

Stirring by squirmers

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We analyse a simple ‘Stokesian squirmer’ model for the enhanced mixing due to swimming micro-organisms. The model is based on a calculation of Thiffeault & Childress (*Phys. Lett. A*, vol. 374, 2010, p. 3487), where fluid particle displacements due to inviscid swimmers are added to produce an effective diffusivity. Here we show that, for the viscous case, the swimmers cannot be assumed to swim an infinite distance, even though their total mass displacement is finite. Instead, the largest contributions to particle displacement, and hence to mixing, arise from random changes of direction of swimming and are dominated by the far-field stresslet term in our simple model. We validate the results by numerical simulation. We also calculate non-zero Reynolds number corrections to the effective diffusivity. Finally, we show that displacements due to randomly swimming squirmers exhibit probability distribution functions with exponential tails and a short-time superdiffusive regime, as found previously by several authors. In our case, the exponential tails are due to ‘sticking’ near the stagnation points on the squirmer’s surface.

Key words: mixing, micro-organism dynamics

1. Introduction

Swimming creatures affect their environment in many ways, and one which has received attention recently is how they mix the surrounding fluid. This phenomenon is called biogenic mixing or biomixing. The most striking and controversial setting is the ocean: Dewar *et al.* (2006) suggested that marine life might have an impact on vertical mixing in the ocean.

Katija & Dabiri (2009) proposed that the dominant effect involved in biomixing is the mass displacement due to a swimming body. This phenomenon is called Darwinian drift, after Darwin (1953), though the displacement due to a moving cylinder was obtained by Maxwell (1869). Thiffeault & Childress (2010) derived the effective diffusivity of an ‘ideal gas’ of randomly distributed non-interacting swimmers, and showed that it depends on the induced squared displacement of fluid particles by the swimmers, as opposed to the net mass displaced.

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In this paper, we apply the techniques of Thiffeault & Childress (2010) to swimmers in the low-Reynolds-number regime. Since the experiments of Wu & Libchaber (2000), there has been considerable work in that direction. Two general types of swimmer arise: pushers or pullers, depending on whether the propulsion takes place ahead or behind the swimmer's centre of mass. Several authors (Dombrowski *et al.* 2004; Hernandez-Ortiz, Dtolz & Graham 2006; Saintillan & Shelley 2007; Underhill, Hernandez-Ortiz & Graham 2008) have pointed out that, at high volume fractions, the pushers align spontaneously with their neighbours, producing large-scale motions. At low volume fractions, pushers and pullers behave similarly, moving in a relatively uncorrelated manner. It is this limit that we treat in this paper. We use the 'squirmers' model of Lighthill (1952) and Blake (1971), where a swimmer is modelled as a sphere in Stokes flow with a prescribed tangential velocity distribution. These have been recently studied by Ishikawa & Pedley (2007) and Drescher *et al.* (2009) as models of the green alga *Volvox*. Squirmers could also be appropriate for *Chlamydomonas* (Leptos *et al.* 2009; Drescher *et al.* 2010; Guasto, Johnson & Gollub 2010), as the observed velocity fields resemble those of the models described here. We find a formula for the effective diffusion coefficient due to the squirmers, and show that it depends predominantly on the far-field displacements imposed by the swimmer. Moreover, the dominant contributions arise from the turning motion of the swimmers, in sharp contrast to the potential flow case (Thiffeault & Childress 2010) where the path length of straight swimming could be considered infinite for all practical purposes. We also show that the probability distribution function (p.d.f.) of displacements due to squirmers has exponential tails, as in Leptos *et al.* (2009), and that it exhibits a short-time superdiffusive regime as in Wu & Libchaber (2000).

The formula we derive for the effective diffusivity has a wide applicability beyond squirmers, for instance to swimmers at larger Reynolds numbers with wakes. In that spirit, we derive finite (but small) Reynolds number corrections to the effective diffusivity using the Oseen form for the far field, and find that the effective diffusivity falls off as $Re^{-0.61}$ from its Stokes (zero Re) value.

