

Hydroelastic scattering and trapping of microswimmers

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Deformable boundaries are omnipresent in the habitats of swimming microorganisms, leading to intricate hydroelastic couplings. Employing a perturbation theory, valid for small deformations, we study the swimming dynamics of pushers and pullers near instantaneously deforming boundaries, endowed with a bending rigidity and surface tension. Our results reveal that pushers can either reorient away from the boundary, leading to overall hydroelastic scattering, or become trapped by the boundary, akin to the enhanced trapping found for pullers. These findings demonstrate that the complex hydroelastic interactions can generate behaviors that are in striking contrast to swimming near planar walls.

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Swimming microorganisms represent fascinating exemplars of nonequilibrium systems and their dynamics have been widely studied in the realm of fluid mechanics and statistical physics [1–6]. Owing to their small size and typical swimming velocity, the effects of fluid inertia are negligible compared to viscous ones, thus requiring cells to perform nonreciprocal swimming strokes to propel through their low-Reynolds-number fluid environments [7]. Unraveling their swimming behavior in their natural habitats is paramount for gaining new insights into the formation of bacterial colonies and biofilms [8,9], the complexities of disease spreading bacteria [10], and sperm motility in the reproductive tract [11], to name a few. They further lay the foundation for advancing technology through the design of novel cargo carriers [12–15].

Many microorganisms live in confined environments, where long-ranged hydrodynamic interactions with nearby boundaries can strongly affect their swimming behaviors, leading to various interesting physical phenomena [3]. Seminal experiments revealed a change from clockwise [16] to counterclockwise circular motion [17] of *Escherichia coli* bacteria by varying the boundary from a rigid no-slip wall to an air-water interface. These dynamics have been predicted to change for spherical microswimmers and phoretic colloids, which can scatter, perform oscillatory dynamics, or hover near the wall, depending on the propulsion modes and their initial orientation [18–22]. Introducing a boundary slip [23] or a nonplanar boundary shape [24,25] can further strongly modify

the dynamics, demonstrating that details of the hydrodynamic interactions are crucial for active systems.

In contrast to rigid walls, many biological surfaces [26–31], such as membranes, are soft and can deform in response to hydrodynamic stresses. The inherent nonlinearity due to the coupling of the flow and the deformation leads to unexpected physics [29–34], while rendering these problems challenging to handle analytically and numerically. Instrumental insights come from the context of externally driven spheres, where the hydroelastic coupling induces a lift force, pushing the sphere away from the surface—a phenomenon not possible near planar walls due to the time reversibility of Stokes flows [35–38]. Theoretical progress was made possible by employing the Lorentz reciprocal theorem [39], providing insights for particle lift near fluid-fluid interfaces [40,41] and compliant surfaces [38,42]. In contrast to their driven, passive counterparts, swimming microorganisms are force- and torque-free, thus producing different flow signatures [43,44], which are expected to fundamentally change the hydroelastic interaction. Recent work discovered the emergence of directed motion of agents with reciprocal swim strokes near deformable boundaries [32,33], their enhanced swim speed through deformable channels [34], and their swimming velocities at the timescale of the deformation [45,46]. Yet, a comprehensive understanding of the swimming dynamics near a deformable boundary at larger timescales, their stationary state, and its dependence on both material and swimmer properties remains lacking and poses a fundamental ingredient towards unraveling more complex many-body systems [28–31].

Here, we study the dynamics of a microswimmer near a deformable boundary, characterized by a bending rigidity and surface tension, by means of a perturbation theory, valid for small deformations. To describe the flows induced by the microswimmer, we rely on a far-field description, which has been successful in providing physical insights into a range of phenomena involving swimmer-surface interactions

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[17,32,47,48]. Our main findings demonstrate that the deformable boundary induces scattering of pusher swimmers away from the boundary and enhanced attraction of pullers. For small Föppl-von Kármán numbers, measuring the relative importance of surface tension to bending rigidity, pushers can reorient towards the boundary, leading to a trapping state. Most importantly, these features emerge from a hydroelastic interaction, reorienting the active agents, in contrast to the deformation-induced lift of the passive counterpart.

Model. We consider a microswimmer in an incompressible fluid of viscosity μ near an elastic boundary S_M . It creates a flow described by the spatially varying fluid velocity field $\mathbf{u}(\mathbf{r})$ and pressure field $p(\mathbf{r})$, with $\mathbf{r} = (\mathbf{r}_\parallel, z)^T$. Here, $\mathbf{r}_\parallel$ denotes the components on the undeformed surface S_0 (corresponding to the xy plane) and z is the normal component. In the low-Reynolds-number limit, the flow fields are governed by the quasisteady Stokes equations [49–51]: $\nabla p = \mu \nabla^2 \mathbf{u}$ and $\nabla \cdot \mathbf{u} = 0$. As a response to its swimming stroke and the presence of surrounding boundaries, the microswimmer translates at a velocity $\mathbf{U}$ and rotates at an angular velocity $\mathbf{\Omega}$. Here, we consider an infinitesimally thin elastic boundary S_M (unbounded in the other directions), which can deform in response to the viscous stresses $\boldsymbol{\sigma} = -p\mathbb{I} + \mu(\nabla \mathbf{u} + \nabla \mathbf{u}^T)$. Its deformation $z = \delta(\mathbf{r}_\parallel)$ obeys the stress balance [26,42]

$$(\kappa \nabla_\parallel^4 - \Sigma \nabla_\parallel^2) \delta = \boldsymbol{\sigma} : \mathbf{nn}|_{S_M}, \quad (1)$$

where κ and Σ denote the bending rigidity and surface tension, respectively, $\mathbf{n}$ is the normally outward-pointing unit vector, and $\nabla_\parallel$ is the in-plane gradient. Note that we have assumed no in-plane deformation of the boundary. The problem setup is complete after imposing the kinematic and no-slip boundary conditions on S_M [51], and assuming that the velocity field vanishes far from the microswimmer (see the Supplemental Material [52]).

