

Hydrodynamic attraction and hindered diffusion govern first-passage times of swimming microorganisms

Yanis Baouche ¹, Magali Le Goff ², Thomas Franosch ² and Christina Kurzthaler ^{1,3,4,*}

¹Max-Planck-Institut für Physik komplexer Systeme, Nöthnitzer Straße 38, 01187 Dresden, Germany

²Institut für Theoretische Physik, Universität Innsbruck, Technikerstraße 21A, A-6020 Innsbruck, Austria

³Center for Systems Biology Dresden, Pfotenhauerstraße 108, 01307 Dresden, Germany

⁴Cluster of Excellence, Physics of Life, TU Dresden, Arnoldstraße 18, 01062 Dresden, Germany



(Received 22 September 2025; accepted 5 June 2026; published 29 June 2026)

The motion of microorganisms in their natural habitat is strongly influenced by their propulsion mechanisms, geometrical constraints, and random fluctuations. Here, we study numerically the first-passage-time (FPT) statistics of microswimmers, modeled as force dipoles, to reach a no-slip wall. Our results demonstrate that hindered diffusion near the wall can increase the median FPT by orders of magnitude compared to “dry” agents, while the intricate interplay of active motion and hydrodynamic attraction speeds up the arrival at large Péclet numbers (measuring the importance of self-propulsion relative to diffusion). Strikingly, it leads to a nonmonotonic behavior as a function of the dipole strength, where pushers reach the wall significantly faster than pullers. The latter become slower at an intermediate dipole strength and are more sensitive to their initial orientation, displaying a highly anisotropic behavior.

DOI: [10.1103/physrevresearch.8.L022060](https://doi.org/10.1103/physrevresearch.8.L022060)

Introduction. Microorganisms have evolved ingenious strategies for surviving and performing a multitude of biological functions, ranging from bacterial infections [1,2] to fertilization [3,4]. Many reside in aqueous settings and employ swimming mechanisms to navigate their surroundings [5–8], where the interplay of viscous forces and strong stochastic fluctuations dictates their dynamics. These processes are expected to play a fundamental role for their ability to find specific targets and their approach toward boundaries [9], where they accumulate to withstand harsh conditions [10–13]. Long-ranged hydrodynamic interactions with the target can generate attraction toward its boundary and reorientation [14,15], while modifying the noise strength [16]. These aspects render the study of the first-passage-time (FPT) statistics, capturing how long these agents require to find their target, a fascinating topic of research with far-reaching implications for both biology and nanotechnology, which aims at designing efficient cargo carriers [17–19].

Theoretical insights come from two main approaches, where the first emanates from entailing the active agents with some internal “intelligence” [20–26] and the second deals with FPT statistics of different stochastic processes describing microswimmer motion at the mesoscale [27–31]. In the first

approach, using control theory optimal strategies for reaching a target have been identified in different force fields [20–22] and near boundaries [23], where hydrodynamic interactions can crucially impact the fastest path toward a target. Furthermore, recent machine learning approaches, relying on genetic algorithms [24] and reinforcement learning [25,26], have been developed to endow active particles with intrinsic mechanisms for their gait control toward target locations.

Standard target-search problems, on the other hand, have been put forward in the 20th century in order to quantify chemical kinetics [32,33], and rely on deriving FPT statistics for specific dynamics. In the context of “dry” active agents, where hydrodynamics are ignored, these properties have been addressed analytically for run-and-tumble particles in one dimension [28–31,34]. Additionally, they have been studied analytically [35,36] and numerically [37] for active Brownian particles (ABPs) hitting a wall in two dimensions, showing anisotropic behavior with respect to the initial swimming direction. Yet, the aspect of hydrodynamic interactions has, despite its abundance in many biological systems, not been accounted for.

While the detention times of noisy microswimmers near walls depend strongly on the details of the hydrodynamic interactions [38], the impact of noise in such situations remains largely unexplored. Hydrodynamic studies, ignoring the aspect of stochastic fluctuations, have demonstrated intriguing physics, such as accumulation [9,15,39,40] and circular near-surface motion [41,42], emerging from the coupling of the velocity field produced by the microswimmers with boundaries. Thus, establishing a fundamental understanding of both hydrodynamics and noise will be of paramount importance for microbiology, for instance, in the transition from a planktonic swimming state to a surface-attached biofilm and

*Contact author: ckurzthaler@pks.mpg.de

Published by the American Physical Society under the terms of the Creative Commons Attribution 4.0 International license. Further distribution of this work must maintain attribution to the author(s) and the published article's title, journal citation, and DOI. Open access publication funded by Max Planck Society.

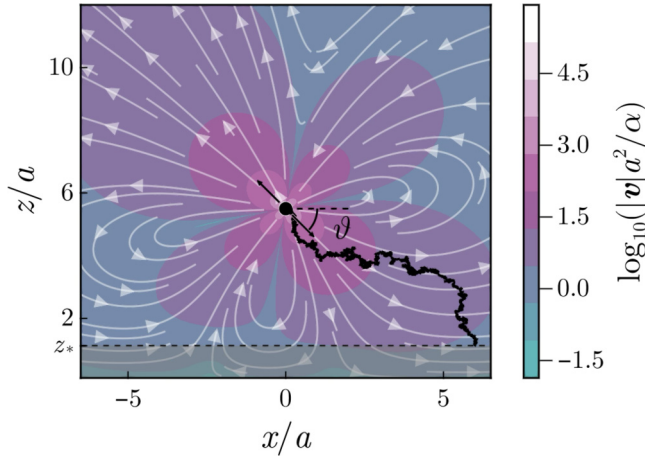


FIG. 1. Velocity field $\mathbf{v}$ induced by the swimmer with force dipole strength $\hat{\alpha} = 4$ and orientation $\vartheta = -\pi/4$, shown in the xOz plane. The black line is an exemplary trajectory. The heatmap represents the magnitude of the velocity field. Further, z^* represents the target height.

target-search efficiency at the microscale, relevant for advancing biomedical applications.

Here, we study the FPT statistics of swimming microorganisms by accounting for the hydrodynamic interactions through both the flow field produced by the agents and the spatially varying diffusivities in terms of a far-field description. Our results reveal a drastic slowdown due to hydrodynamically hindered diffusion close to the wall, which can be compensated by the hydrodynamic attraction of pusher like microswimmers that become faster than their “dry” counterpart at high Péclet numbers. We thus demonstrate how the swimming gait and slowdown of diffusion determine the efficiency of active target-search processes.