2. Computing the effective diffusivity

We first consider a single swimmer in two or three dimensions that moves in a straight line at constant speed U for a distance λ . For simplicity, the swimmer is assumed axially symmetric with characteristic size ℓ , and moves along its axis of symmetry. We are concerned with the effect of the swimmer on a target Lagrangian particle. There are two 'impact parameters' necessary to describe such a situation: the initial perpendicular distance to the particle, $a \geq 0$, and the relative distance b of the start of the trajectory to the point of initial closest approach (see figure 1). Note that b may be positive or negative, and is positive if closest approach would occur at a positive time. After the swimmer traverses its full path length λ , the target particle is displaced by a distance $\Delta_\lambda(a, b)$.

Inspired by Einstein's theory of Brownian motion (Einstein 1956) and following Thiffeault & Childress (2010), we now model the displacement of the target particle after M encounters with swimmers as a series of 'kicks', each of which moves the particle by $\Delta_\lambda(a_k, b_k)$ in some random direction $\hat{\mathbf{r}}_k$. The position \mathbf{x}_M of the particle is

$$\mathbf{x}_M = \mathbf{x}_0 + \sum_{k=1}^M \Delta_\lambda(a_k, b_k) \hat{\mathbf{r}}_k, \quad (2.1)$$

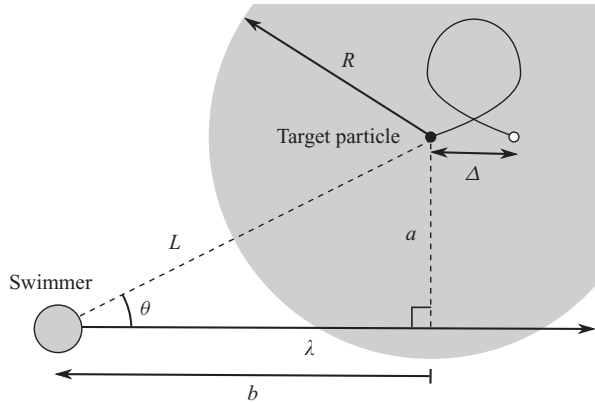


FIGURE 1. Definition of impact parameters a and b , displacement $\Delta = \Delta_\lambda(a, b)$, and swimming path length λ . In this figure, the parameter b is positive; negative b corresponds to the swimmer starting its trajectory past the point of initial closest approach. The filled dot is the initial position of the target particle and the hollow dot is its final position after the swimmer has moved by a distance λ . The ‘interaction disk’ of radius R is also shown.

and we will assume that $\mathbf{x}_0 = 0$. The swimmers are assumed identical and non-interacting, and the encounters are taken to be statistically independent. Their directions of swimming are assumed isotropically distributed. In this case, the mean-squared displacement after M such encounters is given by

$$\langle |\mathbf{x}_M|^2 \rangle = \sum_{k=1}^M \langle \Delta_\lambda^2(a_k, b_k) \rangle = M \langle \Delta_\lambda^2(a, b) \rangle, \quad (2.2)$$

because a_k and b_k are identically distributed for each encounter, with the brackets denoting an average over a and b . (We could also average over distributions of λ and U , but we assume constant values for simplicity.) Our theory will apply in the dilute limit, which we will define more carefully below.

The displacement Δ_λ is assumed small compared to λ , so that we can regard the target particle as approximately fixed during an encounter. We assume that each swimmer advances by a fixed length λ and then changes direction randomly, so after a time t , Ut/λ such direction changes have occurred. For the two-dimensional case, the number of swimmers in a ring of radius L and thickness dL around the target particle is $2\pi nL dL$, where n is the number density of swimmers. To define an encounter, we introduce an ‘interaction disk’ (sphere in three dimensions) of radius R around the target particle (see figure 1), and consider an encounter as occurring when a swimmer enters that disk. If a swimmer does not enter the interaction disk, then the motion of the target particle is negligible. The interaction disk allows us to be more precise about what we mean by a dilute suspension of swimmers: we require $nR^2 \ll 1$ ($nR^3 \ll 1$ in three dimensions) so that encounters are isolated from each other.

The expected number M of such encounters after a time t is best written in terms of integrals over $a = |L \sin \theta|$ and $b = L \cos \theta$:

$$M = \frac{2nUt}{\lambda} \int_0^R \int_{-\sqrt{R^2-a^2}}^{\lambda+\sqrt{R^2-a^2}} db da = 2nRUt + \pi nUt \frac{R^2}{\lambda}. \quad (2.3)$$

For large path length, $\lambda \gg R$, the final term can be neglected, and we obtain the same expression as in Thiffeault & Childress (2010), where an infinite path length was assumed: for large path length, the frequency of encounters is independent of λ .

