1. Summary of the method of generalized Taylor dispersion.

First, let us suppose that a population satisfies the following advection-diffusion equation:

$$\frac{\partial n}{\partial t} = -\nabla.(\boldsymbol{x}.\mathsf{G}n - \mathsf{D}.\nabla n).$$

Here we are assuming the cells have no preferred direction and so the advection term only represents the fluid velocity which is homogeneous shear and the reference frame is chosen so the fluid velocity is zero at the origin.

If we change to a reference frame deforming with the fluid, the codeformational transformation,

$$\boldsymbol{x}^1 = \boldsymbol{x}.e^{-\mathsf{G}t},$$

which in Cartesian components under standard summation convention can be written as

$$x_j^1 = x_i \left(e^{-\mathsf{G}t}\right)_{ij},$$

we can remove the fluid advection term from the governing equation:

$$\frac{\partial n}{\partial t} = \nabla_{\boldsymbol{x}^1}.(e^{-\mathsf{G}^T t}.\mathsf{D}.e^{-\mathsf{G}t}).\nabla_{\boldsymbol{x}^1} n.$$

We shall drop the ^{1} in the subsequent analysis for notational simplicity.

We define the spatial moments of concentration:

$$M_m = \int \boldsymbol{x}^m n d\boldsymbol{x}.$$

Computing the second spatial moment of the governing equation gives an expression relating the diffusion tensor to the second spatial moment of concentration:

$$\frac{dM_2}{dt} = 2e^{-\mathsf{G}^T t}.[\mathsf{D}]^{sym}.e^{-\mathsf{G}t} M_0. \tag{1.1}$$

This result is derived under the assumption that n decays sufficiently rapidly to zero at the outer spatial boundary. We now have an explicit expression describing the effect of the shear on the dispersion.

Now, let us instead start with the following micro-scale model for $P(\boldsymbol{p}, \boldsymbol{x}, t)$, the probability of finding a cell with orientation $\boldsymbol{p}$ at position $\boldsymbol{x}$ at time t, given by the equation:

$$\frac{\partial P}{\partial t} + \nabla_{\boldsymbol{x}}.((\boldsymbol{x}.\mathsf{G} + v_s \boldsymbol{p})P) + d_r \mathcal{L} P = 0.$$

Here we have again assumed the fluid velocity is homogeneous shear and the reference frame is chosen so the fluid velocity is zero at the origin.

Generalized Taylor dispersion aims to obtain a governing equation for the cell concentration $n(\boldsymbol{x}, t) = \int P d\boldsymbol{p}$. Here we outline the method in the case where there is no swimming bias. Extending to the case where bias is included is fairly straightforward, and can be derived by following the details given in Frankel & Brenner (1991, 1993).

Changing to the codeformational reference frame, and then non-dimensionalising based on a length-scale L and diffusion time-scale $d_r L^2/v_s^2$, we obtain the following governing equation:

$$\epsilon^2 \frac{\partial P}{\partial t} + \epsilon \nabla_{\boldsymbol{x}^1}.(\boldsymbol{p}.e^{-\mathsf{G}t} P) + \mathcal{L} P = 0,$$

where ϵ is as defined by equation:

$$\epsilon = \frac{v_s}{L d_r}. \tag{1.2}$$

. On integrating this governing equation, we find that the spatial moments of P, given by

$$P_m = \int \boldsymbol{x}^m P d\boldsymbol{x},$$

satifsy the following coupled equations:

$$\epsilon^2 \frac{\partial P_0}{\partial t} + \mathcal{L} P_0 = 0$$
$$\epsilon^2 \frac{\partial P_1}{\partial t} + \mathcal{L} P_1 = \epsilon \boldsymbol{p}.e^{-\mathsf{G}t} P_0$$
$$\epsilon^2 \frac{\partial P_2}{\partial t} + \mathcal{L} P_2 = 2\epsilon[\boldsymbol{p}.e^{-\mathsf{G}t} P_1]^{sym}.$$

c.f. equation (3.6a), Frankel & Brenner (1991). This result is derived under the assumption that P decays sufficiently rapidly to zero at the outer spatial boundary.

As detailed in Frankel & Brenner (1991), on timescales long compared to the microscopic relaxation time d_r, that is for $\epsilon \ll 1$, the non-stationary contribution to the density vanishes exponentially rapidly and we can relate P_0 and P_1 to f and $\boldsymbol{b}$ defined in the main paper:

$$\lim_{t\to\infty} P_0 = f$$
$$\lim_{t\to\infty} P_1 = \epsilon \boldsymbol{b}.e^{-\mathsf{G}t}.$$

Integrating the equation for P_2 over orientation space gives the following expression for the second moment of cell concentration, $M_2 = \int P_2 d\boldsymbol{p}$:

$$\frac{dM_2}{dt} = 2e^{-\mathsf{G}^T t}.[\int \boldsymbol{p}\boldsymbol{b} d\boldsymbol{p}]^{sym}.e^{-\mathsf{G}t}. \quad (1.3)$$

Comparing the expressions for the second moments, equations (1.1, 1.3), and noting that $M_0 = 1$, we assert that if the population of cells undergoing a random walk in homogeneous shear satisfies an advection-diffusion equation, then the diffusion tensor is given by

$$\mathsf{D} = [\int \boldsymbol{p}\boldsymbol{b} d\boldsymbol{p}]^{sym}. \quad (1.4)$$

If we compare this with the expression given in the main paper for the diffusion:

$$\mathsf{D} = \int_0^{2\pi} [\boldsymbol{b}\boldsymbol{p} + \frac{Pr}{f}\boldsymbol{b}\boldsymbol{b}.\hat{\mathsf{G}}]^{sym} d\theta, \quad (1.5)$$

) we see that there is additional term to ensure that the diffusion tensor is positive definite. This has been shown not to alter the long term spatial moments (Frankel & Brenner 1991, 1993).

