Fertilization in the sea: sperm chemotaxis in physiological shear flows

Steffen Lange\textsuperscript{1,2} and Benjamin M. Friedrich\textsuperscript{1,2}

\textsuperscript{1}Center for Advancing Electronics Dresden (cfaed), TU Dresden, 01062 Dresden, Germany
\textsuperscript{2}Cluster of Excellence Physics of Life (PoL), TU Dresden, 01062 Dresden, Germany

(Dated: December 21, 2019)

Many motile biological cells navigate along concentration gradients of signaling molecules: This chemotaxis guides for instance sperm cells from marine invertebrates, which have to find egg cells in the ocean. While chemotaxis has been intensively studied for idealized conditions of perfect gradients in still water, natural gradients are usually distorted, e.g., by turbulent flows in the ocean. Recent experiments with bacteria and sperm cells surprisingly revealed the existence of an optimal flow strength at which chemotaxis is more effective than for still water. We use sperm chemotaxis in simple shear flow as a prototypical example to understand the origin of such an optimal flow strength theoretically: We quantify how flow accelerates spreading of signaling molecules released by the egg, but distorts the resulting concentration field into long and thin filaments. The competition between these two effects sets an optimal flow strength that maximizes sperm-egg encounter. We characterize how sperm cells ‘surf’ along concentration filaments, typical for scalar turbulence, revealing a general navigation paradigm in the presence of flow. We compare both simulation and theory with previous experimental results and find good agreement.

Chemotaxis - the navigation of biological cells guided by chemical gradients - is crucial for bacterial foraging, neuronal development, immune responses, and sperm-egg encounter during fertilization. For fertilization, sperm cells employ chemotaxis to steer up concentration gradients of signaling molecules, called chemoattractant, released by the egg. This sperm chemotaxis has been intensively studied for external fertilization of marine invertebrates, where sperm and egg cells are spawned directly into the sea [1–5]. In this case, sperm and egg cells become strongly diluted. Besides synchronized spawning [6, 7], sperm chemotaxis is important to enhance sperm-egg encounter rates [8]. The mechanism of sperm chemotaxis in marine invertebrates is well established theoretically [9, 10] and has been experimentally confirmed [11]: Sperm cells swim along helical paths $r(t)$, while probing the surrounding concentration field $c(r)$. A cellular signaling system rotates the helix axis $\mathbf{h}$ to align with the gradient $\nabla c$ at a rate proportional to $|\nabla c|/(c + c_0)$ limited by sensory adaption with sensitivity threshold $c_0$.

Previous work on sperm chemotaxis focused predominantly on idealized conditions of still water [5, 12]. However, natural habitats like the ocean are characterized by turbulent flow, which convects gametes and distorts concentration fields into filamentous plumes [3, 13–17], see Fig. 1A for illustration. Turbulence in typical spawning habitats of marine invertebrates has been characterized [13, 18, 19], e.g., in terms of local energy dissipation rates $\epsilon$ or typical shear rates $\alpha = 0.3 \times 10^{3} \text{s}^{-1}$, which are often similar to those in mammalian reproductive tracts [2]. Turbulent flow rapidly mixes sperm and egg cells, yet only down to the Kolmogorov length-scale $\eta_{\text{Kol}} = (\nu^3/\epsilon)^{1/4} = 1 - 10 \text{mm}$ (with kinematic viscosity $\nu$). Previous predictions based on turbulent mixing [20] underestimated fertilization probability $P_{\text{fert}}$ [17, 21], since these early studies neglected active swimming and sperm chemotaxis inside the smallest eddies, whose size is comparable to the Kolmogorov length $\eta_{\text{Kol}}$. At these small length-scales, the Reynolds number of the flow is below one, and gametes perceive turbulence as unsteady shear flow [19, 22] with a typical shear rate $\alpha$ set by the inverse of the Kolmogorov time $\tau_{\text{Kol}} = \sqrt{\nu/\epsilon}$. Intriguingly, fertilization experiments conducted at physiological shear rates revealed the existence of an optimal shear rate $\alpha^* > 0$, corresponding to an optimal turbulence strength $\epsilon^* > 0$, at which the fertilization probability $P_{\text{fert}}$ was maximal [14, 18, 23]. Similar observations have been made for bacterial chemotaxis [15]. Obvious biological effects can be ruled out as the origin of the optimum [13, 18], including flow damaging the gametes or sperm-egg bonds being broken by shear forces. Despite an early two-dimensional model [23], a physical explanation and quantitative understanding of the observed optimum is still missing [14, 17].

Here, we examine sperm chemotaxis in small-scale turbulence both numerically and theoretically using a prototypical model: We consider three-dimensional sperm chemotaxis in simple shear flow, which convects and co-rotates sperm cells and distorts the chemoattractant field that surrounds the egg. We find an optimal shear rate $\alpha^*$ in simulations, as previously observed in experiments [14, 18]. We explain and quantify this optimum from theory. In particular, we describe how sperm cells ‘surf’ along filaments of the concentration field, see Fig. 1B. The optimum $\alpha^*$ arises from the competition between flow-accelerated spreading of the concentration field, which enhances chemotaxis, and the distortion of this concentration field into long and thin filaments, which impairs chemotaxis. We apply our theoretical description to two previous experiments on sperm chemotaxis, one with moderate flow, mimicking fertilization in shallow coastal waters [14], and one with strong turbulence, mimicking fertilization in the surf zone [18]. In both cases, simulation and theory match the experimental data. For the regime of strong turbulence, a the-
ory based on ballistic swimmers convected by the flow

I. SIMULATIONS: OPTIMAL SHEAR RATE

We simulate sperm chemotaxis around an egg suspended at \( r = 0 \) in a simple shear flow \( \mathbf{v}_{\text{ext}}(r) = \alpha y \mathbf{e}_x \) by extending a generic theory of helical chemotaxis [10] to incorporate convection and co-rotation of sperm cells by the flow. We use a spherical periodic boundary at radius \( r_{\text{max}} \), which mimics an ensemble of eggs with density \( \rho_{\text{egg}} = (4\pi r_{\text{max}}^3/3)^{-1} \), and assume an exposure time \( t_{\text{max}} \). (Materials and Methods provides details on simulation setup and chosen parameters.) The resulting sperm-egg-encounter probability \( P_{\text{sperm,egg}} \) displays a maximum at an optimal shear rate \( \alpha^* \approx 0.1 \text{ s}^{-1} \), see Fig. 2, which uses parameters for sea urchin \textit{A. punctualia}. At the optimal shear rate \( \alpha^* \), \( P_{\text{sperm,egg}} \) is 8-fold higher than without flow. Only for larger shear rates \( \alpha > 0.3 \text{ s}^{-1} \), chemotaxis becomes less effective than without flow and finally ineffective at very strong shear rate with \( \alpha \geq 1 \text{ s}^{-1} \). Note that without chemotaxis, the encounter probability would be 2-3 orders of magnitude smaller for the chosen parameters.

Surprisingly, the numerical results show that convection and co-rotation of sperm cells are not necessary for the existence of an optimal shear rate: Simulations without co-rotation yield very similar results, see Fig. 2, while switching-off convection only changes \( \alpha^* \) (not shown). Consequently, the existence of an optimal shear rate \( \alpha^* \) should be a consequence of the distortion of the concentration field by the flow. Typically, shear flow generates long filaments, or plumes, of high concentration. Simulations show how sperm cells enter these filaments and ‘surf’ along them, see Fig. 1B, with trajectories resembling a damped oscillation, see also Fig S4. Damped oscillations occur when sperm cells move towards the egg, yet oscillations are amplified when sperm cells move away from the egg. The latter sometimes causes sperm cells to turn around, thus redirecting them towards the egg.

In conclusion, sperm chemotaxis in external flows is a two-stage search problem of first finding a concentration
II. THEORY: FILAMENT SURFING

We develop a theory of sperm chemotaxis in filamentous concentration fields generated by simple shear flows. This theory describes surfing along filaments and allows to predict the sperm-egg-encounter probability, see Fig. 2. We consider a simple shear flow \( \mathbf{v}_{\text{ext}}(r) = \alpha y \mathbf{e}_x \) and a spherical egg of radius \( r_{\text{egg}} \), without loss of generality located at \( r = 0 \), releasing chemoattractant at a constant rate for a time \( t \). Far from the source \( |\mathbf{r}| \gg r_{\text{egg}} \), the concentration field \( c(r,t) \) established by diffusion and convection takes a generic form, see Fig. 1B for illustration,

\[
c(r,t) = c_0 \exp\left(-k|x|\right) \exp\left(-\frac{(y-y_0)^2}{2\sigma^2} + \frac{z^2}{2\sigma^2}\right).
\]

The parameters \( c_0(t), k(t), \sigma(|x|, t), a_y, \) and \( y_0(x, t) \) obey phenomenological power-laws, see SI C for details. Eq. 1 describes a filament with exponential decay along its centerline \((x, y_0(x,t), 0)\) and a Gaussian cross-sectional profile. We generalize an effective equation for the helix axis, previously derived for simple radial concentration fields \cite{10} to concentration filaments given by Eq. (1). We obtain a one-dimensional effective equation of motion, which explains and quantifies filament surfing, see SI D for details. To leading order, this effective equation of motion represents a damped harmonic oscillator, whose frequency and damping ratio matches the damped oscillation observed in simulations, see Fig. 1 and Fig. S4. The strong gradient in the cross-section of the filament causes sperm cells to navigate towards the centerline of the filament. Yet, cells continuously pass through this centerline due to their finite chemotactic turning rate and consequently oscillate within the filament. The much weaker gradient along the concentration filament in Eq. (1) damps this oscillation when sperm cells move towards the egg, and amplifies it when they move away.