Dimensional analysis reveals that our system has two nondimensional parameters: (1) A generalized elastoviscous number, $\epsilon = \mu a^2 U_{\text{free}} / (\kappa + \Sigma a^2)$, measuring the relative importance of the hydrodynamic stress induced by the microswimmer (of size a and free-space swimming speed U_{free}) to the elastic resistance of the boundary [40], and (2) the Föppl-von Kármán (FvK) number, $\Gamma = \Sigma a^2 / \kappa$, comparing the strength of surface tension with bending rigidity. Typical estimates for bacteria and synthetic colloids near lipid membranes (comprising a majority of biological membranes) are of the order of $\epsilon = \mathcal{O}(10^{-2}) - \mathcal{O}(1)$ and $\Gamma = \mathcal{O}(0.1) - \mathcal{O}(10)$ [28,30,53].

Small-deformation limit. In this work, we focus on the regime of small elastoviscous numbers, $\epsilon \ll 1$, i.e., the elastic resistance of the boundary is large compared to the viscous stresses. This allows considering small surface deformations and employing a perturbation ansatz of the form

$$\{\delta, \mathbf{u}, \mathbf{U}, \mathbf{\Omega}, p\} = \{\delta^{(0)}, \mathbf{u}^{(0)}, \mathbf{U}^{(0)}, \mathbf{\Omega}^{(0)}, p^{(0)}\} + \epsilon \{\delta^{(1)}, \mathbf{u}^{(1)}, \mathbf{U}^{(1)}, \mathbf{\Omega}^{(1)}, p^{(1)}\} + \mathcal{O}(\epsilon^2),$$

where the first set of terms are the solution variables near a planar wall ($\delta^{(0)} = 0$) and the second set of terms are the leading-order corrections. Furthermore, employing a Taylor series expansion in δ about the reference surface S_0 in Eq. (1) [52], we find that the leading-order deformation is governed

by $(\kappa \nabla_\parallel^4 - \Sigma \nabla_\parallel^2) \delta^{(1)}(\mathbf{r}_\parallel) = -p^{(0)}(\mathbf{r}_\parallel)|_{z=0}$, permitting a solution in Fourier space ($\mathbf{r}_\parallel \rightarrow \mathbf{k}$) of the form

$$\delta^{(1)}(\mathbf{k}) = -\frac{p^{(0)}(\mathbf{k})|_{z=0}}{\kappa |\mathbf{k}|^4 + \Sigma |\mathbf{k}|^2}. \quad (2)$$

A numerical inverse transform then provides $\delta^{(1)}(\mathbf{r}_\parallel)$ [52]. Note that Eq. (2) is reminiscent of the thermal fluctuation spectrum of a membrane [54].

Deformation-induced swimming velocities. Using the Lorentz reciprocal theorem [42,55] and exploiting that the microswimmer is force- and torque-free yields a relation for the deformation-induced swimming velocities, $\mathbf{U}^{(1)}$ and $\mathbf{\Omega}^{(1)}$ (see the Supplemental Material [52] for details):

$$\mathbf{U}^{(1)} \cdot \hat{\mathbf{F}} + \mathbf{\Omega}^{(1)} \cdot \hat{\mathbf{L}} = \int_{S_0} \mathbf{n} \cdot \hat{\boldsymbol{\sigma}} \cdot \mathbf{u}_{S_M} dS, \quad (3)$$

where the contribution of the surface deformation enters via an effective slip velocity [42,52]

$$\mathbf{u}_{S_M} = \frac{\partial \delta^{(1)}}{\partial t} \mathbf{e}_z - \delta^{(1)} \frac{\partial \mathbf{u}^{(0)}}{\partial z} \Big|_{z=0} - \mathbf{U}_\parallel^{(0)} \cdot \nabla_\parallel \delta^{(1)} \mathbf{e}_z. \quad (4)$$

It comprises the deformation rate ($\partial_t \delta^{(1)}$) and the contribution due to the deformation shape ($\delta^{(1)}$), reminiscent to that of a rigid, structured surface [24]. The last term represents the advection of the deformation by the swimming agent, where $\mathbf{U}_\parallel^{(0)}$ denotes its zeroth-order velocity parallel to S_0 . Equation (3) further depends on the stress tensor $\hat{\boldsymbol{\sigma}}$ of a passive object of the same shape as the microswimmer (referred to as auxiliary problem), moving near a planar (no-slip) wall at velocities $\hat{\mathbf{U}}$ and $\hat{\mathbf{\Omega}}$, under the application of an external force $\hat{\mathbf{F}}$ and torque $\hat{\mathbf{L}}$.

Due to the linearity of the Stokes equations, we can generalize Eq. (3) by introducing third-rank tensors $\hat{\mathcal{T}}_F$ and $\hat{\mathcal{T}}_L$, relating the stresses and velocities of the auxiliary problem via $\mathbf{n} \cdot \hat{\boldsymbol{\sigma}} = \mathbf{n} \cdot \hat{\mathcal{T}} \cdot (\hat{\mathbf{U}}, \hat{\mathbf{\Omega}})^T$ with $\hat{\mathcal{T}} = (\hat{\mathcal{T}}_F, \hat{\mathcal{T}}_L)$ [56]. We further note that external forces and torques balance the hydrodynamic forces and torques,

$$\begin{pmatrix} \hat{\mathbf{F}} \\ \hat{\mathbf{L}} \end{pmatrix} = - \int_{S_p} \begin{pmatrix} \mathbf{n} \cdot \hat{\boldsymbol{\sigma}} \\ \mathbf{R} \times \mathbf{n} \cdot \hat{\boldsymbol{\sigma}} \end{pmatrix} dS = \hat{\mathcal{R}} \cdot \begin{pmatrix} \hat{\mathbf{U}} \\ \hat{\mathbf{\Omega}} \end{pmatrix}, \quad (5)$$

