straining parameters, respectively, describing bacteria retention to solid phases. The ψ_t was calculated by following Langmuirian dynamics equation (Adamczyk et al., 1994):

$$\psi_t = 1 - \frac{S}{S_{max}} \tag{10}$$

where S and S_{max} represent the solid-phase concentration and the maximum solid-phase concentration of bacteria on sorption sites, respectively.

The suggested depth-dependent blocking coefficient for straining processes (ψ_x) is given as (Bradford et al., 2003):

$$\psi_x = \left(\frac{d_c + x + x_0}{d_c} \right)^{-\beta} \tag{11}$$

where d_c is sand media size (median diameter); x_0 is the coordinate of the location where the straining process starts. An optimal value of $\beta = 0.432$ was suggested by Bradford et al. (2003) and thus used in this study for simulations. The output parameters, including attachment coefficient (k_{att}), straining coefficient (k_{str}) and the maximum solid-phase concentration of bacteria on sorption sites (S_{max}), were predicted simultaneously from breakthrough curve data by Hydrus-1D modeling.

2.8. Statistical analysis

Significant differences between bacterial cells in EPS+ and EPS-experiments were determined according to lease significant difference test (LSD, p ≤ 0.05) using the PROC GLM procedure in SAS (SAS Institute, 2001).

3. Results

3.1. Characterization of bacteria and quartz sand affected by EPS

Bacterial cells with extra EPS addition (EPS+) were hydrophobic with MATH value of 15.6%, as compared to those without EPS addition (EPS-) of 3.2% (Table 3). It indicates that exogenous EPS increases hydrophobicity of the cell surface. Zeta potential estimations showed that both surfaces of bacteria and quartz sand particles were negatively charged. Bacterial cells in EPS+ solutions were more negatively charged than those in EPS- ones (Table 3), indicating that EPS would likely enhance electrostatic repulsion between bacteria and quartz sand particles. The measured bacterial angles of three selected liquids for EPS+ scenarios were significantly greater than those of EPS- ones (Table 3). Absorption of EPS onto bacterial cells barely alternated cell size, with an equivalent average *E. coli* cell radius estimated as 0.25 μm.

Table 3
Properties of bacteria and quartz sand in different background solution.

Properties		EPS-	EPS+
Zeta potential of bacteria (mV)		-16.4 a	-20.3 b
Zeta potential of quartz sand (mV)		-31.7 a	-33.1 a
Bacteria hydrophobicity (%)		3.2 b	16.5 a
Contact angle (°)	Water	28.1 b	40.0 a
	Glycerol	34.1 b	52.5 a
	Diiodomethane	39.0 b	54.1 a
Surface tension components (mJ m^{-2})	γ^{LW}	40.1	31.9
	$\gamma+$	1.3	0.4
	$\gamma-$	43.3	47.0
Hamaker constant (10^{-21} J), A		4.9	2.9
$\Delta G_{h_0}^{AB}$ (mJ m^{-2})		26.4	30.3

Different letters indicate significantly difference between EPS+ and EPS- bacteria (LSD-test, n = 4, p ≤ 0.05).

3.2. XDLVO energy interactions affected by EPS

We hypothesized that the EPS induced alternation in bacterial hydrophobicity and surface charge would hinder bacterial attachment onto quartz sand surface. Therefore, XDLVO interaction energies were calculated, as used in numerous publications to quantify the effect of extracellular macromolecules on bacterial transport (Feriancikova et al., 2013; Johanson et al., 2012). The interfacial tension parameters (γ^{LW}, γ^+ and γ^-) for bacteria were calculated using Eq. (7). Then they were used to evaluate the Hamaker constant (A) and $\Delta G_{h_0}^{AB}$ values for bacteria, with the estimated values of 4.9×10^{-21} J (A) and 26.4 mJ m^2 ($\Delta G_{h_0}^{AB}$), and 2.9×10^{-21} J (A) and 30.3 mJ m^{-2} ($\Delta G_{h_0}^{AB}$) for EPS- and EPS+ scenarios, respectively, (Table 3). The positive values of $\Delta G_{h_0}^{AB}$ reflected repulsive AB interactions between a bacterium and a quartz sand particle, comparable with those reported by previous literatures ranging from 24.1 to 31.4 mJ m^{-2} (Johanson et al., 2012, 2014; Feriancikova et al., 2013). Similarly, lower values A of *E. faecium* and *E. coli* with extracellular protein were found by Johanson et al. (2012) and Feriancikova et al. (2013), respectively, indicating lower attractive LW force in adhesion behavior. Our results indicated that variations in cell surface-associated (or adsorbed) macromolecules, such as polysaccharides and proteins, may alter bacterial surface tension components and consequently the interactions energy between a bacterium and a quartz sand particle.