Next we compute the average squared displacement (see (2.2)) by integrating Δ_λ^2 :

$$M\langle\Delta_\lambda^2\rangle = \frac{2nUt}{\lambda} \int_0^R \int_{-\sqrt{R^2-a^2}}^{\lambda+\sqrt{R^2-a^2}} \Delta_\lambda^2(a, b) db da. \quad (2.4)$$

We assume that $\Delta_\lambda(a, b)$ decays rapidly for large $a \gg \ell$, where ℓ is the characteristic size of a swimmer. In that case, we can replace $R \gg \ell$ by infinity; after also replacing \mathbf{x}_M by $\mathbf{x}(t)$ we obtain

$$\langle|\mathbf{x}(t)|^2\rangle = \frac{2nUt}{\lambda} \int_0^\infty \int_{-\infty}^\infty \Delta_\lambda^2(a, b) db da =: 4\kappa t \quad (\text{two dimensions}), \quad (2.5)$$

where we introduced the effective diffusivity κ . In three dimensions, the analogous expression can be easily shown to be

$$\langle|\mathbf{x}(t)|^2\rangle = \frac{2\pi nUt}{\lambda} \int_0^\infty \int_{-\infty}^\infty a \Delta_\lambda^2(a, b) db da =: 6\kappa t \quad (\text{three dimensions}). \quad (2.6)$$

Note that the ‘interaction disk’ of radius R has disappeared from (2.5) and (2.6): because of the rapid decay of $\Delta_\lambda(a, b)$ with a , we are free to overcount encounters when computing $\langle|\mathbf{x}(t)|^2\rangle$ because faraway encounters hardly displace the target particle.

Thiffeault & Childress (2010) discussed models based upon potential flow past a cylinder or a sphere and made use of an approximate form of (2.5)–(2.6). The approximate form effectively assumes that the particle does not move unless the swimmer actually crosses the point of initial closest approach (a good approximation for potential flow; see figure 4a). Thus, $\Delta_\lambda(a, b)$ takes the ‘top-hat’ form:

$$\Delta_\lambda(a, b) = \begin{cases} \Delta(a), & \text{if } 0 < b < \lambda, \\ 0, & \text{otherwise.} \end{cases} \quad (2.7)$$

This approximation works very well for potential flow. With the approximate form (2.7), the effective diffusivities defined by (2.5)–(2.6) become

$$\kappa = \begin{cases} \frac{1}{2}Un \int_0^\infty \Delta^2(a) da, & (\text{two dimensions}), \\ \frac{\pi}{3}Un \int_0^\infty a \Delta^2(a) da, & (\text{three dimensions}), \end{cases} \quad (2.8)$$

as in Thiffeault & Childress (2010). Because the potential flow approximation is inappropriate for micro-organisms, we will not use (2.8) but rather take the full form (2.5)–(2.6).

Note that the number density scaling of (2.5)–(2.6) was derived by Underhill *et al.* (2008) using the Green–Kubo formula, but here we get explicit values for the prefactor. As we will see below, this allows us to determine where the dominant contribution to κ arises from. In addition, the dimensionless prefactor can vary significantly depending on the swimmer under consideration.

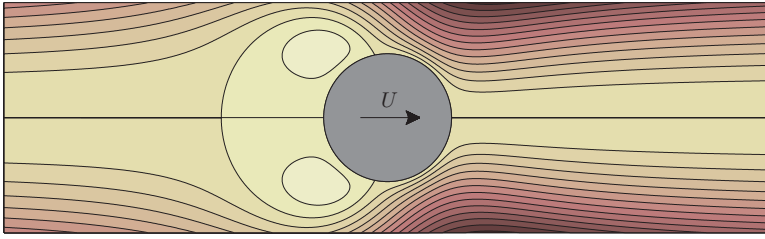


FIGURE 2. (Colour online) Streamfunction contours for a steady squirmer with $\beta = 5$ in a comoving reference frame. Note the wake or closed ‘bubble’ behind the squirmer.

