

Swimming of Biological Filamentous Microorganisms in Quasi-2D Membranes

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Abstract

The locomotion of microscopic biological swimmers is governed by the viscous drag of the fluid that surrounds them and is independent of their inertia. We have studied, theoretically and computationally, microorganisms that pass transverse waves along thin, elastic, inextensible, whip-like appendages and are confined to thin incompressible membranes embedded in bulk fluid of a different viscosity. Microscopic swimmers must continually deform their bodies to propagate and, in their motion, they disturb the fluid in both the membrane and bulk. The flows that emerge feature both two-dimensional (2D) and three-dimensional (3D) hydrodynamics, and so such flows are often referred to as "quasi" 2D. Our theoretical model generalizes the Levine and Mackintosh theory for the fluid response to a localized point-like force in a quasi-2D membrane. We applied a boundary element method to numerically investigate the 2D to 3D crossover effects on the swimming velocities of flagellated microorganisms, both finite and infinite in length.

Introduction

Biological microorganisms have adapted to live in an environment where the viscous damping forces greatly exceed their inertia. For a microscopic critter with a body size on the order of tens of micrometers and swimming in water with a speed of a few body lengths per second, the Reynolds number \mathcal{R} , a dimensionless parameter that is the ratio of inertial forces to viscous forces, is small, $\mathcal{R} \sim 10^{-4} - 10^{-3}$. In such a viscous environment if a critter stops paddling, its motion is slowed to a halt in mere microseconds, coasting only Angstrom scale distances. One category of biological swimmers, including spermatozoa, *E. coli*, and *C. crescentus*, swim by passing transverse waves along the length of their flagella, which are long and thin extensions (tails) on their bodies. Due to the geometrical asymmetry of the flagella, the critters experience an anisotropic viscous drag from the surrounding fluid, which generates their propulsion. We studied microorganisms that swim by moving a single flagellum in a wavelike manner.

