An Analytic Approach to the Modeling of Microbial Locomotion in Porous Media

Meena Jagadeesan

Abstract

Much research has been done to study swimming cell motility in bulk fluids. However, many swimming cells' environments are rife with porous, microstructured materials and boundaries. The goal of the overarching project (which this study is a part of) is to establish a quantitative framework that models microbial locomotion in porous media. In this study, we focus on an analytic approach that complements the overarching project's lab experiments and computer models.

In the low particle density case, we consider the microscopic model of a random walk with one-step memory on the dual graph defined by a porous media's fluid pockets and tunnels. We study the long-term macroscopic particle distribution and present an analytic solution to our generalization of the overarching project's computer-generated numerical solutions. We present properties of our analytic solution that can be tested in an experimental setting to determine the microscopic model's accuracy and validity.

Our approach uses Markov analysis to prove that the stationary distribution of a large class of n-dimensional porous media can be split into $n+1$ probability classes, so that the ratio of interior particles to boundary particles is proportional to the number of interior tunnels. We also prove that the stationary distribution of uniform merged media is determined by the placement of connecting tunnels.

For the mid-density case, we present our preliminary work in constructing a microscopic model to consider shifts in the density distribution rather than the motion of individual particles. We consider a simple microscopic model and prove that it yields unexpected results for the stationary distribution.

1 Introduction

Swimming cells play important roles in many fields of biology: for example, in human health through reproduction and the spread of infection from biomedical devices [14, 10] and in ecology through the recycling of organic matter [4, 9, 11]. With thin actuated flagella that typically range in length from 5-50 microns on 1-10 micron individual cells, swimming cells actively seek out nutrients, light, and mates, unlike their passive counterparts [2]. Much research has been done to study cell motility in the simplified situation of cells in bulk fluid without any boundaries or interior obstructions. For example, Guasto presents an extensive analysis of this situation in his 2004 review article [6]. In bulk fluids, swimming cells are generally assumed to diffuse outward in a fashion similar to passive cells [8].

However, in many cases, the realistic environments of swimming cells are often rife with porous, microstructured materials and boundaries, which significantly affect cell motion. For example, marine bacteria which are involved in biogeochemical cycling live in porous environments such as marine snow [4, 11]. In addition, swimming bacteria are used for bioremediation of oils and chemicals in porous soils [10]. Human parasites swim through complex vascular networks to spread infection [13]. Motile sperm in the female reproductive tract swim through biopolymer networks in cervical mucus and complex tissue topology [5]. Microalgae cells use porous glass microstructures for light distribution and efficient cell growth [7]. Thus, developing a model for cell motion in porous media would enhance our understanding of many natural and manmade systems. This could foster the development of technologies that stifle bacterial infection, mediate infertility, and provide clean drinking water.

The goal of the overarching project (which this study is a part of) is to establish a quantitative framework that accurately models key aspects of microbial locomotion in porous media. There are three components to the project: lab experiments, a computer model, and a mathematical analysis. The lab experiments track the motion of cells in a media with complex boundary structures (Figure 1 [3]). Organisms, also referred to as particles hereafter, can travel around pillars, which are placed in various symmetric patterns. The computer-generated numerical model computes the long-term macroscopic distribution associated to a specific microscopic model for a small class of porous media. In this study, we focus on a complementary analytic approach, presenting an analytic solution for a generalization of the computer-based numerical solutions to a significantly larger class of porous media. We present properties of our analytic solution that can be tested in experimental settings to determine the validity and accuracy of the microscopic model.

The microscopic models considered in the overarching project are derived from a graph theory-based model. Cell motion is conventionally modeled as either a simple random walk, where organisms move independently at each step, or as run-and-tumble motion, where organisms such as flagellated bacteria migrate stochastically towards a more favorable location

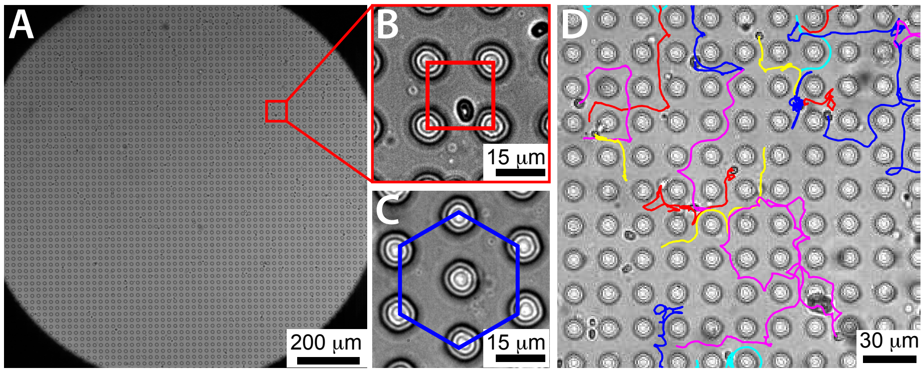

Figure 1: Schematic of experimental set-up

[1, 12]. In order to simulate cell motion in porous media in the case of low particle density, we consider an intermediate model: a random walk with one-step memory, where particles move according to their current position and direction of their previous move. For example, in a persistent random walk, each particle is more likely continue in the direction that it came from with a probability associated to the persistence value. The random walk with memory takes place on a dual graph, which we construct by placing vertices in the fluid pockets between the obstructions and placing edges through the channels between the fluid pockets. We mostly consider finite dual graphs that simulate a boundary. Particles are modeled to travel from vertex to vertex, through the fluid pocket channels. To investigate the long-term behavior of the cells, we study the stationary distribution of the associated Markov chain of a random walk with one-step memory of a single particle, ignoring the effect of particle-particle interactions.

In Section 2, we present definitions and notation. In Section 3 and 4, we analytically prove that for a large number of types of n-dimensional porous media, the stationary distribution can be broken into $n+1$ classes. Within each class, the stationary distribution is local, while between classes, there can be global shifts in probability density. In the case of 2-dimensions, these classes are vertices in the interior, on the boundary edges, and on the corners. We compute the stationary distribution in terms of the reflection coefficient, persistence value at the boundaries, and the local degree of vertices. This solution generalizes the numerical solutions of the overarching project's computer model.

Biologically, it is also interesting to consider the amount of information about the structure of the interior of the porous medium that can deduced from information about the boundary and boundary concentration. For example, this is applicable to a 3D-medium where only the boundary is visible. We find that the boundary ratio - the ratio of the percentage of particles in the interior to the percentage of particles on the boundary - is proportional to the number of edges in the interior. This result can be verified in the experimental setting through the addition of edges (tunnels in a known medium).

In Section 5, we study the merging of multiple porous media through tunnel connections between some of the fluid pockets of each medium. We consider the case where the original media have uniform stationary distributions and outline the constraints for the stationary distribution of the merged porous media to be splittable into classes. We prove that for a large number of types of porous media whose transition probabilities satisfy a set of symmetry constraints, the stationary distribution is determined by the structure of the tunnel connections between the original media. Notably, these stationary distributions are independent of the transition probability values. In an experimental setting, this means that the long-term distribution of particles in merged media is determined by placement of the connecting tunnels, rather than any properties about cell motion in and out of the tunnels.

In Section 6, we present our preliminary work for the mid density case in constructing a microscopic model to consider shifts in the density distribution rather than the motion of individual particles. We also consider a simple microscopic model that takes place on the dual graph of a porous medium and whose transition probabilities are based on the neighboring densities. We prove that this model yields unexpected results for the stationary distribution in the one-dimensional case. For a dual graph with 7 vertices, no stationary distribution exists. For many other small values, the particle densities in the stationary distribution increase up and down unpredictably along the media.

2 Dual Graph, Embedding, and Markov Chains

To each porous medium we associate a dual graph G and an embedding G^* of G into $\mathbb{R}^2$ or $\mathbb{R}^3$ depending on the dimension of the medium. The vertices are defined by the fluid pockets of the medium and the edges are defined by the tunnels between fluid pockets. We define two ways of expressing each vertex: v, to represent the vertex in G, and v^* to represent the embedded vertex in $\mathbb{R}^2$ or $\mathbb{R}^3$. We let V be the set of all v and V^* be the set of all v^*. We similarly define two ways of expressing each edge. Suppose that an edge connects the vertices $v_1, v_2 \in V$ in the graph G and connects $v_1^*, v_2^* \in V^*$ in the embedding G^*. We let $e = (v_1, v_2)$, and we let e^* be the line segment between $\overline{v_1^* v_2^*}$. We let E be the set of all e and E^* be the set of all e^*.

