Multiscale modeling of chemotaxis in homogeneous porous media

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[1] We present a predictive, multiscale modeling framework for chemotaxis in porous media. This model results from volume averaging the governing equations for bacterial transport at the microscale and is expressed in terms of effective medium coefficients that are predicted from the solution of the associated closure problems. As a result, the averaged chemotactic velocity is an explicit function of the attractant concentration field and diffusivity, rather than an empirical effective chemotactic sensitivity coefficient. The model was validated by comparing the transverse bacterial concentration profiles with experimental measurements for Escherichia coli HCB1 in a T-sensor. The averaged chemotactic velocity predicted by the model was found to be within the range of values reported in the literature. Reasonable agreement (approximately 10% mean absolute error) between theory and experiments was found for several flow rates. In order to assess the potential for decreasing the computational demands of the model, the macroscale domain was divided into subdomains for the coupling of bacterial transport to that of the attractant. Sensitivity analysis was performed regarding the number of subdomains chosen, and the results indicate that bacterial transport (as measured by concentration profiles) was not highly affected by this choice. Overall, these results suggest that the predictive, multiscale modeling framework is reliable for modeling chemotaxis in porous media when chemotactic transport is significant compared to convective transport.


1. Introduction

[2] Chemotaxis is the directed movement of microorganisms toward or away from a chemical gradient. This phenomenon was first observed by Pfeffer [1884], and it is now well understood within a homogeneous solution [Adler, 1969; Berg and Brown, 1972; Tsang et al., 1973; Adler, 1975; Lauffenburger, 1991; Tindall et al., 2008a, 2008b]. Studies have shown that many bacterial strains are attracted to (and subsequently degrade) numerous contaminants commonly found in subsurface environments [see Pandey and Jain, 2002; Harms and Wick, 2006; Ford and Harvey, 2007]. Thus, engineered applications of chemotactic bacteria (bioaugmentation) for subsurface bioremediation have been suggested as potential alternatives to traditional remediation methods (i.e., pump and treat) [see Ford and Harvey, 2007]. However, there exists a considerable amount of uncertainty regarding the role of chemotaxis in subsurface environments at the field scale [see Wang et al., 2008].

[3] In an effort to remedy these uncertainties, numerous laboratory investigations have focused solely on bacterial chemotaxis in porous media [e.g., Reynolds et al., 1989; Sharma et al., 1993; Barton and Ford, 1995; Frymier, 1997; Witt et al., 1999; Lanning and Ford, 2002; Pedit et al., 2002; Sherwood et al., 2003; Zaval’skii and Voloshin, 2003; Olson et al., 2004; Roush et al., 2006; Wang et al., 2008; Long and Ford, 2009; Wang and Ford, 2009, 2010]. In addition to controlled experiments, there has been great interest in quantifying effective medium coefficients required for Darcy scale (millimeter to centimeter) models [e.g., Barton and Ford, 1995, 1996; Lanning and Ford, 2002; Pedit et al., 2002; Olson et al., 2004; Roush et al., 2006; Wang et al., 2008; Long and Ford, 2009; Wang and Ford, 2009, 2010; Valdés-Parada et al., 2009]. In this context, effective medium coefficients refer to average parameters that capture the essential details of the processes taking place at the microscale. These coefficients are commonly quantified by adopting an empirical definition (e.g., scaling the bacterial random motility by the porous medium porosity and tortuosity) and subsequently fitting one (or more) of these effective parameters to measured attractant and bacterial concentration data [e.g., Barton and Ford, 1995, 1996; Lanning and Ford, 2002; Pedit et al., 2002; Olson et al., 2004; Roush et al., 2006; Wang et al., 2008; Long and Ford, 2009; Wang and Ford, 2009, 2010]. Although fundamentally sound, this approach has some drawbacks from a modeling perspective. These include the following: (1) the empirical definitions often contain ambiguously defined parameters such as the porous...
medium tortuosity, \(\tau\), (2) the resulting best fit effective medium coefficients only apply to the specific conditions of the controlled experiments, and (3) the process is inherently a posteriori, requiring detailed attractant and bacterial concentration data, which is often expensive and difficult to measure. As an example, Long and Ford [2009] combined best fit values for attractant and bacterial dispersion with reported data from the literature to quantify effective medium coefficients for chemotaxis, which resulted in concentration profiles that did not agree with their measured data. They resorted to arbitrarily increasing the effective chemotactic sensitivity coefficient, \(\chi_{\text{eff}}\), by 2 orders of magnitude in order to qualitatively reproduce the bacterial concentration peaks observed in their experiments [see Long and Ford, 2009, Figure 3]. Additional modeling approaches that are not dependent upon fitting procedures or arbitrary adjustment of coefficients should be explored.

[1] An alternative approach is to formally upscale the governing pore-scale equations to produce macroscale models that contain rigorously defined effective medium coefficients [Bear, 1988; Whitaker, 1999; Pinder and Gray, 2008]. The upscaling procedure connects the essential pore-scale physics to appropriately defined effective medium coefficients and constitutive relationships, while simultaneously reducing the number of degrees of freedom required for solution. One such upscaling technique is the method of volume averaging [Whitaker, 1999]. An attractive feature of this approach is that it is predictive, only requiring representative information about the porous medium microstructure for estimating the effective medium coefficients. Recently, Valdés-Parada et al. [2009] developed a macroscale model for bacterial chemotaxis in porous media using this upscaling technique, resulting in a model containing two effective medium coefficients, namely, the total (fluid and chemotactic) velocity vector, \(\mathbf{v}_{\text{eff}}\), and the total motility tensor, \(\mathbf{\mu}_{\text{eff}}\) (similar to the total dispersion tensor for a passive solute). Valdés-Parada et al. [2009] demonstrated that chemotaxis could be a significant transport mechanism at flow rates commonly encountered in natural subsurface environments. Despite this finding, the model requires further validation, especially in regard to its ability to reproduce experimental observations.

[2] The primary goal of this work is to demonstrate an application of the upscaled model developed by Valdés-Parada et al. [2009] and to validate the model by comparison with experimental observations. To this end, we focus our analysis on the transverse chemotaxis experiments reported by Long and Ford [2009]. In these experiments, transverse concentration profiles for chemotactic bacteria (Escherichia coli HCB1) were measured at three locations within a homogeneous, periodic porous T-sensor for three different mean pore water velocities. Figure 1 illustrates the experimental and multiscale system addressed in this work. We also highlight an equation for the average chemotactic velocity that is not a function of \(\chi_{\text{eff}}\) and provide an inequality that estimates the conditions under which chemotactic transport is negligible with respect to convective transport.