where $\mathbf{R}$ is the position vector directed from the center to the surface of the swimmer (S_p) and

$$\hat{\mathcal{R}} = - \int_{S_p} \begin{pmatrix} \mathbf{n} \cdot \hat{\mathcal{T}} \\ \mathbf{R} \times \mathbf{n} \cdot \hat{\mathcal{T}} \end{pmatrix} dS \quad (6)$$

is the resistance matrix. Combining Eqs. (5) and (3), the leading-order corrections to the translational and angular velocities take the form

$$\begin{pmatrix} \mathbf{U}^{(1)} \\ \mathbf{\Omega}^{(1)} \end{pmatrix} = \hat{\mathcal{R}}^{-1} \cdot \int_{S_0} \mathbf{n} \cdot \hat{\mathcal{T}} \cdot \mathbf{u}_{S_M} dS. \quad (7)$$

The above expression is generic and can be evaluated for any microswimmer, provided the flow fields of the microswimmer near a planar wall and the equivalent auxiliary problem are known.

Far-field description. We employ our theoretical predictions to investigate the dynamics of an axisymmetric microswimmer, whose far-field flow is described as a combination of a force and torque dipole of strengths α_{FD} and α_{RD} , respectively [57]. While the force-dipole term is the minimal term for the flow field generated by any force-free microswimmer, we include the torque-dipole term capturing the frequently observed counter-rotation of a bacterial body and the flagella. For a symmetric swimmer, the instantaneous position $\mathbf{r}_0(t) = (x_0(t), y_0(t), h(t))^T$ and orientation $\mathbf{e}(t) = (\cos \vartheta(t) \cos \varphi(t), \cos \vartheta(t) \sin \varphi(t), \sin \vartheta(t))^T$, parametrized in terms of the pitch angle ϑ (with $\vartheta = 0$ being parallel to $\mathbf{S}_0$) and polar angle φ , obey the equations of motion: $d\mathbf{r}_0/dt = \mathbf{U}^{(0)} + \epsilon \mathbf{U}^{(1)}$ and $d\mathbf{e}/dt = (\mathbf{\Omega}^{(0)} + \epsilon \mathbf{\Omega}^{(1)}) \times \mathbf{e}$, where the zeroth-order contributions, $\mathbf{U}^{(0)}$ and $\mathbf{\Omega}^{(0)}$, represent the translational and angular velocities near a planar wall [52,57] and include both the free-space swimming velocity and the rigid-wall-induced velocity. Further, $\mathbf{U}^{(1)}$ and $\mathbf{\Omega}^{(1)}$ [Eq. (3)] are the contributions due to the deformation. We use parameters for a typical *E. coli* bacterium, swimming at a velocity $U_{\text{free}} \approx 22 \mu\text{m s}^{-1}$ and having a body radius $a \approx 1 \mu\text{m}$. Its force- and torque-dipole strengths have been measured experimentally [44] and through simulations [58]: $\alpha_{FD} \approx 32 \mu\text{m}^3 \text{s}^{-1}$ and $\alpha_{RD} \approx 25 \mu\text{m}^4 \text{s}^{-1}$. Different swimmer shapes can be modeled by a spatial distribution of point forces and torques [48], including higher-order terms in the multipole expansion, and a shear-induced reorientation accounting for elongated shapes [57], which we leave for future work.

Furthermore, we assume the deformation to be instantaneous compared to the swimming timescale $\tau = a/U_{\text{free}}$, so that $\partial_t \delta \approx 0$. The near-field and steric interactions of the microswimmer with the boundary are mimicked by a short-ranged repulsive force, so that the closest particle-surface distance is $h_{\min} = 1.5a$ and the swimmer does not collide with the boundary [23,52,57]. We study the trajectories of the microswimmers starting from a position $\mathbf{r}_0(0) = (0, 0, 4a)$ with pitch angles $\vartheta(0) \in [-\pi/2, \pi/2]$ and $\varphi(0) = 0$ until the swimmer attains a stable orientation in the xz plane, i.e., $d\vartheta/dt = -\Omega_y = 0$ at $\vartheta = \vartheta^*$. We further vary the elastoviscous and FvK numbers, $\epsilon \in [0.01, 0.1]$ and $\Gamma \in [0.01, 10]$, respectively.

Hydroelastic scattering of pushers. We begin our analysis by considering *E. coli*, i.e., a pusher-type microswimmer, oriented toward a deformable boundary at $\vartheta(0) = -0.23\pi$ with $\epsilon = 0.1$ and $\Gamma = 1.13$. Importantly, we observe that the swimmer reorients and is scattered away from the boundary [Fig. 1(a)(i)], attaining a stationary orientation $\vartheta^* > 0$ and a positive vertical velocity $U_z > 0$ taking the swimmer away from the boundary. This is primarily due to the deformation-induced velocity field giving rise to an angular velocity (Ω_y) rotating the swimmer. The shape of the deformation changes with the swimmer position and orientation: As the swimmer moves towards the surface, it pushes fluid toward it, leading to a valley, while it pulls fluid inwards from below, creating a hill. For a swimmer aligned parallel to $\mathbf{S}_0$, the deformation becomes symmetric. As it moves away from the boundary, the deformation shape changes to a valley at the back and a hill in front.