We now define the set of possible states of our Markov process, corresponding to particle states. Our random walk with memory model requires that we keep track of both the vertex position of each particle and the direction that it came from. We define the state space $S(G)$ to be $\{(v, e) \mid v \in e \in E(G)\}$, where v represents the current position and e represents the memory direction. We often abbreviate $S(G)$ as S. We define certain quantities associated to each state $s \in S$. Since s is an ordered pair of a vertex and an edge, we refer to the associated vertex as v_s and the associated edge as e_s. Notice that $e_s \in E$ is an ordered pair (w, v_s) for some $w \in V$ which is the position of the state s during the previous time step. We thus define the **preceding vertex** of s, to be $p(s) = w$.

We now define a Markov chain D to model a random walk with memory on the porous medium by representing the probability distribution $\tilde{P}$ of a single particle in the medium. We first consider the case of low density in which particle-particle interactions are negligible. We assume that $\tilde{P}$ represents the macroscopic particle distribution, with the probabilities representing percentage of particles in each state. The state space of D is defined to be $S(G)$. The transition matrix P has the property that for $s_1, s_2 \in S(G)$, the probability $P(s_1, s_2) > 0$ if and only if $v_{s_1} \in e_{s_2}$. The stationary distribution at vertices SD_V^D of the porous medium represents the long-term distribution of $\tilde{P}$. In order to study SD_V^D, we study the stationary distribution of the states SD^D. Notice that SD^D is related to SD_V^D, according to the following equation

$$SD_V^D(v) = \sum_{s \in S, v_s = v} SD^D(s).$$

3 Two Dimensions

First, we focus on the case where the porous medium is in two-dimensional space. (The results of this section can be generalized to n-dimensional porous media using similar methods. In Section 5, we present the generalization in the case of three dimensions.) We work with a large class of Markov chains and dual graphs where we can study the stationary distribution of the vertices in the following classes: the vertices in the interior, I, the vertices of the

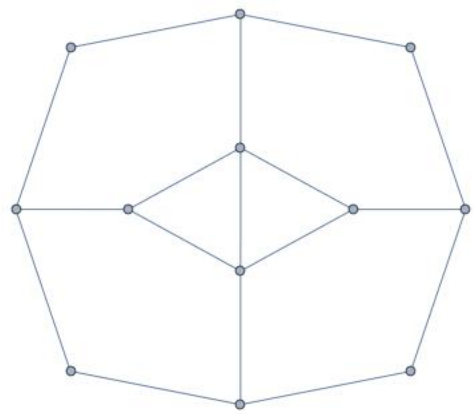

Figure 2: A graph and embedding that satisfies the constraints in Section 3

boundary edges BE, and the verticles on the corners, C. Within each class, the stationary distribution is local, but globally, the probability density can shift between classes.

We first outline certain restrictions on the dual graph G and embedding G^* in $\mathbb{R}^2$. The general idea is that G must be a three-class graph with vertex sets I, BE, and C such that there do not exist any edges between I and C. We will use the following definitions in our constraints. We let the boundary vertices B be $BE \cup C$. We partition the edges E into boundary edges E_B and interior edges E_I so that $E_B = \{(v, w) \mid v, w \in B\}$ and $E_I = E \setminus E_B$. Figure 2 shows an example of a graph and embedding that satisfies the constraints.

These are the precise constraints on G and G^*:

- The graph G is connected.
- The set B^* is exactly the set of vertices on the boundary of the convex hull of V^* in G^*.
- The set E_B^* exactly forms the non-self intersecting, simple convex polygon boundary of the convex hull.

- For $v \in BE$, the degree of v in G is 3.

- For $v \in C$, the degree of v in G is 2.

We define the following partition of $S(D)$ which will help us calculate SD^D:

- $S_\alpha = \{s \in S \mid e_s \in E_I\}$

- $S_\beta = \{s \in S \mid e_s \in E_B\}$

Now, we outline constraints on the transition matrix for us to be able to study the SD_V^D in the classes I, BE, and C. We translate this into constraints on SD^D.

Definition 1. We call the stationary distribution SD^D of the states of a Markov Chain $D(G)$ **splittable** if the following conditions are satisfied:

- There exists α such that for all $s \in S_\alpha$, $SD^D(s) = \alpha$.

- There exists β such that for all $s \in S_\beta$, $SD^D(s) = \beta$.

We denote the splittable stationary distribution as (α, β).

For simplicity of calculation, given an irreducible Markov Chain D, we define SD^{D*} to be an unnormalized stationary distribution of D if it is a scalar multiple of SD^D. In the case that SD^D is splittable, we refer to SD^{D*} as (α^*, β^*).

Lemma 2. *A Markov chain D has an unnormalized splittable stationary distribution* (α^*, β^*) *if and only if the following conditions are satisfied:*

For $s \in S_\alpha$ *such that* $p(s) \in I$,

$$\sum_{s_1 \in S, v_{s_1} = p(s)} P(s_1, s) = 1. \tag{1}$$

For $s \in S_\beta$ such that $p(s) \in C$,

$$\sum_{s_1 \in S, v_{s_1} = p(s)} P(s_1, s) = 1. \tag{2}$$

For $s \in S_\alpha$ such that $p(s) \in BE$,

$$\beta \sum_{s_1 \in S_\beta, v_{s_1} = p(s)} P(s_1, s) + \alpha P(s_2, s) = \alpha, \tag{3}$$

where s_2 is the only state in S_α such that $v_{s_2} = p(s)$. For $s \in S_\beta$ such that $p(s) \in BE$,

$$\beta \sum_{s_1 \in S_\beta, v_{s_1} = p(s)} P(s_1, s) + \alpha P(s_2, s) = \beta, \tag{4}$$

where s_2 is the only state in S_α such that $v_{s_2} = p(s)$.

Proof. This follows from the definition of splittable coupled with the conditions on the graph. □

We outline a more specific set of sufficient constraints on the transition matrix for SD^D to be splittable, defining parameters q and r that we will later relate to the unnormalized splittable stationary distribution, (α^*, β^*).

Definition 3. We call a Markov Chain $D[q, r]$ of a random walk on (V, E) **travellable** if its transition matrix P satisfies (1), (2), and the following conditions:

For all $s \in S_\alpha$ such that $p(s) \in BE$,

$$P(s_1, s) = q,$$

for all $s_1 \in S_\beta$ such that $v_{s_1} = p(s)$.

For all $s \in S_\alpha$ such that $p(s) \in BE$,

$$P((p(s), e_s), s) = r.$$

For all $s \in S_\beta$ such that $p(s) \in BE$,

$$\sum_{s_1 \in S_\beta, v_{s_1} = p(s)} P(s_1, s) = 1 - q.$$

For $s \in S_\beta$ such that $p(s) \in BE$,

$$P(s_1, s) = (1 - r)/2,$$

for the one and only $s_1 \in S_\alpha$ such that $v_{s_1} = p(s)$.

It is important to note that all of these conditions are local and do not impose any additional constraints on the structure of the graph.

Notice that the first condition of the travellable definition imposes certain constraints on the transition probabilities of the states of each vertex $v \in V$. We thus define the following matrix for each vertex:

Definition 4. Given a vertex $v \in G$, we define the **vertex transition matrix** $M[v]$ to be a $\deg(v)$ by $\deg(v)$ square matrix defined by the rows of P associated to s such that $v_s = v$ and columns of P associated to s such that $e_s \setminus v_s = v$.

Notice that each row of $M[v]$ must sum to 1. The condition imposes the additional constraint that the each column of $M[v]$ must sum to 1. Combined, these two conditions imply that $M[v]$ must be doubly stochastic. It is important to note that the other conditions of the travellable definition do not affect the matrix $M[v]$ for any $v \in I$. Furthermore, the values of one vertex transition matrix do not influence the values of any other vertex transition matrix. Thus, the values of each vertex transition matrix can be chosen independently. This means that the only constraint imposed on the vertex transition matrices by the travellable condition is the doubly stochastic property.