Model. We consider an active (spherical) particle swimming near a wall in a quasisteady low-Reynolds-number flow in three dimensions. The swimmer has a radius a and propels at speed v along its orientation $\mathbf{e}$. We describe the flow field produced by the swimmer at distances $z \gg a$ in terms of a force dipole along $\mathbf{e}$ of strength α . The spatially varying velocity and pressure fields, $\mathbf{v}(\mathbf{r})$ and $p(\mathbf{r})$, obey the Stokes equations: $\mu \nabla^2 \mathbf{v} = \nabla p$ and $\nabla \cdot \mathbf{v} = 0$, where μ denotes the fluid dynamic viscosity. Using the image method, the velocity fields have been obtained analytically [14,43]: $\mathbf{v} = \mathbf{v}'' + \mathbf{v}^*$, where $\mathbf{v}''$ corresponds to the velocity field produced by a force dipole in an unbounded domain and $\mathbf{v}^*$ is the (image) contribution due to the nearby wall (Fig. 1). The latter affects the instantaneous position $\mathbf{r}(t)$ and orientation $\mathbf{e}(t)$ of the active agent via

$$\frac{d\mathbf{r}}{dt} = v\mathbf{e} + \mathbf{v}^{\text{HI}} + \mathbf{v}^{\text{noise}} + \mathbf{v}^{\text{drift}}, \quad (1a)$$

$$\frac{d\mathbf{e}}{dt} = (\boldsymbol{\omega}^{\text{HI}} + \boldsymbol{\omega}^{\text{noise}} + \boldsymbol{\omega}^{\text{drift}}) \wedge \mathbf{e}, \quad (1b)$$

which contain contributions from the hydrodynamic interactions with the wall ($\mathbf{v}^{\text{HI}}$ and $\boldsymbol{\omega}^{\text{HI}}$) and Brownian noise ($\mathbf{v}^{\text{noise}}$ and $\boldsymbol{\omega}^{\text{noise}}$), and their associated drifts ($\mathbf{v}^{\text{drift}}$ and $\boldsymbol{\omega}^{\text{drift}}$).

Assuming that the swimmer is described by a force dipole, we can obtain the hydrodynamic contributions using Faxén’s law [44]:

$$\mathbf{v}^{\text{HI}} = \mathbf{v}^*(\mathbf{r}) = \frac{3\alpha}{16z^2} (1 - 3\cos(2\vartheta))\hat{\mathbf{z}} + \frac{3\alpha}{8z^2} \sin(2\vartheta)\hat{\boldsymbol{\phi}}, \quad (2a)$$

$$\boldsymbol{\omega}^{\text{HI}} = \frac{1}{2} \nabla \wedge \mathbf{v}^*(\mathbf{r}) = \frac{3\alpha}{16z^3} \sin(2\vartheta)\hat{\boldsymbol{\phi}}^\perp, \quad (2b)$$

with pitch angle ϑ , measuring the angle relative to the nearby wall, $\hat{\boldsymbol{\phi}} = \cos(\phi)\hat{\mathbf{x}} + \sin(\phi)\hat{\mathbf{y}}$, and $\hat{\boldsymbol{\phi}}^\perp = \hat{\mathbf{z}} \wedge \hat{\boldsymbol{\phi}}$.

Next, we introduce the contributions due to Brownian motion, assuming that the diffusivities are the same as for their passive counterparts:

$$\mathbf{D} = k_B T \mathbf{M} = k_B T \begin{pmatrix} \mathbf{M}^t & \mathbf{M}^{\text{tr}} \\ \mathbf{M}^{\text{rt}} & \mathbf{M}^r \end{pmatrix}, \quad (3)$$

where k_B denotes the Boltzmann constant, T is the temperature, and $\mathbf{M}^{t,r,\text{tr},\text{rt}}$ [45] represent the mobilities for translation, rotation, and the translational/rotational coupling. In the far-field regime ($a/z \ll 1$), to leading order the components of the diffusion tensor are

$$\frac{D_\perp^t}{D_0^t} = 1 - \frac{9}{8} \left(\frac{a}{z} \right), \quad \frac{D_\parallel^t}{D_0^t} = 1 - \frac{9}{16} \left(\frac{a}{z} \right), \quad (4a)$$

$$\frac{D_\perp^r}{D_0^r} = 1 - \frac{1}{8} \left(\frac{a}{z} \right)^3, \quad \frac{D_\parallel^r}{D_0^r} = 1 - \frac{5}{16} \left(\frac{a}{z} \right)^3, \quad (4b)$$

where $\perp$ and $\parallel$ correspond to the direction perpendicular and parallel to the wall, respectively. The coefficients D_0^t and D_0^r are the diffusion coefficients in bulk. In a first approximation, we neglect the translational/rotational coupling $\mathbf{D}^{\text{rt}} = \mathbf{D}^{\text{tr}} = \mathbf{0}$ and focus on the wall-induced effect on translational and rotational diffusion, such that the diffusion matrix (for a sphere) is diagonal $\mathbf{D} = \text{diag}(D_\parallel^t(z), D_\perp^t(z), D_\parallel^r(z), D_\perp^r(z))$, and the Brownian noise is given by $(\mathbf{v}^{\text{noise}}, \boldsymbol{\omega}^{\text{noise}})^T = \sqrt{2\mathbf{D}}\boldsymbol{\xi}$, where $\boldsymbol{\xi}$ is Gaussian white noise of zero mean and delta-correlated variance, $\langle \xi_i(t)\xi_j(t') \rangle = \delta_{ij}\delta(t-t')$ for $i, j = 1, \dots, 6$. Near a planar wall, the diffusive processes are anisotropic and z dependent $[\mathbf{D}(z)]$ and thus drift terms emerge (see the Supplemental Material [46]):

$$\mathbf{v}^{\text{drift}} = D_0^t \frac{9a}{8z^2} \hat{\mathbf{z}} \quad \text{and} \quad \boldsymbol{\omega}^{\text{drift}} = \mathbf{e} \wedge \mathbf{D}^r \cdot \mathbf{e}. \quad (5)$$

