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Caenorhabditis elegans swimming in a saturated particulate system

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Caenorhabditis elegans (C. elegans) is a nematode that often swims in saturated soil in nature. We investigated the locomotive behavior of *C. elegans* swimming in a fluid with particles of various sizes and found that the nematode swims a greater distance per undulation than it does in a fluid without particles. The Strouhal number (a ratio of lateral to forward velocity) of *C. elegans* significantly decreases in a saturated particulate medium (0.50 ± 0.13) in comparison to a fluid without particles (1.6 ± 0.27). This result was unexpected due to the generally low performance of a body moving in a high drag medium. In our model, a saturated granular system is approximated as a porous medium where only the hydrodynamic forces on the body are considered. Combining these assumptions with resistive force theory, we find that a porous medium provides more asymmetric drag on a slender body, and consequently that *C. elegans* locomotes with a greater distance per undulation. © *2010 American Institute of Physics*. [doi:10.1063/1.3359611]

I. INTRODUCTION

Many organisms have adapted to live in aqueous media on other fluid environments. In order for these organisms to survive in nature, an efficient strategy in locomotory behavior has presumably developed. For example, large animals, such as fish or birds, achieve the maximum of propulsive efficiency.[1,2] For smaller organisms, such as bacteria or spermatozoa, changing stroke patterns is one possible way to maximize the locomotory ability.[3–5] However, some organisms are not capable of changing their stroke forms and therefore must utilize the fluidic environment to increase their efficiency.

Caenorhabditis elegans (C. elegans) is a model system used to understand questions arising in various areas of biology.[6] Despite common usage of *C. elegans* in the laboratory, there is little known about its natural habitat. In particular, the crawling motion of *C. elegans* has been studied on an agar plate.[7] They found that *C. elegans* does not change its locomotory pattern over various agar compositions.[8] The stroke form of swimming is found to be different from that of crawling, while swimming *C. elegans* maintains the same amplitude and wavelength over various fluid viscosities. Wallace[9] studied the movement of *C. elegans* in a particulate system, which more closely resembles the natural environment of *C. elegans* than other previous studies. However, this work considers only the frictional force in rigid particles although this organism lives in a wet soil where is often immersed in fluid. The crawling motion on a substrate patterned with posts has also been studied.[10] They found that the crawling speed is increased by contact between the body and several posts. In addition to *C. elegans*, a sandfish lizard moves in a dry granular medium by generating more normal than tangential drag along its body.[11]

In an unbounded fluid, the typical swimming motion of *C. elegans* occurs at a low Reynolds number $(\text{Re} = V_{\text{swim}} L / \nu \sim 10^{-1})$. At such a low Reynolds number, a

locomoting slender body feels and exerts an asymmetric hydrodynamic force that depends on the body orientation. To understand such dynamics, resistive force theory,[12] slender body theory,[13,14] and many others[15,16] have been used. Resistive force theory considers only the local force, which has been widely used to describe the locomotion of a slender body.[16] However, the locomotion in *C. elegans*' natural environment, saturated soil, is not well understood.

Soil immersed in a fluid can be approximated as porous media because of a fluid flowing through porous gaps. For a saturated particulate or fibrous system, the Brinkman equation[17] is often used to describe both viscous stress and Darcy's drag with a single parameter (*permeability*). The resultant force from the Brinkman equation, however, takes into account only the hydrodynamic resistance and does not include the elastic and adhesive force at the particles. This simplification is used in our study to describe the locomotion in different fluidic environments varying from a fluid to a wet particulate system. Mathematically, the Brinkman equation is equivalent to the unsteady creeping flow equation, which has been extensively studied.

In this paper, we compare *C. elegans* swimming in a wet granular medium and in a fluid. We present experimental observations and compare them with the resistive force theory combined with a simple porous-media model.