The threshold \( c_0 \) of sensory adaption limits chemotaxis to the part of the filament with concentration at least of the order of \( c_0 \). This defines a cross-sectional area \( A(x) \), where \( c(\mathbf{r}) \geq c_0 \), as well as circumference \( S(x) \), at each centerline position \( x \) of the filament. We decompose the search for the egg into an outer search, i.e., finding the concentration filament, and an inner search, i.e., surfing along the filament, see SIE. For the outer search, we introduce the flux \( j_{\text{out}} \) of sperm cells arriving at the surface of the concentration filament and assume that \( j_{\text{out}} \) is approximately independent of the position \( x \) along the filament. Given that the egg has to be found within the exposure time \( t_{\text{max}} \), we also introduce the outer search time \( t_{\text{out}}(x, t_{\text{max}}) < t_{\text{max}} \) available to arrive at the filament at \( x \) as specified below. For the inner search, using the effective equation of motion, we compute the probability \( p_{\text{in}}(x, t_{\text{max}}) \) that a sperm cell entering the filament at position \( x \) reaches the egg within time \( t_{\text{max}} \). We also compute the conditional mean surfing time \( t_{\text{in}}(x, t_{\text{max}}) \), i.e., the average time successful sperm cells require to reach the egg after entering the filament at \( x \). Correspondingly, we set the time for the outer search as \( t_{\text{out}}(x, t_{\text{max}}) = t_{\text{max}} - t_{\text{in}}(x, t_{\text{max}}) \) for \( p_{\text{in}} > 0 \) (and \( t_{\text{out}} = 0 \) for \( p_{\text{in}} = 0 \)). We compute the encounter probability \( P_{\text{sperm:egg}} \) by

\[
P_{\text{sperm:egg}} \approx \int_{-\infty}^{\infty} dx \int_{-\infty}^{\infty} dx' \int_{-\infty}^{\infty} dx'' \int_{-\infty}^{\infty} dx''' \int_{-\infty}^{\infty} dx'''' \int_{-\infty}^{\infty} dx'''', \]

\[
\left[A(x)\rho_{\text{egg}} + S(x)j_{\text{out}}(x, t_{\text{max}})\right].
\]

The first term approximates the contribution from sperm cells that are initially within the filament. This contribution is negligible compared to the second term for low \( \rho_{\text{egg}} \) or large \( t_{\text{max}} \). The second term quantifies the contribution from sperm cells that successfully find the concentration filament and surf along it to the egg. The flux \( j_{\text{out}} \) can be determined either from a fit to full simulations or approximated as \( j_{\text{out}} = \rho_{\text{egg}} v_h/4 \) by treating sperm cells outside the filament as ballistic swimmers with speed \( v_h \), both of which gives similar results. Note that for the chosen parameters, the volume \( V_{\text{tot}} = \int_{-\infty}^{\infty} dx A(x) \) of the filament (and its surface area \( \int_{-\infty}^{\infty} dx S(x) \)) increases monotonically with shear rate \( \alpha \). Hence, the optimal \( \alpha^* \) is not explained by a flow-dependent ‘chemotactic volume’ \( V_{\text{tot}} \). Instead, the optimum emerges from two effects related to filament surfing, which reduce \( p_{\text{in}} \) and \( t_{\text{out}} \) in Eq. (2) at high \( \alpha \): First, when the filament is too thin at the entry point \( x \) to enable the first oscillation, the sperm cells simply pass through the filament. Second, if the time required to surf from the entry point \( x \) to the egg is too long, the sperm cells will not reach the egg during the exposure time \( t_{\text{max}} \). Higher shear rates generate longer and thinner filaments, which aggravates both effects.

Comparison of full simulations and the theoretical prediction Eq. (2) shows good agreement, see Fig. 2. This agreement strongly suggests that the optimal shear rate \( \alpha^* \) originates from two competing effects: Higher shear flow spreads the chemoattractant faster, which facilitates sperm navigation to the egg, but results in longer and thinner filaments, which impairs chemotactic filament surfing.

The optimal shear rate \( \alpha^* \) is slightly smaller in simulations, compared to the theory. Inspection of simulated trajectories suggest that this is due to sperm cells, which miss the egg at least once while surfing along the filament, which increases the mean surfing time \( t_{\text{in}} \). Amplitude and position of the peak of the sperm-egg-encounter probability depend on chosen parameters. According to our theory, the presence of an optimal flow strength is a
generic feature at low egg densities and relatively long exposure times, as chosen in Fig. 2. Shorter exposure time $t_{\text{max}}$ or higher egg density $\rho_{\text{egg}}$ diminish $p_{\text{in}}$ by effectively cutting off the outer parts of the filament.

III. COMPARISON WITH EXPERIMENTS

Previous experiments measured the fraction of fertilized eggs $P_{\text{fert}}$ for an exposure time $t_{\text{max}}$. This fraction directly relates to the encounter probability $P_{\text{sperm:egg}}$ by fertilization kinetics [25, 26] when the respective densities of sperm and egg cells, $\rho_{\text{sperm}}$ and $\rho_{\text{egg}}$, are known

$$P_{\text{fert}}(t_{\text{max}}) = 1 - \exp \left( -p_{\text{i}} P_{\text{sperm:egg}}(t_{\text{max}}) \frac{\rho_{\text{sperm}}}{\rho_{\text{egg}}} \right).$$

(3)

The fertilizability $p_{\text{i}}$ is the probability that a sperm-egg encounter results in successful fertilization.

A. Moderate shear

In a previous experiment by Zimmer and Riffell, fertilization was studied for red abalone $H. rufescens$ in a Taylor-Couette chamber for moderate shear rate $\alpha$, mimicking flow conditions in their natural spawning habitat [13, 14]. The measured fertilization probability decreased with increasing $\alpha > 0$, both for normal chemotaxis and a case of chemically inhibited chemotaxis, see Fig. 3 for a reproduction of the original data [14, Fig. 5c]. At low shear rate, the measured fertilization probability is twice as high with chemotaxis than without, while there was little difference at high shear rates. This suggests that the performance of sperm chemotaxis is reduced at high shear rates. We performed simulations of sperm chemotaxis in external flow, using parameters that match the specific experimental setup of Refs. [13, 14], see SI G. Specifically, the time span between preparation of the egg suspension and the actual fertilization experiment results in a background concentration of chemottractant, which we estimate as $c_{\text{bg}} \sim 4 \text{ nM}$ and account for in the simulations. We compare results of these simulations and the experiments, using fertilizability $p_{\text{i}}$ as single fit parameter, see Fig. 3. We find good agreement for the case with normal chemotaxis, and reasonable agreement for the case of inhibited chemotaxis (potentially due to residual chemotaxis in the latter case). An exception is the data point at $\alpha = 0 \text{ s}^{-1}$. In fact, a different experimental protocol was used for this data point, corresponding to different initial mixing of sperm and egg cells, which is not modeled in the simulations. In Fig. 3, we neglected co-rotation of sperm cells for simplicity. We find similar results if we account for co-rotation, except for the highest shear rates, where fertilization probability is reduced, see Fig. S1. A shear-rate dependent chemokinesis suggested by Refs. [13, 14], i.e., regulation of sperm swimming speed, is not included in the simulations, yet is expected to change results only slightly. In our comparison, we focused on the case of low sperm density considered in Refs. [13, 14], thereby avoiding confounding effects of sperm-sperm interactions and reduced fertilization rates due to polyspermy at high sperm densities [27, 28].

Due to the high background concentration $c_{\text{bg}}$, the part of the filament with sufficiently high concentration $c(r) \gtrsim c_{\text{bg}}$ is situated only in the vicinity of the egg and has an approximately spherical shape. While our far-field theory of filament surfing does not directly apply to this special near-field case, a simple estimate for $p_{\text{in}}$ and $t_{\text{out}}$ assuming straight sperm trajectories aligned...
with the local concentration gradient inside the plume, see SIE, yields a similar decay of fertilization probability, see Fig. 3. The fitted flux of sperm cells into the concentration plume $j_{\text{out}} = 4.8 \cdot 10^3 \text{ m}^{-2}\text{s}^{-1}$ is consistent with the limit $j_{\text{out}} = \rho_{\text{egg}} v_h/4 = 7.5 \cdot 10^3 \text{ m}^{-2}\text{s}^{-1}$ for a ballistic swimmer. This validates our interpretation of chemotaxis in external shear as a two-stage search, consisting of blind random search for a chemotactic volume and subsequent navigation inside this volume.