[3] The paper is organized as follows: In section 2, we briefly summarize the experiments conducted by Long and Ford [2009]. Next, we describe the essential details of the upscaling procedure and the resulting macroscale chemotaxis model developed by Valdés-Parada et al. [2009]. Finally, we explain the multiscale numerical simulations that were conducted to model transverse chemotactic bacteria. These include three-dimensional (3-D) computations for the estimation of the effective medium coefficients and vertically averaged, two-dimensional (2-D) computations for macroscale chemotaxis within the main channel of the T-sensor. In addition, we explain how the attractant computations were coupled to those for bacteria by dividing the macroscale solution domain for the attractant into a specified number of subdomains. In section 3, we first present the predicted transverse chemotactic velocity for each experiment, followed by the comparison between the measured and predicted transverse concentration profiles. We conclude section 3 with a sensitivity analysis regarding the influence of the number of subdomains on the predicted concentration profiles. Finally, we discuss our general conclusions in section 4.

2. Methodology

2.1. Experimental Data

[7] In this work, we focus on the bacterial control (i.e., without a chemical attractant) and chemotaxis experiments that were conducted by Long and Ford [2009]. These experiments were performed in a microfluidic porous T-sensor (see Figure 1) with a main channel length of 8.3 cm, a width of 0.6 cm, and a depth of 13 \(\mu\)m. The pore structure consisted of staggered cylinders with a radius of 100 \(\mu\)m (separated by pore throats of 46 \(\mu\)m) and a porosity of 0.40. In the bacterial control experiments a bacteria suspension of E. coli HCB1 and phosphate buffer were injected into the T-sensor. In the chemotaxis experiments a bacteria suspension of E. coli HCB1 and a 3 \(\times\) 10^{-4} M \(\alpha\)-methylaspartate solution (the attractant) were injected into the T-sensor. In both sets of experiments the solutions were injected through the inlets of the T-sensor as illustrated in Figure 1. Each solution was prepared with a 10% random motility buffer as the solvent (see Long and Ford [2009] for details). Measurements were taken in the main channel of the T-sensor for mean pore water velocities of 5, 10, and 20 m d^{-1}. After steady state was achieved for each mean pore water velocity, images were recorded across three transverse profiles (consisting of 25 pores) at 2, 4, and 6 cm from the head of the main channel. Ten bright-field snapshots were taken within a 50 \(\times\) 50 \(\mu\)m^{2} region within each pore, and the number of bacteria was counted using an ImageJ (National Institutes of Health) batch script. The total bacteria from the 10 snapshots were used to normalize the bacteria concentration within each pore. Thus, the macroscale experimental transverse concentration profiles consist of concentration estimates within each of the 25 pores along each T-sensor transect. The molecular diffusion coefficient for the attractant is \(D_A = 8.6 \times 10^{-10} \text{ m}^2 \text{ s}^{-1}\), and the random motility coefficient (equivalent to molecular diffusion) of the bacteria is \(D_B = 3.0 \times 10^{-10} \text{ m}^2 \text{ s}^{-1}\) [Lewus, 2006]. On the basis of previous studies [Mesibov et al., 1973; Lewus, 2000; Lanning et al., 2008], the chemotactic sensitivity coefficient and dissociation constant were taken as \(\chi_0 = 2.4 \times 10^{-9} \text{ m}^2 \text{ s}^{-1}\) and \(K_d = 0.125 \text{ mol m}^{-3}\), respectively.
For the system under consideration, the governing pore-scale equations consist of (1) momentum transport (i.e., continuity and Stokes equations) for the fluid phase, (2) mass transport for the attractant, \( c_A \), and (3) mass transport for the bacteria, \( c_B \). For the sake of brevity, we only show the governing equations for bacteria here; further details are given by Valdés-Parada et al. [2009]. It is assumed that bacterial transport is driven by convection, diffusion, and chemotaxis (i.e., the contributions of bacterial growth and death, as well as chemical reactions, are assumed to be negligible). The governing equation, boundary conditions (B.C.), and initial condition (I.C.) for bacterial transport are expressed as

\[
\frac{\partial c_B}{\partial t} + \nabla \cdot (v_f c_B) + \nabla \cdot (v_c c_B) = \nabla \cdot (D_B \nabla c_B), \tag{1a}
\]

in the \( \gamma \) phase,

B.C. 1 \( \mathbf{n}_{\gamma} \cdot (D_B \nabla c_B) = 0 \) at \( A_{\gamma \kappa} \), \tag{1b} \\
B.C. 2 \( \mathbf{n}_{\gamma \kappa} \cdot v_c = 0 \) at \( A_{\gamma \kappa} \), \tag{1c} \\
B.C. 3 \( c_B = \mathcal{F}_B(r, t) \) at \( A_{\gamma \varepsilon} \), \tag{1d} \\
I.C. \( c_B = \mathcal{G}_B(r) \) at \( t = 0 \). \tag{1e} 

In equations (1a)-(1e), \( v_f \) and \( v_c \) are the fluid and chemotactic velocity vectors, respectively. The vector \( \mathbf{n}_{\gamma \kappa} \) represents the unit normal vector directed from the fluid (\( \gamma \) phase) to the solids (\( \kappa \) phase). The fluid-solid interface and the entrance and exit surfaces for the system are represented by \( A_{\gamma \kappa} \) and \( A_{\gamma \varepsilon} \), respectively. The functions \( \mathcal{F}_B(r) \) and \( \mathcal{G}_B(r) \)
and \( \mathbf{F}_{B}(\mathbf{r}, t) \) (where \( \mathbf{r} \) is the position vector) represent the unknown initial and boundary conditions for bacterial transport. Equation (1b) states that the solutes are impermeable to the bacteria, whereas equation (1c) indicates that the chemotactic velocity is zero at the fluid-solid interface. At this same boundary, the no-slip condition applies for the fluid velocity, \( \mathbf{v}_f \).