The dynamics of the agent is characterized by two nondimensional numbers: the Péclet number $\text{Pe} = va/D_0^t$, characterizing the relative importance of active motion and diffusion, and the reduced dipole strength $\hat{\alpha} = \alpha/(va^2)$. We use the hydrodynamic radius $a = \sqrt{3D_0^t/(4D_0^r)}$ as length scale. Here, we consider pushers $\hat{\alpha} > 0$, pullers $\hat{\alpha} < 0$, and neutral swimmers $\hat{\alpha} = 0$, whose hydrodynamic interaction with the wall only appears in the diffusivities. We perform stochastic simulations (see Appendixes A and B) and compute the FPT properties of agents starting at a distance $z(0) = z^* + z_0$ from the boundary, where $z^*/a = 1.125$ denotes the target distance and is set to ensure positive diffusivities. Varying the cutoff z^* shows that, as expected, the hydrodynamic effects disappear for large $z^*/a \gtrsim 4$, while for smaller z^* the qualitative features remain the same, highlighting the robustness of our findings

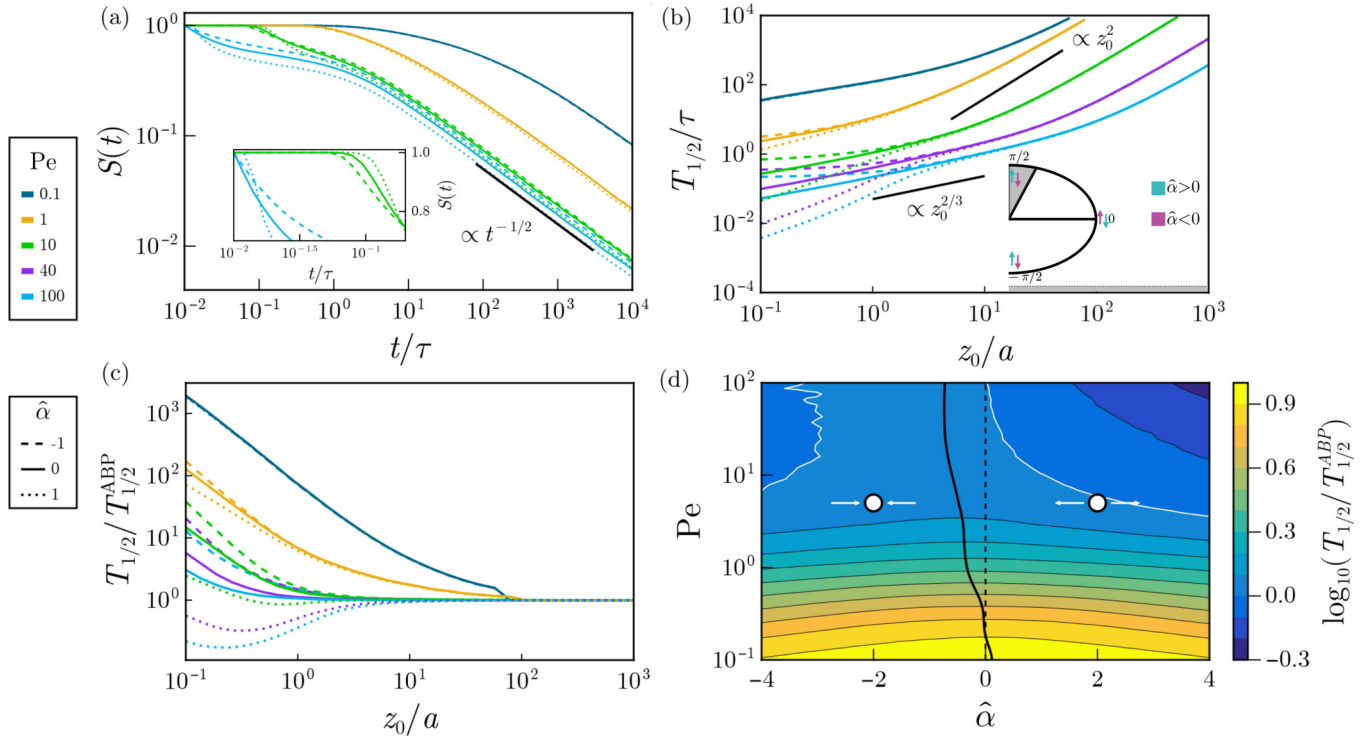


FIG. 2. (a) Survival probability $S(t)$ as a function of time t for several Péclet numbers Pe and reduced dipole strengths $\hat{\alpha}$. Here, the initial distance is $z_0/a = 2.0$. Inset shows a magnification of $S(t)$ at short times. (b) Median FPT $T_{1/2}$ as a function of the initial distance z_0 . (c) Ratio $T_{1/2}/T_{1/2}^{ABP}$ as a function of z_0 . (d) Contour plot of the ratio $T_{1/2}/T_{1/2}^{ABP}$ as a function of Pe and $\hat{\alpha}$ for $z_0/a = 5$. White lines indicate $T_{1/2} = T_{1/2}^{ABP}$ and the black line corresponds to the maximum $\max [T_{1/2}/T_{1/2}^{ABP}]$ for different Pe numbers.

(see Sec. II G of the Supplemental Material [46]). Unless stated otherwise, agents are oriented at random initial pitch angles ϑ_0 .

Hydrodynamic attraction speeds up pushers. The FPT statistics are typically studied through the survival probability $S(t)$ (i.e., the probability that the agent has not reached the target distance z^* up to time t). In an unconfined domain, it commonly behaves as $S(t) \sim t^{-\sigma}$ at long times, with exponent σ depending on the underlying dynamics [47]. Despite hydrodynamic interactions, our simulations [Fig. 2(a)] show $\sigma = 1/2$, just like the “dry” counterpart with small activity [36]. However, the short-time behavior and the tail’s amplitude depend sensitively on the Péclet number. On the one hand, a diffusion-dominated dynamics ($Pe = 0.1$) will lead to a lower probability to be absorbed at short times because diffusion is hindered close to the boundary. On the other hand, the regime of high activity ($Pe \gg 1$) displays a higher absorption probability, as persistent motion becomes the main locomotory mechanism, thus allowing the agent to circumvent slow diffusion. We further note that the impact of the flow signature ($\hat{\alpha}$) becomes mainly apparent at short times and will become clear later. Additionally, as a consequence of the slow decay of the survival probability, the mean FPT diverges, therefore not giving any information about the completion time. Consequently, we use the median $T_{1/2}$ as a metric to provide a quantitative description of the speed of completion [48].