As shown in Fig. 1, the magnitude of XDLVO interaction energy barrier between bacterial cell and sand surface was estimated at 30,548 kT and 35,815 kT for EPS- and EPS+ scenarios, respectively. The
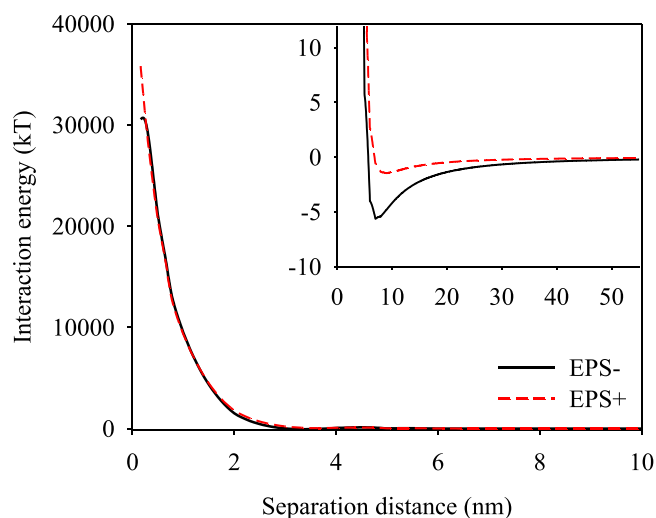
dominant influence of XDLVO forces (e.g., LW, EDL and AB) vary in separation distances, probably resulting in a secondary energy minimum followed by the primary energy minimum. The secondary minimum of bacteria-sand interaction energy is typically found in relatively high IS conditions (Feriancikova et al., 2013; Johanson et al., 2014), due to enhanced repulsive EDL force. An *E. coli* cell has only an average thermal kinetic energy of about 0.5 kT. Therefore, the bacteria may not be retained in primary minimum by overcoming the large energy barriers. The bacterium can be trapped as the depth of secondary energy minimum exceeding 0.5 kT (Redman et al., 2004). Higher absolute value of secondary minimum suggested that bacteria retention could occur within secondary energy minimum (Feriancikova et al., 2013; Johanson et al., 2014; Redman et al., 2004). The data obtained showed that the secondary minimum was -5.6 kT and -1.5 kT in separation distance of 7 nm and 9 nm for bacteria suspended in EPS- and EPS+ solution, respectively (Fig. 1). Overall, higher interaction energy calculated in EPS+ scenario revealed relatively unfavorable conditions for bacterial cells to attach onto quartz sand surface, and thereby facilitated *E. coli* transport in sand column.

3.3. Influence of EPS on bacterial transport and deposition

A clear drop in deposition of bacterial population was observed in the presence of EPS, reflecting facilitated bacterial transport. The breakthrough plateaus were significantly increased by EPS from 0.81 to 0.94 (sand-II), from 0.77 to 0.86 (sand-III) and from 0.68 to 0.78 (sand-IV), respectively (Fig. 2). Addition of EPS significantly reduced bacterial deposition rate in columns packed with sand-I (from 23.4% to 19.6%), sand-II (from 26.2% to 23.8%), sand-III (from 31.3% to 26.5%) and sand-IV (from 36.9% to 30.3%), respectively (Table 2). Interesting, the presence of EPS significantly (Fig. 4) inhibited bacterial retention within 0–5 cm depth from bacteria injection points in sand columns, with mass percentage of bacteria retained decreasing from 14.6% to 11.6% (sand-I), from 16.8% to 14.8% (sand-II), from 24.9% to 20.0% (sand-III) and from 33.3% to 26.9% (sand-IV), respectively. It reflected that EPS reduced straining. Furthermore, this observation was also confirmed by Hydurs-1D simulation, indicated by lower K_{str} values predicted in EPS+ circumstances than those in EPS- ones (Fig. 3). To the best of the authors' knowledge, this study was the first to show the decrease of straining by the presence of EPS. As shown in Fig. 3, S_{max} and K_{att} were decreased with the presence of EPS, suggesting that less retention sites may be exposed to attachment processes than those under EPS- condition. Similarly, some workers focused on the impacts of additional macromolecules (e.g., humic acid and cultured nutrients) present in background solution on bacterial transport behavior (Han et al., 2013; Yang et al., 2012). Those authors attributed the enhancement of bacterial transport to competition of deposition sites between bacteria and macromolecules.