\[ \text{[8] The constitutive equation for } \mathbf{v}_c \text{ is expressed as } [\text{Riviero et al., 1989; Chen et al., 1998}] \]

\[
\mathbf{v}_c = \frac{\chi_0 K_d}{3(K_d + c_{B,t})} \nabla c_{A,t}, \tag{2}
\]

where \( \chi_0 \) is the chemotactic sensitivity coefficient and \( K_d \) is the dissociation coefficient that represents the tendency of the bacteria to sense attractant gradients. Note that equation (2) couples the bacterial transport equations to those of the attractant, and that the chemotactic velocity is not solenoidal (i.e., \( \nabla \cdot \mathbf{v}_c \neq 0 \)).

\[ \text{[10] Solution of the equations describing transport processes at the pore scale is generally not feasible for large, complex porous systems typically encountered at the laboratory and field scales. For such systems, it is often necessary to use a macroscale (also called the Darcy scale) form of the equations that applies to a representative elementary volume [Bear, 1988]. To this end, we used the method of volume averaging [Whitaker, 1999] to arrive at a macroscale model for chemotaxis.} \]

\[ \text{[11] The volume-averaging procedure transforms the pore-scale continuum equations to effective medium equations within a supporting averaging region, } V', \text{ as illustrated in Figure 1. Within } V', \text{ the governing equations for both } c_{A,t} \text{ and } c_{B,t} \text{ are spatially smooth, which results in an unclosed macroscale equation that is a function of average quantities and corresponding deviations. The process of eliminating the deviations from the unclosed macroscopic equations is known as closure. The first step in the closure procedure involves developing the boundary value problem (BVP) for the deviations by subtracting the unclosed macroscale equation from the pore-scale equation (equation (1a)). Second, a reasonable set of assumptions and length-scale constraints, } \ell_{c} \ll r_0 \ll L \text{ (i.e., scaling laws [see Wood, 2009]), are imposed on the resulting deviation equations, which simplify the BVP and greatly reduce the number of degrees of freedom required for solution. Here } \ell_{c} \text{ is the length of a pore throat, } r_0 \text{ is the radius of the averaging volume, and } L \text{ is the width of the T-sensor (see Figure 1). Finally, the BVP is solved numerically in a representative region of the porous medium in order to determine the effective medium coefficients. The closure problems for } c_{A,t} \text{ and } c_{B,t} \text{ are provided in Appendix A, and further details regarding the upscaling procedure are given by Valdés-Parada et al. [2009].} \]

\[ \text{[12] The resulting macroscale transport model for bacteria is expressed as} \]

\[
\frac{\partial (c_{B,t})^\gamma}{\partial t} + \nabla \cdot (\mathbf{v}_{eff} (c_{B,t})^\gamma) = \nabla \cdot (\mathbf{m}_{eff} \cdot \nabla (c_{B,t})^\gamma), \tag{3}
\]

where \( \langle c_{B,t} \rangle^\gamma \) is the intrinsic averaged bacterial concentration, \( \mathbf{m}_{eff} \) is the total motility tensor, and \( \mathbf{v}_{eff} \) is the total velocity vector. In equation (3), \( \mathbf{m}_{eff} \) is the sum of the effective motility, the hydrodynamic dispersion, and the chemotactic dispersion tensors (see equation (A9)). In addition, \( \mathbf{v}_{eff} \) is the sum of the intrinsic averaged fluid velocity, \( \langle \mathbf{v}_f \rangle^\gamma \), and the chemotactic velocity, \( \langle \mathbf{v}_c \rangle^\gamma \), as well as two additional terms that are functions of the bacterial closure variables (see equation (A6)).

\[ \text{[13] Applying the method of volume averaging to the governing equations for the attractant results in the well-known convection-dispersion equation [see Whitaker, 1999, chapter 3]:} \]

\[
\frac{\partial (c_{A,t})^\gamma}{\partial t} + \nabla \cdot (\langle \mathbf{v}_f \rangle^\gamma (c_{A,t})^\gamma) = \nabla \cdot (\mathbf{D}_{A,t eff}^\gamma \cdot \nabla (c_{A,t})^\gamma), \tag{4}
\]

where \( \mathbf{D}_{A,t eff}^\gamma \) is the total dispersion tensor that is the sum of the effective diffusivity, \( \mathbf{D}_{A,t eff} \) and the hydrodynamic dispersion, \( \mathbf{D}_{A,t} \) tensors (see equations (A10) and (A11), respectively).

\[ \text{[14] Equations (3) and (4) are coupled through the average chemotactic velocity, which can be expressed (assuming } K_d \text{ and } \chi_0 \text{ are constant, while } K_d + \langle c_{A,t} \rangle^\gamma \gg \langle c_{B,t} \rangle^\gamma) \text{ in terms of the average concentration by [Valdés-Parada et al., 2009, Appendix A]} \]

\[
\langle \mathbf{v}_c \rangle^\gamma = \frac{\chi_0 K_d}{3(K_d + \langle c_{A,t} \rangle^\gamma)} \mathbf{D}_{A,t eff}^\gamma \cdot \nabla (c_{A,t})^\gamma. \tag{5}
\]

Note that equation (5) does not contain an effective chemotactic sensitivity coefficient, \( \chi_{eff} \), which is common in many models [Lanning and Ford, 2002; Sherwood et al., 2003; Olson et al., 2004; Roush et al., 2006; Long and Ford, 2009; Wang and Ford, 2009, 2010]. Instead, \( \langle \mathbf{v}_c \rangle^\gamma \) is scaled by \( \mathbf{D}_{A,t eff}^\gamma / \mathbf{D}_{A,t}^\gamma \), which is a convenient feature since these coefficients are already required for the solution of the macroscale attractant model.