Reynolds number \mathcal{R} = inertia/viscous friction

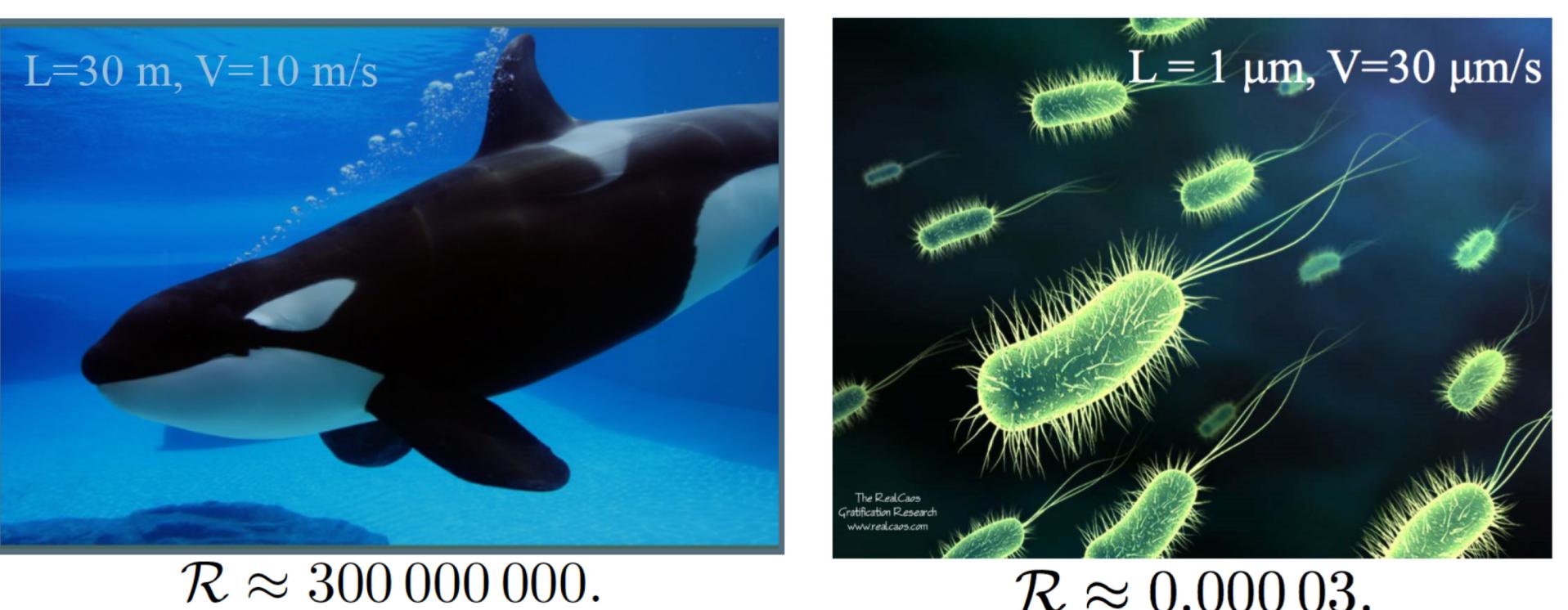


Fig. 1 The Reynolds numbers for a macroscopic organism (*Orcinus orca*, left) and a microorganism (*E. coli*, right) swimming in water. Microscopic critters react instantaneously to any forces, oblivious to any history of prior dynamics and so, *recoil swimming*, the primary method of propagation for macroscopic swimmers (humans, sharks, whales, etc.) which relies on trading momentum with the fluid to induce a net force for propulsion, is ineffective here. The net force on micro-critters is zero at all times.

Quasi 2D Fluid

Oftentimes, microscopic critters are confined to swim in thin membranes surrounded by bulk fluid of a different