3.4. Effect of collector size on bacterial transport and deposition

Our results based on breakthrough curves for different collector size columns indicated that bacterial deposition increased with decreasing sand collector size. The C/C$_0$ at flat breakthrough plateaus decreased with decreasing collector size, which kept at 0.88, 0.81, 0.77 and 0.68 for sand-I, sand-II, sand-III and sand-IV columns, respectively (Fig. 2). Bacterial retention rate in the column increased with decreasing sand collector size, with the estimated deposited bacterial cells (expressed as mass percentage) of 23.4%, 26.2%, 31.3% and 36.9% for the sand-I, sand-II, sand-III and sand-IV columns, respectively (Table 2 and Fig. 3). Bacterial deposition profiles decreased monotonically from the injection point to elution point.

Bacterial transport occurred faster in coarser (larger sand collector sizes) sand column with higher porosity. As shown in Fig. 3, fitted results revealed that S_{max}, k_{att} and k_{str} increased with decreasing sand particle size, indicating more retention locations in fine media. k_{str} values were

Fig. 1. Bacterial cell-sand interaction energy profile as a function of separation distance in different background solution.
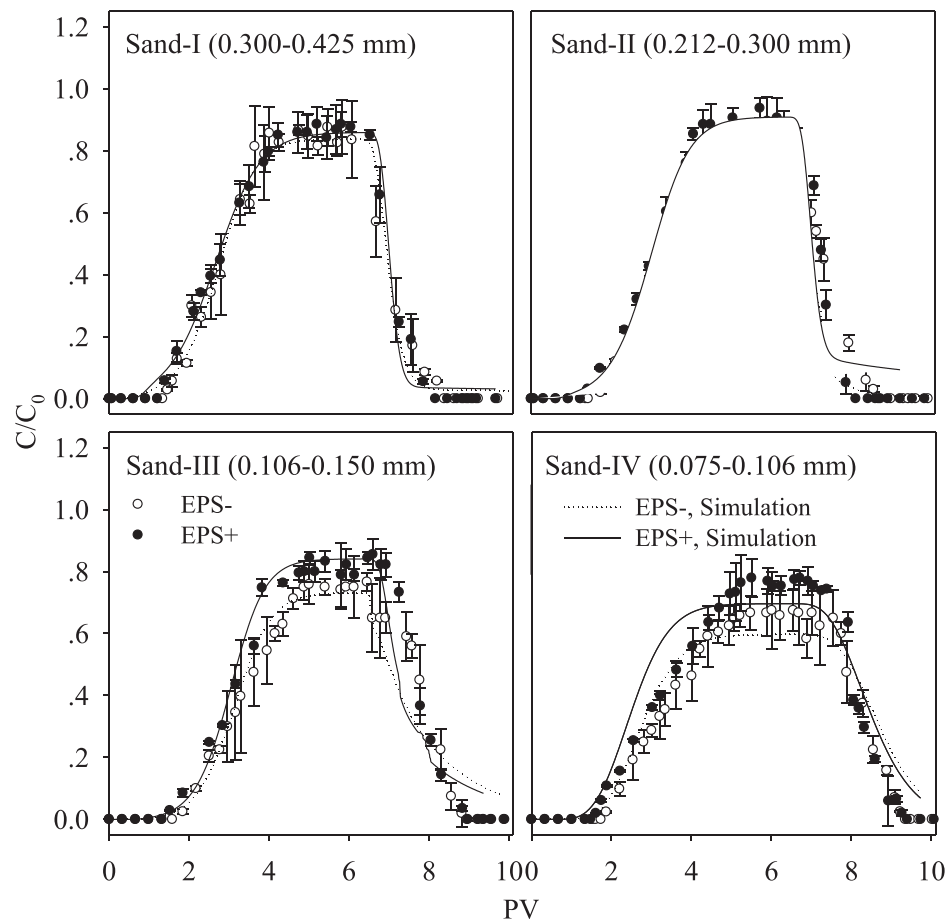
Fig. 2. Observed (symbols) and simulated (lines) breakthrough curves for *E. coli* through quartz sand columns within four porous media. C_0 is the concentration of bacterial suspension injected in paced columns. The R^2 value of simulation performed by Hydrus-1D was 0.985, 0.957, 0.887 and 0.950 for I, II, III and IV sand (EPS-condition), respectively; 0.951, 0.954, 0.943 and 0.896 for I, II, III and IV sand (EPS+ condition), respectively.