\[ \text{[15] Equations (3) and (4) constitute the upscaled macroscale model for chemotactic transport in porous media when convection and diffusion are the dominant transport mechanisms. The macroscale equation for the bacteria (equation (3)), however, contains terms that are not typically found in macroscale chemotaxis models. For example, } \mathbf{m}_{eff} \text{ contains a chemotactic dispersion tensor that accounts for spreading due to local chemotactic velocity variations at the pore scale. Moreover, } \mathbf{v}_{eff} \text{ incorporates two new terms in addition to the average fluid and chemotactic velocities. The importance of the additional terms in our model is discussed further in section 3.} \]

\[ \text{[16] Before concluding this section it is important to point out that the effective medium coefficients in equations (3) and (4) are obtained through the solution of the corresponding closure problems within a representative sample of the porous medium (i.e., a unit cell). It should be noted that detailed knowledge of the microscale structure of the porous medium is not necessarily required to define the unit cell. A variety of simple unit cells have been used to successfully compute effective medium coefficients for random porous media in which the microscale geometric details were unknown [e.g., Eidsath et al., 1983; Quintard and Whitaker, 1994; Whitaker, 1999; Wood, 2007]. The boundary conditions at the entrances and exits of the unit} \]
cell are frequently replaced by periodic boundary conditions, with the idea that the boundary data do not dominate the solution within a unit cell [Eames and Bush, 1999; Renard and de Marsily, 1997]. This does not imply that the actual geometry of the porous medium is periodic. This assumption only implies that a periodic model of the porous medium provides sufficient representation of the actual pore geometry, and this constitutes a scaling law in the sense of Wood [2009]. The ability to directly evaluate the effective medium coefficients within a periodic unit cell gives rise to the predictive, multiscale numerical framework discussed in section 2.3. For the system under consideration the periodic 3-D unit cell is taken directly from the T-sensor, which is illustrated in Figure 2. In this case the periodicity assumption is fully justified since the pore geometry of the T-sensor is, indeed, periodic.

2.3. Numerical Simulations

[17] A series of numerical simulations were performed using the commercial finite element solver COMSOL Multiphysics™ (version 3.5a). The default element types and solvers were used in all simulations. In addition, a conventional mesh-refining procedure was conducted in order to verify that the results were independent of the number of computational elements. All closure problems were solved in the 3-D unit cell illustrated in Figure 2. Periodic boundary conditions were applied at the entrances and exits of the unit cell. The vertically averaged macroscale models were solved in a 2-D representation of the main channel of the T-sensor (see Figure 3). At \( x = 0 \) cm, the half of the T-sensor inlet (i.e., \( 0 \text{ cm} \leq y \leq 0.3 \text{ cm} \)) in which the attractant was injected was set to a constant concentration equal to 0.3 mol m\(^{-3}\), whereas the other half (i.e., \( 0.3 \text{ cm} < y \leq 0.6 \text{ cm} \)) was set to a zero concentration. Similarly, at \( x = 0 \) cm, the half of the T-sensor inlet in which the bacteria were injected (i.e., \( 0.3 \text{ cm} < y \leq 0.6 \text{ cm} \)) was set to a normalized constant concentration, \( C_B \), equal to 1 and the other half (i.e., \( 0 \text{ cm} < y \leq 0.3 \text{ cm} \)) was set to a zero concentration. For both the attractant and bacteria the dispersive flux was set equal to zero at the T-sensor outlet boundary. The model input parameters (i.e., \( D_A \), \( D_B \), \( K_D \), and \( \chi_0 \)) were the same as those used by Long and Ford [2009] (see section 2.1).

[18] The predictive multiscale numerical algorithm was implemented in the MATLAB module for COMSOL Multiphysics. The algorithm consists of the following steps:

1. Solve the momentum transport equations (continuity and Stokes equations) within the 3-D unit cell to obtain the pore-scale fluid velocity field associated with the given mean pore water velocity (i.e., 5, 10, and 20 m d\(^{-1}\)).
2. Solve problem 1 (equations (A2a)–(A2d)) in the 3-D unit cell (for both the \( x \) and \( y \) components) using the velocity field from step 1.
3. Compute \( D_{A,x} \) (equations (A10) and (A11)) using the solutions obtained in step 2.
4. Use \( D_{A,x} \), and the given mean pore water velocity to solve the steady state, vertically averaged 2-D macroscale model for the attractant (equation (4)) in the main channel of the T-sensor.
5. Compute average values of \( \langle c_A \rangle \) and \( \nabla \langle c_A \rangle \) for a specified number of subdomains within the T-sensor.

![Figure 2](image1.png)

**Figure 2.** Periodic unit cell in which the closure problems for the attractant and bacteria were solved.

![Figure 3](image2.png)

**Figure 3.** Illustration of the 2-D representation of the T-sensor and division into 25 subdomains.
expected that taking average values of $\langle c_{A^r} \rangle$ and $\nabla \langle c_{A^r} \rangle$ within subdomains larger than a unit cell will not significantly influence the overall solution for the bacteria. In order to test this hypothesis, we divided the T-sensor into 100 (10 in the $x$ direction and 10 in the $y$ direction), 25 (5 in the $x$ direction and 5 in the $y$ direction), and 1 (the whole T-sensor) subdomains and present a sensitivity analysis in section 3.3. Steps 6 and 7 provide $\langle v_{c^r} \rangle$, $\mu_{eff}$, and the last two terms in $v_{eff}$ (see equation (A6)) for each subdomain in the T-sensor. Finally, step 8 provides the spatially dependent effective medium coefficients for each mesh node in the T-sensor, which are subsequently used to solve the macroscale bacterial chemotaxis model in step 9. The resulting bacterial concentration field for $\langle v_{c^r} \rangle = 5$ m d$^{-1}$ is illustrated in Figure 5. Clearly, the majority of the transverse migration of the bacteria occurs between $x = 0$ and $x = 2$ cm. Similar behavior was observed for the other experimental flow rates.

3. Results

3.1. Predicted Chemotactic Velocity

[20] Figure 6 shows a contour plot of the predicted transverse chemotactic velocity, $||\langle v_{c^r} \rangle ||$, as a function of $\langle c_{A^r} \rangle$ and $||\nabla \langle c_{A^r} \rangle ||$ for each mean pore water velocity. The magnitudes of the attractant concentration gradients and transverse chemotactic velocity (for similar attractant concentrations) are on the same order of magnitude as those reported by Ahmed and Stocker [2008]. The highest transverse chemotactic velocities occur when $\langle c_{A^r} \rangle < K_d$ and $||\nabla \langle c_{A^r} \rangle || > 5$ mM cm$^{-1}$, which corresponds to a small region centered near the inlet of the T-sensor (not shown). In this region the variations in $||\langle v_{c^r} \rangle ||$ are mostly caused by variations in $\langle c_{A^r} \rangle$. In the majority of the T-sensor, the attractant gradients are small (i.e., $||\nabla \langle c_{A^r} \rangle || < 5$ mM cm$^{-1}$), which primarily corresponds to transverse chemotactic velocities that are less than 0.8 m d$^{-1}$. Figure 6 also shows that for any particular pair of $\langle c_{A^r} \rangle$ and $||\nabla \langle c_{A^r} \rangle ||$ values, $||\langle v_{c^r} \rangle ||$ is slightly different for each simulation. In previous modeling efforts [e.g., Lanning and Ford, 2002; Sherwood et al., 2003; Olson et al., 2004; Roush et al., 2006; Long and Ford, 2009; Wang and Ford, 2009, 2010], $\langle v_{c^r} \rangle$ is not explicitly a function of the fluid velocity. In contrast, $\langle v_{c^r} \rangle$ in our model (equation (5)) is a function of $D_{A^r, eff}$, which is dependent upon the average pore water velocity at these