**B. Strong flows**

![Figure 4: Fertilization in strong flows and high egg density.](image)

**FIG. 4. Fertilization in strong flows and high egg density.** Previous measurements of fertilization probability $P_{\text{fert}}(\epsilon)$ for sea urchin *S. purpuratus* at strong turbulence, characterized by density-normalized dissipation rate $\epsilon$ (filled gray triangles) [18, 29] and our corresponding simulations $P_{\text{fert}}(\alpha)$ as function of shear rate $\alpha$ (open blue circles, mean ± SD) match well, using a single fit parameter $a = 0.075$ that relates dissipation rate $\epsilon$ and typical shear rate $\alpha$ (using the known relationship $\alpha(\epsilon) = a \sqrt{\nu/\epsilon}$ [19, 22]). Both simulation and experiment are well captured by a minimal model of a ballistic swimmer in simple shear flow (red), see SIA. Fertilization probability $P_{\text{fert}}$ rapidly drops above a characteristic flow strength $\alpha > 100 \text{ s}^{-1}$, which is consistent with a scale estimate $\alpha = 2\pi v_h/(0.1 r_{\text{egg}})$ (vertical dotted line). At these high shear rates, active swimming becomes negligible compared to convection. The case of low shear rates is well described by the limit case of a ballistic swimmer in the absence of flow $\alpha = 0 \text{ s}^{-1}$ (dotted horizontal line, Eq. (3) with $P_{\text{sperm-egg}}(t) = 1 - \exp(-qt)$ and rate $q = \pi v_h^2 r_{\text{egg}}/\rho_{\text{egg}}$). The fertilizability $p_t = 10\%$ is obtained from an independent experiment [18], see Fig. S2. From the experimental protocol, we estimate a high background concentration $c_{bg} = 500 - 4000 \text{ nM}$ of chemotracant, which renders sperm chemotaxis ineffective. Corresponding results for simulations with co-rotation are shown in Fig. S3.

Mead and Denny studied fertilization in the sea urchin *S. purpuratus* in turbulent flow, mimicking physiological conditions in the oceanic surf zone [18, 29, 30]. The measured fertilization probability slightly increased as function of turbulence strength, quantified in terms of local dissipation rate $\epsilon$, and decreased rapidly at larger dissipation rate $\epsilon > 1 \text{ m}^2\text{s}^{-3}$, see Fig. 4 for a reproduction of the original data (taken from Fig. 3 of Ref. [29], representing a re-calibration of data from Fig. 5 of Ref. [18]). We determined fertilization probability $P_{\text{fert}}$ in simple shear flow from simulations, using parameters that match the specific experimental setup, see SIE. For the experiments by Mead and Denny, we estimate a high background concentration of chemotracant $c_{bg} = 500 - 4000 \text{ nM}$, which renders sperm chemotaxis ineffective, which is thus neglected in the simulations. Fully developed turbulence is characterized by a spectrum of local shear rates, with a characteristic shear rate $\alpha$ related to the dissipation rate by $\alpha(\epsilon) = a \sqrt{\nu/\epsilon}$ with proportionality factor $a$ [19, 22]. In the simulations, we assume a simple shear flow $v_{\text{ext}} = \alpha y e_x$, and determine $a = 0.075$ by a single-parameter fit, see Fig. 4. For sake of simplicity, co-rotation of sperm cells is neglected. Results with co-rotation are qualitatively very similar, yet the fertilization probability $P_{\text{fert}}$ drops at a smaller shear rate $\alpha$ and thus yields a smaller fit parameter $a = 0.023$, see Fig. S3. Note that these fits for $a$ are smaller than values commonly used in the literature $a \sim 0.15 - 1.8$ [22, 31, 32]. Nevertheless, our minimal model already reproduces the experimentally observed characteristic drop in fertilization probability $P_{\text{fert}}(\epsilon)$ at high flow rates, implying that this is a robust, general feature.

We can capture the functional dependence of the fertilization probability $P_{\text{fert}}$ observed in both experiment and simulations by a minimal theory of a ballistic swimmer in simple shear flow, see Fig. 4 and SIA. In particular, for small shear rate $\alpha$, $P_{\text{fert}}$ is close to the asymptotic limit $P_{\text{fert}}(\alpha = 0)$ of a ballistic swimmer without flow. The drop of $P_{\text{fert}}$ at strong flow can be estimated from a simple scaling argument: At high shear rate $\alpha \geq v_h/r_{\text{egg}}$, the active swimming of sperm cells is negligible compared to the external flow, except in the direct vicinity of the egg. This vicinity is set by a characteristic distance $\delta \sim 0.1 r_{\text{egg}}$ from the egg, up to which the flux of sperm cells is elevated (due to the geometry of the streamlines around the egg). To reach the egg, these sperm cells have to traverse a distance $\sim \delta$ within the typical time $t_\delta \sim 2\pi/\alpha$ that corresponding streamlines spend in the vicinity of the egg (time for half rotation of the egg). Thus, the characteristic flow strength at which $P_{\text{fert}}$ drops can be estimated as $\alpha \sim 2\pi v_h/\delta$, see Fig. 4.

For Fig. 4, we obtain the fertilizability $p_t \approx 10\%$ from an independent experiment in the absence of flow [18], which is well described by the fertilization kinetics, Eq. (3), see Fig. S2. This $p_t$ is larger than a value $p_t = 3.4\%$ previously reported for sea urchin *S. franciscanus* [25, 26]. However, these previous experiments...
were conducted at much higher sperm densities, where sperm-sperm interactions and polyspermy [27, 28] may reduce the fertilization probability. Interestingly, the estimated fertilizability for sea urchin is smaller than our estimate for red abalone $p_t = 60\%$. Note that for red abalone, sperm cells are considered to arrive directly on the egg surface, whereas for sea urchin, sperm cells are considered to arrive at a jelly coat surrounding the egg, which sperm cells have to penetrate before fertilization.

IV. DISCUSSION

We presented a theoretical framework for chemotaxis at small-scale turbulence, using marine sperm chemotaxis in physiological shear flow as prototypical example. We explain the existence of an optimal flow strength at which chemotaxis is more effective than for still water. Our theory can serve as a building block for future work, which should address increasingly more realistic models of small-scale turbulence beyond the simple shear flow considered here. Chemotactic navigation in fully developed turbulence comprises multiple intercalated scales, including chaotic mixing at large scales [20, 33, 34], where active swimming of sperm cells is negligible, and active navigation below the Kolmogorov length (the last millimeter to the target), captured by our theory. Specifically, refined models of small-scale turbulence include unsteady shear flows, Burger vortices and Direct Numerical Simulations (DNS) [15, 19, 22, 35–37]. While we described co-rotation of sperm cells in external shear flow by an effective Jeffrey equation, hydrodynamic simulations of flagellated microswimmers can be used to refine these models [38–40], which will become relevant at high shear rates. We expect that shear flows change the shape of the flagellar beat at $\alpha \geq 10^5 \text{s}^{-1}$ [41]. For the sperm-egg exposure times considered here, we treated concentration fields as static. Future work will go beyond this reference case and address time-varying concentration gradients [42, 43], and the role of sensing noise [44, 45], relevant at the boundaries of concentration filaments.

We expect that our findings of two-stage chemotactic search, comprising finding a filament and subsequent surfing along this filament, will be also relevant for bacteria and plankton foraging on marine snow, which play an important role for oceanic ecosystems [15, 19, 46–51]. While our theory addresses the experimentally more accessible model system of external fertilization as employed by marine invertebrates [1], chemotaxis in external flows is relevant also for internal fertilization, where sperm cells navigate complex environments [52, 53], likely guided by both chemotaxis [2] and rheotaxis [54, 55]. More generally, we characterized sperm chemotaxis in external flow as a combination of random exploration, followed by local gradient ascent, which corroborates a general paradigm for cellular and animal search behavior [56]. The minimalistic information processing capabilities of sperm cells (comparable to that of a single neuron [5]) can inspire navigation strategies for artificial microswimmers with limited information processing capabilities intended for navigation in dynamic and disordered environments [24, 57]. Previous work proposed navigation strategies in strong scalar turbulence based on Bayesian update rules, which, however, require advanced information processing capabilities of search agents [58], which may be limited to higher organisms. In conclusion, our work contributes to a recent endeavor to characterize cellular function in physiological environments.

V. NUMERICAL METHODS

The encounter probability $P_{\text{sperm-egg}}$ is computed numerically by simulating sperm trajectories $r(t)$ in the presence of both a concentration field $c(r)$ of chemoattractant and an external fluid flow field $v_{\text{ext}}(r)$ according to equations of motion for $r(t)$, see SI B. These equations extend a previous, experimentally confirmed theory of sperm chemotaxis along helical paths [10, 11] by incorporating convection and co-rotation of cells by the external flow. For co-rotation, we employ Jeffrey equation for prolate spheroids by assigning sperm cells an effective aspect ratio $\gamma = 5$. For the shear rates considered here, the effect of external flow on sperm flagellar beat patterns is negligible [41]. Each sperm cell is simulated for an exposure time $t_{\text{max}}$ or until it hits the surface of the egg.

As external flow, we assume a simple shear flow around a freely-rotating spherical egg, see SI A. The concentration field is established by diffusion and convection from the egg releasing chemoattractant at a constant rate. We consider the reference case of a static concentration field corresponding to a chemoattractant release time equal to exposure time $t_{\text{max}}$. To account for an ensemble of eggs at density $\rho_{\text{egg}}$, we consider a single egg with radius $r_{\text{egg}}$ at the origin $r = 0$ and a spherical domain with radius $r_{\text{max}} = (4\pi \rho_{\text{egg}}/3)^{-1/3}$ and appropriate periodic boundary conditions. Initially, sperm cell positions $r$ ($r_{\text{egg}} \leq |r| \leq r_{\text{max}}$) and directions of the helix axis $h$ are uniformly distributed, representing the distribution after initial turbulent mixing of egg and sperm cells. If sperm cells leave the simulation domain, they re-enter with random initial conditions $r$ and $h$ with $|r| = r_{\text{max}}$, whose distribution $P_b(r, h)$ is defined by the theoretical in-flux of cells due to active swimming and convection

$$P_b(r, h) \sim -p_{\text{sperm}}(r, h) \left[ (v_{\text{ext}} \cdot h) \cdot e_r(r) \right]$$

with uniform and isotropic distribution of sperm cells $p_{\text{sperm}}(r, h)$. In principle, co-rotation of non-spherical particles by shear flow leads to a non-uniform distribution of directions $h$, see analytic solutions in SIF, but the effect on simulation results is negligible.