higher than k_{att} values in sand-II, sand-III and sand-IV, while the opposite trend was observed in sand-I. Furthermore, k_{str} values were 6.5%, 21.8% and 33.1% greater than k_{att} values in II, III and IV porous media, respectively. The results suggested that straining was the dominant mechanism for bacterial transport in finer-textured media. Consistent with simulated results, bacterial retention rates in 0–5 cm depth from bacteria injection points significantly increased with decreasing collector size, which were 14.8% for sand-II, 20.0% for sand-III and 26.9% for sand-IV, respectively (Fig. 4). It indicates that bacteria may be funneled to small and tortuous pore space and restricted the regions adjacent to sand-sand contact points (straining locations) (Bradford et al., 2007; Hoek and Agarwal, 2006). Enhanced bacterial deposition in packed columns was expected to occur at those straining locations due to pore size limitations, lower hydrodynamic forces and decreased repulsive DLVO energy (Hoek and Agarwal, 2006; Shen et al., 2018). In line with several researches (Bai et al., 2016; Bradford et al., 2006; Gargiulo et al., 2007; Syngouna and Chrysikopoulos, 2011), the result suggested that straining played a more important role in finer porous media.

4. Discussion

4.1. EPS facilitating bacterial transport by altering cell surface properties

Both experiment and simulation result clearly demonstrated that EPS facilitated the transport of bacteria in packed columns, consistent with other previous studies (Kuznar and Elimelech, 2005; Kim et al., 2009; Feriancikova et al., 2013). This can be partially explained by following factors changed with the presence of EPS.