Figure 4. Illustration of the $||\nabla \langle c_{A^r} \rangle ||$ field near the entrance of the T-sensor for a mean pore water velocity of 20 m d$^{-1}$.

6. Compute $\langle v_{c^r} \rangle$ using equation (5).

7. Solve problems 2 (equations (A3a)-(A3d)) and 3 (equations (A4a)-(A4d)) in the 3-D unit cell (for both the $x$ and $y$ components) for each subdomain in step 5.

8. Interpolate each solution from steps 6 and 7 to the mesh nodes in the T-sensor and compute $\mu_{eff}$ (equation (A5)) and $v_{eff}$ (equation (A6)).

9. Use the spatially dependent $\mu_{eff}$ tensor and $v_{eff}$ vector, as well as the given mean pore water velocity, to solve the steady state, vertically averaged 2-D macroscale model for bacteria (equation (3)).

Steps 1–4 constitute a typical algorithm required to solve the closure problem and corresponding macroscale model for dispersion of a passive tracer. Step 5 provides the $\langle c_{A^r} \rangle$ and $\nabla \langle c_{A^r} \rangle$ values used to compute $\langle v_{c^r} \rangle$ and solve the bacterial closure problems. In theory, the $\langle c_{A^r} \rangle$ and $\nabla \langle c_{A^r} \rangle$ values should correspond to the area (top view) of a unit cell in the 2-D T-sensor representation since we have already assumed that $\langle c_{A^r} \rangle$ and $\nabla \langle c_{A^r} \rangle$ are constant in each unit cell. If we divided the T-sensor into subdomains corresponding to the area of the unit cell, there would be approximately 4700 subdomains. This does not present an issue for $\langle v_{c^r} \rangle$ since equation (5) can be utilized; however, 4700 subdomains become computationally intensive for the solution of the bacterial closure problems (problems 2 and 3 in Appendix A), which is counter to the upscaling procedure. In order to reduce the number of closure problems we observe that $\nabla \langle c_{A^r} \rangle$ (see Figure 4) and $\partial \langle c_{A^r} \rangle / \partial x$ (not shown) only vary significantly in a small region near the entrance of the T-sensor; everywhere else the values are similar in magnitude. Thus, it is
flow rates [see Valdés-Parada et al., 2010, Figure 7]. This constitutes a potentially significant difference between our model and that typically reported in the literature. It should be noted that a sufficiently large average pore water velocity would dominate over the chemotactic velocity, making chemotactic transport negligible. This is discussed in more detail in section 3.2.

3.2. Comparison With Experiments

[21] Figure 7 shows the comparison between the concentration profiles from the experiments and our multiscale model simulations using 100 subdomains. The simulated results represent true predictions of the experimental data using only the measured parameters from Long and Ford [2009] as input. The control experiments are also included in Figure 7 in order to show the extent of the observed chemotactic response; clearly, pronounced chemotactic peaks were only observed in the experiments at $x = 4$ and 6 cm for the 5 m d$^{-1}$ mean pore water velocity. While there are discrepancies between the measured and predicted concentration profiles, the model results are encouraging, especially for the 10 m d$^{-1}$ experiment. In the 5 m d$^{-1}$ experiments the model predicts chemotactic peaks at $x = 4$ and 6 cm; however, the magnitudes of the predicted peaks are smaller than those observed in the experiment. In addition, the predicted peaks occur at $y \approx 0.3$ cm, whereas the experimental peaks occur in the range of $0.10 \text{ cm} < y < 0.25 \text{ cm}$. Overall, the chemotactic peaks in our predicted concentration profiles decrease as the mean pore water velocity increases, which is similar to the trends observed in the experimental data. It is noted that in the modeling efforts reported by Long and Ford [2009], no chemotactic peaks were obtained using the same input parameters in their model. Moreover, when they arbitrarily increased their effective chemotactic sensitivity coefficient by 2 orders of magnitude, their model produced pronounced chemotactic peaks for all flow rates, which is not observed in the experiments. The mean absolute error (MAE) between our predictions and the observations for each concentration profile is listed in Table 1. The largest MAE (17%) is observed at $x = 6$ cm for the 5 m d$^{-1}$ experiment. In all other cases the predicted concentration profiles have a MAE less than 13%.

[22] The lack of a clear distinction between the control and chemotaxis experimental concentration profiles presented in Figure 7 for a mean pore water velocity of 20 m d$^{-1}$ suggests that chemotaxis may not be a dominant transport mechanism at this flow rate. In order to determine the importance of chemotactic transport, we conducted an order of magnitude analysis (see Appendix B) for the total convection and total dispersion terms in equation (3). Our analysis shows that if the flow conditions are such that $\chi_0/L \ll \langle v_c \rangle^3$, chemotactic transport is negligible with respect to convection in both $v_{eff}$ and $\mu_{eff}$. For the experimental setup of Long and Ford [2009], $\chi_0 = 2.4 \times 10^{-8} \text{ m}^2 \text{ s}^{-1}$ and $L = 0.6 \text{ cm}$; thus, $\chi_0/L = 0.35 \text{ m d}^{-1}$. Thus, all of the experimental flow rates are greater than $\chi_0/L$, and it is expected that for the flow rate of 20 m d$^{-1}$ the above inequality is met, implying that convection dominates over chemotactic transport. On the basis of this analysis we modeled all of the chemotaxis experiments without chemotactic transport (i.e., $\chi_0 = 0$), which effectively reduces equation (3) to a convection-dispersion equation for bacterial transport. The results from these simulations are presented in Figure 8, and the MAEs between the model predictions and chemotaxis data are shown in Table 2. Clearly, the convection-dispersion model for bacteria represents the 20 m d$^{-1}$ chemotaxis data better than the chemotaxis model. Thus, it can be concluded that chemotactic transport is not an important transport mechanism at mean pore water velocities greater than 20 m d$^{-1}$. Interestingly, the convection-dispersion model provides better predictions for the chemotaxis data for all flow rates at 2 cm. This suggests that the experimental system at hand is not at steady state and that a chemotaxis model with time-dependent effective medium coefficients should be explored.