viscosity. We explore the effect of confinement on the hydrodynamics of swimming microorganisms in a thin film. As the critters move, they excite flows in both the membrane and the bulk. The presence of a bulk fluid allows one to introduce a length scale, the so-called Saffman length l_s , given by the ratio of 2D membrane viscosity to 3D viscosity of the embedding fluid. This length scale governs whether energy is dissipated primarily in the membrane or in the bulk and determines the spatial decay rate of the flow field in the membrane due to a perturbation.

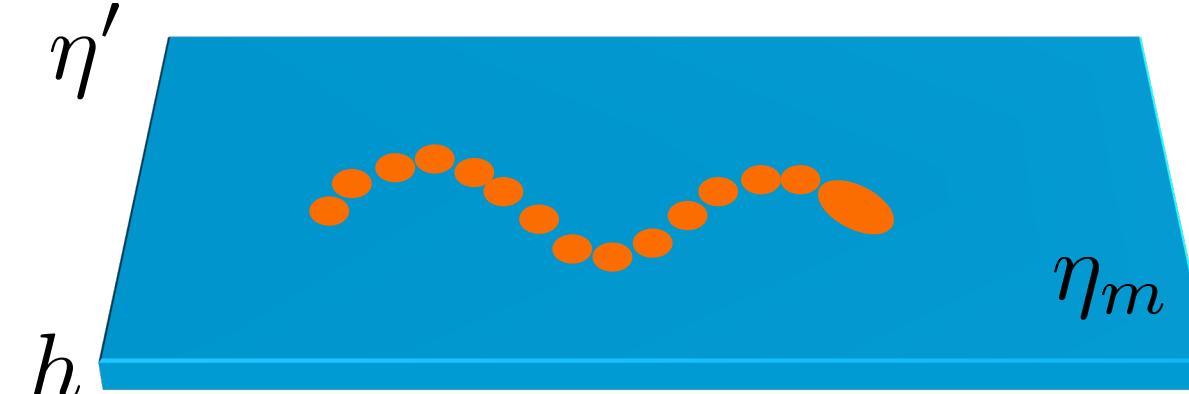


Fig. 2 Cartoon illustrating a micro-swimmer confined to a membrane of thickness h embedded in a bulk fluid of different viscosity.