We first consider the median $T_{1/2}$ for a range of Pe and $\hat{\alpha}$ as a function of initial distance z_0/a to study how the interplay

of all processes affects the absolute time it takes the agent to reach the boundary [Fig. 2(b)]. For neutral swimmers ($\hat{\alpha} = 0$), the median FPT scales as $z_0^{2/3}$ at distances smaller than the persistence length $z_0 \lesssim \ell_p = v/D_0'$. This behavior remains for constant diffusivities (Fig. S2 in the Supplemental Material [46]) and can thus be attributed to the coupling between persistent motion and diffusive rotational motion. Indeed, an ABP typically displays a superballistic regime in its mean-squared displacement $\langle \Delta z(t)^2 \rangle \propto t^3$ through the influence of its initial angle [49]. The latter is captured by the median, as it does not pick up particles that do not reorient to eventually reach the wall. Thus, the typical time to reach the boundary from a distance z_0 leads to a median such that $T_{1/2} \propto z_0^{2/3}$. The effective diffusive regime of an ABP manifests itself at large initial distances ($z_0 \gg \ell_p$), where the median behaves as $T_{1/2} \propto z_0^2$ and where the dipole strength has no impact.

At short and intermediate initial distances $z_0 \lesssim \ell_p$, the hydrodynamic contributions allow differentiating the type of swimmer [Fig. 2(b)]. In particular, the prominent feature that emerges is that pushers almost always exhibit a smaller median than pullers when the initial angle is randomized. Inspecting the survival probability, our results show that pullers reach the wall in two populations: the first swimming toward the wall and actually reaching it faster than pushers, which becomes manifest in a smaller survival probability [Fig. 2(a), inset]; and the second population departs away from the wall and reaches it after a very long time due to reorientation toward the wall via rotational diffusion (or never), leading to a slower decay of S at long times. The latter eventuates in

spite of the hydrodynamic attraction for pullers, as persistent motion $v \gtrsim v_z^{\text{HI}}$ [corresponding to $1 \gtrsim 3|\alpha|/(4vz^2)$] prevails.

To understand the differences between pushers and pullers, we elucidate the distinct contributions due to the hydrodynamic coupling. First, neglecting the hydrodynamic reorientation by setting $\omega^{\text{HI}} = \mathbf{0}$ does not change the results, while for $\mathbf{v}^{\text{HI}} = \mathbf{0}$ the results for various $\hat{\alpha}$ are almost indistinguishable (see Fig. 6 in the Supplemental Material [46]), indicating that hydrodynamic attraction is what causes the difference in the medians. We argue that this discrepancy results from the fact that out of half of the population that reach the wall at long times $t \gtrsim T_{1/2}$, most agents first swim persistently away from the wall and thus an unbalance of hydrodynamic attraction arises between pushers and pullers. In particular, pullers from a certain part of their attractive region are not represented in the median [corresponding to the gray-shaded area in the inset of Fig. 2(b)]. If we let $\vartheta^* \in [0, \pi/2]$, then averaging the attraction over the orientations $\int_{-\pi/2}^{\vartheta^*} v_z(\vartheta) \sin(\vartheta) d\vartheta \propto -\alpha/z^2$ shows that pushers experience a net attraction and pullers a net repulsion. Overall, this demonstrates that hydrodynamic attraction is the prime cause of the speedup of pushers, while their reorientation plays a minor role. It is important to note that hydrodynamic reorientation becomes important for postarrival phenomena [14,41,50] and dictate their detention times [38]. It is important to note that our results are robust to statistical uncertainties, as shown in Sec. II F of the Supplemental Material [46], where we use bootstrapping to provide a 95% confidence interval for the median.

Slowdown due to hindered diffusion. In order to obtain a quantitative idea of how hydrodynamic interactions and height-dependent diffusion affect the median, we compare $T_{1/2}$ with that of a simple ABP $T_{1/2}^{\text{ABP}}$ ($\hat{\alpha} = 0$ and constant bulk diffusivities D_0^r, D_0^t). Figure 2(c) shows an increase by up to two orders of magnitude of the median FPT—a significant slowdown in comparison to “dry” agents—revealing that hindered diffusion at the boundary is the leading cause of this slowdown, even at high Péclet numbers ($\text{Pe} = 100$). We further note that we have also split the contributions of translational and rotational diffusion and observed that the latter does not influence the FPT statistics (Sec. II B of the Supplemental Material [46]), thus supporting our first approximation, in which the rotation-translation coupling term (of same order) was neglected.

Nonmonotonic behavior. To unravel the interplay between activity and flow signature, we plot the same ratio as before as a function of Pe and $\hat{\alpha}$ for $z_0/a = 5$ [Fig. 2(d)]. Through the black line representing the maximum of $T_{1/2}/T_{1/2}^{\text{ABP}}$, we observe that pullers are slightly faster than pushers at very low Péclet number ($\text{Pe} \ll 1$), as activity is too low to prevent the hydrodynamic attraction at these distances. This picture reverses for increasing activity and pushers become faster than pullers. Moreover, larger dipole strength $\hat{\alpha}$ can decrease the median FPT due to hydrodynamic attraction of both pullers and pushers, leading to a nonmonotonic behavior of the median with a maximum at $\hat{\alpha} \lesssim 0$. (We note that the latter $\hat{\alpha}^{\text{max}}(\text{Pe})$ does not follow a simple scaling law.) This indicates that at an intermediate dipole strength, pullers take longer to reach the wall: For large $\hat{\alpha}$, hydrodynamic attraction takes