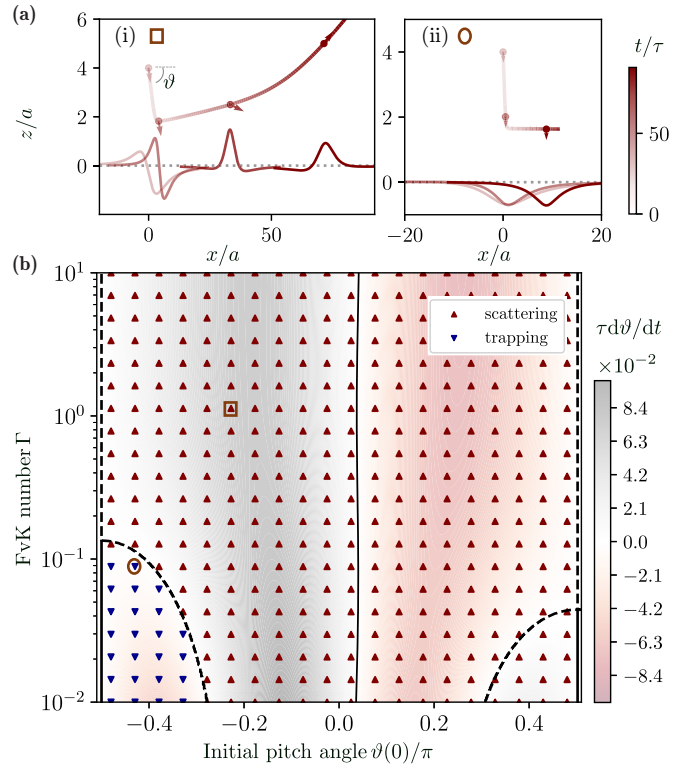


FIG. 1. (a) Chronophotographies of a pusher-type microswimmer moving near a deformable boundary in the xz plane. (i) Hydroelastic scattering event with parameters $\vartheta(0) = -0.23\pi$ and $\Gamma = 1.13$. (ii) Hydroelastic trapping event with parameters $\vartheta(0) = -0.43\pi$ and $\Gamma = 0.088$. The trajectories are color coded by time, where $\tau = a/U_{\text{free}}$ denotes the characteristic swimming timescale. The swimmer's orientation and the boundary deformation are shown at selected times. The latter are magnified by a factor of 10 for visualization in panel (a)(i). (b) Phase diagram for a pusher as a function of the initial orientation $\vartheta(0)$ and FvK number Γ . Background colors indicate $d\vartheta/dt = -\Omega_y(\epsilon, \Gamma, \vartheta(0), h_{\min})$. Black solid and dashed lines correspond to the stable and unstable fixed points of $d\vartheta/dt$, respectively. The trajectories in panel (a) correspond to the square and circle in the phase diagram. We use $\epsilon = 0.1$ in panels (a) and (b).

Our observation of hydroelastic scattering stands in stark contrast to the behavior of pushers aligning parallel to planar walls [57]—a phenomenon that promotes surface trapping of bacteria [47]. It is worth pointing out that due to the scattering the nature of the circular motion observed near planar walls [16] becomes negligible. This implies that the torque-dipole actuated angular velocity normal to the wall (Ω_z) is not decisive in the scattering trajectory for these parameters. Hence, it suffices to look at the trajectory of the swimmer in the xz plane as in [Fig. 1(a)]. While the torque-dipole contribution to the trajectory is negligible, it contributes to the nonaxisymmetric deformation of the membrane in the xy plane (Fig. S2 in the Supplemental Material [52]).

Moreover, it is paramount to note that the hydroelastic scattering appears reminiscent to the lift observed for their driven spherical counterparts [42], yet the mechanism is profoundly different as the latter do not have a characteristic orientation.

While the contribution to the deformation-induced velocity of spheres translating parallel to the elastic boundary becomes positive $U_z^{(1)} > 0$, leading to the lift, the one of the pushers is purely attractive $U_z^{(1)} < 0$ for $\vartheta = 0$ [Fig. S2(a) in the Supplemental Material [52]], indicating that the overall scattering of pushers away from the wall results from a hydroelastic reorientation. Further differences can be observed in the deformation that are relatively symmetric for pushers aligned parallel to the wall [Fig. 1(a)(i)], but display highly asymmetric shapes for sedimenting spheres irrespective of their distance to the boundary [42].

Hydroelastic trapping of pushers. Studying the trajectories of a pusher initially oriented toward the boundary at $\vartheta(0) = -0.43\pi$ and a smaller FvK number $\Gamma = 0.088$, we find a notably different behavior: The microswimmer reorients towards the surface due to the hydroelastic interaction and finally ends up in a trapping state, with stationary orientation $\vartheta^* = -\pi/2$ and height $h^* = h_{\min}$. This can be rationalized by investigating Eq. (1) and the deformation shapes in [Fig. 1(a)(ii)]. For $\Gamma \ll 1$, the bending resistance of the membrane dominates over the surface tension, with an increased penalty for higher-order gradients, producing deformations with smaller curvatures compared to situations with $\Gamma \gtrsim 1$. This appears to rotate the swimmer towards the boundary, leading to a symmetric deformation reminiscent of a pusher digging its own trap.

Phase diagram of pushers. To further characterize the emergence of these behaviors as a function of initial angles $\vartheta(0)$ and FvK numbers Γ (keeping $\epsilon = 0.1$ fixed), we plot a phase diagram where different phases are quantified based on their stationary orientation ϑ^* [Fig. 1(b)]. Our findings demonstrate that the hydroelastic scattering appears across various $\vartheta(0) < 0$ and Γ , showing that it is a persistent feature for interactions between pushers and deformable boundaries. For $\vartheta(0) > 0$ pushers also scatter away, similar to their behavior near rigid walls. The phase diagram further reveals an extended trapping phase at small $\Gamma \lesssim 0.1$ and initial pitch angles close to $\vartheta(0) \sim -\pi/2$. To quantify the transition between both phases, we assume that the orientational dynamics close to the surface are important and thus we consider $d\vartheta/dt$ evaluated close to the surface at $h_{\min}$, indicated in the background of the phase diagram. Our results show that different stationary orientations emerge depending on Γ : For $\Gamma \gtrsim 0.1$, the only stable fixed point is $\vartheta^* \sim 0.04\pi$, while for decreasing $\Gamma \lesssim 0.1$, the unstable fixed point at $\vartheta^* = -\pi/2$ becomes stable (corresponding to the trapping state) and, akin a pitchfork bifurcation, two new unstable fixed points arise close to $\pm\pi/2$. The unstable fixed point near $-\pi/2$ captures exactly the crossover between hydroelastic scattering and trapping in our phase diagram, emphasizing that the hydroelastic reorientation determines the overall dynamics.