These observations are closely related to the well-known fact that the transition matrix of an irreducible Markov chain with a finite state space is doubly stochastic if and only if its stationary distribution is uniform over S.

Theorem 5. *Every travellable Markov Chain $D[q, r]$ has an unnormalized splittable stationary distribution $(\alpha^*, \beta^*) = (2q, 1 - r)$.*

Theorem 5 essentially demonstrates that the unnormalized stationary distribution of the states of $D(G)$ is a function of these two local parameters and completely independent of the structure of the graph.

Proof. Substituting the conditions from Definition 3 into Lemma 2 causes all the equations except (3) and (4) to be satisfied. We are left with the following two equations:

$$2q\beta + r\alpha = \alpha. \tag{5}$$

$$\beta(1 - q) + \alpha(1 - r)/2 = \beta. \tag{6}$$

Notice that (5) can be rearranged into (6). Solving yields that $(2q, 1-r)$ is an unnormalized simple stationary distribution of D. □

We will translate our result to the stationary distribution at the vertices.

Corollary 6. *Given a travellable Markov Chain D, the unnormalized stationary distribution*

SD_V^{D*} *is defined as follows:*

$$\begin{cases} \deg(v)\alpha & v \in I \\ \\ \alpha + 2\beta & v \in BE \\ \\ 2\beta & v \in C. \end{cases}$$

This demonstrates that the stationary distribution of the vertices is a function of only the interior degrees and the local parameters q and r. We now define certain ratios that are associated to the stationary distributions at the vertices and have experimental applications. The boundary ratio represents the ratio of the percentage of particles in the interior to the percentage of particles on the boundary.

Definition 7. For a travellable Markov Chain D, we define the **boundary ratio** $Br(D)$ as

$$\frac{\sum_{v \in I} SD_V^D(v)}{\sum_{v \in B} SD_V^D(v)}.$$

In the case of travellable Markov chains D, notice that $Br(D)$ is a function of q, r, $|C|$, and $|BE|$, and $|E_I|$. In an experimental setting, it is interesting to consider what can be deduced about the structure of the interior of the porous medium from information about the boundary and boundary concentration. For example, this is applicable to a closed medium where only the boundary is visible. We find that the boundary ratio - the ratio of the percentage of particles in the interior to the percentage of particles on the boundary - is proportional to the number of edges in the interior. For a fixed q, r, $|C|$, and $|BE|$, notice that $Br(D)$ is proportional to $|E_I|$. This has two implications. First, $Br(D)$ is independent of the structure of the graph when $|E_I|$ is fixed. This means that adding edges to the interior of the graph should cause $Br(D)$ to increase linearly. This result can be verified in the experiment through the addition of interior tunnels. Furthermore, in a situation where only the boundary is visible, given $Br(D)$ and the boundary-local parameters q, r, $|C|$, and $|BE|$, the number of interior edges, $|E_I|$, can be determined.

3.1 Example: Rectangular Grid

As an example, we apply the results of the previous section to particles travelling in an m by n grid. This dual graph structure is particularly pertinent to the lab component of the overaching project, since pillar patterns corresponding to a rectangular grid are used in the experiment. We will let $q = 1/3 - p/3$ where p is the persistence value, defined so that when $p = 0$, the particles travelling along the boundary have a 1/3 probability of shifting to the interior and as $p \to 1$, these particles have a 0 probability of shifting to the interior. The value r represents the probability that a particle that hits the boundary bounce back into the interior.

The example of a square n by n grid also served as the motivation to guess the stationary distribution in the previous section. It was initially computed by using the transition matrix to create a system of equations to solve for the stationary distribution. The system can be represented by the $N+1$ by $N+1$ matrix $Q(i,j)$ which is defined as follows:

$$\begin{cases} 1 & i = n+1 \\ 0 & j = n+1, i \neq n+1 \\ P(i,j) - 1 & i = j < n+1 \\ P(j,i) & i \neq j, i, j \neq n+1. \end{cases}$$

Notice that the rows are linearly dependent, but upon the deletion of one of the first $i-1$ rows, they become linearly independent. Taking the row reduced echelon form enabled us to find the the solution. This was computed for $n = 4, 6$ and the general solution was guessed from these values.

By Corollary 6, we can compute that:

Theorem 8. *The stationary distribution SD^D of the travellable Markov Chain $D[1/3 - p/3, r]$ of an m by n grid is defined as follows:*

$$\begin{cases} \frac{8(-1+p)}{2(-1+p)(4mn-6m-6n+8)+3(-1+r)(4m+4n-8)} & v \in I \\ \frac{2(-1+p)+6(-1+r)}{2(-1+p)(4mn-6m-6n+8)+3(-1+r)(4m+4n-8)} & v \in BE \\ \frac{6(-1+r)}{2(-1+p)(4mn-6m-6n+8)+3(-1+r)(4m+4n-8)} & v \in C. \end{cases}$$

The analytic solution was obtained by normalizing the values of α and β using the properties of an m by n grid. Notice that the interior points all have the same percentage of particles, regardless of the values of p and r. For a fixed r, in the limit as $p \to 1$, the interior cells become empty and the particles rest on the boundaries, with a slightly higher concentration at the boundary edges than on the corners. This follows from the fact that S_β becomes the only essential communicating class of D in the limit. For a fixed p, in the limit as $r \to 1$, the corners become empty, and particles rest on the boundary edges and the interior.

We now consider the special case where $r = 1/3$, where a particle on the boundary is equally likely to travel in all three directions. In the case that $p = 0$, our Markov process now corresponds to a classical random walk on a graph. In this case, the stationary distribution of a vertex is proportional to its degree, meaning that there are more particles at vertices in the interior than at vertices on the boundary. This is reflected in Theorem 8. As the persistence value increases, the particles in the interior get pushed to the boundaries. An

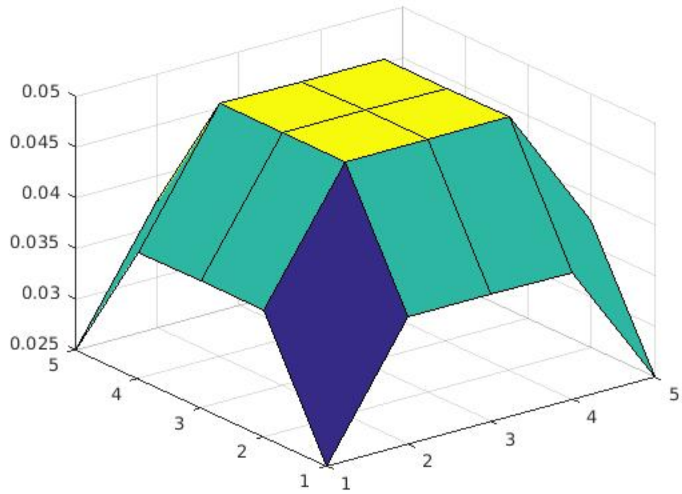

Figure 3: $p = 0$

equilibrium point occurs at $p = 1/3$, when $SD^D(v)$ for $v \in I$ is equal to $SD^D(v)$ for $v \in BE$. The particles in the interior continue to get pushed to the boundaries until at $p = 1/2$, we have that $SD^D(v)$ for $v \in I$ is equal to $SD^D(v)$ for $v \in C$ when $p = 1/2$. For $p > 1/2$, there are more particles at any point on the boundaries than at any point in the interior, and at $p = 1$, there are no particles in the interior.

Figures 3-9 show the distribution of particles in a 5×5 grid for varying persistence values in the case that $r = 1/3$. The two class distribution for $p = 1/3, 1/2$ is shown through the two-color distribution in the plots. For other persistence values, the three class distribution is reflected through the three color distribution.