Parameters for Fig. 2 were chosen to closely match conditions of $A. \ punctula$ sea urchin in their natural
spawning habitat at low egg density $\rho_{\text{egg}}$ and relatively long exposure times $t_{\text{max}}$. Parameters for Figs. 3 and 4 are chosen to match the experiments by Zimmer and Riffell [13, 14] and Mead and Denny [18], respectively. For further details on simulations and parameters used for each scenario, see SI G, SI H. Finally, error bars for simulation results represent simple standard deviation (SD) of the corresponding binomial distribution. Error bars are smaller than symbol sizes in some cases.

ACKNOWLEDGMENTS

We are grateful for discussions with L. Alvarez, M. Wilczek, M. W. Denny, and J. Riffell. We acknowledge support by the DFG under grant FR 3429/3 – 1 and through the Excellence Initiative by the German Federal and State Governments (Clusters of Excellence cfaed EXC 1036 and PoL EXC 2068).

SI. SUPPORTING INFORMATION

FIG. S1. Fertilization probability $P_{\text{fert}}(\alpha)$ as in Fig. 3 but with simulations taking into account co-rotation (green triangles): Previous experimental data [14, Fig. 5c] for red abalone $H. \text{rufescens}$ with and without chemotaxis (filled gray triangles: with chemotaxis, open gray triangles: inhibited chemotaxis) and our corresponding simulations (filled green triangles: with chemotaxis, open green triangles: without chemotaxis; mean ± SD), using fertilizability $p_f = 60\%$ in Eq. (3) as single fit parameter. Experiment and simulation again agree reasonably except for the data point without flow $\alpha = 0$ s$^{-1}$, which corresponds to a different experimental protocol. While the simulations with co-rotation overestimate the reduction of $P_{\text{fert}}$ at high shear rate $\alpha > 6$ s$^{-1}$, these high shear rates are less relevant for the spawning habitat of $H. \text{rufescens}$.

FIG. S2. Calibration of fertilizability without flow ($\alpha = 0$). Fertilization probability $P_{\text{fert}}$ as function of the ratio $\rho_{\text{perm}}/\rho_{\text{egg}}$ of sperm and egg density in the absence of flow $\alpha = 0$ s$^{-1}$ from experiments with sea urchin $S. \text{purpuratus}$ [18, Fig. 4] (filled gray triangles) and fit of fertilization kinetics Eq. (3) (red). From the fit, we obtain $p_f \rho_{\text{perm-egg}} \approx 9\%$ for the product of fertilizability $p_f$ and encounter probability $P_{\text{perm-egg}}$. Assuming a ballistic swimmer that is captured at the egg surface (Eq. (3) with $P_{\text{perm-egg}}(t_{\text{max}}) = 1 - \exp(-qt_{\text{max}})$ and rate $q = \pi r_{\text{egg}}^2 v_{\text{h}} \rho_{\text{egg}} = 0.02$ s$^{-1}$), we find $p_f \approx 10\%$ for exposure time $t_{\text{max}} = 120$ s and $\rho_{\text{egg}} = 1.5 \cdot 10^4$ ml$^{-1}$. This value $p_f$ is used in Figs. 4, S3.
FIG. S3. Fertilization probability $P_{\text{fert}}(\alpha)$ as in Fig. 4 but with simulations taking into account co-rotation of sperm cells (open green triangles): Previous measurements of fertilization probability $P_{\text{fert}}(t)$ for sea urchin $S.\,parpurus$ at strong turbulence, characterized by density-normalized dissipation rate $\epsilon$ (filled gray triangles) [18, 29] and our corresponding simulations $P_{\text{fert}}(\alpha)$ as function of shear rate $\alpha$ (open green triangles, mean ± SD) match well, using a single fit parameter $\alpha = 0.023$ that relates dissipation rate $\epsilon$ and typical shear rate $\alpha$ (with the known relationship $\alpha(\epsilon) = a \sqrt{\nu/\epsilon}$ [19, 22]). Analogous to Fig. 4, the case of low shear rates is well described by the limit case of a ballistic swimmer in the absence of flow $\alpha = 0 \, s^{-1}$ (dotted horizontal line, Eq. (3) with $P_{\text{fert};\text{egg}}(t) = 1 - \exp(-qt)$ and rate $q = \pi r_{\text{egg}}^2 v_{\text{h}} \rho_{\text{egg}}$). The fertilizability $p_{\text{f}} = 10\%$ is obtained from an independent experiment [18], see Fig. S2. From the experimental protocol, we estimate a high background concentration $c_{\text{bg}} = 500–4000\, \text{nM}$ of chemoattractant, which renders sperm chemotaxis ineffective.

A. Shear flow around freely-rotating egg and minimal case of ballistic swimmer

For all simulations (except Fig. 1A), we use a simple shear flow $\alpha y e_z$ as idealized paradigm for small-scale turbulence. At the relevant shear rates $\alpha$ and typical egg radii $r_{\text{egg}} \sim 100\, \mu$m, the Reynolds number $\text{Re} = \alpha r_{\text{egg}}^2 / \nu \lesssim 0.1$ is sufficiently small to justify the use of the analytical Stokes equation for viscous flow $v_{\text{ext}}(r)$. Throughout, we consider the co-moving frame of the egg allowing us to assume that the egg is at the origin $r = 0$. We introduce dimensionless coordinates $\hat{r} = r / r_{\text{egg}}$ and the dimensionless flow field $\hat{v}_{\text{ext}}(\hat{r}) = \frac{2 v_{\text{ext}}(r)}{\alpha r_{\text{egg}}}$. The components of this flow field read [59, Eq. (12)]

$$\hat{v}_{\text{ext},x} = 2 \hat{y} \left( 1 + \hat{\Omega} \right) \hat{\Omega}^3 - 5 \hat{x} \hat{y} \left( \hat{\Omega}^5 - \hat{\Omega}^7 \right)$$

$$\hat{v}_{\text{ext},y} = \hat{x} \left( 1 + \hat{\Omega} \right) \hat{\Omega}^3 - 5 \hat{x} \hat{y} \left( \hat{\Omega}^5 - \hat{\Omega}^7 \right)$$

$$\hat{v}_{\text{ext},z} = -5 \hat{x} \hat{y} \hat{z} \left( \hat{\Omega}^5 - \hat{\Omega}^7 \right)$$

where no-slip boundary conditions on the surface $|\hat{r}| = 1$ of the freely-rotating spherical egg are assumed. The egg rotates according to the undisturbed flow vorticity with the dimensionless rotation rate $\hat{\Omega} = -1$, corresponding to an rotation of the egg with angular velocity $\Omega = -\frac{2}{3} \epsilon z$.

It is instructive to consider a ballistic swimmer in the above flow field $\mathbf{v}_{\text{ext}}$ as a reference for the analysis of more complicated cases, such as swimmers performing chemotaxis. For instance, without flow or chemotaxis, sperm cells are considered to swim along a straight helix with helix radius $r_0$ much smaller than the egg radius. These sperm trajectories are well approximated by a ballistic swimmer moving along the helix axis $\mathbf{h}$ with net swimming speed $v_{\text{h}}$. If the ballistic swimmer and the target eggs (with density $\rho_{\text{egg}}$) are uniformly distributed, the steady-state rate $q$ at which a swimmer hits an egg is given by $q = \pi (r_{\text{egg}} + r_0)^2 v_{\text{h}} \rho_{\text{egg}} = \pi r_{\text{egg}}^2 v_{\text{h}} \rho_{\text{egg}}$. If ballistic swimmers become trapped at the egg on encounter, this corresponds to the encounter probability $P_{\text{fert};\text{egg}}(t) = 1 - \exp(-qt)$ (and fertilization probability $P_{\text{fert}}$ according to fertilization kinetics, see Eq. (3)).

If ballistic swimmers are additionally convected by an external fluid flow field $\mathbf{v}_{\text{ext}}$, we can characterize $q$ (and thus $P_{\text{fert};\text{egg}}$ and $P_{\text{fert}}$) in terms of an universal curve: We introduce the dimensionless parameter $f = \frac{\alpha r_{\text{egg}}}{\sqrt{\pi}}$, which compares shear rate to net swimming speed. The combined velocity field of active swimming and fluid flow is now

$$\mathbf{v}_{\text{ext}}(\hat{r}) + v_{\text{h}} \mathbf{h} = v_{\text{h}} (f \hat{v}_{\text{ext}}(\hat{r}) + \mathbf{h}) = v_{\text{h}} \hat{\mathbf{u}}(\hat{r}, f, \mathbf{h})$$

where $\hat{\mathbf{u}}$ is the dimensionless swimmer velocity.