Model

The flow field due to a moving swimmer is modeled as a superposition of flow fields due to an array of point-like forces \mathbf{F} applied to the membrane. A no-slip boundary condition is enforced at the surface of the swimmer:

$$\mathbf{v}(\mathbf{r}_i) + \mathbf{U} = \sum_j \mathbf{G}(|\mathbf{r}_i - \mathbf{r}_j|) \mathbf{F}(\mathbf{r}_j)$$

Where \mathbf{v} is the surface deformation velocity, \mathbf{U} is the swimming velocity, \mathbf{G} is the Levine-Mackintosh response function. The material points of the flagellum move in a prescribed wavy motion:

$$y(x, t) = b \cos[q(x + ct)]$$

The net force on the swimmer is zero at all times:

$$\sum_j \mathbf{F}(\mathbf{r}_j) = 0$$

These equations form a closed system of algebraic relations that can be solved for the swimmer's propagation velocity \mathbf{U} and the forces \mathbf{F} simultaneously. We solved this system of equations in MATLAB.

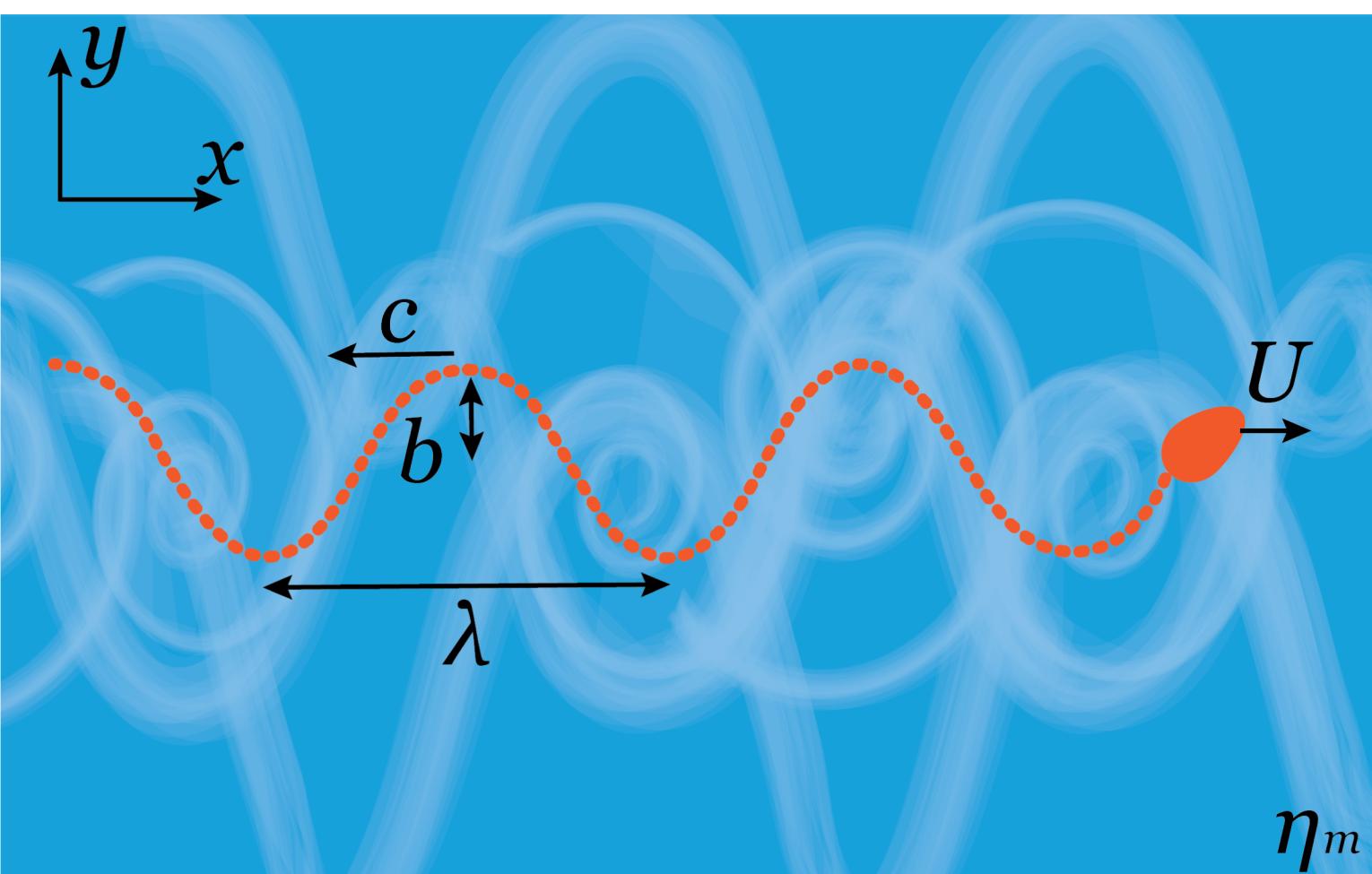


Fig. 3 Top view. This membrane-bounded flagellated swimmer is passing waves of the form $y(x, t) = b \cos[q(x + ct)]$ to the left. The drag anisotropy due to the flagellum geometry and its surface deformation produces a propulsion to the right.