Now, we will explore the boundary ratio for general p and r. The boundary ratio

$$Br(D) = \frac{8(-1+p)(m-2)(n-2)}{2(-1+p)(2m+2n-8)+3(-1+r)(4m+4n-8)}. \tag{7}$$

We consider the situation where the porous media is a very long tube. To model this, we

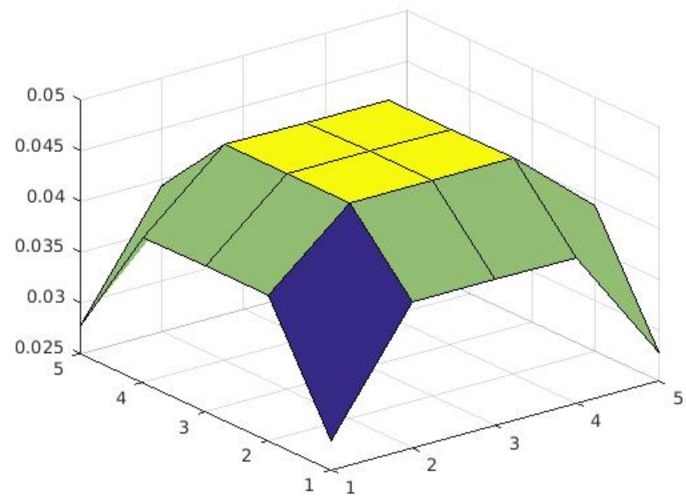

Figure 4: $p = 1/6$

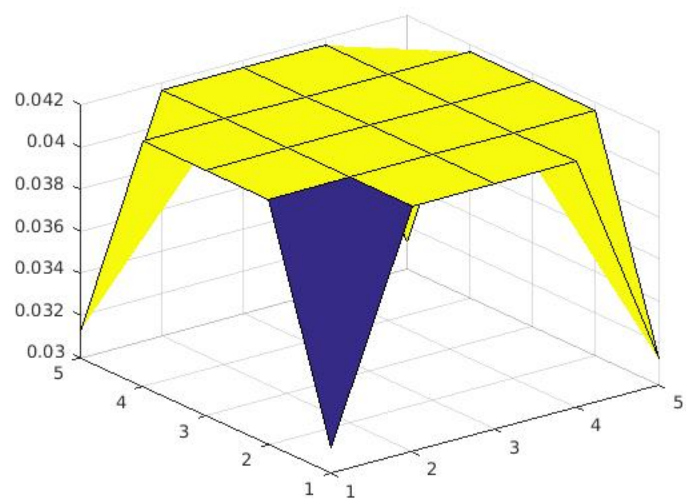

Figure 5: $p = 1/3$

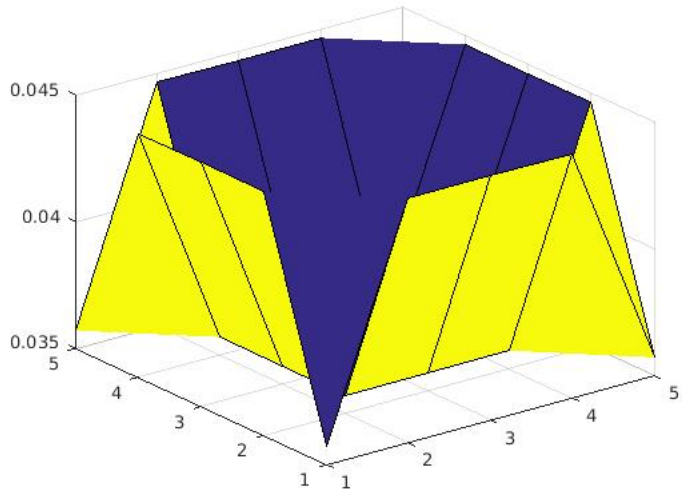

Figure 6: $p = 1/2$

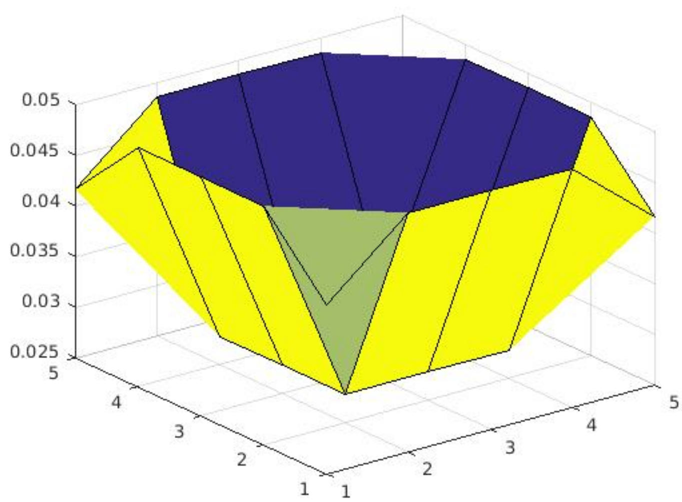

Figure 7: $p = 2/3$

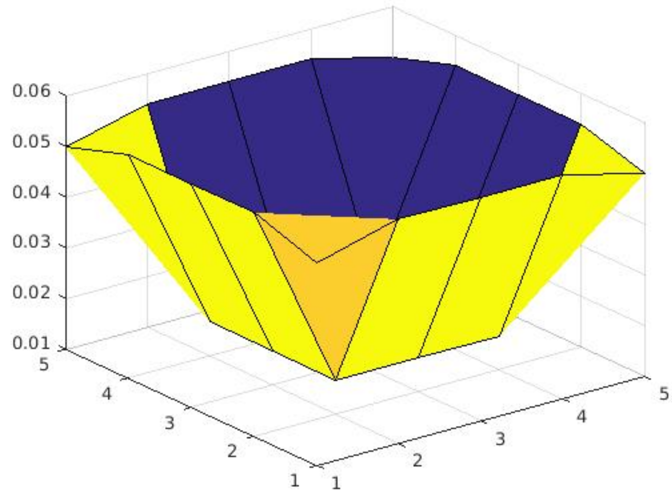

Figure 8: $p = 5/6$

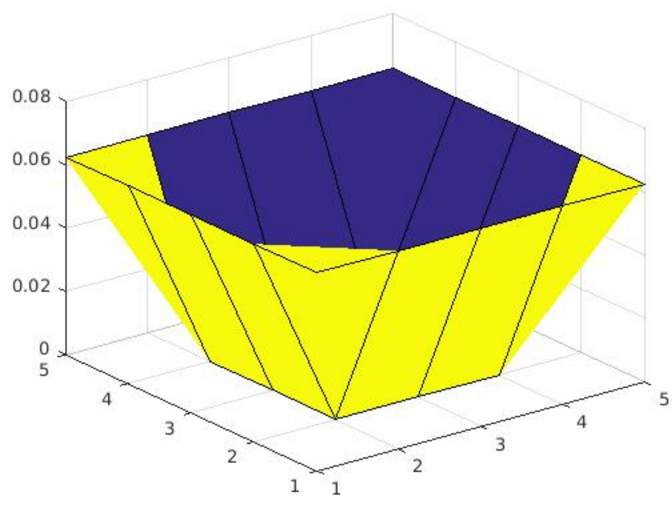

Figure 9: $p = 1$

take the limit as $m \to \infty$. Applying L'Hopital's rule, we obtain the following:

$$Br(D) \to \frac{8(-1+p)(n-2)}{4(-1+p)+12(-1+r)}$$

$$Br(D) \to \frac{2(-1+p)(n-2)}{(-1+p)+3(-1+r))}$$

$$Br(D) \to (n-2) \cdot g(p,r).$$

This demonstrates the boundary ratio is proportional to $n-2$. This can be experimentally tested by measuring the boundary ratio for porous media (of a fixed material) with varying widths.

Figure 3 shows the boundary ratio as a function of p and r in a 3×3 grid. For a fixed r, the boundary ratio decreases as p increases, since particles get pushed out of the interior. For a fixed p, the boundary ratio increases as r increases, since particles bounce off the walls back to the interior with higher probability. Our analytic solution represented in (7) is a generalized version of the numerical solutions of MIT graduate student Aden Forrow's computer model. Our analytic solution is plotted as the surface and the data from the computer model is plotted as the scatter points. Notice the alignment of the scatter points on the surface.