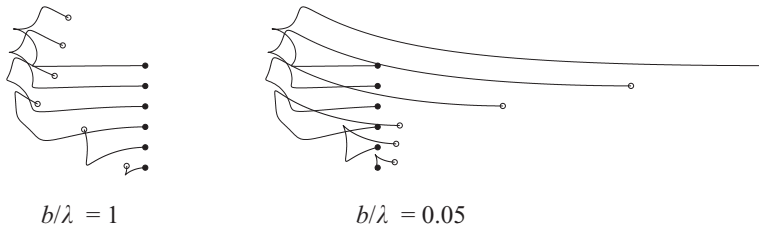


FIGURE 3. Typical trajectories of a target particle in the fixed laboratory frame for different values of a and b due to a single squirmer moving from left to right, with $\ell = U = 1$, $\lambda = 100$ and $\beta = 5$. The trajectories are offset vertically for clarity. The initial positions of the particle are marked by solid dots and the final positions by hollow dots. In each panel, solid dots from top to bottom correspond to $\log(a/\ell) = 2, 1, 0, -1, -2, -3$.

3. Stirring by squirmers

Squirmers are a simple model of swimming micro-organisms in the Stokesian regime. Lighthill (1952) first introduced the model and Blake (1971) later extended the analysis. Recently, the squirmer model has been applied to describe the behaviour of slow-moving ciliates (see, for example, Ishikawa, Simmonds & Pedley 2006, Ishikawa & Pedley 2007 and Drescher *et al.* 2009), whose motion is propelled by arrays of pulsating cilia on their surface. A squirmer is generally a three-dimensional sphere moving in a Stokesian fluid with velocity field prescribed on its boundary. The velocity field generated by such a squirmer is derived by an expansion of solutions obtained by separation of variables. The steady swimming imposes a force-free condition between the fluid and the body which, in turn, translates to algebraic equations for the expansion coefficients of the solution.

Following Ishikawa *et al.* (2006), we choose a specific instance of an axially symmetric squirmer of radius ℓ , swimming along the positive z -axis at a constant speed U . Its free-space, steady, axisymmetric streamfunction in a comoving reference frame is

$$\psi(\rho, z) = \frac{1}{2}\rho^2 U \left(-1 + \frac{\ell^3}{r^3} + \frac{3\beta\ell^2 z}{2r^3} \left(\frac{\ell^2}{r^2} - 1 \right) \right) \quad (3.1)$$

in cylindrical coordinates where $r = \sqrt{\rho^2 + z^2} = \sqrt{x^2 + y^2 + z^2}$. The stresslet coefficient β is a free, dimensionless parameter, and the special case $\beta = 0$ corresponds to a sphere in potential flow; we shall take $\beta = 5$ in numerical examples as in Ishikawa *et al.* (2006). Figure 2 shows the contours of the streamfunction (3.1) for a squirmer swimming from left to right, and figure 3 shows typical trajectories of a passive target particle displaced by the squirmer with different values of the impact parameters

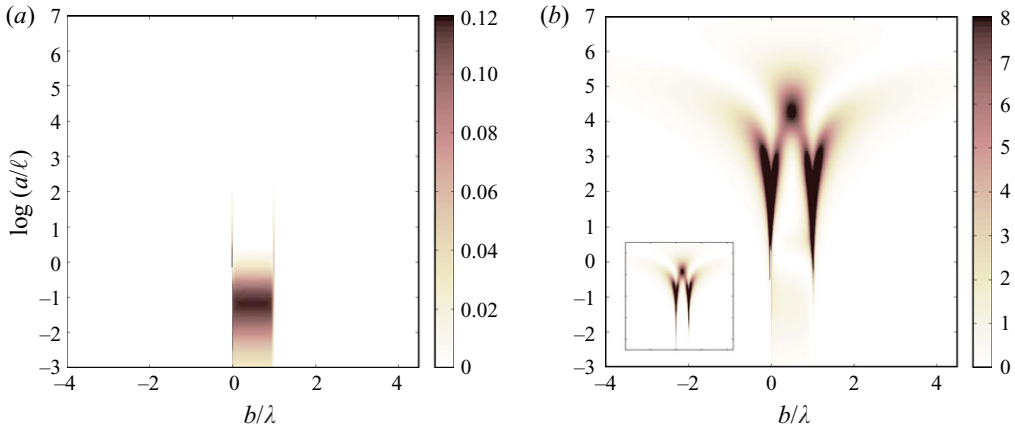


FIGURE 4. (Colour online) Integrand $\ell^{-4}a^2\Delta_\lambda^2(a, b)$ from (3.2) due to (a) potential flow past a sphere; (b) a squirmer with $\beta = 5$; the near-field potential-flow pattern can be dimly seen for $\log a < 0$, but is much weaker than the far-field contribution. Inset: integrand corresponding to the far-field approximation of the squirmer flow. In all figures, $\ell = U = 1$ and $\lambda = 100$.

a and b . These types of trajectories were discussed by Dunkel *et al.* (2010) in the context of swimming organisms.