Finally, we note that the phase diagram remains independent of $h(0)$ (Fig. S5 in the Supplemental Material [52]). Also, for smaller elastoviscous numbers $\epsilon = 0.01$, the hydroelastic scattering and trapping phases disappear and we recover, as expected, the in-plane circular motion. Overall our results suggest the following trend: For small Γ , the transition from circular motion to scattering and trapping occurs at smaller ϵ than for large Γ (Figs. S4 and S5 in the Supplemental Material

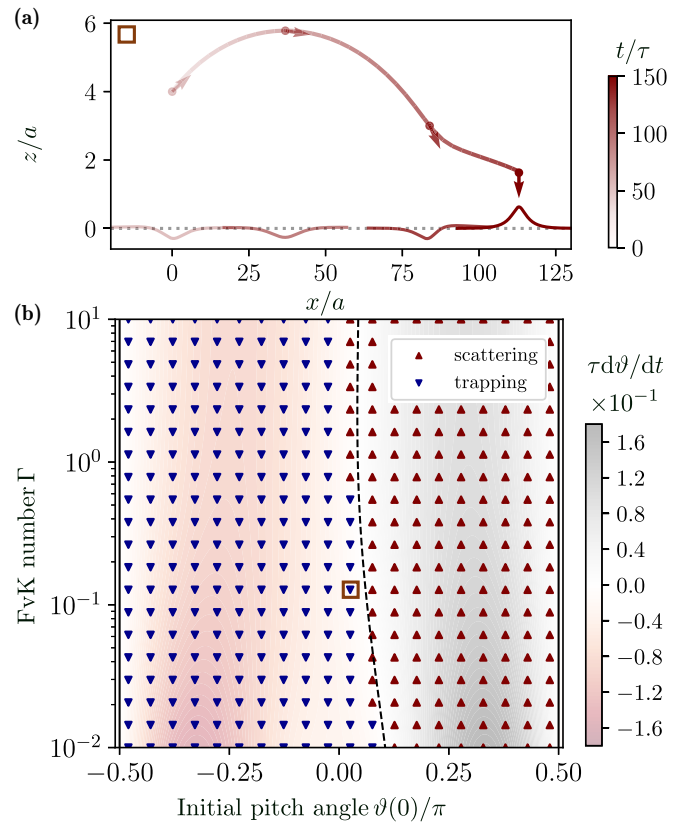


FIG. 2. (a) Chronophotographies of a puller-type microswimmer moving near a deformable boundary: a hydroelastic trapping event. The parameters are $\vartheta(0) = 0.02\pi$ and $\Gamma = 0.13$. The trajectories are color coded by time, where $\tau = a/U_{\text{free}}$ denotes the characteristic swimming timescale. The swimmer's orientation and the boundary deformation are shown at selected times. (b) Phase diagram for a puller as a function of its initial orientation $\vartheta(0)$ and FvK number Γ . Background colors indicate $d\vartheta/dt$ at $h_{\min}$. Black solid and dashed lines correspond to the stable and unstable fixed points of $d\vartheta/dt$, respectively. The trajectory in panel (a) corresponds to the square in the phase diagram. We use $\epsilon = 0.1$ in panels (a) and (b).

[52]). A substantial deformation seems to be necessary to observe these intriguing dynamics.

Enhanced trapping of pullers. While we have established a physical understanding of pusher-type microswimmers near a deformable boundary, we further investigate pullers with $\alpha_{\text{FD}} \rightarrow -\alpha_{\text{FD}}$ (and keeping α_{RD}) in terms of a phase plot for varying $\vartheta(0)$ and Γ . Most prominently, our results show that pullers, which are slightly oriented away from the boundary, exhibit enhanced overall trapping near the deformable boundary (Fig. 2), in contrast to their scattering from a planar wall. A typical trajectory is depicted in Fig. 2(a), indicating that the pullers first swim away from the boundary, before reorienting and moving towards it. In the trapping state, the swimmer pulls the boundary up creating a hill as opposed to the deformation produced by pushers.

The transition between trapping ($\vartheta^* = -\pi/2$) to a scattering state can be captured again by the unstable fixed points of the orientational dynamics $d\vartheta/dt$ at $h_{\min}$, as indicated in Fig. 2(b). Thus, the hydroelastic reorientation is the key ingredient for this intricate behavior, similar to the pusher case. We note

that small deviations between simulation results and our prediction arise at $\Gamma \gtrsim 1$, which result from the fact that pullers reorient further away from the boundary (at $h \gtrsim h_{\min}$) and not near the boundary as pushers.

Summary and conclusions. Our study reveals a profound impact of a deformable boundary on the dynamics of microswimmers, giving rise to behaviors that are distinct to motion near rigid walls. Using a perturbation theory, we find that surface deformations can generate reorientations, effectively scattering pusher-type microswimmers away from the boundary, and can enhance the overall trapping of pullers. Additionally, we observe that pushers, in certain parameter regimes, become trapped near deformable boundaries.