II. EXPERIMENTS

A. Experimental methods

The nematodes in this study were adult hermaphrodite wild-type *C. elegans* (N2). The typical body length (L) is about 1 mm. We conducted experiments in fluid without particles and with six different sizes of particles 41, 58, 69, 98, 138, and 165 μm in diameter. Particles were monodisperse granular particles (MO-SCI Co.), which do not introduce any chemicals to the fluid system. A 8 μl drop of nematode growth medium buffer with particles and a single *C. elegans*
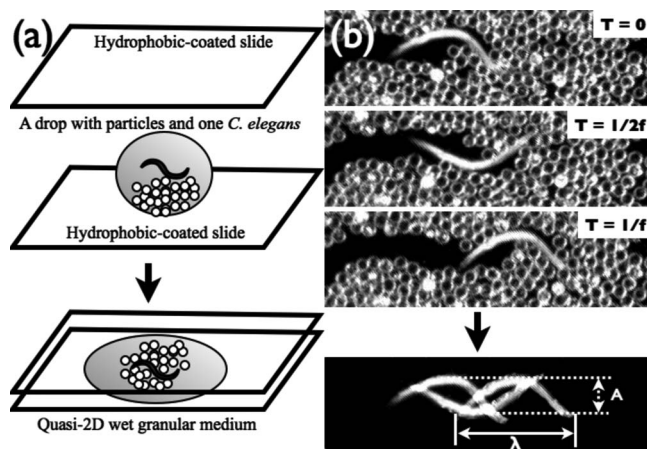
FIG. 1. (a) Schematic procedure of experiments. (b) Three images of *C. elegans* swimming in a wet particulate medium at different times. These images are combined into the bottom image without particles for high contrast.

is placed on a coated hydrophobic plate [see the upper panel in Fig. 1(a)]. Another coated hydrophobic plate is placed on top to create a quasi-two-dimensional (2D) slurry granular system [see the lower panel in Fig. 1(a)]. The distance between two plates changes with the particle diameter.

Particles are initially randomly packed when they settle to the bottom. In experiments, the quasi-2D packing fraction of glass beads (defined as the ratio of the volume occupied by particles to the total volume) does not vary significantly with a range of 0.6 ± 0.04. A charge coupled device camera recorded the motion of *C. elegans* over a few minutes at 8 frames/s. The system was illuminated by a light-emitting diode ring. In Fig. 1(b), three images of locomoting *C. elegans* are shown. For the bottom image, the glass beads were subtracted to yield a high contrast image of the worm. The amplitude was measured as the peak-to-peak distance perpendicular to the swimming direction. In convenience, the wavelength was measured as the distance between the head and tail when *C. elegans* forms a "U" shape. The undulation period is the difference between two successive times when the worm has the same body form. The swimming frequency is defined as the inverse of the undulation period.

B. Experimental observations

Figure 2 shows *C. elegans* swimming in a wet particulate medium with 98 μm particles and in a fluid without particles. The swimming *C. elegans* in a particulate medium more closely simulates the natural environment than swimming in a fluid. In a wet granular medium, *C. elegans* undulates at a lower frequency than in a fluid. However, stroke forms in both configurations are similar. As the body undulates sideways and swims forward, it pushes particles laterally, not along the swimming direction; as illustrated in Fig. 2(a), *C. elegans* swims to the left and leaves voids on the right. Swimming speeds in both cases are comparable; however, swimming distance per undulation is quite different.