4 Three Dimensional Case

We present a generalization of Section 3 in the case of three-dimensions. We work with a large class of Markov chains and dual graphs where we can study the stationary distribution of the vertices in the following classes: the vertices in the corners, C, the vertices on the boundary edges, BE, on the faces, F, in the interior, I. Within each class, the stationary

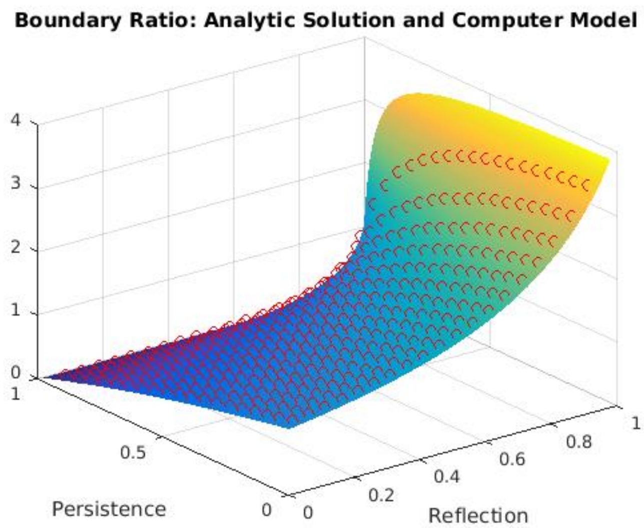

Figure 10: Analytic and computer model calculations of $Br(D)$ as a function of p and r in a 3×3 grid

distribution is local, but globally, the probability density can shift between classes.

We first outline certain restrictions on the dual graph G and embedding G^* in $\mathbb{R}^3$. The general idea is that G must be a four-class graph with vertex sets C, BE, F and I such that there only exist edges within these sets and between C and BE, between BE and F, and between F and I. We will use the following definitions in our constraints. We let the boundary vertices B be $F \cup BE \cup C$. We define the sharp boundary vertices SB to $BE \cup C$. We define the boundary edges E_B, the interior edges E_I, the sharp boundary edges E_{SB}, and the face boundary edges E_{FB} so that $E_B = \{(v, w) \mid v, w \in B\}$, $E_I = E \setminus E_B$, $E_{SB} = \{(v, w) \mid v, w \in SB\}$, and $E_{FB} = E_B \setminus E_{SB}$. These are the precise constraints on G and G^*:

- The graph G is connected.
- The set B is exactly the set of vertices on the boundary of the convex hull of V.

- For $v \in BE$, the degree of v is 4. There are two exactly two vertices $w \in SB$ and exactly two vertices $w \in F$ such that $(v, w) \in E$.
- For $v \in C$, every edge $(v, w) \in E$ must have $w \in SB$.
- The set SB is exactly the set of edges of the non self-intersecting, simple convex polyhedron boundary of the convex hull of V.
- For $v \in F$, there exists exactly 1 edge (v, w) such that $w \in I$.

We now consider the Markov chain $D(G)$. We define the following partition of $S(D)$:

- $S_\alpha = \{s \in S \mid e_s \in E_I\}$.
- $S_\beta = \{s \in S \mid e_s \in E_{FB}\}$.
- $S_\gamma = \{s \in S \mid e_s \in E_{SB}\}$.

Now, we outline constraints on the transition matrix for us to be able to study the stationary distribution of the vertices in the desired classes. We translate this into constraints on the stationary distribution of the states.

Definition 9. We call the stationary distribution SD^D of the states of a Markov Chain D **splittable** if the following conditions are satisfied:

- There exists α such that for all $s \in S_\alpha$, $SD^D(s) = \alpha$.
- There exists β such that for all $s \in S_\beta$, $SD^D(s) = \beta$.
- There exists γ such that for all $s \in S_\gamma$, $SD^D(s) = \gamma$.

We denote the splittable stationary distribution as (α, β, γ).

Given an irreducible Markov Chain D, we will call SD^{D*} an unnormalized stationary distribution of D if it is a scalar multiple of SD^{D}.

Lemma 10. *A Markov chain D has an unnormalized splittable stationary distribution (α, β, γ) if and only if the following conditions are satisfied:*

For $s \in S_\alpha$ such that $p(s) \in I$:

$$\sum_{s_1 \in S_\alpha, v_{s_1} = p(s)} P(s_1, s) = 1. \tag{8}$$

For $s \in S_\gamma$ such that $p(s) \in C$:

$$\sum_{s_1 \in S_\gamma, v_{s_1} = p(s)} P(s_1, s) = 1. \tag{9}$$

For $s \in S_\alpha$ such that $p(s) \in F$:

$$\beta \sum_{s_1 \in S_\beta, v_{s_1} = p(s)} P(s_1, s) + \alpha P(s_2, s) = \alpha,$$

where s_2 is the one and only state in S_α such that $v_{s_2} = p(s)$. For $s \in S_\beta$ such that $p(s) \in F$:

$$\beta \sum_{s_1 \in S_\beta, v_{s_1} = p(s)} P(s_1, s) + \alpha P(s_2, s) = \beta.$$

where s_2 is the one and only state in S_α such that $v_{s_2} = p(s)$. For $s \in S_\beta$ such that $p(s) \in BE$:

$$\beta \sum_{s_1 \in S_\beta, v_{s_1} = p(s)} P(s_1, s) + \gamma \sum_{s_2 \in S_\gamma, p(s) = v_{s_2}} P(s_2, s) = \beta.$$

For $s \in S_\gamma$ such that $p(s) \in BE$:

$$\beta \sum_{s_1 \in S_\beta, v_{s_1} = p(s)} P(s_1, s) + \gamma \sum_{s_2 \in S_\gamma, p(s) = v_{s_2}} P(s_2, s) = \gamma.$$

Proof. This follows from the conditions of a stationary distribution coupled with the conditions imposed by the travellable condition. □

In order to simplify these equations, we now outline a set of sufficient constraints on the transition matrix for the stationary distribution of the states to be splittable.

Definition 11. We call a quasi-travellable Markov Chain $D[q, r_1, r_2, l]$ travellable if its transition matrix P satisfies (8), (9), and the following conditions:

For all $s \in S_\alpha$ such that $p(s) \in F$,

$$\sum_{s_1 \in S_\beta, v_{s_1} = p(s)} P(s_1, s) = q.$$

For all $s \in S_\alpha$ such that $p(s) \in F$,

$$P(s_2, s) = r_2,$$

where s_2 is the one and only state in S_α such that $v_{s_2} = p(s)$. For $s \in S_\beta$ such that $p(s) \in F$,

$$\sum_{s_1 \in S_\beta, v_{s_1} = p(s)} P(s_1, s) = \frac{\deg(p(s)) - q}{\deg(p(s))}.$$

For all $s \in S_\beta$ such that $p(s) \in F$,

$$P(s_2, s) = \frac{1 - r_2}{\deg(p(s))},$$

where s_2 is the one and only state in S_α such that $v_{s_2} = p(s)$. For all $s \in S_\beta$ such that $p(s) \in BE$,

$$\sum_{s_2 \in S_\gamma, p(s) = v_{s_2}} P(s_2, s) = l.$$

For all $s \in S_\beta$ such that $p(s) \in BE$,

$$\sum_{s_1 \in S_\beta, v_{s_1} = p(s)} P(s_1, s) = r_1.$$

For all $s \in S_\gamma$ such that $p(s) \in BE$,

$$\sum_{s_1 \in S_\beta, v_{s_1} = p(s)} P(s_1, s) = 1 - r_1.$$

For all $s \in S_\gamma$ such that $p(s) \in BE$,

$$\sum_{s_2 \in S_\gamma, p(s) = v_{s_2}} P(s_2, s) = 1 - l.$$

Theorem 12. *Every travellable Markov Chain $D[q, r_1, r_2, l]$ has an unnormalized simple stationary distribution of the form $(ql, (1 - r_2)l, (1 - r_1)(1 - r_2))$.*

Proof. Substituting the conditions from Definition 11 into Lemma 10 causes many of the equations to be satisfied. After deleting repeated equations, we are left with the following three equations in four variables:

$$\alpha r_2 + \beta q = \alpha.$$

$$\alpha \frac{1 - r_2}{\deg(p(s))} + \beta \frac{\deg(p(s)) - q}{\deg(p(s))} = \beta.$$

$$\beta r_1 + \gamma l = \beta.$$

$$\beta(1 - r_1) + \gamma(1 - l) = \gamma.$$

Solving yields that $(ql, (1 - r_2)l, (1 - r_1)(1 - r_2))$ is an unnormalized simple stationary distribution of D. □

We will translate this result to stationary distribution at the vertices.