Note that without co-rotation, $\mathbf{h}$ does not change. Thus, for any $\mathbf{h}$, all possible velocity fields $\hat{\mathbf{u}}$ are given by a single one-parameter family parametrized by $f$. For each of these fields, the dimensionless rate of swimmers $\hat{q}(f, \mathbf{h})$ reaching the egg from $|\hat{r}| \gg 1$ specifies the actual rate $q$ for any set of parameters $\alpha, r_{\text{egg}}, v_{\text{h}}, \rho_{\text{egg}}$ with the same parameter $f$ by

$$q(\alpha, r_{\text{egg}}, v_{\text{h}}, \rho_{\text{egg}}) = \hat{q}(f, \mathbf{h}) r_{\text{egg}}^2 v_{\text{h}} \rho_{\text{egg}}$$

We obtain a universal curve for $q$ by computing $\hat{q}(f, \mathbf{h})$ numerically for all $f$ and $\mathbf{h}$ and average $\hat{q}(f) = \langle \hat{q}(f, \mathbf{h}) \rangle_{\mathbf{h}}$ over all directions $\mathbf{h}$, see Fig. 4 for corresponding $P_{\text{fert}}$. A prominent feature of the universal rate is that it vanishes at large shear rates $\hat{q}(f \to \infty) \to 0$. In the absence of flow $\alpha = 0$, we have $\hat{q}(f = 0) = \pi$.

We compute the universal rate $\hat{q}$ efficiently by integrating a uniform grid of initial conditions on the surface of the egg, with $|\hat{r}| = 1$ at $t = 0$, backwards in time according to the velocity field $\hat{\mathbf{u}}$. Each initial condition is integrated until it either returns to the egg $|\hat{r}(t)| = 1$ (fail)
or leaves the outer boundaries \( \mathbf{r}(t) = \mathbf{r}_{\text{max}} \) (success) with \( \mathbf{r}_{\text{max}} \gg 1 \). As the flow is volume conserving, the results are independent of the choice of the outer boundary \( \mathbf{r}_{\text{max}} \), as long as \( \mathbf{r}_{\text{max}} \) is sufficiently large to ensure the absence of closed orbits beyond it. We choose \( \mathbf{r}_{\text{max}} = 4 \) as numerics show that the in- and outflow on this sphere differs only by 4% between the Stokes flow around the freely-rotating sphere and the undisturbed simple shear flow, for which it is known no closed orbits exist. Based on the intersections with the outer boundary, the flow reaching the egg is interpolated. This is done for a grid of swim directions \( \mathbf{h} \). For efficiency, we exploit the symmetries of the Stokes flow \( \mathbf{v}_{\text{ext}}(\hat{x}, \hat{y}, \hat{z}) \cdot (h_x \mathbf{e}_x + h_y \mathbf{e}_y + h_z \mathbf{e}_z) = \mathbf{v}_{\text{ext}}(\hat{x}, -\hat{y}, -\hat{z}) \cdot (h_x \mathbf{e}_x - h_y \mathbf{e}_y + h_z \mathbf{e}_z) = \mathbf{v}_{\text{ext}}(-\hat{x}, \hat{y}, \hat{z}) \cdot (-h_x \mathbf{e}_x - h_y \mathbf{e}_y + h_z \mathbf{e}_z); \) thus, it is sufficient to consider \( h_x \geq 0 \) and \( h_y \geq 0 \), respectively.

### B. Equations of motion for navigating sperm cells

We simulate the swimming path \( \mathbf{r}(t) \) of a sperm cell in a concentration field \( c(\mathbf{r}) \) of chemoattractant in the presence of an external fluid flow field \( \mathbf{v}_{\text{ext}}(\mathbf{r}) \). For this, we extend a previous theory of chemotaxis of marine sperm cells along helical paths [10, 11, 60, 61] by incorporating convection and co-rotation by flow: The sperm cell is described in terms of the time-dependent center position \( \mathbf{r}(t) \), averaged over one flagellar beat cycle, and the set of ortho-normal vectors \( \mathbf{e}_1(t), \mathbf{e}_2(t), \mathbf{e}_3(t) \) of the co-moving coordinate frame, where the vector \( \mathbf{e}_1(t) \) points in the direction of active swimming with speed \( v_0 \). The equations of motion read

\[
\dot{\mathbf{r}} = v_0 \mathbf{e}_1 + \mathbf{v}_{\text{ext}}(\mathbf{r}(t)) ,
\]

\[
\dot{\mathbf{e}}_i = (\Omega_h + \Omega_f) \times \mathbf{e}_i \quad i = 1, 2, 3 ,
\]

(S4)

The two angular velocities, \( \Omega_h \) and \( \Omega_f \), describe the rotation of the coordinate frame due to helical chemotaxis and external flow, respectively. Note that Eq. (S4) is also valid for time-dependent concentration and flow fields.

Without external flow or chemotaxis, cells swim along a helical path with constant path curvature \( \kappa(t) = \kappa_0 \) and torsion \( \tau(t) = \tau_0 \). The angular velocity \( \Omega_h \) is defined by the Frenet-Serret equations

\[
\Omega_h(t) = v_0 \left( \tau(t) \mathbf{e}_1(t) + (\kappa(t) + \kappa_0) \mathbf{e}_3(t) \right) ,
\]

(S5)

where the coordinate frame \( \mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3 \) corresponds to the Frenet-Serret frame of \( \mathbf{r}(t) \), i.e., tangent, normal, and binormal vector. During chemotactic steering, sperm cells dynamically regulate curvature \( \kappa(t) \) and torsion \( \tau(t) \) of active swimming according to the output \( a(t) \) of a chemotactic signaling system

\[
\kappa(t) = \kappa_0 - \rho \kappa_0 (a - 1) ,
\]

\[
\tau(t) = \tau_0 + \rho \tau_0 (a - 1) .
\]

(S6)

Here, the sensori-motor gain factor \( \rho \) characterizes the amplitude of chemotactic steering responses. The chemotactic signaling system takes as input the local concentration \( c(\mathbf{r}(t)) \) at the position of the cell

\[
\mu a = p [c_0 + c(\mathbf{r}(t))] - a ,
\]

\[
\mu \dot{a} = p (1 - a) . \quad \text{(S7)}
\]

This minimal signaling system comprises sensory adaptation with sensitivity threshold \( c_0 \) and relaxation with time scale \( \mu \) to a rest state \( a = 1 \) for any constant stimulus \( c(\mathbf{r}(t)) = c_0 \). The gain factor \( \rho \) sets the rate of chemotactic steering. While \( \rho \) could depend on the chemotactic signal by a feedback mechanism [45], we assume here a constant gain factor \( \rho = 5 \) for simplicity. The values of all parameters are listed and discussed in S1G.

We approximate the angular velocity \( \Omega_f \) for co-rotation by external flow using the Jeffrey equation for a small prolate spheroid with major axis along \( \mathbf{e}_1 \) [62, 63]

\[
\Omega_f(\mathbf{r}) = \frac{1}{2} \mathbf{\omega}(\mathbf{r}) + G \mathbf{e}_1 \times [\mathbf{E}(\mathbf{r}) \cdot \mathbf{e}_1] ,
\]

\[
\mathbf{\omega}(\mathbf{r}) = \nabla \times \mathbf{v}_{\text{ext}}(\mathbf{r}) , \quad \mathbf{E}(\mathbf{r}) = \frac{1}{2} \left[ \nabla \otimes \mathbf{v}_{\text{ext}}(\mathbf{r}) + (\nabla \otimes \mathbf{v}_{\text{ext}}(\mathbf{r}))^T \right]
\]

with the flow vorticity \( \mathbf{\omega} \), the strain rate tensor \( \mathbf{E} \), and a geometric factor \( G = \frac{2 - 1}{2 - 1} \), which depends on the aspect ratio \( \gamma \geq 1 \) of major to minor axis of the spheroid. For a swimming sperm cell, we take the swim direction \( \mathbf{e}_1 \) as effective major axis, and employ an effective aspect ratio, \( \gamma = 5 \), reflecting the ratio of the length of the flagellum and a typical beat amplitude [13]. Note that in general instead of \( \mathbf{e}_1 \), the major axis could be any co-moving vector.

We numerically integrate the equations of motion Eqs. [S4,S7] using an Euler scheme with fixed small time step \( dt \). For efficient computation, Rodrigues rotation formula with respect to the co-moving coordinate frame is used to integrate \( \mathbf{e}_1, \mathbf{e}_2, \mathbf{e}_3 \), resulting in faster computation compared to the algorithm used in Ref. [45].

### C. Analysis of concentration filaments

Turbulent flows cause turbulent mixing of diffusing chemicals and generate filamentous concentration fields. We consider a spherical egg located at the origin \( \mathbf{r} = \mathbf{0} \) releasing chemoattractant with diffusion coefficient \( D \) at a constant rate \( Q \) in the presence of shear flow \( \mathbf{v}_{\text{ext}}(\mathbf{r}) \) given by Eq. (S1). We compute the time-dependent concentration field \( c(\mathbf{r}, t) \) of chemoattractant numerically using Lagrangian particle tracking, see S1G. We empirically find that the far-field at distances \( r \gg r_{\text{egg}} \) is well approximated by a generic profile, see Fig. 1B for illustration,

\[
c(\mathbf{r}, t) = c_0 \exp(-k|x|) \exp \left( -\frac{(y - y_0)^2}{a^2} + \frac{z^2}{2b^2} \right) ,
\]

(S9)
which describes a concentration filament with parameters $c_0(t)$, $k(t)$, $\sigma(x,t)$, $a_y$, and $y_0(x,t)$. This formula for the concentration filament is consistent with results obtained using the analytic solution for the parameters in the following. While these dependencies are not explicitly required for our theory, they demonstrate the universality of our theory.