3.3. Subdomain Sensitivity Analysis

[23] As discussed in section 2.3, the number of subdomains chosen to compute the bacterial closure problems was varied between 100, 25, and 1 in order to reduce the computational demands required for each macroscale bacterial transport solution. Figure 9 compares each of the simulation results for all three mean pore water velocities. The maximum MAE between any two predicted concentration profiles is 8%, which occurs between the 100 and 1 subdomain simulations at $x = 6$ cm for the 20 m d$^{-1}$ pore water
velocity. In all other simulation comparisons, the MAE was less than 5%. As expected (see section 2.3), these results suggest that the predicted concentration profiles are not highly sensitive to the number of subdomains chosen within this homogeneous porous system. However, it should be noted that Figure 9 suggests that the subdomain resolution may need to increase with transport distance in the direction of flow, which could have significant implications for applications of this model to larger systems. Additional applications of the model to larger, more natural systems are required to determine whether or not this is a limitation of the current model.

### Table 1. Percent of Mean Absolute Error for the Chemotaxis Predictions in Figure 7

<table>
<thead>
<tr>
<th>2 cm</th>
<th>4 cm</th>
<th>6 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 m d⁻¹</td>
<td>13</td>
<td>12</td>
</tr>
<tr>
<td>10 m d⁻¹</td>
<td>13</td>
<td>7</td>
</tr>
<tr>
<td>20 m d⁻¹</td>
<td>10</td>
<td>10</td>
</tr>
</tbody>
</table>

4. Discussion and Conclusions

[24] In this study, we presented a predictive, multiscale framework for modeling chemotaxis in porous media on the basis of the upscaled model developed by Valdés-Parada et al. [2009]. This modeling approach is unique in that it only requires an appropriately defined unit cell and measured values of microscale parameters to quantify the...
effective medium coefficients. Moreover, it is worth stressing that the main differences between the macroscale model used in this work and those commonly reported in the literature are the following: (1) the effective motility coefficient, \( l_{eff} \), contains a chemotactic dispersion tensor rather than simply being defined as the sum of the effective diffusion and hydrodynamic dispersion tensors, (2) \( \nu_{eff} \) contains two additional terms other than the averaged fluid and chemotactic velocities, and (3) the average chemotactic velocity is not expressed in terms of empirical coefficients (i.e., tortuosity) but is rather a function of the effective diffusivity of the attractant (equation (A10)). Other common approaches rely on empirically defined effective medium coefficients, therefore requiring statistical fitting of these coefficients to experimental data. Indeed, both approaches (i.e., upscaling and empirical) are justifiable, and the use of one over the other is ultimately a modeling choice. Long and Ford [2009] used the empirical approach without

![Figure 8. Multiscale predictions of transverse chemotaxis within the T-sensor assuming that chemotactic transport is negligible compared to convective transport.](image)

<table>
<thead>
<tr>
<th>Time (m d(^{-1}))</th>
<th>2 cm</th>
<th>4 cm</th>
<th>6 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 m d(^{-1})</td>
<td>5</td>
<td>30</td>
<td>36</td>
</tr>
<tr>
<td>10 m d(^{-1})</td>
<td>6</td>
<td>10</td>
<td>18</td>
</tr>
<tr>
<td>20 m d(^{-1})</td>
<td>9</td>
<td>7</td>
<td>8</td>
</tr>
</tbody>
</table>
successfully reproducing their experimental data. In this work we have shown that the upscaling approach reproduced (MAE on the order of 10%; see Table 1) the experimental concentration profiles. In fact, for low flow rates ($h \nu_i/C_{13}/C_{20}/C_0 < 10$ m d$^{-1}$) our model produced chemotactic peaks similar to those observed in the experiments. For $h \nu_i/C_{13}/C_{20}/C_0 > 10$ m d$^{-1}$, convection became the dominant transport mechanism (as determined by $\nu_i/C_3/L_h$), and we demonstrated that a convection-dispersion model is more consistent with the experimental observations.

Certainly, there were some discrepancies between our predictive approach and the experimental observations. These discrepancies can be attributed to a number of sources related to both the experiments and the theory. For the predictive modeling approach it is stressed that the macroscale equations are only known to be valid as long as the scaling laws (e.g., $\ell_0 \ll r_0 \ll L$) are met. In this particular experimental system, the disparity of characteristic lengths between the pore scale and macroscale is not as evident as in other applications (e.g., groundwater flow, packed bed reactors, column experiments, etc.). Moreover, the influence of the T-sensor boundaries was not taken into account in the upscaling process, which may influence the results under certain conditions. Despite these discrepancies the results are encouraging and should motivate further use of volume averaging for bacterial transport in natural porous media.
Appendix A: Closure Problems

[26] In section 2.2 we explained that the closed upscaled model requires the derivation of the associated BVPs for the deviation fields (i.e., \( \tilde{c}_{x} \) and \( \tilde{c}_{B} \)) [see Gray, 1975]. The formal solution of these problems is given by

\[
\tilde{c}_{x}(r) = b_{x}(r) \cdot \nabla (c_{x})^\gamma, \quad (A1a) \\
\tilde{c}_{B}(r) = b_{B}(r) \cdot \nabla (c_{B})^\gamma + b_{AB}(r) (c_{B})^\gamma, \quad (A1b)
\]

where \( b_{x} \) is the closure variable for the attractant, while \( b_{B} \) and \( b_{AB} \) are the closure variables for the bacteria. Here, a quasi-steady constraint has been imposed, which implies that the microscale transport processes relax to their steady state values much faster than the time scales for variations in the macroscale source terms. It follows that the linear independent closure problem for each closure variable in equations (A1a) and (A1b) is [Valdés-Parada et al., 2009]