We performed typically 20 experiments with different particle sizes from 41 to 165 μm, but only nine runs with 41 μm particles were successful since multiple layers of
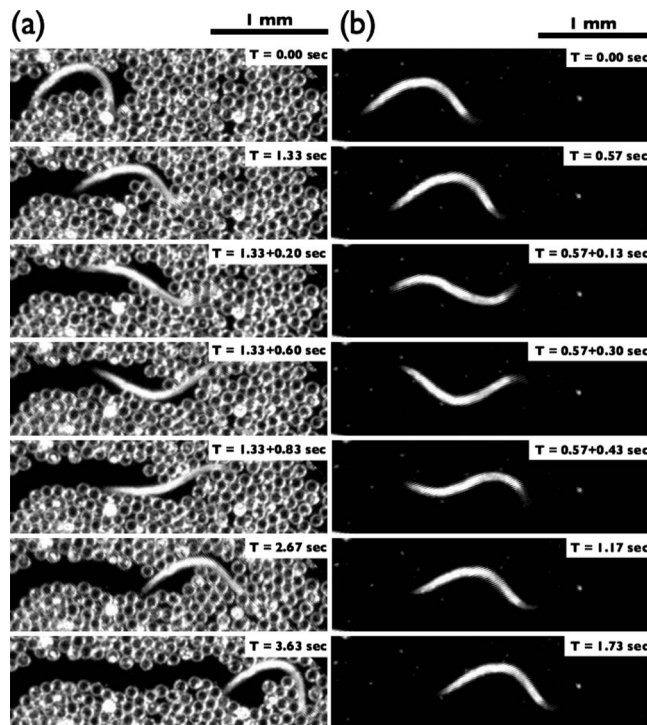

FIG. 2. Swimming motion of *C. elegans* in a wet granular medium of 98 μm particles (a) and in a fluid (b). The body forms of *C. elegans* were captured over three periods of undulation.

particles are easily formed and *C. elegans* becomes hard to observe. For particles above 200 μm in diameter, *C. elegans* can move through voids between particles without pushing the particles. Therefore, our range of particle sizes was limited by these two extreme cases. Table I summarizes the experimental observations of *C. elegans* swimming in fluids with and without particles. As shown, the swimming speed is fluctuating within experimental errors, but the undulation frequency is quite distinct in a particulate medium compared with that in a fluid without particles.

The motion of an undulating body in a plane can be described by two principal velocities: forward swimming velocity and lateral transverse velocity. The swimming velocity is defined as the mean forward speed. This velocity is not directly characterized by the undulation motion, but the transverse velocity is defined as the frequency multiplied by the peak-to-peak amplitude and is directly associated with lateral undulations. Figure 3 shows these two velocities in experiments. The relationship between the two principle velocities is independent of the particle size and is approximately linear. This suggests that regardless of the size of particles involved, the hydrodynamic effect on locomotion is nearly the same. As shown, the data of *C. elegans* moving in a granular-imbedded fluid are scattered in the region above and to the right of those without particles.

Stroke forms of swimming organisms are often characterized by a ratio of amplitude to wavelength. Figure 4 shows that this ratio does not change significantly in fluids with and without particles. The ratio is observed to be 1.1 ± 0.23, which is consistent with other work in crawling and swimming.[7,8,18] In particular, *C. elegans* keeps the same

TABLE I. Measured velocity, frequency, normalized peak-to-peak amplitude, and wavelength with six different sizes of particles and without particles. Here, the amplitude and wavelength were normalized by the body length of *C. elegans*.

Size (μm)	Velocity (cm/s)	Frequency (Hz)	Normalized amplitude	Normalized wavelength	Samples
165	0.478 ± 0.205	0.852 ± 0.336	0.217 ± 0.042	0.679 ± 0.087	17
138	0.327 ± 0.105	0.659 ± 0.215	0.237 ± 0.034	0.645 ± 0.064	20
98	0.282 ± 0.084	0.747 ± 0.299	0.224 ± 0.029	0.675 ± 0.093	20
69	0.317 ± 0.117	0.716 ± 0.236	0.256 ± 0.052	0.697 ± 0.150	18
58	0.342 ± 0.194	0.982 ± 0.600	0.224 ± 0.036	0.625 ± 0.075	19
41	0.206 ± 0.042	0.537 ± 0.175	0.230 ± 0.048	0.695 ± 0.105	9
No particles	0.292 ± 0.057	1.923 ± 0.220	0.259 ± 0.031	0.730 ± 0.072	17

stroke form even with various hydrodynamic drags on the body due to different fluid viscosities.[8] In our experiments, *C. elegans* feels more drag in the presence of granular media, but keeps the same stroke form.