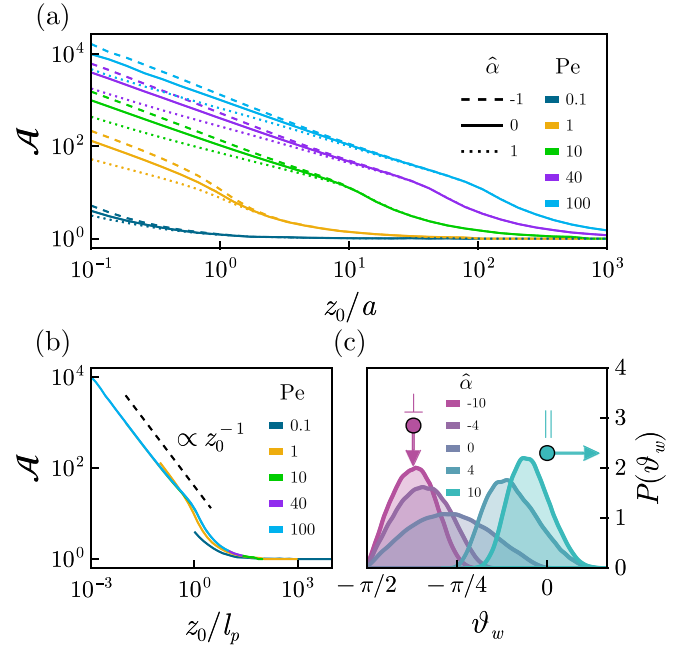


FIG. 3. (a) Anisotropy $\mathcal{A}$ as a function of the initial distance z_0 for several Péclet numbers Pe and dipole strengths $\hat{\alpha}$. (b) Anisotropy rescaled by the persistence length l_p for $\hat{\alpha} = 0$. (c) Distribution of the arrival angles ϑ_w as a function of the dipole strength $\hat{\alpha}$. Here, $z_0/a = 5.6$ and $\text{Pe} = 10$.

over active motion away from the wall ($v \lesssim v_z^{\text{HI}}$), while for small $\hat{\alpha}$ the behavior of a neutral swimmer is approached.

Impact of initial orientation. Our results suggest that the initial orientation plays a major role in the FPT statistics, similar to the dry counterpart [36]. To quantify its role, we introduce an anisotropy metric

$$\mathcal{A} = \frac{T_{1/2}(z_0, \pi/2)}{T_{1/2}(z_0, -\pi/2)}, \quad (6)$$

measuring the ratio of the median FPTs of swimmers departing from and swimming toward the wall. Figure 3(a) shows that the anisotropy decays with the initial distance for all activities and dipole strengths, and relaxes exponentially to one for $z_0/a \gg 1$, where the memory of the initial angle is progressively lost. We note that for $\hat{\alpha} = 0$ rescaling the initial distance by the persistence length collapses our data to a single curve where $\mathcal{A} \propto z_0^{-1}$ up to $z_0/l_p \simeq 1$. This is due to agents facing the wall and reaching it ballistically ($\propto z_0$), while those departing away from it exhibit a median that plateaus until $z_0 \simeq l_p$ (see Sec. II C in Supplemental Material [46]). Their ratio thus linearly decays with initial distance. At $z_0/l_p \gtrsim 1$, rotational diffusion typically decorrelates orientations as $\propto e^{-2D_0^r t}$ and the anisotropy vanishes.

Additionally, we note that pullers ($\hat{\alpha} = -1$) display a bigger anisotropy than pushers ($\hat{\alpha} = 1$). This can be once again explained by the fact that pullers swimming toward the wall experience attraction, making them faster than pushers in this instance. In the departing scenario, pushers experience boundary-aligning torques, making them slightly faster, such that the overall anisotropy is more pronounced for pullers. The

anisotropic behavior can be further understood by studying the angle at which they reach the boundary ϑ_w . Figure 3(c) shows that while pushers tend to approach the wall in a parallel manner, pullers swim straight toward the wall due to hydrodynamic reorientation and subsequent attraction, in agreement with the orientational dynamics of force-dipole swimmers near walls [9,14,51].

Summary and conclusions. Through the study of the FPT properties of different types of swimming organisms, we demonstrated that the time it takes an active agent to reach a no-slip boundary is dictated by the interplay of their swimming gait and diffusion. Using numerical simulations, we find that although hindered diffusion always obstructs wall absorption, hydrodynamic interactions can make the swimmer faster or slower than a “dry” agent, with the outcome dependent on its flow signature. In particular, persistent swimming disrupts the overall balance of wall-induced attraction and repulsion, resulting in a net decrease of the median FPT for pushers and increase for pullers. Our results suggest that for an *Escherichia coli* bacterium, having a reduced dipole strength of $\hat{\alpha} \approx 1.5$ and a Péclet number of $Pe = O(100)$ [52,53], hydrodynamic interactions could expedite their approach toward walls, which remains to be tested in experiments. Moreover, we find that pullers are better at leveraging their initial swimming angle, as attraction and persistent swimming play in concert to make them hit the wall faster than pushers when facing toward it.

Different properties of the boundary, which alter both the hydrodynamic attraction and the diffusivities, are in principle expected to modify our findings. Interestingly, our conclusions still hold for a perfect slip boundary (see Sec. III of the Supplemental Material [46]) [14,54], demonstrating that the main features appear generic, namely, the slowdown due to hindered diffusion and pushers being faster than pullers. This urges the question whether changes of a pusher to puller mode in the gait, as observed in *Vibrio alginolyticus* [55] and *Pseudomonas putida* [56], could be leveraged by microorganisms to optimize their approach toward target boundaries, resulting in a competition between energetic cost of the swim mode [57–60] and fast arrival.

Here, we used a far-field description for the swimmer and neglected near-field effects, which could stem from lubrication flows or steric interactions. Resolving the near-field hydrodynamics through an asymptotic matching with lubrication theory, the use of bispherical coordinates or numerics together with steric repulsion has been shown to yield swimmer-specific interface effects such as scattering and oscillations [61–63]. We have explored the impact of the cutoff distance, defining the near-wall region, in additional simulations, showing no qualitative changes in this regime. While we considered spherical microswimmers, elongated shapes entail anisotropic diffusivities with respect to their body axis and additional hydrodynamic alignment. These aspects may only quantitatively impact our results, as their dependence on the particle-surface distance remains of the same order as for spherical particles [14,64], leading to negligible effects of reorientation for the FPT statistics that could, however, significantly alter the near-surface dynamics.

Our work sheds light on how confined hydrodynamics affects the approach of active agents toward boundaries and is expected to provide grist for future microbiological target-search studies. We anticipate that it will allow for a broader consideration of the role of hydrodynamics in first-passage problems for active particles, which are often only studied through the lens of statistical physics due to the difficulty in resolving hydrodynamic interactions. For biological swimmers, arrival at a boundary represents the first step toward the emergence of phenomena such as biofilm formation [65,66], material degradation [67–69], or microbial predation [70,71], and we expect our study to contribute to their understanding.