Compared with the fore–aft symmetry of the potential flow case, $\beta = 0$, a squirmer with $\beta > 0$ has a downstream wake or ‘bubble’, which we will discuss in §4. In addition, a passive particle displaced by the squirming motion experiences a much larger excursion when the swimmer is still more than several body lengths away from the point of initial closest approach, while, in potential flow, this contribution is negligible to the total displacement. This suggests that the finite-path displacement function $\Delta_\lambda(a, b)$ due to a squirmer has a more complicated dependence on the details of the swimming path through the values of a , b and λ . A direct consequence of this feature is that the diffusivity integral can no longer be reduced to one dimension by restricting the integration domain of b as in (2.7). Instead, the full two-dimensional integral (2.6) has to be computed.

Thiffeault & Childress (2010) showed that the integrals (2.5) and (2.6) for potential swimmers are dominated by ‘head-on’ collisions, namely, significant particle displacement occurs only when the impact parameter $a \lesssim \ell$ and when the swimmer passes by the particle. We next investigate the dominant contribution of the integral for the squirmers (2.6). Transforming the integral as

$$\lambda^{-1}\ell^{-4} \int_{-\infty}^{\infty} \int_0^{\infty} a \Delta_\lambda^2(a, b) da db = \int_{\mathbb{R}^2} \ell^{-4} a^2 \Delta_\lambda(a, b) d \log(a/\ell) d(b/\lambda), \quad (3.2)$$

we compare in figure 4 the spatial distributions of the dimensionless integrand $\ell^{-4}a^2\Delta_\lambda^2(a, b)$ due to a sphere in potential flow and a squirmer in Stokes flow, for $\ell = U = 1$ and $\lambda = 100$, in the $\log(a/\ell)$ – (b/λ) plane. The far-field stresslet-only approximation to the displacement for a squirmer is also plotted as an inset in figure 4(b). The inset plot is almost identical to the full plot for any $\lambda \gg \ell$. Note that there is a vertical strip near $b = 0$ in each figure which corresponds to the situation where the initial particle position is inside the swimmer or its wake and is therefore excluded in the calculations. We shall return to the effect of particles trapped in the wake in §4.

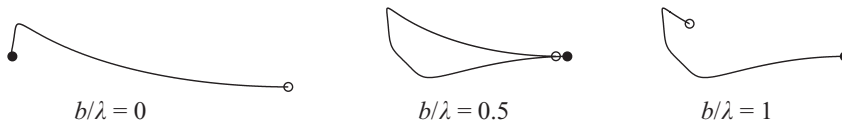


FIGURE 5. Trajectories of target particle for $a/\ell = 1.1$ and different values of b . The filled dot is the initial position of the target particle and the hollow dot is its final position after the swimmer has moved by a distance $\lambda = 100$ to the right. The net displacement is small at $b = \lambda/2$ because of cancellation as the particle moves towards and then follows the swimmer.