The ratio of transverse velocity to swimming velocity gives a Strouhal number that characterizes the undulating body in fluid. Figure 5 shows that the Strouhal number for swimming in wet particulate media is close to 0.50 ± 0.13 ($P > 0.23$), which is three times smaller than the Strouhal number ($\mathrm{St} \sim 1.6 \pm 0.27$) for swimming without granular media. A low Strouhal number suggests that *C. elegans* moves efficiently in the presence of particles.

III. MODELS

A saturated particulate system is complicated, containing various granular effects (arches of particles, long-range and short-range interactions among particles) and hydrodynamic effects (pushing fluid through micropores and shearing fluid around the body). In addition, an undulating *C. elegans* interacts with both the fluid and the particles. The total force on the body can be expressed as the sum of hydrodynamic stress and solid-contact stress as

$$\int \sigma_{\mathrm{fluid}} dS_{\mathrm{fluid}} + \int \sigma_{\mathrm{solid}} dS_{\mathrm{solid}}, \tag{1}$$

where σ_n and S_n are the stress and contact area with either solid or fluid. On the body, the solid particles have point contacts while the fluid contacts the body elsewhere. Thus, the solid contact area S_{solid} is expected to be much smaller than the fluid contact area S_{fluid}. In the limit of zero Reynolds number, S_{solid} is ideally zero since it takes an infinite time (inversely proportional to the Reynolds number) for the body to deplete a thin fluid layer. As the solid fraction increases, σ_{solid} becomes enormously large from various granular effects including reconfiguring particles, jamming, and so on.

In this section, we consider only the hydrodynamic stress σ_{fluid} on the body. This hydrodynamic stress is evaluated by approximating a wet granular system as a porous medium. Such approximation is valid when the granular medium is dilute. When the granular medium has a high packing fraction, this assumption fails due to significant stress from solid contacts. Our experiments vary the packing fraction from low random loose packing to highly ordered arrays. However, the trend of particle effect can be studied from the simple porous medium assumption.
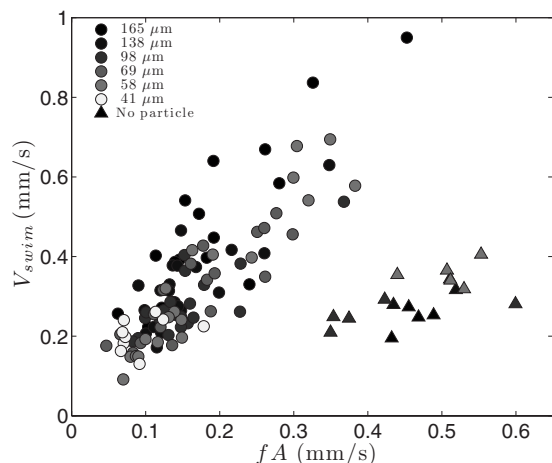

FIG. 3. Swimming velocity (V_{swim}) vs transverse velocity (fA). Six different sizes of particles from 41 to 165 μm are used (darker circular symbols are for larger particles). Swimming without granular particles is marked with closed triangles.
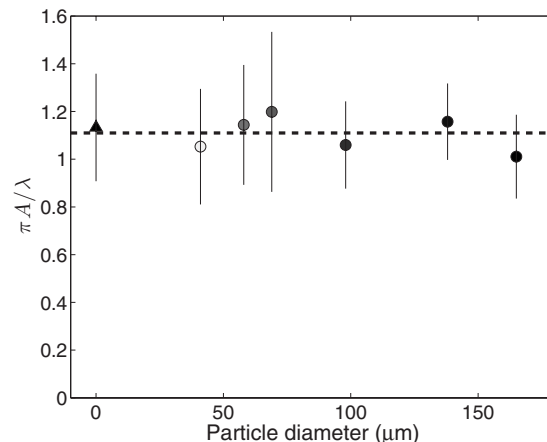