4.1.1. Bacterial surface hydrophobicity

Bacteria suspended in EPS+ solution were significantly hydrophobic (Table 3), and exhibited greater mobility. It is well documented that surface hydrophobicity can influence bacterial transport in packed sand columns (Kim et al., 2009, 2010; Bai et al., 2016). For instance, study showed that bacteria retention clearly decreased with increasing cell hydrophobicity within either finer (0.25–0.54 mm) or coarser (0.58–1.48 mm) sand column (Bai et al., 2016). However, contradictory results exist with respect to the effects of EPS on bacterial hydrophobicity. For example, Johanson et al. (2012) showed that mutant strain with no enterococcal surface proteins secretion were more hydrophilic than wild strain, while Kim et al. (2009) reported that proteinase K treated bacterial cells were more hydrophilic than those of untreated ones. The inconsistent effects of EPS on bacterial surface hydrophobicity would eventually lead to different levels of cell-cell and/or cell-surface interactions and thereby transport performance. Soluble EPS or loosely bonded EPS may serve as surfactants, where their modification capacity on bacterial surface hydrophobicity was strongly concentration dependent (Hua et al., 2003; Kaczorek and Olszanowski, 2011; Lin et al., 2017; Ma et al., 2018). For example, an increase in the concentration of biosurfactants (that originated from EPS sources) from 0 mg L^{-1} to 100 mg L^{-1} likely increased bacterial surface hydrophobicity, while further increasing the concentration from 200 mg L^{-1} to 400 mg L^{-1} resulted in a reduced cell hydrophobicity (Ma et al., 2018). It indicates that variations in presented external EPS concentration would eventually lead to different or even opposite consequences on bacterial surface characteristics under certain circumstances.
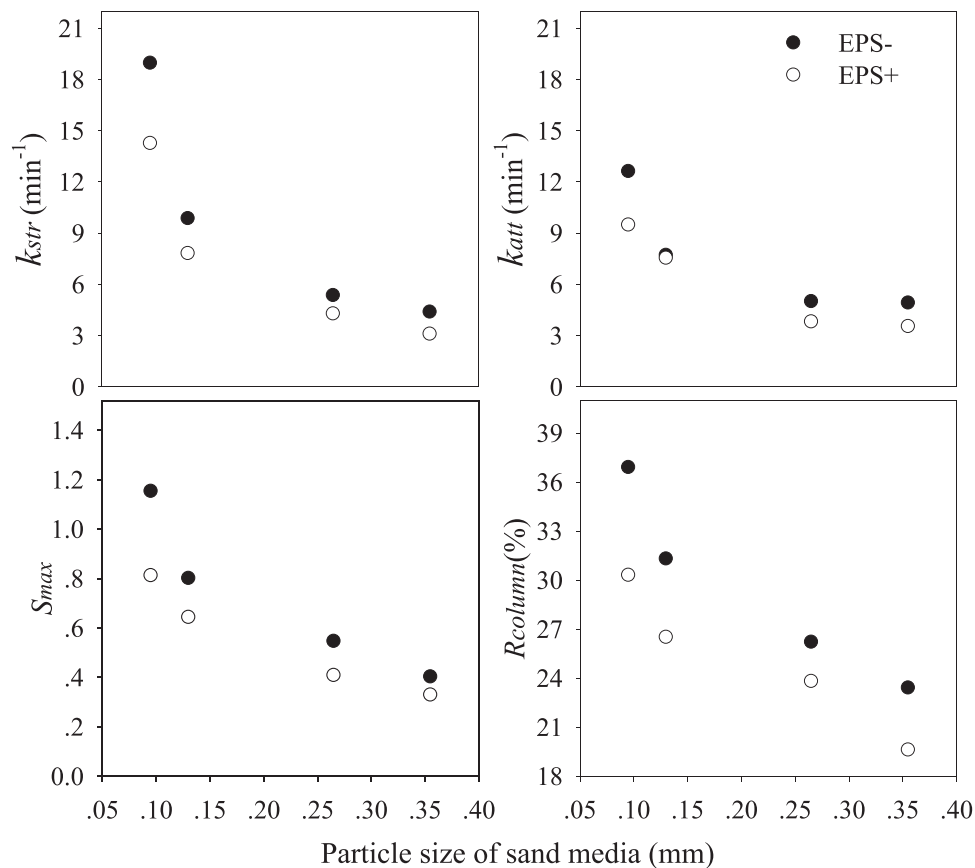
Fig. 3. Simulated parameters (k_{str}, k_{att} and S_{max}) of bacteria breakthrough curves by Hydrus-1D and percentage of deposited bacteria in column (R_{column}). These symbols k_{str}, k_{att} and S_{max} indicate straining coefficient, attachment coefficient and the maximum solid-phase concentration of bacteria on sorption sites, respectively.
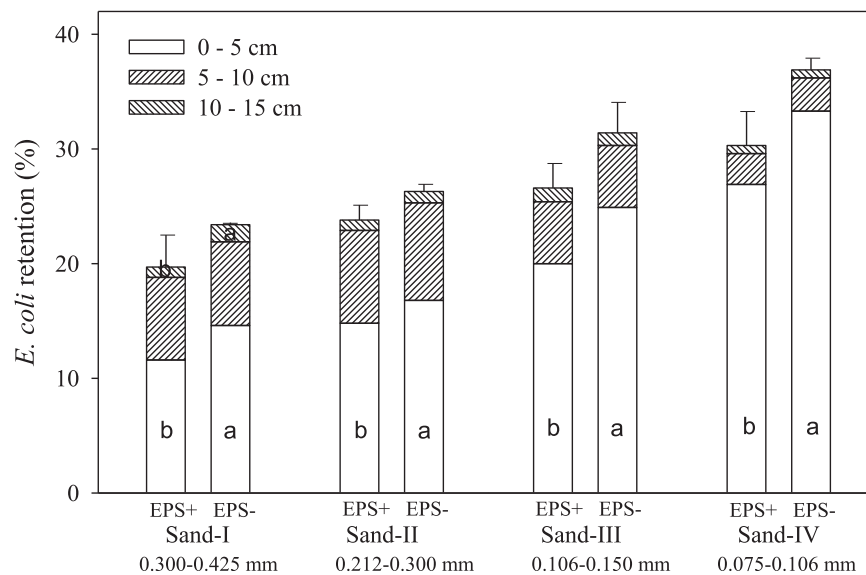

Fig. 4. Retention profiles for *E. coli* through quartz sand columns with four different particle sizes. Different letters indicate significantly different means within the same depth from the injection point (LSD-test, n = 3, p ≤ 0.05).

