



A poroelastic immersed boundary method with applications to cell biology



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ABSTRACT

The immersed boundary method is a widely used mixed Eulerian/Lagrangian framework for simulating the motion of elastic structures immersed in viscous fluids. In the traditional immersed boundary method, the fluid and structure move with the same velocity field. In this work, a model based on the immersed boundary method is presented for simulating poroelastic media in which the fluid permeates a porous, elastic structure of small volume fraction that moves with its own velocity field. Two distinct methods for calculating elastic stresses are presented and compared. The methods are validated on a radially symmetric test problem by comparing with a finite difference solution of the classical equations of poroelasticity. Finally, two applications of the modeling framework to cell biology are provided: cellular blebbing and cell crawling. It is shown that in both examples, poroelastic effects are necessary to explain the relevant mechanics.

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1. Introduction

The immersed boundary (IB) method is a computational method for simulating fluid–structure interaction problems. It has been applied to many biological and physical systems such as blood flow in the heart [1], insect flight [2], and flagellar swimming [3]. In the traditional IB method, the elastic structure moves with the local fluid velocity. The method has been adapted for porous membranes in which the fluid moves through the elastic structure [4,5], and this variant has been applied to problems such as parachute mechanics [4] and suction feeding in jellyfish [6]. However, the porous IB method has been limited to infinitely thin elastic membranes. IB methods have been extended to thick elastic structures, but only for the case when the structure moves with the local fluid velocity [7–9]. Many biological materials, such as the cell cytoplasm [10], brain tissue [11], and blood clots [12], involve immersed structures that are both elastic and porous. In this paper, we are motivated by poroelasticity of the cytoplasm and how its material properties affect cell processes driven by fluid dynamics.

The cytoplasm is the intracellular mixture of organelles, the cytosol, and the cytoskeleton [13]. The cytosol is the liquid portion of the cytoplasm consisting of water, ions, and dissolved molecules. The cytoskeleton is a system of protein filaments in the cytoplasm that give the cell its shape and ability to move. Actin filaments are a major cytoskeletal component that play an important role in cell motility. The cytoplasm has been modeled on the continuum level as an elastic material,

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viscoelastic material, porous gel, and viscous fluid [14–16]. The appropriate rheological description of the cytoplasm depends on the timescale and relevant cellular process under consideration. For example, actin filaments depolymerize and repolymerize on a timescale of minutes. Therefore, an actin network behaves like an elastic material on the timescale of seconds, but a fluid on timescales longer than minutes.

Recent work suggests that cytoplasmic streaming plays an important role in cell motility [17]. The rheological properties of the cytoplasm affect pressure propagation and fluid flow in migrating cells that exhibit cytoplasmic streaming. Some animal cells use blebs, spherical membrane protrusions driven by cytoplasmic flow, for migration [18]. In [19], the authors found cytoplasmic elasticity necessary to limit bleb size. Other recent blebbing experiments support the view of the cytoplasm as a poroelastic material [10]. The relative motion of the cytosol flowing through the cytoskeleton demonstrates that the cytoplasm acts as a two-phase material in blebbing cells. Similarly, in large amoeboid cells, relative motion between cytoplasmic phases has been observed in *Amoeba proteus* [20] and *Physarum polycephalum* [21]. In *Physarum polycephalum* cells, cytoplasmic streaming driven by cytoskeletal contraction corresponds with an increase in cell migration speed [21], which suggests that cytoplasmic streaming drives locomotion. Generally, the role of fluid mechanics in cells that use cytoplasmic streaming for migration is not fully understood.

Motivated by problems involving cytoplasmic steaming and cell locomotion, we propose a novel method for simulating poroelastic structures in a mixed Eulerian/Lagrangian framework. In our formulation, there is a separate force balance equation for the fluid and for the elastic structure, and the two materials are coupled through drag forces. We show that our formulation agrees with the traditional Eulerian formulation of poroelasticity. Elastic forces within the structure are computed using two different methods. The first method extends lattice-spring models, in which elastic structures are discretized by a network of springs, to unstructured grids. We also used the energy-based method for describing hyperelastic materials from [9]. The method is applied to models of cellular blebbing and cell crawling, where we demonstrate the properties of both the fluid and structure are necessary to capture the relevant biological behavior.

2. Mathematical formulation

To describe the mechanics of poroelastic materials, we begin with the two-phase flow model [22], which is often used to describe multicomponent mixtures that consist of an elastic network immersed in a viscous fluid. Each phase moves with its own velocity field and at any given point, the composition of the mixture is described by the volume fractions of the different phases. The velocity of the fluid is denoted by \mathbf{u}_f and the network velocity by \mathbf{u}_n . The volume fraction of the network phase is ϕ and it is assumed to be constant. Since the volume fractions sum to one, the volume fraction of the fluid is $1 - \phi$. For constant density, mass conservation leads to volume averaged incompressibility. For applications in cell biology, the Reynolds number is very small and inertial forces may be neglected. Then, the force density balance for each phase and the volume averaged incompressibility constraint are given by

$$\nabla \cdot \boldsymbol{\sigma}_f - (1 - \phi)\nabla p + \xi(\mathbf{u}_n - \mathbf{u}_f) = 0 \quad (\text{fluid}) \quad (1)$$

$$\nabla \cdot \boldsymbol{\sigma}_e - \phi\nabla p + \xi(\mathbf{u}_f - \mathbf{u}_n) = 0 \quad (\text{network}) \quad (2)$$

$$\nabla \cdot (\phi\mathbf{u}_n + (1 - \phi)\mathbf{u}_f) = 0, \quad (\text{mixture incompressibility}) \quad (3)$$

where the $\boldsymbol{\sigma}_i$'s indicate fluid and elastic stress tensors, p is the pressure, and ξ is the drag coefficient between the network and the fluid. The elastic stress tensor $\boldsymbol{\sigma}_e$ is given by the appropriate constitutive law (provided in the next section). For a Newtonian fluid, the fluid stress is given by

$$\boldsymbol{\sigma}_f = \mu(\nabla\mathbf{u}_f + \nabla\mathbf{u}_f^T) + \lambda(\nabla \cdot \mathbf{u}_f)\mathcal{I}, \quad (4)$$

where μ is the shear fluid viscosity and λ is the second coefficient of viscosity.

We note here that by assuming that $\boldsymbol{\sigma}_f$ is negligible, one can derive the standard model of poroelastic media given in [23]. By adding (1) and (2), the drag term can be eliminated from the network force density balance. Similarly, rearrangement of (1) results in a Darcy law governing the fluid. This yields the system

$$\nabla \cdot \boldsymbol{\sigma}_e - \nabla p = 0 \quad (5)$$

$$\mu(\mathbf{u}_f - \mathbf{u}_n) = -\kappa\nabla p. \quad (6)$$

Here the quantity $\kappa = \mu(1 - \phi)/\xi$ is interpreted as the Darcy permeability of the network. Indeed, for materials of known permeability, we calculate the drag parameter using $\xi = \mu(1 - \phi)/\kappa$. This technique is used for numerical simulations performed in Section 4. Because we wish to investigate problems where regions of porous media exist in contact with regions of viscous fluid, it is inappropriate to assume that fluid stress is negligible throughout the whole domain. By maintaining the term $\boldsymbol{\sigma}_f$, we leverage the machinery of the IB method to treat this scenario in a single unified framework.

Because the aim of this work is to simulate the poroelastic cytoskeleton, and the volume fraction of the cytoskeletal network is negligible in comparison to the fluid phase [24], we consider the case when $\phi \ll 1$. Under the assumption of vanishing network volume fraction, (1)–(3) simplify to

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