Problem 1

\[
\mathbf{v}_{\gamma} + \mathbf{v} \cdot \nabla b_{x} = \nabla \cdot (D_{x} \nabla b_{x}) \quad (A2a)
\]

in the \( \gamma \) phase,

\[
\text{B.C.} - n_{\gamma x} \cdot \nabla b_{x} = n_{\gamma x} \text{ at } A_{\gamma x}, \quad (A2b) \\
b_{x}(r + l) = b_{x}(r) \text{ at } A_{\gamma i} i = 1, 2, 3, \quad (A2c) \\
\langle b_{x} \rangle^\gamma = 0. \quad (A2d)
\]

Problem 2

\[
\mathbf{v}_{\gamma} + \mathbf{v} \cdot \nabla b_{B} = \nabla \cdot (D_{B} \nabla b_{B}) \quad (A3a)
\]

in the \( \gamma \) phase,

\[
\text{B.C.} - n_{\gamma x} \cdot \nabla b_{B} = n_{\gamma x} \text{ at } A_{\gamma x}, \quad (A3b) \\
b_{B}(r + l) = b_{B}(r) \text{ at } A_{\gamma i} i = 1, 2, 3, \quad (A3c) \\
\langle b_{B} \rangle^\gamma = 0. \quad (A3d)
\]

Problem 3

\[
\mathbf{v} \cdot \mathbf{v} + \mathbf{v} \cdot \nabla b_{AB} = \nabla \cdot (D_{AB} \nabla b_{AB}) \quad (A4a)
\]

in the \( \gamma \) phase,

\[
\text{B.C.} - n_{\gamma x} \cdot \nabla b_{AB} = 0 \text{ at } A_{\gamma x}, \quad (A4b) \\
b_{AB}(r + l) = b_{AB}(r) \text{ at } A_{\gamma i} i = 1, 2, 3, \quad (A4c) \\
\langle b_{AB} \rangle^\gamma = 0. \quad (A4d)
\]

In equations (A2)–(A4), \( \mathbf{v} = \mathbf{v}_{\gamma} + \mathbf{v}_{\gamma} \), and problems 1–3 are solved in the periodic unit cell illustrated in Figure 2. Note that problems 2 and 3 are dependent upon the solution of problem 1, but the latter is independent of problems 2 and 3. [27] Directing our attention to the closed macroscale models (equations (3) and (4)), the corresponding effective medium coefficients for bacteria are defined as follows:

\[
\mathbf{u}_{eff} = D_{x, eff} + D_{B} + D_{B, ct}, \quad (A5)
\]

\[
\mathbf{v}_{eff} = \langle \mathbf{v}_{\gamma} \rangle^\gamma + \langle \mathbf{v}_{\gamma} \rangle^\gamma - \frac{D_{B}}{\gamma} \int \mathbf{n}_{\gamma x} b_{AB} dA + \langle b_{AB} \rangle^\gamma, \quad (A6)
\]

where \( D_{x, eff} \), \( D_{B} \), and \( D_{B, ct} \) are the effective motility, hydrodynamic dispersion, and chemotactic dispersion tensors, respectively, which are defined in terms of the solutions to problems 1–3 as

\[
D_{x, eff} = D_{x} \left( 1 + \frac{1}{\gamma} \int \mathbf{n}_{\gamma x} b_{x} dA \right), \quad (A7)
\]

\[
D_{B} = -\langle \mathbf{v}, b_{B} \rangle^\gamma. \quad (A8)
\]

\[
D_{B, ct} = -\langle \mathbf{v}, b_{B} \rangle^\gamma. \quad (A9)
\]

[28] In addition, \( \langle \mathbf{v}_{\gamma} \rangle^\gamma \), as defined in equation (5), depends upon \( D_{x, eff} \), which is expressed as

\[
D_{x, eff} = D_{x} \left( 1 + \frac{1}{\gamma} \int \mathbf{n}_{\gamma x} b_{x} dA \right). \quad (A10)
\]

This coefficient is added to the hydrodynamic dispersion tensor,

\[
D_{B} = -\langle \mathbf{v}, b_{B} \rangle^\gamma \quad (A11)
\]
in order to define the total dispersion tensor, \( D_{AB} \), in equation (4).

Appendix B: Contribution of Chemotactic Transport

[29] In order to determine the conditions for which chemotaxis is a significant transport mechanism (at the macroscale) we present an order of magnitude analysis for the total convection and total dispersion terms in equation (3). To this end, we consider the definition of the total motility tensor, \( \mathbf{u}_{eff} \), which is written in terms of the closure variable, \( b_{B, \gamma} \), as

\[
\mathbf{u}_{eff} = D_{B} \left( 1 + \frac{1}{\gamma} \int \mathbf{n}_{\gamma x} b_{AB} dA - \langle \mathbf{v}, b_{B} \rangle^\gamma - \langle \mathbf{v}, b_{B} \rangle^\gamma \right). \quad (B1)
\]

From the governing boundary value problem for \( b_{B} \), we have \( b_{B} = O(\epsilon) \). In addition, the no-slip condition at the fluid-solid interface implies that \( \mathbf{v} = O(\langle \mathbf{v}_{\gamma} \rangle^\gamma) \).
Finally, from the developments presented by Valdés-Parada et al. [2009], we have the following result:

$$\bar{v}_c = O((v_c)^{\gamma}) = O\left(\frac{\chi_0 K_d}{(K_d + \langle c_{A\gamma}\rangle)^2} \frac{D_{A\gamma}}{\ell_{\gamma}} \nabla \langle c_{A\gamma}\rangle^{\gamma}\right). \tag{B2}$$

Now, assuming that $K_d = O(\langle c_{A\gamma}\rangle)$ and $D_{A\gamma} \frac{\partial}{\partial x} = O(1)$, the above estimate can be simplified to

$$\bar{v}_c = O((v_c)^{\gamma}) = O\left(\frac{\chi_0}{L}\right). \tag{B3}$$

Thus, the estimate of the total motility tensor is given by

$$\mu_{\text{eff}} = O(\mathcal{D}_{B\gamma} + (v_c)^{\gamma} \ell_{\gamma} + \chi_0 \ell_{\gamma}). \tag{B4}$$