Our results provide first insights into the role of hydrodynamics for experimental observations of the trapping of active colloids [28,30] and bacteria [29] at the boundary of vesicles. In qualitative agreement with the finding that longer protrusions emerge for “flaccid” vesicles with low surface tension [28], the trapping state in our work occurs for small Föppl-von Kármán numbers. Furthermore, active Janus colloids, with puller-like flow signature, have been shown to be attracted towards deformable vesicles, which could be qualitatively explained by the enhanced hydrodynamic attraction of pullers predicted by our model. Besides, our theory lays the foundation for elucidating the emergence of collective effects due to the hydroelastic coupling [28–31], in which deformation due to one influences the behavior of all other particles. This would thus complement recent simulations on vesicle deformations due to “dry” active agents [59–61], where hydrodynamics have not been accounted for to date.

In this work, we have considered an infinitely thin planar elastic boundary with fluid on one side. A natural extension is

to include a preferred curvature or closed vesicle, resembling experimental setups, or another fluid or a viscoelastic material on the other side [37]. Insights come from theoretical work on swimming objects near a deformable liquid-liquid interface, which allows for in-plane flows [33,46]. For rigid slender microswimmers, enhanced attraction has been observed at long times [46], similar to our work. Furthermore, motion of reciprocal squirmers has been found due to the interplay of the timescales of the surface deformation and squirming modes [33]. Yet, the stationary dynamics of microswimmers near these interfaces, even in the far-field regime, as a function of material properties of the boundary remain to be explored.

Additionally, the shape of the microswimmer, details of its propulsion mechanism, short-range (steric) interactions [62], and fluctuations at different levels, ranging from diffusion [63] to tumbling dynamics [64–66], represent important aspects that could be incorporated in our framework and are expected to be relevant for the interactions of microswimmers with deformable boundaries in microbiological settings. In the future, it will be important to develop numerical tools to ultimately relax the assumption of small and instantaneous boundary deformations and resolve the full nonlinear hydroelastic coupling, which is expected to reveal more enriching dynamics of the microswimmers.

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Data availability. The data that support the findings of this article are not publicly available. The data are available from the authors upon reasonable request.

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- [1] E. Lauga and T. R. Powers, The hydrodynamics of swimming microorganisms, *Rep. Prog. Phys.* **72**, 096601 (2009).
 - [2] M. C. Marchetti, J. F. Joanny, S. Ramaswamy, T. B. Liverpool, J. Prost, M. Rao, and R. A. Simha, Hydrodynamics of soft active matter, *Rev. Mod. Phys.* **85**, 1143 (2013).
 - [3] C. Bechinger, R. Di Leonardo, H. Löwen, C. Reichhardt, G. Volpe, and G. Volpe, Active particles in complex and crowded environments, *Rev. Mod. Phys.* **88**, 045006 (2016).
 - [4] E. Lauga, *The Fluid Dynamics of Cell Motility*, 1st ed. (Cambridge University Press, Cambridge, 2020).
 - [5] G. Gompper *et al.*, The 2020 motile active matter roadmap, *J. Phys.: Condens. Matter* **32**, 193001 (2020).
 - [6] C. Kurzthaler, L. Gentile, and H. A. Stone, *Out-of-Equilibrium Soft Matter* (The Royal Society of Chemistry, 2023).
 - [7] E. M. Purcell, Life at low Reynolds number, *Am. J. Phys.* **45**, 3 (1977).
 - [8] R. Hartmann, P. K. Singh, P. Pearce, R. Mok, B. Song, F. Díaz-Pascual, J. Dunkel, and K. Drescher, Emergence of three-dimensional order and structure in growing biofilms, *Nat. Phys.* **15**, 251 (2019).
 - [9] O. Hallatschek, S. S. Datta, K. Drescher, J. Dunkel, J. Elgeti, B. Waclaw, and N. S. Wingreen, Proliferating active matter, *Nat. Rev. Phys.* **5**, 407 (2023).
 - [10] S. Otte, E. P. Ipiña, R. Pontier-Bres, D. Czerucka, and F. Peruani, Statistics of pathogenic bacteria in the search of host cells, *Nat. Commun.* **12**, 1990 (2021).
 - [11] S. S. Suarez and A. A. Pacey, Sperm transport in the female reproductive tract, *Hum. Reprod. Update* **12**, 23 (2006).
 - [12] R. Golestanian, Phoretic active matter, *arXiv:1909.03747* [cond-mat.soft].
 - [13] G. Volpe *et al.*, Roadmap for animate matter, *J. Phys.: Condens. Matter* **37**, 333501 (2025).
 - [14] Z. Wu, Y. Chen, D. Mukasa, O. S. Pak, and W. Gao, Medical micro/nanorobots in complex media, *Chem. Soc. Rev.* **49**, 8088 (2020).
 - [15] B. J. Nelson, I. K. Kaliakatsos, and J. J. Abbott, Microrobots for minimally invasive medicine, *Annu. Rev. Biomed. Eng.* **12**, 55 (2010).
 - [16] E. Lauga, W. R. DiLuzio, G. M. Whitesides, and H. A. Stone, Swimming in circles: Motion of bacteria near solid boundaries, *Biophys. J.* **90**, 400 (2006).
 - [17] R. Di Leonardo, D. Dell’Arciprete, L. Angelani, and V. Iebba, Swimming with an image, *Phys. Rev. Lett.* **106**, 038101 (2011).
 - [18] K. Ishimoto and E. A. Gaffney, Squirmer dynamics near a boundary, *Phys. Rev. E* **88**, 062702 (2013).
 - [19] G.-J. Li and A. M. Ardekani, Hydrodynamic interaction of microswimmers near a wall, *Phys. Rev. E* **90**, 013010 (2014).