Acknowledgments. Y.B. gratefully acknowledges discussions with Sagnik Garai and Akhil Varma. This research was funded in part by the Austrian Science Fund (FWF) Grant No. 10.55776/P35580.

Data availability. There are no publicly available research data or software supporting this manuscript. Requests for further information or data should be sent to the authors.

Appendix A: Nondimensional equations of motion. Rescaling the equations of motion with the particle radius a as characteristic length scale, $\mathbf{r} = a\mathbf{R}$, and the rotational diffusion time $\tau = 1/(2D_0^r)$ as characteristic time scale, $t = \tau T$, yields

$$\frac{d\mathbf{R}}{dT} = Pe\mathbf{e} + Pe\hat{\alpha}\mathbf{V}^{\text{HI}} + \mathbf{V}^{\text{noise}} + \mathbf{V}^{\text{drift}}, \quad (\text{A1a})$$

$$\frac{d\mathbf{e}}{dT} = (Pe\hat{\alpha}\boldsymbol{\Omega}^{\text{HI}} + \boldsymbol{\Omega}^{\text{noise}} + \boldsymbol{\Omega}^{\text{drift}}) \wedge \mathbf{e}, \quad (\text{A1b})$$

with

$$\begin{aligned} \mathbf{V}^{\text{HI}} = & \frac{3}{8Z^2} \sin(2\vartheta)(\cos(\varphi_0)\hat{\mathbf{x}} + \sin(\varphi_0)\hat{\mathbf{y}}) \\ & + \frac{3}{16Z^2}(1 - 3\cos(2\vartheta))\hat{\mathbf{z}}, \end{aligned} \quad (\text{A2a})$$

$$\boldsymbol{\Omega}^{\text{HI}} = \frac{3}{16Z^3} \sin(2\vartheta)(-\sin(\varphi_0)\hat{\mathbf{x}} + \cos(\varphi_0)\hat{\mathbf{y}}), \quad (\text{A2b})$$

$$\mathbf{V}^{\text{drift}} = \frac{3}{4Z^2}\hat{\mathbf{z}}, \quad (\text{A2c})$$

$$\boldsymbol{\Omega}^{\text{drift}} \wedge \mathbf{e} = -(\mathcal{D}_{\perp}^r(Z) - \mathcal{D}_{\parallel}^r(Z))(e_z^2\mathbf{e} - e_z\hat{\mathbf{z}}), \quad (\text{A2d})$$

and rescaled diffusivities

$$\begin{aligned} \mathcal{D}_{\perp}^t(Z) &= \frac{2}{3}\left(1 - \frac{9}{8Z}\right), \\ \mathcal{D}_{\parallel}^t(Z) &= \frac{2}{3}\left(1 - \frac{9}{16Z}\right), \end{aligned} \quad (\text{A3a})$$

$$\begin{aligned} \mathcal{D}_{\perp}^r(Z) &= \frac{1}{2}\left(1 - \frac{1}{8Z^3}\right), \\ \mathcal{D}_{\parallel}^r(Z) &= \frac{1}{2}\left(1 - \frac{5}{16Z^3}\right), \end{aligned} \quad (\text{A3b})$$

where we used the Stokes-Einstein-Sutherland relation for a spherical particle in bulk $D_0^t/D_0^r = (4/3)a^2$.

Appendix B: Numerical aspects. The equations of motion are integrated with the following scheme:

$$\mathbf{R}(T + \Delta T) = \mathbf{R}(T) + \Delta T(\text{Pee}(T) + \text{Pe}\hat{\alpha}\mathbf{V}^{\text{HI}} + \mathbf{V}^{\text{drift}}) + \text{diag}\left(\sqrt{2\mathcal{D}_{\parallel}^i(Z)\Delta T}, \sqrt{2\mathcal{D}_{\parallel}^r(Z)\Delta T}, \sqrt{2\mathcal{D}_{\perp}^r(Z)\Delta T}\right) \cdot \mathbf{N}(0, 1), \quad (\text{B1a})$$

$$\mathbf{e}(T + \Delta T) = \mathbf{e}(T) + (\text{Pe}\hat{\alpha}\mathbf{\Omega}^{\text{HI}}\Delta T + \mathbf{\Omega}^{\text{drift}}\Delta T + \text{diag}\left(\sqrt{2\mathcal{D}_{\parallel}^r(Z)\Delta T}, \sqrt{2\mathcal{D}_{\parallel}^i(Z)\Delta T}, \sqrt{2\mathcal{D}_{\perp}^r(Z)\Delta T}\right) \cdot \boldsymbol{\xi}(0, 1)) \wedge \mathbf{e}(T), \quad (\text{B1b})$$

$$\mathbf{e}(T + \Delta T) = \frac{\mathbf{e}(T + \Delta T)}{|\mathbf{e}(T + \Delta T)|}, \quad (\text{B1c})$$

where $\boldsymbol{\xi}(0, 1)$ and $\mathbf{N}(0, 1)$ are independent, normally distributed random variables with zero mean and unit variance. Furthermore, we use a time step $\Delta T = 10^{-4}$ and collect statistics from 10^5 agents.