FIG. 4. The ratio of amplitude to wavelength of *C. elegans* swimming in particulate media (circles) and in fluids without particles (triangles located at zero on the axis of the particle size). This ratio is close to a constant (1.1 ± 0.23) both with and without particles in fluids.
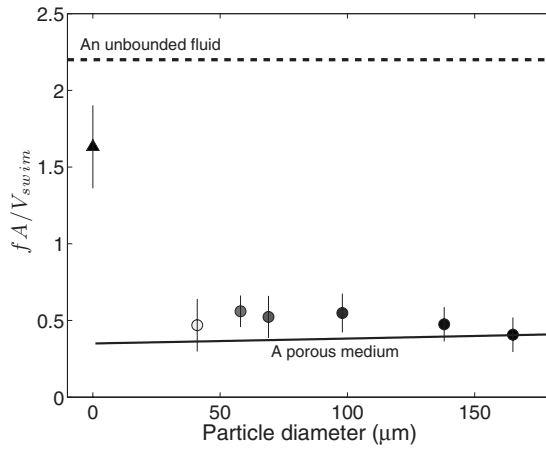
FIG. 5. Strouhal number (St=fA/V_{swim}) vs different particle diameters. Six different sizes of particles were used from 41 to 165 μm (circles). Triangle symbol is for *C. elegans* that swims between two plates without particles. Solid and dashed lines are from resistive force theory with simple model in an unbounded fluid and in a porous medium, respectively.

A. Resistive force theory

Resistive force theory is used to give a description of a slender body swimming in a viscous fluid.[12] It assumes that the fluid force on the body is locally determined by the velocity; $F=C_t u\cdot\hat{t}\hat{t}+C_n u\cdot\hat{n}\hat{n}$, where $\hat{t}$ and $\hat{n}$ are tangential and normal directions to the body's centerline, respectively, and C_t and C_n are tangential and normal drag coefficients. If a slender body swims by undulating sinusoidal motion in the x-y plane, the body's centerline in a moving frame is formulated as $y=(A/2)\cos k(x+V_{wave}t)$, where A is the peak-to-peak amplitude and $k=2\pi/\lambda$ is the wavenumber. Its corresponding velocity becomes $u_x=V_{swim}$, $u_y=dy/dt$. Here, the swimming velocity (V_{swim}) is an unknown parameter to be determined by one constraint, zero force in a swimming direction. The fluid force in the swimming (x) direction is $\int F\cdot\hat{x}dx\approx C_t(I_1 V_{wave}-I_2 V_{swim})L$, where the two integrals I_1 and I_2 are approximately $I_1\sim(C_n/C_t-1)(\pi A/\lambda)^2/2$ and $I_2\sim 1+(C_n/C_t)(\pi A/\lambda)^2/2$ in the limit of small amplitude.[12]

From the above discussion, the swimming velocity is determined in terms of the body shape and the wave speed. Therefore, the Strouhal number is given as

$$\text{St}=\frac{fA}{V_{swim}}=\frac{2}{\pi}\frac{[1+(C_n/C_t)(\pi A/\lambda)^2/2]}{(C_n/C_t-1)(\pi A/\lambda)},\quad(2)$$

which is a function of C_n/C_t and $\pi A/\lambda$ only. Here, the value of $\pi A/\lambda$ is obtained from experiments, which is nearly independent of particle sizes. The only unknown is the drag parameter (C_n/C_t) to be determined from the simple model in Secs. III B and III C. When $\pi A/\lambda=1$, the Strouhal number decreases and converges to 0.32 as C_n/C_t increases. In general, a lower Strouhal number means that the body swims more efficiently by generating less lateral than forward motion.