- [20] W. E. Uspal, M. N. Popescu, S. Dietrich, and M. Tasinkevych, Self-propulsion of a catalytically active particle near a planar wall: from reflection to sliding and hovering, *Soft Matter* **11**, 434 (2015).
- [21] M. Kuron, P. Stärk, C. Holm, and J. de Graaf, Hydrodynamic mobility reversal of squirmers near flat and curved surfaces, *Soft Matter* **15**, 5908 (2019).
- [22] N. Desai and S. Michelin, Instability and self-propulsion of active droplets along a wall, *Phys. Rev. Fluids* **6**, 114103 (2021).
- [23] A. Poddar, A. Bandopadhyay, and S. Chakraborty, Near-wall hydrodynamic slip triggers swimming state transition of microorganisms, *J. Fluid Mech.* **894**, A11 (2020).
- [24] C. Kurzthaler and H. A. Stone, Microswimmers near corrugated, periodic surfaces, *Soft Matter* **17**, 3322 (2021).
- [25] K. Ishimoto, E. A. Gaffney, and D. J. Smith, Squirmer hydrodynamics near a periodic surface topography, *Front. Cell Dev. Biol.* **11**, 1123446 (2023).
- [26] W. Helfrich, Elastic properties of lipid bilayers: Theory and possible experiments, *Z. Naturforsch. C* **28**, 693 (1973).
- [27] F. L. H. Brown, Elastic modeling of biomembranes and lipid bilayers, *Annu. Rev. Phys. Chem.* **59**, 685 (2008).
- [28] H. R. Vutukuri, M. Hoore, C. Abaurrea-Velasco, L. van Buren, A. Dutto, T. Auth, D. A. Fedosov, G. Gompper, and J. Vermant, Active particles induce large shape deformations in giant lipid vesicles, *Nature (London)* **586**, 52 (2020).
- [29] S. C. Takatori and A. Sahu, Active contact forces drive nonequilibrium fluctuations in membrane vesicles, *Phys. Rev. Lett.* **124**, 158102 (2020).
- [30] F. Fessler, M. Wittmann, J. Simmchen, and A. Stocco, Autonomous engulfment of active colloids by giant lipid vesicles, *Soft Matter* **20**, 5904 (2024).
- [31] A. Azadbakht, T. R. Weikl, and D. J. Kraft, Nonadditivity in many-body interactions between membrane-deforming spheres increases disorder, *ACS Nano* **18**, 23067 (2024).
- [32] R. Trouilloud, T. S. Yu, A. E. Hosoi, and E. Lauga, Soft swimming: Exploiting deformable interfaces for low Reynolds number locomotion, *Phys. Rev. Lett.* **101**, 048102 (2008).
- [33] V. A. Shaik and A. M. Ardekani, Motion of a model swimmer near a weakly deforming interface, *J. Fluid Mech.* **824**, 42 (2017).
- [34] R. Ledesma-Aguilar and J. M. Yeomans, Enhanced motility of a microswimmer in rigid and elastic confinement, *Phys. Rev. Lett.* **111**, 138101 (2013).
- [35] J. M. Skotheim and L. Mahadevan, Soft lubrication, *Phys. Rev. Lett.* **92**, 245509 (2004).
- [36] L. Bureau, G. Coupier, and T. Salez, Lift at low Reynolds number, *Eur. Phys. J. E* **46**, 111 (2023).
- [37] B. Rallabandi, Fluid-elastic interactions near contact at low Reynolds number, *Annu. Rev. Fluid Mech.* **56**, 491 (2024).
- [38] H. S. Davies, D. Débarre, N. El Amri, C. Verdier, R. P. Richter, and L. Bureau, Elastohydrodynamic lift at a soft wall, *Phys. Rev. Lett.* **120**, 198001 (2018).
- [39] H. Lorentz, A general theorem concerning the motion of a viscous fluid and a few consequences derived from it, *Versl. Kon. Acad. Wet. Amst.* **5**, 168 (1897).
- [40] S. H. Lee, R. S. Chadwick, and L. G. Leal, Motion of a sphere in the presence of a plane interface. Part 1. An approximate solution by generalization of the method of Lorentz, *J. Fluid Mech.* **93**, 705 (1979).
- [41] C. Berdan II and L. G. Leal, Motion of a sphere in the presence of a deformable interface: I. Perturbation of the interface from flat: the effects on drag and torque, *J. Colloid. Interface Sci.* **87**, 62 (1982).
- [42] B. Rallabandi, N. Oppenheimer, M. Y. B. Zion, and H. A. Stone, Membrane-induced hydroelastic migration of a particle surfing its own wave, *Nat. Phys.* **14**, 1211 (2018).
- [43] K. Drescher, R. E. Goldstein, N. Michel, M. Polin, and I. Tuval, Direct measurement of the flow field around swimming microorganisms, *Phys. Rev. Lett.* **105**, 168101 (2010).
- [44] K. Drescher, J. Dunkel, L. H. Cisneros, S. Ganguly, and R. E. Goldstein, Fluid dynamics and noise in bacterial cell-cell and cell-surface scattering, *Proc. Natl. Acad. Sci. USA* **108**, 10940 (2011).
- [45] A. Daddi-Moussa-Ider, B. Rallabandi, S. Gekle, and H. A. Stone, Reciprocal theorem for the prediction of the normal force induced on a particle translating parallel to an elastic membrane, *Phys. Rev. Fluids* **3**, 084101 (2018).
- [46] S. Nambiar and J. S. Wettlaufer, Hydrodynamics of slender swimmers near deformable interfaces, *Phys. Rev. Fluids* **7**, 054001 (2022).
- [47] A. P. Berke, L. Turner, H. C. Berg, and E. Lauga, Hydrodynamic attraction of swimming microorganisms by surfaces, *Phys. Rev. Lett.* **101**, 038102 (2008).
- [48] P. Prakash, M. Vona, and R. E. Goldstein, Feeders and expellers, two types of animalcules with outboard cilia, have distinct surface interactions, *Phys. Rev. Fluids* **9**, 103101 (2024).
- [49] S. Kim and S. Karrila, *Microhydrodynamics: Principles and Selected Applications*, Butterworth-Heinemann Series in Chemical Engineering (Dover Publications, Mineola, New York, 2005).
- [50] J. Happel and H. Brenner, *Low Reynolds Number Hydrodynamics: With Special Applications to Particulate Media, Mechanics of Fluids and Transport Processes* (Springer Netherlands, Dordrecht, 1983), Vol. 1.
- [51] L. G. Leal, *Advanced Transport Phenomena: Fluid Mechanics and Convective Transport Processes* (Cambridge University Press, Cambridge, 2007), Vol. 7.
- [52] See Supplemental Material at <http://link.aps.org/supplemental/10.1103/rdx-gftq>, for details on the theory and simulations, which includes Refs. [67–76].
- [53] J. F. Faucon, M. D. Mitov, P. Méléard, I. Bivas, and P. Bothorel, Bending elasticity and thermal fluctuations of lipid membranes. Theoretical and experimental requirements, *J. Phys.* **50**, 2389 (1989).
- [54] F. Brochard and J. F. Lennon, Frequency spectrum of the flicker phenomenon in erythrocytes, *J. Phys.* **36**, 1035 (1975).
- [55] H. Masoud and H. A. Stone, The reciprocal theorem in fluid dynamics and transport phenomena, *J. Fluid Mech.* **879**, P1 (2019).
- [56] G. J. Elfring, A note on the reciprocal theorem for the swimming of simple bodies, *Phys. Fluids* **27**, 023101 (2015).
- [57] S. E. Spagnolie and E. Lauga, Hydrodynamics of self-propulsion near a boundary: predictions and accuracy of far-field approximations, *J. Fluid Mech.* **700**, 105 (2012).
- [58] J. Hu, M. Yang, G. Gompper, and R. G. Winkler, Modelling the mechanics and hydrodynamics of swimming *E. coli*, *Soft Matter* **11**, 7867 (2015).