-
- [1] T. Ó. Cróinín and S. Backert, Host epithelial cell invasion by *Campylobacter jejuni*: Trigger or zipper mechanism? *Front. Cell. Infect. Microbiol.* **2**, 25 (2012).
 - [2] 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).
 - [3] S. Suarez and A. A. Pacey, Sperm transport in the female reproductive tract, *Hum. Reprod. Update* **12**, 23 (2006).
 - [4] M. Zaferani and A. Abbaspourrad, Biphasic chemokinesis of mammalian sperm, *Phys. Rev. Lett.* **130**, 248401 (2023).
 - [5] E. Lauga and T. R. Powers, The hydrodynamics of swimming microorganisms, *Rep. Prog. Phys.* **72**, 096601 (2009).
 - [6] 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).
 - [7] E. Lauga, *The Fluid Dynamics of Cell Motility*, Cambridge Texts in Applied Mathematics (Cambridge University Press, Cambridge, 2020).
 - [8] *Out-of-Equilibrium Soft Matter: Active Fluids*, edited by C. Kurzthaler, L. Gentile, and H. A. Stone, Soft Matter Series No. 17 (Royal Society of Chemistry, London, 2023).
 - [9] A. P. Berke, L. Turner, H. C. Berg, and E. Lauga, Hydrodynamic attraction of swimming microorganisms by surfaces, *Phys. Rev. Lett.* **101**, 038102 (2008).
 - [10] C. Hannig and M. Hannig, The oral cavity—A key system to understand substratum-dependent bioadhesion on solid surfaces in man, *Clin. Oral Invest.* **13**, 123 (2009).
 - [11] K. Drescher, Y. Shen, B. L. Bassler, and H. A. Stone, Biofilm streamers cause catastrophic disruption of flow with consequences for environmental and medical systems, *Proc. Natl. Acad. Sci. USA* **110**, 4345 (2013).
 - [12] G. C. L. Wong, Roadmap on emerging concepts in the physical biology of bacterial biofilms: From surface sensing to community formation, *Phys. Biol.* **18**, 051501 (2021).
 - [13] D. L. Kurz, E. Secchi, R. Stocker, and J. Jimenez-Martinez, Morphogenesis of biofilms in porous media and control on hydrodynamics, *Environ. Sci. Technol.* **57**, 5666 (2023).
 - [14] 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).
 - [15] S. E. Spagnolie, G. R. Moreno-Flores, D. Bartolo, and E. Lauga, Geometric capture and escape of a microswimmer colliding with an obstacle, *Soft Matter* **11**, 3396 (2015).
 - [16] X. Bian, C. Kim, and G. E. Karniadakis, 111 years of Brownian motion, *Soft Matter* **12**, 6331 (2016).
 - [17] P. Erkoc, I. C. Yasa, H. Ceylan, O. Yasa, Y. Alapan, and M. Sitti, Mobile microrobots for active therapeutic delivery, *Adv. Ther.* **2**, 1800064 (2019).
 - [18] Y. Alapan, O. Yasa, B. Yigit, I. C. Yasa, P. Erkoc, and M. Sitti, Microrobotics and microorganisms: Biohybrid autonomous cellular robots, *Annu. Rev. Control Rob. Auton. Syst.* **2**, 205 (2019).
 - [19] G. Volpe, Roadmap for animate matter, *J. Phys.: Condens. Matter* **37**, 333501 (2025).
 - [20] L. Piro, E. Tang, and R. Golestanian, Optimal navigation strategies for microswimmers on curved manifolds, *Phys. Rev. Res.* **3**, 023125 (2021).
 - [21] L. Piro, R. Golestanian, and B. Mahault, Efficiency of navigation strategies for active particles in rugged landscapes, *Front. Phys.* **10**, 1034267 (2022).
 - [22] L. Piro, B. Mahault, and R. Golestanian, Optimal navigation of microswimmers in complex and noisy environments, *New J. Phys.* **24**, 093037 (2022).
 - [23] A. Daddi-Moussa-Ider, H. Löwen, and B. Liebchen, Hydrodynamics can determine the optimal route for microswimmer navigation, *Commun. Phys.* **4**, 15 (2021).
 - [24] B. Hartl, M. Hübl, G. Kahl, and A. Zöttl, Microswimmers learning chemotaxis with genetic algorithms, *Proc. Natl. Acad. Sci. USA* **118**, e2019683118 (2021).
 - [25] S. Colabrese, K. Gustavsson, A. Celani, and L. Biferale, Flow navigation by smart microswimmers via reinforcement learning, *Phys. Rev. Lett.* **118**, 158004 (2017).
 - [26] Z. Zou, Y. Liu, Y.-N. Young, O. S. Pak, and A. C. H. Tsang, Gait switching and targeted navigation of microswimmers via deep reinforcement learning, *Commun. Phys.* **5**, 158 (2022).
 - [27] *The Physics of Foraging: An Introduction to Random Searches and Biological Encounters*, edited by G. M. Viswanathan (Cambridge University Press, Cambridge, 2011).
 - [28] G. H. Weiss, Some applications of persistent random walks and the telegrapher's equation, *Phys. A* **311**, 381 (2002).
 - [29] L. Angelani, R. Di Leonardo, and M. Paoluzzi, First-passage time of run-and-tumble particles, *Eur. Phys. J. E* **37**, 59 (2014).
 - [30] K. Malakar, V. Jemseena, A. Kundu, K. Vijay Kumar, S. Sabhapandit, S. N. Majumdar, S. Redner, and A. Dhar, Steady state, relaxation and first-passage properties of a run-and-tumble particle in one-dimension, *J. Stat. Mech.* (2018) 043215.