Corollary 13. *Given a travellable Markov Chain D, the vector SD_V^{D*} is an unnormalized stationary distribution of D: If $v \in I$,*

$$SD_V^{D*}(v) = \deg(v)\alpha.$$

If $v \in F$,

$$SD_V^{D*}(v) = (\deg(v) - 1)\beta + \alpha.$$

If $v \in BE$,

$$SD_V^{D*}(v) = 2\beta + 2\gamma.$$

If $v \in C$,

$$SD_V^{D*}(v) = \deg(v)\gamma.$$

Given travellable Markov chains D, notice that $Br(D)$ is a function of q, r_1, r_2, and $|E_{SB}|$, $|E_{FB}|$, $|E_I|$. For a fixed q, r_1, r_2, and $|E_{SB}|$, and $|E_{FB}|$, notice that $Br(D)$ is proportional to $|E_I|$. This has two implications. First, $Br(D)$ is independent of the structure of the graph when $|E_I|$ is fixed. This means that adding edges to the interior of the graph should cause $Br(D)$ to increase linearly according to this model. Furthermore, in a situation where only the boundary is visible, given $Br(D)$ and the boundary-local parameters q, r_1, r_2,, $|E_{SB}|$, and $|E_{FB}|$, the number of interior edges, E_I, can be determined.

5 Merging Multiple Media

Suppose that we merge the interiors of n media by adding tunnels between certain fluid pockets. In this section, we consider the case where all of the original media have uniform stationary distributions of the states. An example of a porous medium with a uniform stationary distribution is a torous shaped medium with transition probabilities defined by a persistent random walk. A natural question to ask is what constraints on the original medium must exist so that we can split the states of the merged medium into n classes that are divided in a way that is closely related to the divisions of the original media, such that each class has a uniform stationary distribution of the states, but globally, the probability density can shift between classes.

Suppose that the n original media have dual graphs G_1, G_2, ... , G_n and embeddings G_1^*, G_2^*, ... , G_n^*. We assume that SD^{D_i} is uniform for all $1 \leq i \leq n$ Then, a dual graph G and embedding G^* must satisfy the following properties:

- $V^* = \cup_{i=1}^n V_i^*$
- $V = \cup_{i=1}^n V_i$
- For all $i \leq n$, the induced subgraph generated by V_i in G is G_i.

We define the following subsets of V:

- $B_i = \{v \in V_i \mid \exists j \neq i \text{ s.t. } \exists w \in V_j \text{ s.t. } (v, w) \in E\}$.
- $I_i = V_i \setminus B_i$.
- $I = \cup_{i=1}^n I_i$.
- $B = \cup_{i=1}^n B_i$.

It can be shown that this means that the transition matrix is doubly stochastic. We now study the state space S. We partition the state space into the following n classes:

- $S_i = \{s \in S \mid v_s \in I_i\} \cup \{s \in S \mid v_s \in B, p(s) \in V_i\}$.

We now define the n-splittable condition:

Definition 14. We call the stationary distribution SD^D of the states of a Markov Chain D **n-splittable** if for each $i \leq n$, there exists α_i such that for all $s \in S_i$, $SD^D(s) = \alpha_i$. We denote the splittable stationary distribution as $(\alpha_1, \alpha_2, ..., \alpha_i)$.

We refer to an unnormalized n-splittable stationary distribution as $(\alpha_1^*, \alpha_2^*, ..., \alpha_i^*)$.

We will now outline the constraints on the transition matrix that must be satisfied for the stationary distribution to be splittable with respect to the n classes $S_1, S_2, ..., S_n$.

Lemma 15. *For a merged medium to be n-splittable, the following conditions must be satisfied: For $s \in S$ such that $p(s) \in I$,*

$$\sum_{s_1 \in S, v_{s_1} = p(s)} P(s_1, s) = 1. \tag{10}$$

The probabilities $P(s_1, s)$ for $p(s) \in B$ must be chosen such that the solution to the following system of n equations in $(\alpha_1, \alpha_2, ..., \alpha_n)$ must be exactly the infinite class of solutions of the form $(\alpha_1, \alpha_2, ..., \alpha_n) = m(k_1, k_2, ..., k_n)$ where $k_1, ..., k_n$ are fixed and m ranges over $\mathbb{R}$.

For $s \in S$ such that $p(s) \in B$, if $s \in S_{\alpha_i}$,

$$\alpha_i = \sum_{j=1}^{n} \alpha_j \sum_{s_1 \in S_{\alpha_j}, v_{s_1} = p(s)} P(s_1, s). \tag{11}$$

Proof. This follows from the definition of n-splittable and properties of a transition matrix.

□

Definition 16. We call a merged dual graph and embedding **meshable** if condition 2 on System 11 is satisfied and for $s_1, s_2 \in S$ such that $v_{s_1} \in I^{\alpha_j}$,

$$P(s_1, s_2) = P^{\alpha_j}(s_1, s_2).$$

The additional condition of the the meshable definition preserves the transition probabilities coming from $s \in S_i$ with $v_s \in I_i$. This makes sense in an experimental context, because the transition probabilities of particles coming from fluid pockets that are not directly connected to the other media should not be affected, since the composition of tunnels originated from those fluid pockets will not be affected by the merging.

Theorem 17. *A meshable merged medium is n-splittable.*

Proof. The additional condition of the definition guarantees that the conditions on System 10 holds. Thus, by Lemma 15, the medium is n-splittable. □

5.1 Symmetric Case

We study the case where the Markov chain D associated to the meshable, merged medium has transition probabilities that preserve sufficient symmetry to be experimentally relevant. These constraints will not impose additional constraints on the transition probabilities defined in the additional condition of the meshable definition, that is, probabilities $P(s_1, s_2)$ for $s \in S_i$ with $v_s \in I_i$. We show that in many cases, the unnormalized stationary distribution of a meshable, symmetric merged medium is determined by the structure of the connections between the original media and is independent of the transition probability values.

We use the following notation. Let E_{CO} be the set of connecting edges, so that $E_{CO} = E \setminus (E_1 \cup E_2 \cup ... \cup E_n)$. We let $\deg_{j,i}$ be the number of connecting edges between G_i and G_j, so that $\deg_{j,i} = |\{(v,w) \in E_{CO} \mid v \in V_i, w \in V_j\}|$. We let $\deg_i$ be the number of connecting edges coming from the medium G_i, so that $\deg_i = \sum_{j \neq i} \deg_{j,i}$.

We now define the constraints imposed by the symmetric condition.

Definition 18. We call a merged medium **symmetric** if the following two conditions are satisfied:

- Given a state s such that $e_s \in E_{CO}$, we know that $P(s_1, s)$ is equal for all s_1 such that $e_{s_1} \notin E_{CO}$.

- Given a state s such that $e_s \in E_{CO}$, we know that $P(s, s_1)$ is equal for all s_1 such that $e_{s_1} \notin E_{CO}$.

Theorem 19. *If a merged medium is meshable and symmetric, then its normalized stationary distribution* $(\alpha_1^*, \alpha_2^*, ..., \alpha_n^*)$ *satisfies the following system of equations:*

For $1 \leq i \leq n$*,*

$$\deg_i \alpha_i = \sum_{j \neq i} \deg_{j,i} \alpha_j \tag{12}$$

We use the following notation in our proof. For a given i, pick a given vertex $v \in B_i$. We let E_{CO}^v be $\{e \in E_{CO} \mid v \in e\}$. We let $\deg_{j,i}^v$ be $|\{(v,w) \in E_{CO} \mid w \in V_j\}|$. We let $\deg_i^v$ be $\sum_{j \neq i} \deg_{j,i}^v$. We will use the following lemma in our proof:

Lemma 20. *In a meshable and symmetric merged media of* n *original media, for a given* $i \leq n$ *and a given* $v \in B_i$*, we have*

$$\deg_i^v \alpha_i = \sum_{j \neq i} \deg_{j,i}^v \alpha_j \tag{13}$$

Proof. By the symmetry condition, for a given $s \in S_i$ such that $e_s \in E_{CO}^v$, we know that $P(s_1, s)$ is equal for all s_1 such that $e_{s_1} \in E_{CO}$. We let this value be u_s.