Finite Flagellum

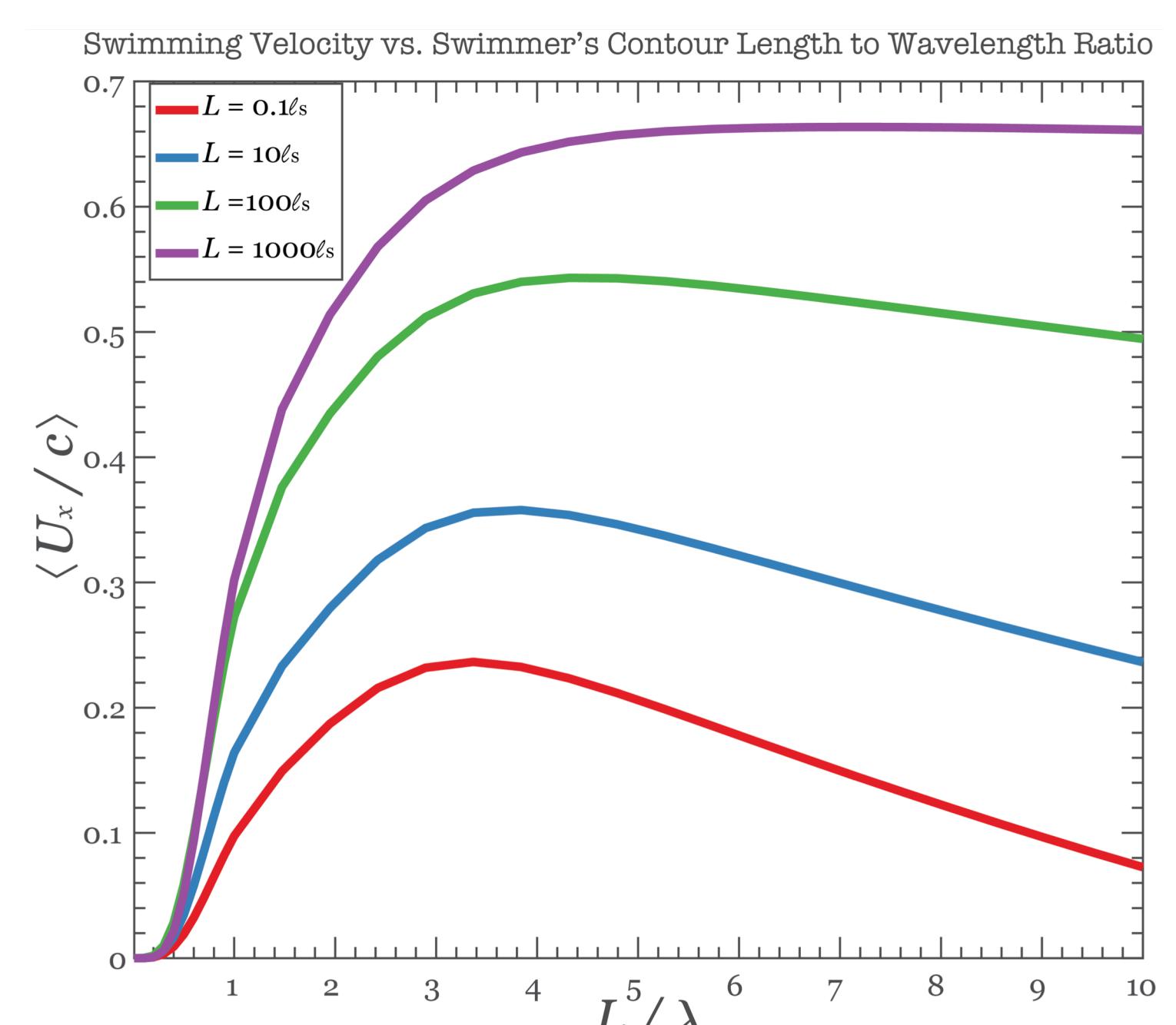


Fig. 4 Swimming velocity of flagellum with contour lengths of various multiples of the Saffman length are plotted. The swimming velocities are averaged over a period of wave motion and scaled by the wave speed c at which the swimmers pass waves of the form $y(x, t) = b \cos[q(x + ct)]$ in quasi-2D fluid. The flagella were traced by 500 mesh points per wave. The amplitude was set to $b = 0.1L$.

- The propulsion of flagellated organisms in viscous flows is owed to the drag anisotropy from their geometry.

Large Saffman Length

- Membrane-bound organisms smaller than the Saffman length generate flows primarily dissipated in the membrane and so feature properties of 2D swimmers.
- On this scale the long range flows on a portion of flagellum, due to other portions, are significant and oppose the drag on the swimmers from which they gain their propulsion.

Small Saffman Length

- Quasi 2D swimmers on length scales larger than the Saffman length perturb flows that are dissipated by the bulk fluid more so than in the membrane fluid.
- On this scale the long range flows on a portion of flagellum, due to other portions, are reduced, and so, the swimmers can utilize the drag anisotropy for propulsion to a greater degree.
- Due to the 2D incompressibility of the membrane, the drag anisotropy is logarithmically dependent on the length scale of the flagellum allowing the organisms to achieve larger swimming velocities.