4.1.2. Bacterial surface charge

EPS promoted electrostatic repulsion between bacterium and quartz sand, as indicated by increased negative zeta potential of bacteria in EPS+ groups (n = 4, p < 0.05, Table 3). Contrary to this observation, the presence of EPS on bacterial cell surface resulted in significantly higher zeta potential values at 0.01–10 mM IS (Kim et al., 2009) and

20 mM IS (Johanson et al., 2012), respectively. Additionally, other researches showed that EPS did not significantly alter zeta potential of a bacterial cell at 10–100 mM IS (Kim et al., 2009), 1–5 mM IS (Johanson et al., 2014) and 1–100 mM IS (Feriancikova et al., 2013), respectively. Similar with our results, Jacobs et al. (2007) suggested that lower zeta potential of bacteria inhibited cell adhesion behavior within quartz sand

media.

In addition to surface hydrophobicity, the surface charge of colloid and bio-colloid was also a function of macromolecule concentration (e. g., dissolved organic matters and/or surfactants) (Bai et al., 2017; Ma et al., 2018; Yan et al., 2019; Carstens et al., 2021). For example, bacterial zeta potential decreased with increasing surfactant concentration in the range of 0–100 mg L^{-1}, while sharply increased when the concentration enhanced from 100 mg L^{-1} to 200 mg L^{-1} (Ma et al., 2018). Furthermore, Liu et al. (2021) suggested the existence of a critical value of colloidal zeta potential squared (e.g., >80 mV^2) within membrane fouling processes, and a slight increase of which could lead to substantially enhanced energy barrier and subsequently dropped colloidal attachment efficiency. Our results revealed that the presence of external EPS resulted in a small yet significant change of zeta potential value of the quartz sands, which was in consistent with Yan et al.'s report where relatively stable zeta potential value of quartz sand was found upon all tested addition of 0–16 mg L^{-1} bovine serum albumin (2019). In addition, EPS recovery test showed a high recovery ratio of 99.5%, indicating barely EPS adsorption onto the quartz sands. Nevertheless, studies also showed that the presence of macromolecules would alternate zeta potential values of colloids and/or bio-colloids, as well as those of quartz sands, which are important measures for numerous electrostatic interactions and subsequent colloids/bio-colloids transport processes (He et al., 2019; Rong et al., 2020).

4.1.3. Steric stabilization

Steric repulsion of extracellular structure, e.g., capsule (Wang et al., 2013), EPS (Zhu et al., 2012), filament and pili (Francius et al., 2016), also influenced bacterial adhesion behavior by hindering the approaching distance of cell to substrate surface, even under favorable attachment circumstances (Kim et al., 2009, 2010). For example, lower adhesion force, measured with tip-immobilization bacteria approached to and retracted from mineral surface by atomic force microscopy, was reported by Zhu et al. (2012). Studies have shown enhanced bacterial transport at the presence of organic matters, such as plant root exudates (16–130 mg L^{-1}) (Jimenez-Sanchez et al., 2015), humic acid (1–180 mg L^{-1}) (Yang et al., 2012; Madumathi, 2017), rhamnolipid (0–400 mg L^{-1}) (Ma et al., 2018), poly (amido amine) (10 μg L^{-1} to 10 mg L^{-1}) (He et al., 2019), bovine serum albumin (1–10 mg L^{-1}) (Rong et al., 2020) and cysteine (100 ppm) (Yang et al., 2014). In addition to the functions of alternating bacterial surface properties, another widely accepted mechanism is that organic matters would compete the adsorption sites of colloidal or bio-colloidal surfaces and thereby inhibit bacterial cell attachment. As a consequence, it likely facilitates bacterial transport through porous media. Nevertheless, such promotion on bacterial transport could be otherwise weakened or even not observed at relatively low concentration (~16 mg L^{-1}) of dissolved organic matters (Jimenez-Sanchez et al., 2015). It indicates that the dosage of organic matters, as well as EPS concentration, are important intergradient impacting bacterial transport.