By (11), we know that

$$\alpha_i = \alpha_i \deg(v) u_s + \sum_{j \neq i} \alpha_j \sum_{s_1 \in S_j, v_{s_1} = v} P(s_1, s)$$

for all $s \in S_i$ such that $e_s \in E_{CO}^v$, where $\deg(v)$ is the degree of v in G. This simplifies to

$$\alpha_i(1 - \deg(v) u_s) = \sum_{j \neq i} \alpha_j \sum_{s_1 \in S_j, v_{s_1} = v} P(s_1, s)$$

for all $s \in S_i$ such that $e_s \in E_{CO}^v$.

If we sum these equations for all $s \in S_i$ such that $e_s \in E^v_{CO}$, we obtain the following:

$$\alpha_i(\deg_i^v - \deg(v) \sum_{s\in S_i \text{ s.t. } e_s\in E^v_{CO}} u_s) = \sum_{j\neq i} \alpha_j \sum_{s_1\in S_j, v_{s_1}=v} \sum_{s\in S_i \text{ s.t. } e_s\in E^v_{CO}} P(s_1, s). \tag{14}$$

By the symmetry condition, for all $j \neq i$, for a given $s_1 \in S_j$ such that $v_{s_1} = v$, we know that $P(s_1, s)$ is equal for all s such that $e_s \notin E_{CO}$. We know this value is

$$\frac{1 - \sum_{s\in S_i \text{ s.t. } e_s\in E^v_{CO}} P(s_1, s)}{\deg(v)}.$$

By (11) and the doubly stochastic condition on each of the original media, we know that

$$\alpha_i = \alpha_i(1 - \sum_{s\in S_i \text{ s.t. } e_s\in E^v_{CO}} u_s) + \sum_{j\neq i} \alpha_j \sum_{s_1\in S_j, v_{s_1}=v} \frac{1 - \sum_{s\in S_i \text{ s.t. } e_s\in E^v_{CO}} P(s_1, s)}{\deg(v)}.$$

This simplifies to

$$\alpha_i \deg(v) \sum_{s\in S_i \text{ s.t. } e_s\in E^v_{CO}} u_s = \sum_{j\neq i} \alpha_j \sum_{s_1\in S_j, v_{s_1}=v} (1 - \sum_{s\in S_i \text{ s.t. } e_s\in E^v_{CO}} P(s_1, s)). \tag{15}$$

Adding (15) and (14), we obtain the following:

$$\deg_i^v \alpha_i = \sum_{j\neq i} \alpha_j \sum_{s_1\in S_j, v_{s_1}=v} (1).$$

This simplifies to the desired equation:

$$\deg_i^v \alpha_i = \sum_{j\neq i} \deg_{j,i}^v \alpha_j.$$

□

Now, we prove Theorem 19.

Proof of Theorem 19. For a given i, we sum (13) over all $v \in B_i$ to obtain the following:

$$\sum_{v\in B_i} \deg_i^v \alpha_i = \sum_{v\in B_i} \sum_{j\neq i} \deg_{j,i}^v \alpha_j$$

If we simplify and consider this equation for $1 \leq i \leq n$, we obtain the following system of equations:

For $1 \leq i \leq n$,

$$\deg_i \alpha_i = \sum_{v \in B_i} \sum_{j \neq i} \deg_{j,i} \alpha_j$$

$\square$

Notice that equations of System 12 sum to 0, demonstrating that they are linearly dependent. Upon deletion of one of the equations, if the remaining equations are linearly independent, then there will be an infinite class of solutions $(\alpha_1, \alpha_2, ..., \alpha_n) = m(k_1, k_2, ..., k_n)$. If $(k_1, k_2, ..., k_n)$ are all nonzero and have the same sign, then there is one unnormalized stationary distribution solution $(\alpha_1^*, \alpha_2^*, ..., \alpha_n^*)$. In this case, the unnormalized stationary distribution is a function of the connecting degrees $\deg_{j,i}$ and is independent of the transition probability values. In an experimental setting, this means that the long-term distribution of particles in the merged media is determined by placement of the connecting tunnels, rather than any properties about cell motion in and out of the tunnels.

In the case of two-dimensions, Theorem 19 significantly limits the possible α and β values. In fact, it follows that:

Corollary 21. *In the case that $n = 2$, if a merged medium is meshable and symmetric, then it has a uniform stationary distribution.*

This corollary essentially states that the symmetry condition coupled with the meshable condition renders impossible a 2-splittable stationary distribution with distinct classes. Thus, our random walk with memory model predicts that if two porous media that each originally have uniform long-term particle distributions are connected by any number of tunnels, then the long-term distribution of particles in the merged media is uniform.

6 Mid Particle Density Case

In this section, we present our preliminary work in constructing a microscopic model for mid particle density that considers shifts in the density distribution rather than the motion of individual particles.

First, we seek to calculate a rough estimate of a transitional density for a given porous medium with dual graph G and associated Markov chain D at which the particle motion leaves the low particle density limit. This is based on the minimum density that yields a nonnegligible probability (say p^*) that a randomly chosen particle collides with one of the other particles. For ease of calculation, we consider particles in the stationary distribution and compute the minimum number of particles on the porous medium necessary for this to occur. Then, it suffices to find the minimum n such that

$$\sum_{v \in V} SD_V^D(v) \cdot (1 - (1 - SD_V^D(v))^{n-1}) > p^*.$$

6.1 Simple Model

In this subsection, we consider a simple microscopic model takes place on the dual graph G defined in Section 2. The particle clumps at a given fluid pocket break apart and move to neighboring fluid pockets, so that the amount of flow to a neighboring fluid pocket is inversely proportional to the density of that fluid pocket.

We define the state space to be V. For a given state v, we define the set of states $n(v) \subset V$

to be the neighbors of v, so that

$$n(v) = \{w \in V \mid (v, w) \in E\}.$$

We model the process as a step-wise process that transforms the density function $\rho : V \to \mathbb{R}$. At stage i, let the density function be ρ_i. Order V as $\{v_1, v_2, \ldots, v_{|V|}\}$. We can represent ρ_i as a row vector $\rho_i^{\to}$ of length $|V|$ so that the j'th element of $\rho_i^{\to}$ is $\rho_i(v_j)$. Then, we obtain $\rho_{i+1}^{\to}$ by $\rho_i^{\to} \cdot P^{\rho_i}$ where P^{ρ_i} is a $|V| \times |V|$ square matrix with $P^{\rho_i}(k, l)$ representing the flow of particles from v_k to v_l from the stage i to the stage $i + 1$. We define $P^{\rho_i}(k, l)$ so that $P(k, l) > 0$ only if $v_k \in n(v_l)$. In that case,

$$P^{\rho_i}(k, l) = \frac{\frac{1}{\rho_i(v_l)}}{\sum_{v \in n(v_k)} \frac{1}{\rho_i(v)}}.$$

Notice that $\sum_{v \in V} P^{\rho_i}(v_k, v) = 1$, as desired. This flow distribution models a higher percentage of particles moving into fluid pockets with a lower density.