From numerical simulations, we empirically find the following scaling laws of the parameters from Eq. (S9)

\[
k(t) \sim t^{-\delta_k}, \quad \delta_k = 1.5 \ldots 1.6
\]

\[
c_0(t) \sim t^{-\delta_c}, \quad \delta_c = 1.6 \ldots 1.8
\]

\[
\sigma^2(x,t) = 2Dt_0(x,t), \quad t_0 \sim t
\]

\[
y_0(x,t) = \text{sgn}(x) p_{0,0}, p_{1,0} \cdot t^{\delta_{y0}} x, \quad \delta_{y0} = 0.9 \ldots 1
\]

\[
p_{1,0} = (1 \ldots 1.4) \cdot a^{-\delta_{y0}}, \quad a_y = 0.5 \ldots 0.6
\]

where all parameters except $p_{2,0}$ are positive. We also found power-law dependencies for the coefficients $p_{0,0}, p_{1,0}, p_{2,0}$. The factor $a_y$ appears to be constant for sufficient large $t$. These numerical observations become plausible by analysis of a point source in shear flow. The Fokker-Planck equation for this case can be written in dimensionless form

\[
\partial_t c = -a_y \partial_x c + D \triangle c + \partial_t c = -c \partial_x c + \Delta c \quad (S10)
\]

by re-scaling to dimensionless coordinates

\[
x = x \sqrt{\frac{\alpha}{D}}, \quad y = y \sqrt{\frac{\alpha}{D}}, \quad t = t \alpha, \quad \tilde{c} = c \sqrt{\frac{D^3}{\alpha Q}} \quad (S11)
\]

with shear rate $\alpha$, and release rate $Q$ of the source. Consequently, the solution $\tilde{c}(\tilde{x},\tilde{t})$ of this equation can be re-scaled to the solution $c(x,t)$ for any set of parameters $\alpha, D, Q$. For the above form of the far-field of the filament, this implies that the parameters $\delta_k, \delta_{y0}$ and $p_{2,0}$ are universal as they are invariant under the re-scaling Eq. (S11). The analytical solution for the dimensionless concentration $\tilde{c}$ reads [64, Eq. (18)]

\[
\tilde{c}(\tilde{x}, \tilde{t}) = \int_0^\tilde{t} d\tilde{s} \tilde{G}(\tilde{x}, \tilde{s}) = \int_0^t d\tilde{s} \tilde{G}(\tilde{x}, \tilde{s}) \quad (S12)
\]

with Greens function $\tilde{G}$, i.e., the solution for an instantaneous source at the origin [65, Eq. (26)]

\[
\tilde{G}(\tilde{x}, \tilde{t}) = \frac{\exp \left[ \left( \frac{\tilde{x}^2 + \tilde{y}^2}{4(1 + \frac{\tilde{t}^2}{4})} \right) \cdot \frac{\tilde{y}^2 + \tilde{z}^2}{4} \right]}{(4\pi \tilde{t})^{\frac{3}{2}} \sqrt{1 + \frac{\tilde{t}^2}{4}}} \quad (S13)
\]

While the integral Eq. (S12) cannot be solved analytically, it explains the empirical scaling for the parameters in Eq. (S9) heuristically: It is reasonable to assume that for any $\tilde{x}$, the parameter $\tilde{y}_0(\tilde{t})$ is close to the point $\tilde{y}_{\text{max}}$ of the maximal concentration of $\tilde{G}(\tilde{x}, \tilde{t})$. From $\partial_{\tilde{y}} \tilde{G}(\tilde{x}, \tilde{y}, \tilde{z}) |_{\tilde{y} = \tilde{y}_{\text{max}}} = 0$, it follows (for $\tilde{t} > \sqrt{3}$)

\[
\tilde{y}_0(\tilde{x}, \tilde{t}) \approx \tilde{y}_{\text{max}}(\tilde{x}, \tilde{t}) = \frac{3\tilde{x} \tilde{t}}{2(\tilde{t}^2 + 3)} \Rightarrow p_{1,0} \approx \frac{3}{2} \tilde{t}^{-1} \quad (S14)
\]

in accordance with the fitted power-law.

The power law $c_0(t) \sim t^{-\frac{2}{3}}$, as suggested by numerics, is plausible since $\tilde{G}(\tilde{0}, \tilde{s} \gg 1) \sim \tilde{s}^{-\frac{2}{3}}$, which implies $\tilde{c}(\tilde{0}, \tilde{t} \gg 1) \sim \int_0^\tilde{t} d\tilde{y} \tilde{s}^{-\frac{2}{3}} \sim \tilde{t}^{-\frac{2}{3}}$. We introduce the concentration $\tilde{c}_{\text{max}}$ at the centerline of the filament $\tilde{c}_{\text{max}}(\tilde{x}, \tilde{t}) = \tilde{c}(\tilde{x}, \tilde{y}_0(\tilde{x}, \tilde{t}), \tilde{z} = 0)$. We make the ansatz $\tilde{c}_{\text{max}}(\tilde{x}, \tilde{t}) = \tilde{c}_0(\tilde{t}) \exp(-\tilde{k}(\tilde{t}) |\tilde{x}|)$ and derive a power-law for $\tilde{k}(\tilde{t})$ in the following. We expect that $\tilde{c}_{\text{max}}$ scales proportional to the summed contributions of the Greens functions at the time-dependent centerline, hence we estimate (assuming $\tilde{t} \gg 1$, we approximate $\tilde{t}^2 + 3 \rightarrow \tilde{t}^2, 1 + \tilde{t}^2/12 \rightarrow \tilde{t}^2/12$ in $\tilde{G}$)

\[
\tilde{c}_{\text{max}}(\tilde{x}, \tilde{t}) \sim \int_0^\tilde{t} d\tilde{s} \tilde{G}(\tilde{x}, \tilde{y}_0(\tilde{x}, \tilde{s}), \tilde{z} = 0, \tilde{s}) \sim \frac{\text{erfc}(\sqrt{\frac{2}{4\pi \tilde{x}}})}{6\pi \tilde{x}} \quad (S15)
\]

We are interested in the shape of the concentration filament up to a maximal distance $\tilde{x}_{\text{max}}$ at which the concentration at the centerline decayed to a fraction $u$ of $\tilde{c}_0$. $\tilde{c}_{\text{max}}(\tilde{x}_{\text{max}}, \tilde{t}) = u \tilde{c}_0(\tilde{t})$. Any asymptotic tails beyond this distance will likely not be relevant for chemotaxis. Since the decay of $\tilde{c}_{\text{max}}$ as function of $\tilde{x}$ is dominated by the numerator in Eq. (S15), the distance $\tilde{x}_{\text{max}}$ has a time-dependency $\tilde{x}_{\text{max}}(\tilde{t}) \sim \tilde{t}^2$ according to the argument of the complementary error-function erfc. Using Eq. (S15), we estimate the time-dependency of $\tilde{k}(\tilde{t})$ from

\[
\tilde{k}(\tilde{t}) \tilde{x} = \ln \left( \frac{\tilde{c}_{\text{max}}(\tilde{x})}{\tilde{c}_0} \right) \sim \ln \left( \frac{\text{erfc}(a)}{a} \right) \sim \ln \text{erfc}(a) \sim -a \quad (S16)
\]

where we introduced $a(\tilde{x}, \tilde{t}) = \sqrt{3/4 \tilde{t}^{-\frac{2}{3}} \tilde{x}}$. The crucial point is that for $0 \leq \tilde{x} \leq \tilde{x}_{\text{max}}(\tilde{t})$, the variable $a$ varies only in a finite interval $0 \leq a \leq a_{\text{max}}$ with upper bound $a_{\text{max}} = a(\tilde{x}_{\text{max}}(\tilde{t}), \tilde{t}) \sim \tilde{t}^{-\frac{2}{3}} \tilde{x}_{\text{max}}(\tilde{t})$ independent of time $\tilde{t}$. This allows us to approximate $\ln \text{erfc}(a)$ by its Taylor expansion for small $a \ll 1$ in the last step of Eq. (S16). We conclude $\tilde{k}(\tilde{t}) \sim a_{\text{max}}/\tilde{x}_{\text{max}}(\tilde{t}) \sim \tilde{t}^{-\frac{2}{3}}$, as suggested by numerics.