B. In a fluid without particles

Here, we briefly review the calculation of drag on a cylinder as described by Lighthill.[19] For *C. elegans* swimming in an unbounded fluid, the flow can be modeled by the Stokes equations

$$\nabla p=\mu\nabla^2 u,\quad \nabla\cdot u=0.\quad(3)$$

First, we assume constant forces along the centerline (f). Then, it is convenient to represent the velocity field using a distribution of singular forces

$$u_i=F_j\int G_{ij}ds,\quad(4)$$

where $G_{ij}=[\delta_{ij}/r+x_i x_j/r^3]/(8\pi\mu)$, s is the longitudinal coordinate along the body, and a is the radius of the body. A few indefinite integrals are $\int(1/r)ds=\ln 2(s+r)$, $\int(a^2/r^3)ds=s/r$, and $\int(s^2/r^3)ds=-s/r+\ln 2(s+r)$, where $r^2=a^2+s^2$ are integrated over a domain $s(\in[-L/2,L/2])$. In the limit of $a/L\ll 1$, the normal component of Eq. (4) in the middle of a body becomes

$$u_n=\frac{F_n}{8\pi\mu}\left[\int\frac{1}{r}ds+\cos^2\theta\int\frac{a^2}{r^3}ds\right]$$
$$=\frac{F_n}{8\pi\mu}\left[\frac{L\cos^2\theta}{\sqrt{a^2+L^2/4}}+\ln\left(\frac{L+\sqrt{4a^2+L^2}}{-L+\sqrt{4a^2+L^2}}\right)\right]$$
$$=\frac{F_n}{8\pi\mu}[1+\cos(2\theta)+2\ln(L/a)]+\mathcal{O}(a/L)^2,\quad(5)$$

where θ is the angle between the arbitrary principal axis and the direction of motion. This approximation is given by taking the slender limit as done in Refs. 13 and 20. Similarly, the tangential component is given as

$$u_t=\frac{F_t}{8\pi\mu}\left[\int\frac{1}{r}ds+\int\frac{s^2}{r^3}ds\right]$$
$$=\frac{F_t}{8\pi\mu}\left[-\frac{L}{\sqrt{a^2+L^2/4}}+2\ln\left(\frac{L+\sqrt{4a^2+L^2}}{-L+\sqrt{4a^2+L^2}}\right)\right]$$
$$=\frac{F_t}{8\pi\mu}[-2+4\ln(L/a)]+\mathcal{O}(a/L)^2.\quad(6)$$

Then, the drag coefficients are

$$C_n=\frac{4\pi\mu}{\ln(L/a)+\frac{1}{2}},\quad C_t=\frac{2\pi\mu}{\ln(L/a)-\frac{1}{2}}.\quad(7)$$

Asymptotically, $C_n/C_t=2[\ln(L/a)-1/2/\ln(L/a)+1/2]$ approaches 2 in the limit of an infinite slender body.

For a body shape like a blunt *C. elegans*, we find that C_n/C_t is close to 1.5 from physical parameters ($L\sim 1$ mm and $a\sim 0.03$ mm). While swimming in a fluid, *C. elegans* keeps a ratio of amplitude and wavelength ($\pi A/\lambda$) close to 1.1. Hence, the Strouhal number becomes 2.2 for undulating *C. elegans* in an unbounded Stokes fluid. However, this value differs from experimental measurement (1.6±0.27). The possible error comes from the boundary effects from the top and bottom plates, which are neglected in this analysis.

C. In a porous medium

The description of *C. elegans* swimming in a wet granular medium is complex. For simplicity, we approximate this fluidic system as a porous medium in which *C. elegans* pushes particles as well as fluid around. Hence, the dominant forces on *C. elegans* originate from viscous stresses and Darcy's flow. To derive the local force in a porous medium, we use the Brinkman model where

$$\nabla p = \mu(\nabla^2 - \alpha^2)\boldsymbol{u}, \quad \nabla \cdot \boldsymbol{u} = 0. \tag{8}$$

As mentioned in Sec. I, the Brinkman equation is mathematically equivalent to the unsteady Stokes equation if α^2 is redefined as the frequency parameter.