We will focus on the case where G is a $1 \times n$ grid. Label the vertices $v_1, v_2, v_3, \ldots, v_n$ in order. We will study the density distribution of the stationary distribution(s) associated to the step-wise model described above. Notice that the stationary distributions are infinite classes of vectors of the form $\alpha \cdot v^{\to}$ for $\alpha \in \mathbb{R}$. For a given stationary distribution $S(G)$, we define ρ_S to be the corresponding density distribution. Notice that $P^{\rho_S}(v_i, v_{i+1}) = P^{\rho_S}(v_{i+1}, v_i)$ for all $1 \leq i \leq n - 1$ and $P^{\rho_S}(v_i, v_j) = 0$ unless $j - 1 = -1, 1$. Also, notice that $\rho_S(v_i) = P^{\rho_S}(v_{i+1}, v_i) + P^{\rho_S}(v_{i-1}, v_i)$, where $P^{\rho_S}(v_i, v_{i+1})$ is taken to be 0 if $i = n$ or $i = 0$. We derive the following relation:

Lemma 22. *In a stationary distribution of a dual graph that is a $1 \times n$ grid, we have*

$$P^{\rho_S}(v_i, v_{i+1}) \cdot \rho_S(v_i) = P^{\rho_S}(v_{i+1}, v_{i+2}) \cdot \rho_S(v_{i+2}).$$

for all $1 \le i \le n-1$.

Proof. We know that

$$P^{\rho_S}(v_{i+1}, v_i) = \rho_S(v_{i+1}) \cdot \frac{\frac{1}{\rho_S(v_i)}}{\frac{1}{\rho_S(v_i)} + \frac{1}{\rho_S(v_{i+2})}}.$$

This means that

$$\frac{P^{\rho_S}(v_{i+1}, v_i)}{P^{\rho_S}(v_i, v_{i+1}) + P^{\rho_S}(v_{i+2}, v_{i+1})} = \frac{\frac{1}{\rho_S(v_i)}}{\frac{1}{\rho_S(v_i)} + \frac{1}{\rho_S(v_{i+2})}}.$$

Taking the inverse gives us,

$$\frac{P^{\rho_S}(v_i, v_{i+1}) + P^{\rho_S}(v_{i+2}, v_{i+1})}{P^{\rho_S}(v_{i+1}, v_i)} = \frac{\frac{1}{\rho_S(v_i)} + \frac{1}{\rho_S(v_{i+2})}}{\frac{1}{\rho_S(v_i)}}.$$

Hence,

$$\begin{aligned}\frac{P^{\rho_S}(v_{i+2}, v_{i+1})}{P^{\rho_S}(v_{i+1}, v_i)} &= \frac{\frac{1}{\rho_S(v_{i+2})}}{\frac{1}{\rho_S(v_i)}} \\ &= \frac{\rho_S(v_i)}{\rho_S(v_{i+2})},\end{aligned}$$

which gives us the desired statement. This relation, coupled with the reflective symmetry about the center of G, enables us to calculate the stationary distributions for small n. We pick a single scalar value of α for each infinite class in the stationary distribution. We have the following approximations (rounded to the nearest hundredth) for $n = 1, 2, 3, 4, 5, 6, 7, 8, 9$.

n	$\rho_{\vec{S}}$
1	[1]
2	[1, 1]
3	[1, 2, 1]
4	[1.62, 2.62, 2.62, 1.62]
5	[1.41, 2.41, 2, 2.41, 1.41]
6	[1.28, 2.15, 1.87, 1.87, 2.15, 1.28]
7	no solution
8	[1.35, 2.28, 1.96, 2.04, 2.04, 1.96, 2.28, 1.35]
9	[1.34, 2.26, 1.95, 2.03, 2, 2.03, 1.95, 2.26, 1.34]

Notice that there is no stationary distribution in the case $n = 7$, but there is exactly one stationary distribution (up to scalar multiplication) for all other n. Notice that each distribution is non-monotonic towards the center and the values have no perceivable closed form. This is unexpected given the simplicity of the microscopic model. □

7 Conclusion

In this study, we conducted a mathematical analysis of a microscopic model of swimming cell motion in porous media. We considered a random walk with one-step memory on the dual graph defined by the fluid pockets on the medium. In the case of low particle density, we presented an analytic solution that generalized the overaching project's computer-generated numerical solutions to a significantly larger class of porous media. We presented properties of the analytic solution that can be implemented in an experimental setting to test the accuracy and validity of the random walk with memory model.

We proved that the splittability of the stationary distribution of porous media whose associated Markov chain is travellable. This implied that the boundary ratio was proportional to the number of tunnels in the interior. We also proved that the long-term distribution of particles in a symmetric, meshable merged media is determined by the placement of connecting tunnels.

We also presented our preliminary work in constructing a microscopic model for mid particle density that considers shifts in the density distribution rather than the motion of individual particles. We considered a simple microscopic model where particle flow was inversely proportional to the density. In the 1-dimensional case, we paradoxically found this model had no stationary distribution for a 1×7 dual graph and yielded an alternating up/down stationary distribution for other small cases.

8 Acknowledgments

I would like to thank my mentor, Andrew Rzeznik of MIT, for his invaluable guidance, and Prof. Jorn Dunkel of MIT for his suggestions and help. I would also like to thank the MIT Math Department — Prof. Jerison and Prof. Moitra — for organizing my research. Furthermore, I would like to thank Dr. Khovanova and Dr. Rickert for their help with my paper and presentation. I would also like to thank RSI, the CEE, MIT, and the following sponsors: Mr. Zelimir Galjanic, Head of Strategic Growth at D. E. Shaw Research, Dr. Ellen J. Maycock, Associate Executive Direction at American Mathematical Society, Ms. Susan Lee Ko, Mr. Klee Dienes, Dr. and Mrs. David E. Keyes, Chaired Professor at Columbia

University, Drs. Phillip and Gina Smith, Director and Engineer Fellow at BAE Systems, Professor Robert Hansen, Senior Associate Dean at Dartmouth, Mr. Dean Kamen, President at DEKA Research and Development, and Dr. Anthony G. Oettinger, Chairman, Program on Information Resources Policy at Harvard University. Lastly, I would like to thank my parents for their continued support.

References

[1] Howard C. Berg. *Random Walks in Biology.* Princeton University Press, 1983.

[2] H. Winet C. Brennen. Fluid mechanics of propulsion by cilia and flagella. *Annu. Rev. Fluid Mech.*, 9(1):339–398, 1977.

[3] Guasto Dunkel. Transport and chemotaxis of swimming cells in porous media flows. *NSF Grant Proposal*, 2014.

[4] J. Field F. Azam, T. Fenchel. The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser*, 10:257–263, 1983.

[5] F. Lopez-Gatius J. Rutllant, M. Lopez-Bejar. Ultrastructural of bovine vaginal fluid and its relation to sperm motility and fertilization: a review. *Reprod. Domest. Anim.*, 40(2):79–86, 2005.

[6] R. Stocker J. S. Guasto, R. Rusconi. Fluid mechanics of planktonic microorganisms. *Annu. Rev. Fluid Mech.*, 44(1):373–400, 2012.

[7] A. Jacob, E. C. Bucharsky, and K. GuenterSchell. The application of transparent

glass sponge for improvement of light distribution in photobioreactors. *J. Bioprocess. Biotech.*, 02(01):1–8, 2012.

[8] George Gaspari Joseph Rudnick. *Elements of the Random Walk*. Cambridge University Press, 2004.

[9] A. K. Mukherjee K. Das. Crude petroleum-oil biodegradation efficiency of bacillus subtilis and pseudomonas aeruginosa strains isolated from a petroleum-oil contaminated soil from north-east india. *Bioresour. Technol.*, 98(7):1339—-45, 2007.

[10] M. Muller K. Dohnt, M. Sauer. An in vitro urinary tract catheter system to investigate biofilm development in catheter-associated urinary tract infections. *J. Microbiol. Meth.*, 87(3):302–308, 2011.

[11] D. L. Kirchman. New light on an important microbe in the ocean. *Proc. Natl. Acad. Sci. U. S. A.*, 105(25):8487–8, 2008.

[12] Ronald G. Larson Nobuhiko Watari. The hydrodynamics of a run-and-tumble bacterium propelled by polymorphic helical flagella. *Biophysical*, 98:12–17, 2010.

[13] E. Stellamanns S. Uppaluri, N. Heddergott. Flow loading induces oscillatory trajectories in a bloodstream parasite. *Biophys. J.*, 103(6):1162–9, 2012.

[14] N. D. Kashikar U. B. Kaupp. Mechanisms of sperm chemotaxis. *Annu. Rev. Physiol.*, 70:93–117, 2008.