D. Chemotactic navigation within filament

We derive an effective equation of motion for chemotactic navigation within a typical concentration filament. For simplicity, we initially ignore interaction with the flow and assume that the motion is effectively two-dimensional, i.e., in the xy-plane. Additionally, we em-
ploy a two-dimensional version of Eq. (S9) for the concentration filament, setting \( a_y = 1 \),
\[
c(x, y, t) = c_0 \exp \left( -k |x| \right) \exp \left( -\frac{(y - y_0)^2}{2\sigma^2} \right). \tag{S17}
\]
We introduce the centerline \( r_h(t) = (x(t), y(t), 0) \) of the helical swimming path \( r(t) \), with \( r_h = v_h \mathbf{h} \). From a previously established equation for \( r_h \) [10, 60], we have
\[
\dot{x} = v_h \cos(\varphi), \quad \dot{y} = v_h \sin(\varphi), \nonumber
\]
\[
\dot{\varphi} = -\frac{v_\varphi}{c + c_b} |\nabla c| \sin \Psi, \quad \Psi = \angle (\nabla c, \mathbf{h}), \tag{S18}
\]
describing the alignment of the helix axis \( \mathbf{h} \) with the local gradient \( \nabla c(r_h(t)) \) of a concentration field \( c(r) \). The first equation corresponds to ballistic motion along the helix axis \( \mathbf{h}(\varphi) = \cos \varphi \mathbf{e}_x + \sin \varphi \mathbf{e}_y \) with net swimming speed \( v_h = v_0 \gamma \sigma / \sqrt{\kappa_0^2 + \tau_0^2} \). The second equation describes chemotactic turning of the orientation angle \( \varphi \), where \( \Psi \) denotes the angle enclosed by \( \mathbf{h} \) and the local gradient \( \nabla c(r_h(t)) \). Here, \( c_b \) adapts the adaption threshold and \( v_\varphi \) the chemotactic turning speed, \( v_\varphi = \rho v_h \kappa_0^2 / \left( \kappa_0^2 + \tau_0^2 \right) \), \( v_\varphi > 0 \), with the gain factor \( \rho \) and helix parameters \( \kappa_0, \tau_0 \). We apply this general theory, Eq. (S18), to the filamentous profile Eq. (S17) and obtain a single dimensionless ODE
\[
\dot{Y} = \left( \frac{\dot{X}^2 Y^2}{c + c_b} + \frac{\text{sgn}(X)}{c + c_b} \gamma \dot{X} \dot{Y} \right), \tag{S19}
\]
with \( \dot{X}^2 + \dot{Y}^2 = 1, \dot{X} \neq 0 \) and a single dimensionless parameter
\[
\gamma = k \sigma \sqrt{\frac{v_\varphi}{v_h}} = k \sigma \sqrt{\frac{\rho v_0 \kappa_0^2}{\kappa_0^2 + \tau_0^2}}. \tag{S20}
\]
Here, we introduce a characteristic time-scale \( \tau \),
\[
\tau = \sqrt{\frac{\sigma}{v_\varphi}} \frac{\sigma}{v_h}, \tag{S21}
\]
as well as re-scaled coordinates \( Y(T) = (y(t) - y_0) / L, \)
\[
X(T) = x(t) / L, \quad L = v_h \tau. \nonumber \]
Dots denote differentiation with respect to re-scaled time \( T = t / \tau \), e.g., \( \dot{Y} = \text{d}Y / \text{d}T \). The time scale \( \tau \) is the geometric mean of a characteristic time-scale \( \sigma / v_\varphi \) of chemotactic steering and a typical time \( \sigma / v_h \) for traversing the cross-sectional width \( \sigma \) of the filament if steering was absent. We have an equation for \( X \) analogous to Eq. (S19) (which requires \( \dot{Y} \neq 0 \) and covers the case \( \dot{X} = 0 \)),
\[
\ddot{X} = \left( \dot{X} \dot{Y} Y - \text{sgn}(X) \gamma \dot{Y}^2 \right) \frac{c}{c + c_b}. \tag{S22}
\]
The factor \( c/(c + c_b) \) in the effective equations of motion, Eqs. [S19, S22], represents a ‘dimmer switch’ that attenuates chemotactic navigation at low concentration \( c \). Thus, it is reasonable to define the filament as the region where \( c(r) > c_b \). In the following, we focus on the dynamics within the filament and approximate \( c/(c + c_b) \approx 1 \).

The effective equation of motion, Eq. (S19), describes a damped, non-linear oscillator: The first term \( \dot{X}^2 \dot{Y}^2 \) originates from the perpendicular component \( \nabla \perp c = (\mathbf{e}_x \cdot \nabla c) \mathbf{e}_y \) of the concentration filament and governs the observed oscillations of sperm cells around the centerline \( Y = 0 \) of the filament. Heuristically, these oscillations result from sperm cells slowly aligning their helix axis \( \mathbf{h} \) parallel to \( \nabla \perp c \) while approaching \( Y = 0 \). At \( Y = 0 \), \( \nabla \perp c \) changes its direction, yet sperm cells overshoot due to their finite chemotactic turning speed \( v_\varphi < \infty \), before they eventually make a ‘U-turn’. The second term \( \text{sgn}(X) \gamma \dot{X} \dot{Y} \) in Eq. (S19) originates from the exponential decay of concentration along the centerline of the filament and changes the amplitude of the oscillation. In particular, for \( \text{sgn}(X) \dot{X} < 0 \), i.e., sperm cells surfing towards the egg, the oscillation is damped, whereas for \( \text{sgn}(X) \dot{X} > 0 \), i.e., sperm cells surfing away from the egg, it is amplified. This increase in amplitude can cause sperm cells that are surfing away from the egg to eventually turn around, redirecting them towards the egg. A linear stability analysis of Eq. (S19) around the case of a non-oscillating trajectory \( (Y, \dot{Y}) = (0, 0) \) yields the eigenvalues \( \omega_{1,2} \) of the Jacobian of the linearization,
\[
\omega_{1,2} = \zeta \pm i \sqrt{1 - \zeta^2}, \quad \zeta = \text{sgn}(X) \frac{\gamma}{2}, \tag{S23}
\]
which define a harmonic oscillator with dimensionless damping ratio \( \zeta \) and dimensionless oscillation frequency \( \sqrt{1 - \zeta^2} \). This analytic result agrees with full simulations of helical chemotaxis in three-dimensional space, see Fig. S4.

Note that the predicted exponential decay of oscillation amplitude, \( \exp(\zeta T) = \exp(\gamma / 2 \cdot t / \tau) \), is independent of \( x \) since \( \gamma / \tau \) is independent of \( \sigma^2 \). Interestingly, both for Eq. (S19) and full simulations, the angle at which trajectories intersect the centerline \( Y = 0 \) of the concentration filament is essentially independent of the angle, at which they first entered the filament at \( Y(c = c_b) \), provided \( Y(c = c_b) \) is sufficiently large: For smaller \( Y(c = c_b) \), i.e., outer and thus thinner parts of the filament, trajectories will simply pass through the filament, unable to execute a successful turn before they have left the filament again. As the width of the filament decreases away from the egg, this implies that filament surfing will be operative, at most, up to a maximal distance from the egg (which depends on the entry angle), characterized by \( \rho_{in} \). If we account for convection by shear flow \( v_{ext} = \alpha y \mathbf{e}_x \), Eq. (S22) changes to \( \ddot{X} \rightarrow \ddot{X} + \alpha \tau (Y + y_0(X)/L) \). Note that due to \( \text{sgn}(y_0(x)) = \text{sgn}(x) \), sperm cells that surf within the filament towards the egg swim on average against the external flow.
E. Minimal theory for sperm-egg-encounter probability

We provide an estimate for the encounter probability $P_{\text{sperm:egg}}$, building on the effective equation of motion of the helix axis derived in SID. The fertilization probability $P_{\text{fert}}$ is obtained then from $P_{\text{sperm:egg}}$ using fertilization kinetics, Eq. (3). For $P_{\text{sperm:egg}}$, we decompose the search problem for the egg into an outer search problem of finding the concentration filament and an inner search problem of surfing along the filament. We obtain (exploiting the symmetry between the two branches of the filament for $x < 0$ and $x > 0$)

$$P_{\text{sperm:egg}} \approx 2 \int_0^\infty dx \rho_{\text{egg}}(x) \left[ A(x) \rho_{\text{egg}} + S(x) j_{\text{out}} t_{\text{out}}(x, t_{\text{max}}) \right].$$

(S24)

Here, we introduce the following quantities:

- the cross-sectional area $A(x)$ at the position $x$ of the filament, which is defined by $c(r) \geq c_0$, i.e., $A(x) = \int_{-\infty}^\infty dy \Theta(c(x, y, z) - c_0)$, with the Heavyside-function $\Theta(\Theta(c > 0) = 1$ and $\Theta(c \leq 0) = 0$),
- the circumference $S(x)$ corresponding to the cross-section,
- the average probability $p_{\text{in}}(x, t_{\text{max}})$ that a trajectory entering the filament at $x > 0$ will surf along it and reach the egg within exposure time $t_{\text{max}}$,
- the mean steady-state flux $j_{\text{out}}$ of trajectories arriving at the surface of the filament, and
- the time limit $t_{\text{out}}$ for the outer search problem.

These quantities are explained in detail below. The first term in Eq. (S24) accounts for sperm cells found inside the concentration filament already at $t = 0$, assuming a random uniform distribution of initial positions. The second term in Eq. (S24) accounts for trajectories, which first search for the filament and, after encountering the filament, surf along it towards the egg.

We compute the probability $p_{\text{in}}(x, t_{\text{max}})$ of successful inner search numerically using the effective equation of motion for the helix axis Eq. (S19) as function of entry position $x$ and exposure time $t_{\text{max}}$. Specifically, we average over simulations of Eq. (S19) with uniformly distributed initial entry points and isotropic initial directions, i.e., entry angles. In order to account for the ellipsoidal cross-section of the concentration filament with $\sigma_y = \sigma_a q_y$, $\sigma_z = \sigma$, we average results for $\sigma_y$ and $\sigma_z$ from the successful trajectories, we also obtain the mean travel time $t_{\text{in}}$ within the filament, which represents a conditional mean first passage time. Accordingly, we set the maximal time $t_{\text{out}}$ allowed for the outer search $t_{\text{out}}(x, t_{\text{max}}) = t_{\text{max}} - t_{\text{in}}(x, t_{\text{max}})$ if $p_{\text{in}} > 0$ and $t_{\text{out}} = 0$ else.