- [31] M. Guéneau, S. N. Majumdar, and G. Schehr, Run-and-tumble particle in one-dimensional potentials: Mean first-passage time and applications, *Phys. Rev. E* **111**, 014144 (2025).
- [32] E. Gudowska-Nowak, K. Lindenberg, and R. Metzler, Preface: Marian Smoluchowski's 1916 paper—A century of inspiration, *J. Phys. A: Math. Theor.* **50**, 380301 (2017).
- [33] D. Grebenkov, R. Metzler, and G. Oshanin, Target search problems, in *Target Search Problems*, edited by D. Grebenkov, R. Metzler, and G. Oshanin (Springer Nature Switzerland, Cham, 2024), pp. 1–29.
- [34] M. Guéneau, S. N. Majumdar, and G. Schehr, Optimal mean first-passage time of a run-and-tumble particle in a class of one-dimensional confining potentials, *Europhys. Lett.* **145**, 61002 (2024).
- [35] F. Di Trapani, T. Franosch, and M. Caraglio, Active Brownian particles in a circular disk with an absorbing boundary, *Phys. Rev. E* **107**, 064123 (2023).
- [36] Y. Baouche, M. Le Goff, C. Kurzthaler, and T. Franosch, First-passage-time statistics of active Brownian particles: A perturbative approach, *Phys. Rev. E* **111**, 054113 (2025).
- [37] U. Basu, S. N. Majumdar, A. Rosso, and G. Schehr, Active Brownian motion in two dimensions, *Phys. Rev. E* **98**, 062121 (2018).
- [38] K. Schaar, A. Zöttl, and H. Stark, Detention times of microswimmers close to surfaces: Influence of hydrodynamic interactions and noise, *Phys. Rev. Lett.* **115**, 038101 (2015).
- [39] J. Elgeti and G. Gompper, Wall accumulation of self-propelled spheres, *Europhys. Lett.* **101**, 48003 (2013).
- [40] 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).
- [41] 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).
- [42] J. Elgeti, U. B. Kaupp, and G. Gompper, Hydrodynamics of sperm cells near surfaces, *Biophys. J.* **99**, 1018 (2010).
- [43] J. R. Blake and A. T. Chwang, Fundamental singularities of viscous flow, *J. Eng. Math.* **8**, 23 (1974).
- [44] L. G. Leal, *Advanced Transport Phenomena: Fluid Mechanics and Convective Transport Processes*, Cambridge Series in Chemical Engineering (Cambridge University Press, Cambridge, 2007).
- [45] W. E. Usual, The boundary element method for fluctuating active colloids, in *Non-Equilibrium Particle Dynamics*, edited by A. S. Kim (IntechOpen, London, UK, 2019), pp. 23–45.
- [46] See Supplemental Material at <http://link.aps.org/supplemental/10.1103/qdl8-kk9h> for details on the theory and simulations, which includes Refs. [14,44,54,72–76].
- [47] N. Levernier, M. Dolgushev, O. Bénichou, R. Voituriez, and T. Guérin, Survival probability of stochastic processes beyond persistence exponents, *Nat. Commun.* **10**, 2990 (2019).
- [48] S. Belan, Median and mode in first passage under restart, *Phys. Rev. Res.* **2**, 013243 (2020).
- [49] B. ten Hagen, S. van Teeffelen, and H. Löwen, Brownian motion of a self-propelled particle, *J. Phys.: Condens. Matter* **23**, 194119 (2011).
- [50] S. Garai, U. Makanga, A. Varma, and C. Kurzthaler, Hydroelastic scattering and trapping of microswimmers, *Phys. Rev. Res.* **7**, L042005 (2025).
- [51] R. E. Goldstein, Green algae as model organisms for biological fluid dynamics, *Annu. Rev. Fluid Mech.* **47**, 343 (2015).
- [52] 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).
- [53] 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).
- [54] 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).
- [55] K.-T. Wu, Y.-T. Hsiao, and W.-Y. Woon, Entrapment of pusher and puller bacteria near a solid surface, *Phys. Rev. E* **98**, 052407 (2018).
- [56] Z. Alirezaeizanjani, R. Großmann, V. Pfeifer, M. Hintsche, and C. Beta, Chemotaxis strategies of bacteria with multiple run modes, *Sci. Adv.* **6**, eaaz6153 (2020).
- [57] 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).
- [58] B. Nasouri, A. Vilfan, and R. Golestanian, Minimum dissipation theorem for microswimmers, *Phys. Rev. Lett.* **126**, 034503 (2021).
- [59] A. Daddi-Moussa-Ider, B. Nasouri, A. Vilfan, and R. Golestanian, Optimal swimmers can be pullers, pushers or neutral depending on the shape, *J. Fluid Mech.* **922**, R5 (2021).
- [60] L. Piro, A. Vilfan, R. Golestanian, and B. Mahault, Energetic cost of microswimmer navigation: The role of body shape, *Phys. Rev. Res.* **6**, 013274 (2024).
- [61] D. Crowdy, Treadmilling swimmers near a no-slip wall at low Reynolds number, *Int. J. Non Linear Mech.* **46**, 577 (2011).
- [62] G.-J. Li and A. M. Ardekani, Hydrodynamic interaction of microswimmers near a wall, *Phys. Rev. E* **90**, 013010 (2014).
- [63] K. Ishimoto and D. G. Crowdy, Dynamics of a treadmilling microswimmer near a no-slip wall in simple shear, *J. Fluid Mech.* **821**, 647 (2017).
- [64] M. Lisicki, B. Cichocki, and E. Wajnryb, Near-wall diffusion tensor of an axisymmetric colloidal particle, *J. Chem. Phys.* **145**, 034904 (2016).
- [65] S. Sharma, J. Mohler, S. D. Mahajan, S. A. Schwartz, L. Bruggemann, and R. Aalinkel, Microbial biofilm: A review on formation, infection, antibiotic resistance, control measures, and innovative treatment, *Microorganisms* **11**, 1614 (2023).
- [66] A. Zhao, J. Sun, and Y. Liu, Understanding bacterial biofilms: From definition to treatment strategies, *Front. Cell. Infect. Microbiol.* **13**, 1137947 (2023).
- [67] M. S. Datta, E. Sliwerska, J. Gore, M. F. Polz, and O. X. Cordero, Microbial interactions lead to rapid micro-scale successions on model marine particles, *Nat. Commun.* **7**, 11965 (2016).
- [68] J. Słomka, U. Alcolombri, E. Secchi, R. Stocker, and V. I. Fernandez, Encounter rates between bacteria and small sinking particles, *New J. Phys.* **22**, 043016 (2020).

- [69] U. Alcolombri, F. J. Peaudecerf, V. I. Fernandez, L. Behrendt, K. S. Lee, and R. Stocker, Sinking enhances the degradation of organic particles by marine bacteria, *Nat. Geosci.* **14**, 775 (2021).
- [70] M. Saleem, I. Fetzer, H. Harms, and A. Chatzinotas, Diversity of protists and bacteria determines predation performance and stability, *ISME J.* **7**, 1912 (2013).
- [71] H. H. Tuson and D. B. Weibel, Bacteria–surface interactions, *Soft Matter* **9**, 4368 (2013).
- [72] 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).
- [73] C. Kurzthaler, S. Leitmann, and T. Franosch, Intermediate scattering function of an anisotropic active Brownian particle, *Sci. Rep.* **6**, 36702 (2016).
- [74] J. Happel and H. Brenner, *Low Reynolds Number Hydrodynamics: With Special Applications to Particulate Media, Mechanics of Fluids and Transport Processes*, 2nd ed (Kluwer Academic Publishers, Dordrecht, 1991).
- [75] R. B. Jones and F. N. Alavi, Rotational diffusion of a tracer colloid particle: IV. Brownian dynamics with wall effects, *Phys. A* **187**, 436 (1992).
- [76] B. Efron, Nonparametric estimates of standard error: The jack-knife, the bootstrap and other methods, *Biometrika* **68**, 589 (1981).