In the case where the eigenvalues of G have zero real part, Frankel & Brenner (1991, 1993), carefully considered all the higher order moments and were able to show that all the spatial moments agree with the expected solution of the advection-diffusion equation and therefore the cells do satisfy an advection-diffusion equation. What is still not understood is what the population model should be for straining-dominated flow.

2. Calculation of two-dimensional spatial distribution, small Pe asymptotics.

For gravitactic cells, at equilibrium, the cell concentration satisfies the following:

$$\nabla.((Pe\boldsymbol{V} + \frac{1}{\epsilon}\overline{p}_y\boldsymbol{j})n - \mathsf{D}.\nabla n = 0, \tag{2.1}$$

where the non-dimensional diffusion tensor, D, is diagonal. The no-flux boundary conditions are given by

$$-D_{xx}\frac{\partial n}{\partial x} = 0, \quad \text{at} \quad x = 0, 1$$
$$\frac{1}{\epsilon}\overline{p}_y n - D_{yy}\frac{\partial n}{\partial y} = 0, \quad \text{at} \quad y = 0, 1.$$

When $Pe = 0$, the equilibrium solution is $n_0 e^{\nu y}$. Inserting an asymptotic solution for small Pe:

$$n = n_0 e^{\nu y} + Pe n'(x, y) + O(Pe^2),$$

into equation (2.1) gives the following expression at $O(Pe)$:

$$\frac{1}{\epsilon}\overline{p}_y\frac{\partial n'}{\partial y} - D_{xx}\frac{\partial^2 n'}{\partial x^2} - D_{yy}\frac{\partial^2 n'}{\partial y^2} = -n_0\nu V_y e^{\nu y}.$$

For the simple convection flow field, $V_y = -\pi\cos(\pi x)\sin(\pi y)$, we can let

$$n' = n_0 \cos(\pi x) f(y)$$

which automatically satisfies the no-flux boundary conditions at $x = 0, 1$ and results in a linear constant coefficient differential equation for $f(y)$:

$$\nu f' + r\pi^2 f - f'' = \frac{\nu\pi}{D_{yy}} \sin(\pi y) e^{\nu y},$$

where r is the ratio of the diagonal entries in the diffusion tensor, $r = D_{xx}/D_{yy}$. This has general solution

$$f = ae^{\alpha y} + be^{\beta y} + (A\sin(\pi y) + B\cos(\pi y))e^{\nu y},$$

where the following constants are defined:

$$\alpha = \nu/2 + \sqrt{(\nu/2)^2 + r\pi^2}, \quad \beta = \nu/2 - \sqrt{(\nu/2)^2 + r\pi^2}$$
$$A = \frac{\pi(r+1)\nu}{D_{yy}(\pi^2(r+1)^2 + \nu^2)}, \quad B = \frac{\nu^2}{D_{yy}(\pi^2(r+1)^2 + \nu^2)}.$$

The constants a and b are found by imposing the no-flux boundary conditions at the walls $y = 0, 1$:

$$\nu f - f' = 0, \quad \text{at} \quad y = 0, 1,$$

which yields

$$a = \frac{A\pi(e^{\beta} + e^{\nu})}{(e^{\beta} - e^{\alpha})(\nu - \alpha)}, \quad b = \frac{A\pi(e^{\alpha} + e^{\nu})}{(e^{\alpha} - e^{\beta})(\nu - \beta)}.$$

The validity of this approximation is examined in figure 1 for a range of Pe and κ: for increasing gravitactic bias in swimming, κ, the approximation is valid for a decreasing range of values of Pe.

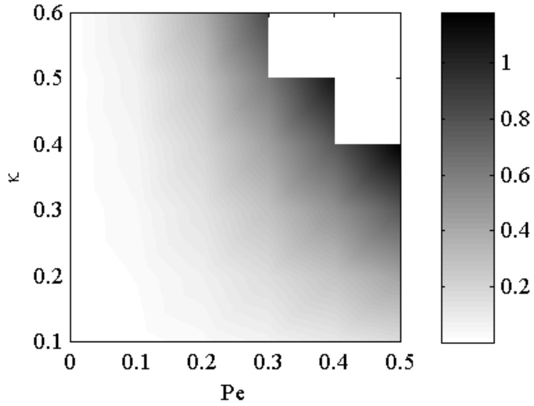

FIGURE 1. The absolute error maximised over all computational mesh points computed as a function of Pe and κ. The error is the difference between the asymptotic approximation and the numerical solution of the full advection-diffusion equation for spherical cells. Maximum values of the error were computed at increments of 0.1 in Pe and κ and interpolated bilinearly. (κ, Pe) pairs in the top right corner yield regions of negative concentration in the asymptotic approximation and so were removed from the analysis.

REFERENCES

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