Infinitely Long Flagellum

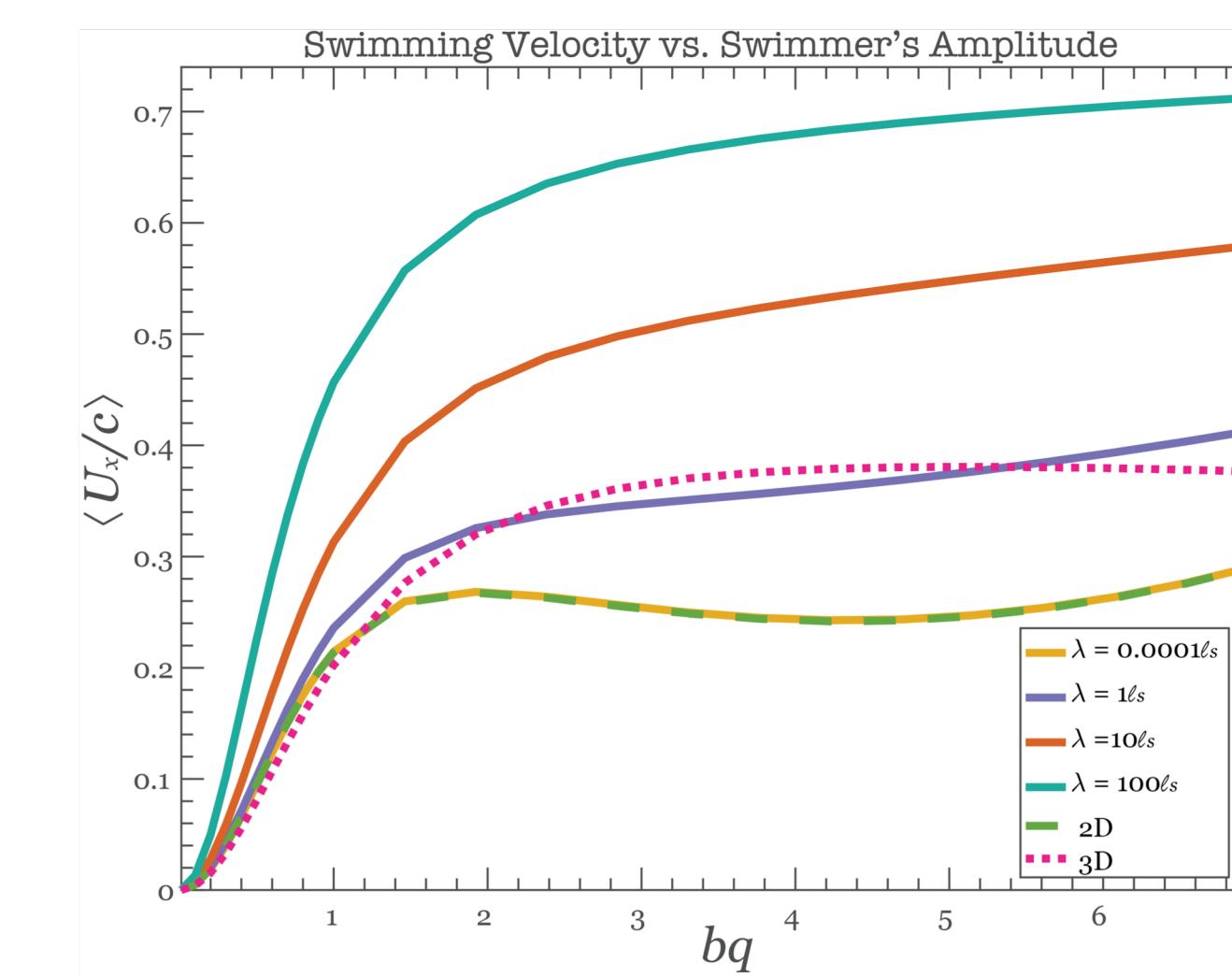


Fig. 5 Average swimming velocity scaled by wave speed c vs. dimensionless amplitude parameter bq for an infinitely long swimmer with a modulation $y(x, t) = b \cos[q(x + ct)]$ in 2D, 3D, and quasi-2D fluid. The quasi 2D velocity is plotted for various values of the wavelength scaled by the Saffman length. The flagella were traced by 500 mesh points per wave. Cortez' regularized force-point response functions [5] were used to calculate the swimming velocities in 2D and 3D fluid, setting the regularization parameters to 0.25δ and 0.9δ , respectively, where δ is the mesh point spacing.