- [59] M. Paoluzzi, R. Di Leonardo, M. C. Marchetti, and L. Angelani, Shape and displacement fluctuations in soft vesicles filled by active particles, *Sci. Rep.* **6**, 34146 (2016).
- [60] Y. Li and P. R. ten Wolde, Shape transformations of vesicles induced by swim pressure, *Phys. Rev. Lett.* **123**, 148003 (2019).
- [61] C. Wang, Y.-k. Guo, W.-d. Tian, and K. Chen, Shape transformation and manipulation of a vesicle by active particles, *J. Chem. Phys.* **150**, 044907 (2019).
- [62] V. Kantsler, J. Dunkel, M. Polin, and R. E. Goldstein, Ciliary contact interactions dominate surface scattering of swimming eukaryotes, *Proc. Natl. Acad. Sci. USA* **110**, 1187 (2013).
- [63] N. Fares, M. Lavaud, Z. Zhang, A. Jha, Y. Amarouchene, and T. Salez, Observation of Brownian elastohydrodynamic forces acting on confined soft colloids, *Proc. Natl. Acad. Sci. USA* **121**, e2411956121 (2024).
- [64] M. Molaei, M. Barry, R. Stocker, and J. Sheng, Failed escape: Solid surfaces prevent tumbling of *Escherichia coli*, *Phys. Rev. Lett.* **113**, 068103 (2014).
- [65] G. Junot, T. Darnige, A. Lindner, V. A. Martinez, J. Arlt, A. Dawson, W. C. Poon, H. Auradou, and E. Clément, Run-to-tumble variability controls the surface residence times of *E. coli* bacteria, *Phys. Rev. Lett.* **128**, 248101 (2022).
- [66] C. Kurzthaler, Y. Zhao, N. Zhou, J. Schwarz-Linek, C. Devailly, J. Arlt, J.-D. Huang, W. C. K. Poon, T. Franosch, J. Tailleur, and V. A. Martinez, Characterization and control of the run-and-tumble dynamics of *Escherichia coli*, *Phys. Rev. Lett.* **132**, 038302 (2024).
- [67] M. J. Lighthill, On the squirming motion of nearly spherical deformable bodies through liquids at very small Reynolds numbers, *Commun. Pure Appl. Math.* **5**, 109 (1952).
- [68] R. Golestanian, T. B. Liverpool, and A. Ajdari, Propulsion of a molecular machine by asymmetric distribution of reaction products, *Phys. Rev. Lett.* **94**, 220801 (2005).
- [69] M. N. Popescu, W. E. Uspal, and S. Dietrich, Self-diffusiophoresis of chemically active colloids, *Eur. Phys. J.: Spec. Top.* **225**, 2189 (2016).
- [70] S. Michelin, Self-propulsion of chemically active droplets, *Annu. Rev. Fluid Mech.* **55**, 77 (2023).
- [71] M. Deserno, Fluid lipid membranes: From differential geometry to curvature stresses, *Chem. Phys. Lipids* **185**, 11 (2015).
- [72] K. Kamrin, M. Z. Bazant, and H. A. Stone, Effective slip boundary conditions for arbitrary periodic surfaces: The surface mobility tensor, *J. Fluid Mech.* **658**, 409 (2010).
- [73] A. T. Chwang and T. Y.-T. Wu, Hydromechanics of low-Reynolds-number flow. Part 2. Singularity method for Stokes flows, *J. Fluid Mech.* **67**, 787 (1975).
- [74] H. Bateman and B. M. Project, *Tables of Integral Transforms* (McGraw-Hill Book Company, New York, 1954).
- [75] K. Aderogba and J. R. Blake, Action of a force near the planar surface between two semi-infinite immiscible liquids at very low Reynolds numbers, *Bull. Aust. Math. Soc.* **18**, 345 (1978).
- [76] M. Abramowitz, *Handbook of Mathematical Functions, With Formulas, Graphs, and Mathematical Tables* (Dover Publications, Inc., Mineola, New York, 1974).