We can use the boundary integral formula as in Eq. (4) with the unsteady Stokeslet defined by[17]

$$G_{ij} = \frac{1}{8\pi\mu}\left(\frac{2}{\alpha^2 r^3}[(1 + \alpha r + \alpha^2 r^2)e^{-\alpha r} - 1]\delta_{ij}\right.$$
$$\left. + \frac{6}{\alpha^2 r^5}\left[1 - \left(1 + \alpha r + \frac{1}{3}\alpha^2 r^2\right)e^{-\alpha r}\right]x_i x_j\right). \tag{9}$$

When α is small, the Green's function from the previous equation is modified to become

$$G_{ij} = \frac{1}{8\pi\mu}\left[\left(\frac{1}{r} - \frac{4\alpha}{3}\right)\delta_{ij} + \frac{x_i x_j}{r^3}\right] + \mathcal{O}(\alpha^2). \tag{10}$$

By following the same method as in Sec. III B, the drag coefficients are

$$C_n = \frac{4\pi\mu}{\ln(L/a) + \frac{1}{2} - 2\alpha L/3}, \quad C_t = \frac{2\pi\mu}{\ln(L/a) - \frac{1}{2} - \alpha L/3}. \tag{11}$$

This shows a trend of increasing the drag in both directions. Moreover, the drag parameter $C_n/C_t = 2[\ln(L/a) - 1/2 - \alpha L/3/\ln(L/a) + 1/2 - 2\alpha L/3]$ gets larger as α increases. This trend of increasing asymmetry, which results in a greater swimming distance per undulation, decreases the Strouhal number.

For large α, the exact solution of drag on a cylinder or a disk has been calculated in an unsteady Stokes flow.[21] For the porous medium, we can employ these solutions of the drags on a cylinder by replacing the frequency parameter with the inverse permeability. In the limit of large α, the drag is expressed by

$$C_n = \pi\mu(2\alpha L + 8)\alpha L, \quad C_t = 4\pi\mu\alpha L. \tag{12}$$

Additionally, for large αL, $C_n/C_t \to \alpha L/2$ showing that the normal drag is considerably larger than the tangential drag. For a 2D array of particles, the permeability is calculated based on various configurations including periodic cells,[22] random arrays,[23] and so on. For random arrays, the permeability α in a range of packing fraction $(0.5 < \phi < 0.7)$ is estimated to be $3.4/a < \alpha < 8.5/a$, giving the drag coefficient as approximately $1.7L/a < C_n/C_t < 4.2L/a$, where a is the particle diameter. In Fig. 5, the corresponding Strouhal numbers in resistive force theory are in the range of 0.37–0.41. These numbers depend on the packing fraction $(0.5 < \phi < 0.7)$ and are not far from the experimental result (0.5 ± 0.13).

IV. DISCUSSION

We have studied the dynamics of *C. elegans* swimming both in a fluid and in a wet particulate medium. It was found that *C. elegans* moves efficiently with a low undulation frequency in a particulate medium, and that the stroke form of undulations does not change significantly. Despite varying particle sizes, *C. elegans* keeps a constant ratio of forward to transverse velocities. This ratio, the Strouhal number, decreases significantly in the presence of particles. The resistive force theory in a porous medium predicts the Strouhal number changing from 0.39 in the presence of porous media to 2.2 in a fluid without particles. From experiments, we observed St $\sim 0.50 \pm 0.13$ in a saturated particulate medium and St $\sim 1.63 \pm 0.27$ in a fluid without particles.

Large animals such as fish or birds use inertia by shedding coordinated vortices, and then achieving a Strouhal number close to 0.3 with a high propulsion speed.[1] It is assumed that this high efficiency is not attained by small organisms due to viscous forces. However, our experiments reveal that small organisms such as *C. elegans* can achieve efficient locomotion by using nearby porous medium, which is found in their natural environment.

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