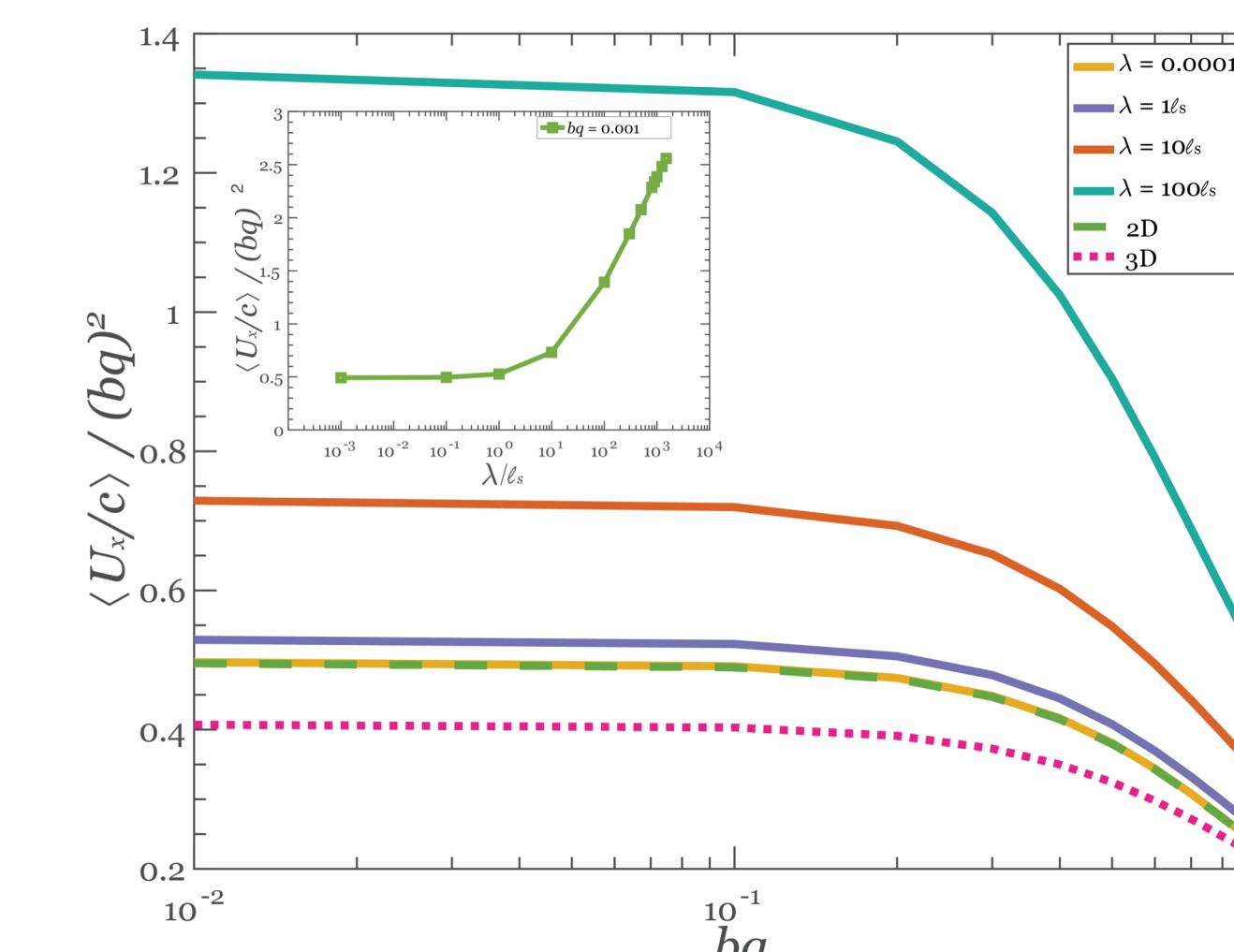


Fig. 6 Average swimming velocity scaled by the squared non-dimensional amplitude parameter bq . At large wavelengths in comparison to the Saffman length, the swimming velocity at small bq in quasi 2D fluid is logarithmically dependent on the wavelength.

- At small amplitudes, drag can be approximated as local and linear in velocity.
- In simple viscous fluids, the drag anisotropy at small amplitudes is very close to 2:1.
- In a quasi-2D membrane, the drag anisotropy, on length scales larger than the Saffman length, becomes logarithmically dependent on the length scale.
- At large amplitudes, long range flows reduce the propulsion of swimmers in simple fluid.
- In quasi 2D fluid, these long range flows are dissipated to a greater degree due to the presence of the bulk fluid and the 2D incompressibility of the membrane.
- Quasi 2D swimmers can achieve swimming speeds that logarithmically approach the wave speed at the largest length scales.

Flagellum Flow Field

As flagellated organisms propagate through fluid, by passing transverse waves, they create vortices near the troughs and crests of their waves. For a flagellum passing waves to the left, propulsion is produced towards the right and its crests' vortices are clockwise oriented, while those near the troughs are counter-clockwise oriented. Since the swimmers deformations are planar, the swimmer remains in the same plane only producing planar shearing flows that decay with distance in all directions. In figure 7 below, the flow field of swimmers at different length scales are shown. It can be seen that the spacial decay rates of the generated flows due to the swimmers perturbing the membrane as they swim is larger for swimmers that are larger in comparison to the Saffman length ζ .