From this result, we notice that for cases in which

$$\chi_0 \ll \langle v_c \rangle^{\gamma}, \tag{B5}$$

the contribution of convection dominates that of chemotaxis in the total motility tensor. Under these conditions, the values of the total motility tensor are driven by diffusion and convection, and its estimate is given by

$$\mu_{\text{eff}} = O(\mathcal{D}_{B\gamma} + (v_c)^{\gamma} \ell_{\gamma}). \tag{B6}$$

[30] Directing our attention to the total velocity vector, we have

$$\mathbf{v}_{\text{eff}} = \langle v_c \rangle^{\gamma} + \langle v_{\gamma} \rangle^{\gamma} - \frac{\mathcal{D}_{B\gamma}}{\ell_{\gamma}} \int_{A_{\kappa}} n_{\kappa} b_{\kappa \beta} \mathbf{d}A + \langle b_{\kappa \beta} \rangle \bar{v}. \tag{B7}$$

Recall that $b_{\kappa \beta}$ is a closure variable for the bacteria; using its associated boundary value problem (equations (A4a)–(A4d)), we obtain the estimate

$$b_{\kappa \beta} = O\left(\frac{\frac{\rho}{\chi_0} + (v_{\gamma})^{\gamma} + \overline{\sigma_{\beta \gamma}}}{\ell_{\gamma}}\right). \tag{B8}$$

Moreover, the estimate for $\bar{v}$ is

$$\bar{v} = O((v_c)^{\gamma}) + O\left(\langle v_{\gamma} \rangle^{\gamma} + \chi_0 \ell_{\gamma}\right). \tag{B9}$$

Combining equations (B8) and (B9), the order of magnitude estimate of the total velocity vector is given by

$$\mathbf{v}_{\text{eff}} = O\left(\langle v_c \rangle^{\gamma} + \chi_0 \ell_{\gamma}\right). \tag{B10}$$

Thus, the inequality in equation (B5) provides the conditions under which chemotaxis is negligible with respect to convection in both $\mu_{\text{eff}}$ and $\mathbf{v}_{\text{eff}}$.

**Notation**

- $A_{\kappa \beta}$ surface of the fluid-solid interface.
- $A_{\beta \gamma}$ surface of the boundary entrances and exits.
- $b_{\kappa \beta}$ attractant closure variable, m.
- $b_{\kappa \beta}$ bacterial closure variable, m.
- $b_{\kappa \beta}$ microscale attractant concentration, mol m$^{-3}$.
- $c_{A\gamma}$ spatial deviations of the microscale attractant concentration, mol m$^{-3}$.
- $\langle c_{A\gamma}\rangle^{\gamma}$ intrinsic average of the attractant concentration, mol m$^{-3}$.
- $c_{B\gamma}$ microscale bacteria concentration, mol m$^{-3}$.
- $\langle c_{B\gamma}\rangle^{\gamma}$ spatial deviations of the microscale bacteria concentration, mol m$^{-3}$.
- $\langle c_{B\gamma}\rangle^{\gamma}$ intrinsic average of the bacteria concentration, mol m$^{-3}$.
- $C_B$ normalized bacteria concentration.
- $D_{A\gamma}$ molecular diffusion coefficient of the attractant, m$^2$ s$^{-1}$.
- $D_{A\gamma}$ attractant hydrodynamic dispersion tensor, m$^2$ s$^{-1}$.
- $D_{A\gamma}$ total attractant dispersion tensor, m$^2$ s$^{-1}$.
- $D_{B\gamma}$ random motility coefficient of the bacteria, m$^2$ s$^{-1}$.
- $D_{B\gamma}$ bacteria hydrodynamic dispersion tensor, m$^2$ s$^{-1}$.
- $D_{B\gamma}$ bacteria effective motility tensor, m$^2$ s$^{-1}$.
- $D_{B\gamma}$ bacteria chemotactic dispersion tensor, m$^2$ s$^{-1}$.
- $D_{B\gamma}$ total bacteria dispersion tensor, m$^2$ s$^{-1}$.
- $\mathcal{F}_{B\gamma}$ boundary conditions for the bacteria.
- $g_{B\gamma}$ initial conditions for the bacteria.
- $I$ identity tensor.
- $K_d$ bacterial dissociation coefficient, mol m$^{-3}$.
- $\ell_{\gamma}$ characteristic length associated with the microscale, m.
- $l_{\kappa}$ unit cell lattice vector, m.
- $L$ characteristic length associated with the macroscale, m.
- $n_{\kappa \kappa}$ unit normal vector directed from the $\gamma$ phase toward the $\kappa$ phase.
- $r$ position vector, m.
- $r_0$ radius of the averaging region, m.
- $t$ time, s.
- $\nu_{\gamma}$ fluid velocity vector, m s$^{-1}$.
- $\bar{v}_{\gamma}$ spatial deviations of the fluid velocity vector, m s$^{-1}$.
- $\langle v_{\gamma}\rangle^{\gamma}$ intrinsic average of the fluid velocity vector, m s$^{-1}$.
- $v_{\gamma}$ chemotactic velocity vector, m s$^{-1}$.
- $\overline{\sigma_{\beta \gamma}}$ spatial deviations of the chemotactic velocity vector, m s$^{-1}$.
- $\langle v_{\gamma}\rangle^{\gamma}$ intrinsic average of the chemotactic velocity vector, m s$^{-1}$.
- $\bar{v}$ total velocity vector, m s$^{-1}$.
- $\mathbf{v}$ spatial deviations of the total velocity vector, m s$^{-1}$.
- $\langle \mathbf{v}\rangle^{\gamma}$ intrinsic average of the total velocity vector, m s$^{-1}$.
- $V$ averaging region.
- $y_{\gamma}$ volume of the pore space contained within the averaging region, m$^3$.
- $x, y$ longitudinal and transverse directions in the T-sensor, m.
- $\epsilon$ porosity of the porous medium.
- $\chi_0$ chemotactic sensitivity coefficient, m$^2$ s$^{-1}$.
\( \chi_{\text{eff}} \) effective chemotactic sensitivity coefficient, \( \text{m}^2 \text{s}^{-1} \)

\( \mu_{\text{eff}} \) effective motility tensor, \( \text{m}^2 \text{s}^{-1} \)

\( \omega_{\text{eff}} \) effective total velocity vector, \( \text{m} \text{s}^{-1} \)

\( \tau \) tortuosity of the porous medium.

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