4.2. The contradictory effect of EPS on bacterial transport observed in publications

It should be noted that enhanced (Liu et al., 2007) or hindered (Kim et al., 2009) cell deposition occurred in the presence of EPS at similar IS. Those opposite trends may be related to different treated methods applied to bacteria (Table 1). For example, three *Pseudomonas aeruginosa* strains with different EPS secretion capacity were involved by Liu et al. (2007), while proteinase treated cells (to remove extracellular macromolecules) were selected by Kim et al. (2009). Another treated method for evaluating the impact of EPS on bacterial deposition was applied by Long et al. (2009) and Tong et al. (2010), where cation exchange resin treatment was used to remove EPS on four bacteria surfaces. Besides, other factors may also contribute to the different transport behaviors. For example, quartz sand (0.417–0.600 mm, d_{50} = 0.510 mm) and

spherical glass beads (d = ~0.55 mm) were selected as the porous media by Tong et al. (2010) and Liu et al. (2007), respectively. However, this study involved four sand media with different collector sizes ranging from 0.075 to 0.425 mm (Table 2). Also, flow rate of Tong et al. (2010) (1.0 mL min^{-1} vs. 2.93 mL min^{-1}) and Darcy velocity of Liu et al. (2007) (0.181–0.201 cm min^{-1} vs. 0.66 cm min^{-1}) were higher compared with those used in our transport experiments. It suggested that greater hydrodynamic shear stress existed in their packed column, which could decrease the attachment of bacterial cells onto silica surface. In this study, the extrinsic EPS (200 mg L^{-1}), to some extent, increased shear stress (from 0.273 to 0.276 Pa) and viscosity (from 0.911 to 0.980 mPa s) of background solution within transport columns. Therefore, the EPS induced changes in hydrodynamic characteristics of background solutions might not be neglected, especially in experimental conditions with relatively high EPS concentration. Interestingly, even in the same abiotic experimental conditions, variations of bacterial strains and macromolecule species may have different effects on transport. For example, Feriancikova et al. (2013) showed that outer membrane protein *TolC* facilitated *E. coli* transport (IS ≥ 20 mM), while Johanson et al. (2012) reported that *enterococcal* surface protein hindered *E. faecium* mobility.

Furthermore, EPS are susceptible to many factors that govern bacterial metabolism, of which composition and amount are thereby continuously dynamic. Bacterial species and growth phases can be listed as two dominant biological factors. For example, Sheng and Yu (2006) reported that EPS concentration decreased with cultivation time during exponential growth phase, while kept constant in stationary stage. Furthermore, Harimawan and Ting (2016) analyzed EPS composition of by *Pseudomonas aeruginosa* and *Bacillus subtilis*. The results verified that EPS secreted by different bacterial species and even by the same strain under various growth phases was not compositionally identical. Accordingly, a variety of bacterial growth stage (Gargiulo et al., 2007; Saini et al., 2011) and species (Bai et al., 2016; Johanson et al., 2014) led to different transport and deposition in packed sand columns. Consequently, further investigation is still necessary to clarify these discrepancies.

5. Conclusion

Both experiment and simulation results showed a clear drop in the retention of bacterial population in the presence of EPS, reflecting facilitated bacterial transport by EPS. This can be partially explained by the facts that the presence of EPS significantly enhanced bacterial cell hydrophilicity and electrostatic repulsion between bacteria and quartz sand. Besides, steric repulsion of EPS can hinder the approaching distance of bacteria to sand and thereby bacterial attachment onto the substrate surface. This study was also the first to show that the EPS could decrease straining. Bacterial retention increased with decreasing sand collector size, indicating that straining played an important role in fine-textured media. These findings provide new insight into the functional effects of extrinsic EPS on bacterial transport behavior in the saturated soil environment, e.g., aquifers. In addition, it may also have potential implications for bioremediation processes and/or other bacterial activities in soils or aquifers where bacteria with novel metabolic properties are expected to actively respond to contaminant and/or other gradients. Nevertheless, due to the conflicting effect of EPS on bacterial mobility in porous media, further study is still needed for better elucidating such interactions, with treated methods and precise control of EPS (e.g., concentration and composition) being key factors taken into consideration.

CRediT authorship contribution statement

MD: Experiment, Data analysis, Manuscript writing and revision. **LW:** Experiment and data analysis. **AE:** Manuscript writing and revision. **GWC:** Manuscript writing and revision. **SYS:** Experiment. **KZ:**

Manuscript revision. **CYS**: Manuscript revision. **BL**: Manuscript revision. **GW**: Conceptualization, Data analysis, Manuscript writing and revision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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