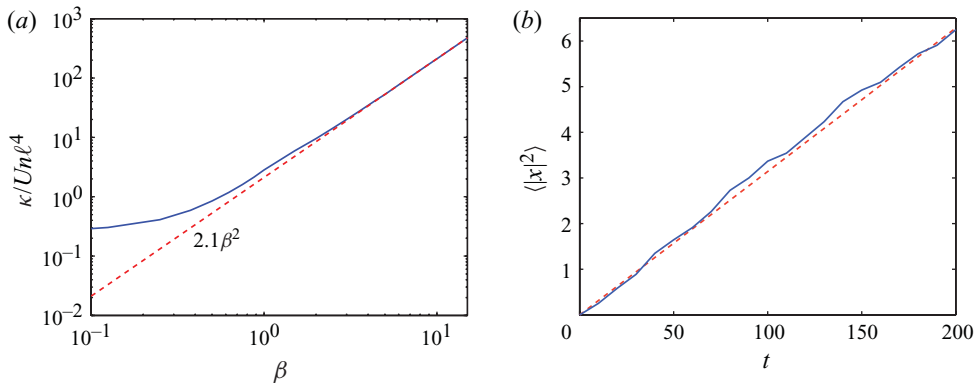


FIGURE 6. (Colour online) (a) Dependence of effective diffusivity on β for $\lambda \gg \ell$: the solid line is the numerical integration of (2.6) with Δ_λ computed with the streamfunction (3.1). For large λ , κ is independent of λ . The dashed line is the effective diffusivity only due to the stresslet term. (b) The mean-squared displacement (solid line) of a target particle for 2×10^6 realisations of 10 squirmers, with $\ell = U = 1$. The dashed line is the squared displacement predicted by (3.3), using a number density $n = 10^{-8}\ell^{-3}$.

For a sphere in potential flow, the dominant contributions to (3.2) come from a rectangle (figure 4a) where the values of the integrand are nearly uniform in b for $b \in [0, \lambda]$. This justifies the approximation (2.7). However, for a squirmer, the dominant contributions to the integral (3.2) come from a much larger and irregular region with $a/\ell \gtrsim 1$. The contribution from this region is negligible in the potential case.

What explains the strong peaks in figure 4(b) along the lines $b/\lambda = 0$, $b/\lambda = 1$? Figure 5 provides the answer: a target particle with $b/\lambda = 1/2$ undergoes a sizable excursion, but has a small net displacement since it moves towards and then follows the squirmer, giving back a large part of the displacement it first underwent. In contrast, for $b/\lambda = 0$ and $b/\lambda = 1$ the squirmer starts or stops (i.e. changes direction) before the particle reverses direction and gives back its displacement.

Now that we know where the contributions to (3.2) arise from, we apply the basic theory to the squirmer model and find that

$$\kappa = 57.0 Un\ell^4, \quad \lambda \gg \ell, \quad (3.3)$$

which is more than 200 times bigger than the effective diffusivity due to potential swimmers under the same set of parameters. One source of this large enhancement comes from the free parameter β , equal to 5 here. Since, at far field, the dominant perturbation to the uniform flow in the streamfunction (3.1) is multiplied by β , we expect that for large β , $\kappa \approx 2.1\beta^2 Un\ell^4$ (the far-field value, with coefficient fitted in figure 6a), whereas the diffusivity converges to the potential value $0.266 Un\ell^4$ as

$\beta \rightarrow 0$. Figure 6(a) shows how different values of β change the effective diffusivity κ . Using the far-field form of our model, we can recover the diffusivity $1.53 \mu\text{m}^2 \text{s}^{-1}$ measured by Leptos *et al.* (2009), for volume fraction 1.6 %, velocity $U = 100 \mu\text{m s}^{-1}$ and size $\ell = 5 \mu\text{m}$, using a stresslet amplitude $\beta = 0.6$. The linearity of the diffusivity in the velocity and volume fraction (for dilute suspensions) has been pointed out by Underhill *et al.* (2008) and Leptos *et al.* (2009), but is verified here from first principles with computed prefactors.

Next we validate the results with direct simulations conducted as in Thiffeault & Childress (2010). For each trial, we use 10 randomly distributed, non-interacting squirmers with $\ell = U = 1$ moving in random initial directions in a large periodic box of size 1000. Each squirmer moves in a straight line for a length $\lambda = 100$ and then turns in a new random direction. The turning times are randomised so that all the squirmers do *not* turn simultaneously. The displacement statistics are identical when this asynchrony is relaxed. The target particle initially at the origin is displaced by the superposition of the flows created by each squirmer. (This is a good approximation at such low densities.) Figure 6(b) shows the mean-squared displacement $\langle |x|^2 \rangle$ of a target particle over 2×10^6 trials (realisations). The agreement between the solid curve (numerically simulated $\langle |x|^2 \rangle$) and the dashed line ($6\kappa t$ with κ computed with the integral (2.6)) verifies the theoretical prediction. We also simulated a large number of particles advected by a single realisation of 30 squirmers: the squared displacement averaged over all the particles obeys the theory for large times, as expected.