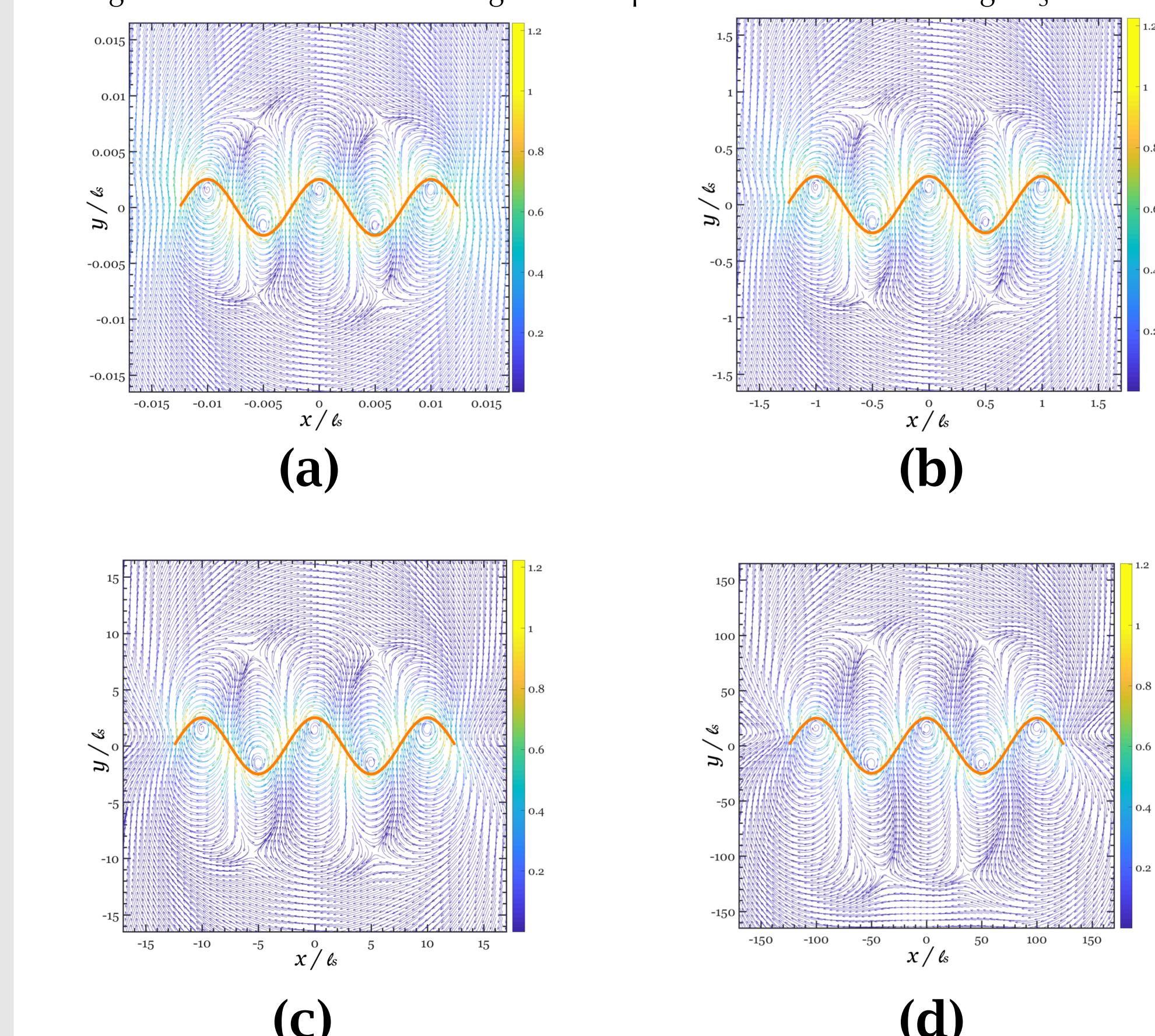


Fig. 7 $t = 0$ snap shots of the flow field of wavy flagella of different wavelengths in quasi 2D fluid. The flow field was represented as that due to an array of 100 force points per wave of wavy flagellum and calculated via our boundary element model. The non-dimensional amplitude parameter was set to $bq = \frac{\pi}{2}$ and the flagellum contour length was set to $L = 2.5\Lambda$, where Λ is the arc length of a single wave of the form $y(x, t) = b \cos(qx)$. The wavelength was set to (a) $\lambda = 0.01L_s$, (b) $\lambda = 1L_s$, (c) $\lambda = 10L_s$, (d) $\lambda = 100L_s$. The velocity intensities are color coded.

Conclusion

We studied propulsion of microorganisms confined to a viscous membrane embedded in bulk fluid. We investigated the dependence of the swimming speed on the hydrodynamic length scale (the Saffman length) and thus studied the crossover from two-dimensional to three-dimensional behavior. In the limiting case of the flagellum length much smaller than the Saffman length, the energy is primarily dissipated in the membrane, and the swimmer exhibits properties of a purely 2D swimmer. In the opposite limit of the flagellum much larger than the Saffman length the swimmer's speed is greater than that in purely 2D or 3D fluids and approaches the upper bound: the wave propagation velocity.

References

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