4. Wake transport

In the previous section, we have ignored the wake or closed ‘bubble’ behind the squirmer, visible in figure 2, since it is helpful to treat it separately. Assume that a particle is initially trapped in the swimmer’s wake: it will then be displaced by the full swimmer’s path length λ , until the swimmer changes direction and new particles are introduced in the wake. We can thus approximate the displacement Δ_λ to be equal to λ if the particle is inside the wake. The wake contribution to the effective diffusivity is then obtained from (2.6) as

$$\kappa_{\text{wake}} = \frac{Un}{6\lambda} \lambda^2 \int_{\text{wake}} 2\pi a \, da \, db = \frac{1}{6} Un V_{\text{wake}} \lambda, \quad (4.1)$$

where V_{wake} is the volume of the wake ‘bubble’. Note that nV_{wake} is the total volume fraction of wake bubbles in the fluid. The wake effective diffusivity (4.1) is potentially much larger than that due to displacements outside the wake bubble, since (4.1) is directly proportional to λ . In practice, many swimmers do not exhibit a wake bubble, and even for those that do the time dependence of the velocity field near the swimmer and the effect of other swimmers can cause particles to jump in and out of the wake, which may lower (4.1) considerably. Molecular diffusivity will also limit the path length over which material remains trapped in the wake: for $\lambda \gtrsim U V_{\text{wake}}^{2/3} / \kappa_{\text{molecular}}$, significant amounts of material will have leaked out.

5. Non-zero Reynolds number

In the previous section, the basic theory was applied to model squirmer-induced mixing in Stokes flow, for which the Reynolds number $Re = 0$ and inertial effects are neglected. We identified the dominant contributions as arising from the far field (stresslet). To generalise the squirmer far field and to account for finite (but small)

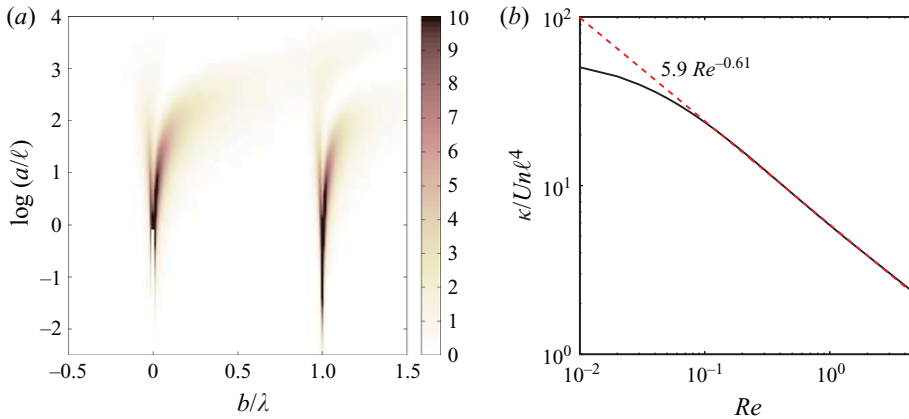


FIGURE 7. (Colour online) The role of the Reynolds number Re . (a) Integrand $\ell^{-4}a^2\Delta_\lambda^2(a, b)$ from (3.2) for displacements due to the far-field Oseen flow (5.1), for $Re = 0.5$ and $\lambda = 100$. (b) The effective diffusivity κ from (2.6) as a function of Re . For small Re , we recover (3.3).

Reynolds number effects on diffusion, we consider the analogous problem for the Oseen equations, which linearise the inertial forces (Oseen 1910). The singularity analogous to the squirmer far-field has streamfunction

$$\psi = -\frac{1}{2}U\rho^2 + \frac{U\ell^2\rho^2}{r^2} \left(\exp(-Re(r-z)/2\ell) + \frac{2}{Re} \frac{\ell}{r} (\exp(-Re(r-z)/2\ell) - 1) \right). \quad (5.1)$$

It is easily checked that, as $Re \rightarrow 0$, this recovers the far-field displacement due to a Stokesian squirmer. Using this streamfunction, we obtain $\Delta_\lambda(a, b)$ numerically for different values of Re and summarise the results for the effective diffusivity in figure 7(b). For small Re , we recover the Stokes value of the effective diffusivity; for larger values of Re , the effective diffusivity drops off as $Re^{-0.61}$ due to smaller particle displacements.

6. Probability distribution function of displacements

We close with some comments regarding the typical size of displacements imparted by the squirmers. In a recent letter, Leptos *et al.* (2009) experimentally measured the p.d.f. of displacements of a target particle due to repeated ‘kicks’ by swimming micro-organisms. They observe that, unlike in Einstein’s theory of Brownian motion, the p.d.f. is non-Gaussian with clear exponential tails. We now show that squirmers also exhibit such tails, due to the stagnation points at their surface.

The large displacements for squirmers are due to particles that lie very close to the axis of motion, i.e. with $a \ll \ell$. For small a , the displacement function can be well-approximated with a ‘top-hat’ function as in (2.7). The probability of $\Delta_\lambda(a, b)$ being larger than a given value δ is then

$$P(\Delta_\lambda > \delta) = \frac{1}{V} \int_{\Delta_\lambda(a, b) > \delta} \pi a \, da \, db = \frac{\lambda}{V} \int_{\Delta(a) > \delta} \pi a \, da. \quad (6.1)$$

For $a \ll \ell$, the squirmer displacement $\Delta(a)$ diverges as $C\ell \log(\ell/a)$, where C is a numerical constant. Hence, the contribution for large δ comes from small a , and we

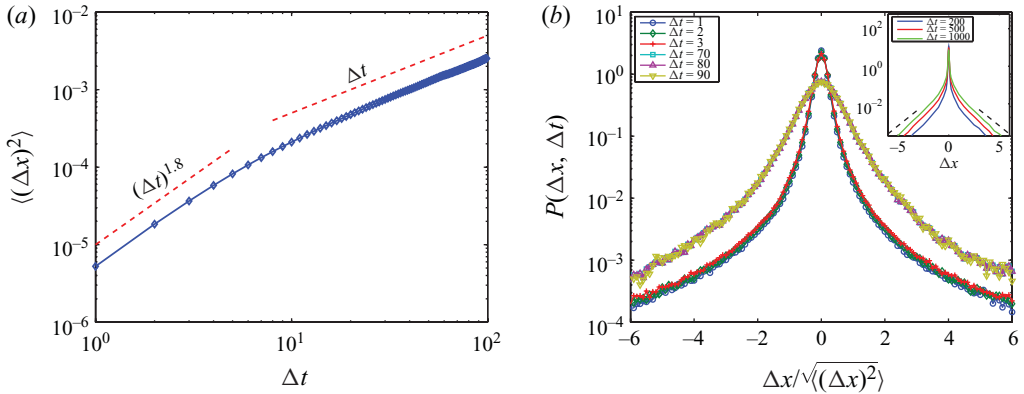


FIGURE 8. (Colour online) (a) Growth of mean-squared displacement $\langle(\Delta x)^2\rangle$ with time, with superdiffusive (short-time) and diffusive (long-time) regimes. (b) Rescaled x -displacement distributions in the two regimes, showing the collapse after scaling. Inset: unscaled p.d.f.s with exponential tails (6.2).

have that

$$P(\Delta_\lambda > \delta) \approx \frac{\lambda}{V} \int_{C\ell \log a^{-1} > \delta} \pi a \, da = \frac{\pi\lambda}{2V} e^{-2\delta/\ell C}, \quad (6.2)$$

which exhibits exponential tails, as in Leptos *et al.* (2009). A simple argument using large-deviation theory shows that the p.d.f. of a superposition of such exponential tails retains the same exponential tails.

To make contact with Leptos *et al.* (2009), we statistically analyse displacements for our biomixing model via particle simulations. We examine the displacement histograms for different sampling intervals Δt up to 90, over which each swimmer travels a distance $U\Delta t$. Figure 8(a) shows the mean-squared displacement $\langle(\Delta x)^2\rangle$ as a function of time: for short times, this grows as $(\Delta t)^{1.8}$, in good accordance with the superdiffusive regime observed by Wu & Libchaber (2000): they found an exponent between 1.5 and 2. For longer times, we recover a linear diffusive regime, as expected, with slope given by our theoretical prediction 2κ . Figure 8(b) shows that the incremental displacement probability distribution along the x -axis, $P(\Delta x, \Delta t)$, rescales to a single distribution function in terms of the similarity variable $\Delta x/\sqrt{\langle(\Delta x)^2\rangle}$ in each of the two scaling regimes. However, note that the exponential tails (6.2) are independent of Δt , and are visible only in simulations after integrating for a long time (see inset in figure 8b). Thus, it is not clear if these are related to the exponential tails observed by Leptos *et al.* (2009).

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