Note that the first term in Eq. (S24) can be written as $V_{\text{eff}} \rho_{\text{egg}}$ with an effective volume $V_{\text{eff}} = 2 \int_0^\infty dx A(x) \rho_{\text{egg}}(x, t_{\text{max}})$ of the concentration filament, weighted by the probability $p_{\text{in}}$ of successful chemotaxis to the egg. This contribution is negligible compared to the second term for long exposure times $t_{\text{max}}$ and low egg densities $\rho_{\text{egg}}$.

The flux $j_{\text{out}}$ of trajectories arriving at the surface of the concentration filament can be determined by a fit to $P_{\text{sperm:egg}}(\alpha)$ from simulations at different shear rates $\alpha$. Alternatively, we can estimate $j_{\text{out}}$ by treating sperm cells outside of the filament as ballistic swimmers with net swimming speed $v_h$ and uniformly distributed random positions $r$ and orientations $\mathbf{h}$ with probability distribution $p_{\text{perm}}(r, \mathbf{h})$ by probability distribution $p_{\text{perm}}(r, \mathbf{h}) = \left( \frac{3}{2} \pi (r_{\text{max}}^3 - r_{\text{egg}}^3) \right)^{-3} (4\pi)^{-1} \approx \rho_{\text{egg}} (4\pi)^{-1}$. Assuming that the filament is convex, each point on its surface is reached at time $t$ from initial conditions on a surface of a half-sphere with radius $v_h t$. The flux of trajectories with direction $\mathbf{h}$ into the filament at $r_0$ is $j_{\text{out}}(r_0, \mathbf{h}) = -\mathbf{n} \cdot v_h p_{\text{perm}}(r_0, \mathbf{h})$ for $\mathbf{n} \cdot \mathbf{h} < 0$ and $j_{\text{out}}(r_0, \mathbf{h}) = 0$ else, where $\mathbf{n}$ denotes the outer surface normal vector at $r_0$. For

![Graph](image-url)
the constant density $p_{\text{perm}}(r_0, h) = p_{\text{perm}}$ the total flux of sperm cells into the filament is $j_{\text{out}} = j_0^{2\pi} d\varphi \int_0^{\pi/2} d\theta \sin \theta j_{\text{out}}(r_0, h(\varphi, \theta)) = p_{\text{perm}} \pi v_h$, where we use spherical coordinates $\varphi, \theta$ with $e_z = n$ to express $h$. Note that an isotropic distribution of orientations $h$ is a simplification, since co-rotation by flow alters this distribution, see SI F.

Despite the simplifications made, Eq. (S24) can quantitatively account for the encounter probability in full simulations, see Fig. 2. In particular, we find that the numerical fit for $j_{\text{out}} = 0.063 \text{ m}^{-2} \text{s}^{-1}$ is close to our simple estimate for a ballistic swimmer $j_{\text{out}} = p_{\text{egg}} v_h / 4 = 0.04 \text{ m}^{-2} \text{s}^{-1}$. Of course, our simple theory has limitations: First, trajectories are three-dimensional, not two-dimensional, and are characterized by oscillations both in $y$- and $z$-direction. As a result, sperm trajectories are super-helical, which reduces the effective speed along the filament. Second, our theory does not account for the fact that some sperm cells may miss the egg on the first attempt, and find it only after reversing their motion in $x$-direction, which increases the mean time $t_{\text{in}}$ to find the egg. Preliminary simulations suggest that the difference between simulations and theory in Fig. 2 indeed originate from this effect. Finally, co-rotation is neglected in the simple theory. However, this is justified for $\alpha \ll \tau^{-1}$, see Eq. (S21), i.e., when rotation due to navigation is much faster than co-rotation due to flow. Note that simulations with neither convection nor co-rotation exhibit also an optimal shear rate $\alpha^*$, but at higher shear rate and different encounter probability. The reason is that convection implies a flow opposing surfing towards the egg, which increases $t_{\text{in}}$ compared to the case without convection. Thus, $P_{\text{perm(egg)}}$ increases for large $\alpha$ when convection is not included, resulting in a shift of $\alpha^*$.

For the experiment of Zimmer and Riffell (data reproduced in Figs. 3, S1), we estimate a high background concentration of chemotactrant $c_{\text{bg}} \approx 4 \text{ nM}$, see SI G. Adding a background concentration $c \rightarrow c + c_{\text{bg}}$ in Eq. (S17) leads to an effective, higher threshold $c_{\text{bg,eff}} = c_h + c_{\text{bg}}$ in Eq. (S19). Consequently, the volume of the filament with sufficiently high concentration $c(r) \geq c_{\text{bg,eff}}$ is situated only in the vicinity of the egg. While our far-field theory of filament surfing does not apply directly to this special near-field case, we can make a simple estimate: We assume that sperm cells always swim directly towards the egg within the concentration plume defined by $c(r) \geq c_{\text{bg,eff}}$ due to the close-to-spherical shape of the plume. Thus, sperm cells entering the plume at $x_0 = 0$ approach it with net radial speed $v_h$, as the external flow only convects the sperm cells parallel to the egg surface, see Eq. (S1). A second, alternative calculation applies if sperm cells enter the plume at $x_0 \gg r_{\text{egg}}$: In this case, we can estimate the net speed towards the egg by $\hat{x} = \alpha_0 v(x) - v_h$. This yields for the distance $x(t)$ from the egg, $x(t) = \frac{x_0}{\alpha_0} + \left( x_0 - \frac{x_0}{\alpha_0} \right) \exp (\alpha_0 t)$ (using $v_0(x) \approx bx$, see SI C). We use these two limit cases to compute $p_{\text{in}}$ and $t_{\text{out}}$ for Eq. (S24) and obtain similar fertilization probabilities $P_{\text{fert}}(\alpha)$ in both cases. For these limit cases, $P_{\text{fert}}(\alpha)$ displays a similar decay as function of $\alpha$ as the simulation results without co-rotation, see Fig. 3. In particular, the fitted flux $j_{\text{out}} = 4.8 \cdot 10^3 \text{ m}^{-2} \text{s}^{-1}$ is consistent with the theoretical value $j_{\text{out}} = p_{\text{egg}} v_h / 4 = 7.5 \cdot 10^3 \text{ m}^{-2} \text{s}^{-1}$.

F. Analytic solution of Jeffrey equation in shear flow

As shear flow is a fundamental paradigm for small-scale turbulence, we present here the analytic solution to the Jeffrey equation, Eq. (S8), for particles suspended in simple shear flow. The application to helical swimmers is discussed. The results provide the distribution of helix orientations $h$ on the periodic boundary used in the simulations, i.e., $p_{\text{perm}}$ in Eq. (4). In particular, the results quantify the common notion that non-spherical swimmers align their major axis parallel to the flow direction. In fact, these swimmers rotate all the time, but with non-constant rotation rate, causing these swimmers to spend more time aligned with the flow axis. Consequently, the time-average of the orientation vector is not zero, but aligned with the flow axis. Note that analytic results for Poiseuille flow can be found in Refs. [66, 67].

For simple shear flow $v_{\text{ext}} = \alpha y e_z$, the dynamics of the unit vector $e$ along the major axis of a prolate spheroid, i.e., $e = \Omega_t \times e$ with $\Omega_t$ given by Eq. (S8), can be rewritten in terms of spherical coordinates $0 \leq \theta \leq \pi, 0 \leq \varphi \leq 2\pi$ of $e = (\sin \theta \cos \varphi, \sin \theta \sin \varphi, \cos \theta)$

\[
\begin{align*}
\dot{\varphi} &= \frac{\alpha}{2} \left[ G \cos 2\varphi - 1 \right], \\
\dot{\theta} &= \frac{\alpha}{4} \sin 2\theta \sin 2\varphi,
\end{align*}
\]

(S25)

The range $1 \leq \gamma < \infty$ of the aspect ratio $\gamma$ (with $\gamma = 0$ for a sphere and $\gamma \rightarrow \infty$ for an infinitesimal thin rod) implies $0 \leq G < 1$ for the geometric factor $G$. The dynamics of the polar angle $\varphi(t)$ is independent of the azimuthal angle $\theta(t)$. By integration, we find

\[
\varphi(t) = \arctan \left[ \frac{G - 1}{\sqrt{1 - G^2}} \tan (\Psi(t)) \right]
\]

(S26)

with short-hand

\[
\Psi(t) = \frac{\alpha t}{2} \sqrt{1 - G^2} + \arctan \left[ \frac{\sqrt{1 - G^2}}{G - 1} \tan \varphi_0 \right]
\]

(S27)

and initial condition $\varphi(0) = \varphi_0$. Note that $\varphi \leq 0$, i.e., $-\varphi (1 + G) \leq \varphi \leq -\frac{\varphi}{2} (1 - G)$. Hence, the polar angle $\varphi(t)$ rotates clockwise with period

\[
T = \frac{4\pi}{\alpha \sqrt{1 - G^2}}
\]

(S28)

with $T \geq 4\pi / \alpha$. Substituting Eq. (S26) for $\varphi(t)$ into Eq. (S25), we find

\[
\theta(t) = \arccot \left[ \frac{\cot (\theta_0)}{\sqrt{1 + G \cos (2\Psi(0))}} \right]
\]

(S29)
with initial condition \( \theta(0) = \theta_0 \).

We also compute the density \( \rho_e(\theta, \varphi) \) of directions for an ensemble of ballistic microswimmers obeying Eq. (S25). The distribution of polar angles \( \rho_\varphi(\varphi) \) is proportional to \( 1/|\dot{\varphi}| \)

\[
\rho_\varphi(\varphi) = \frac{\sqrt{1-G^2}}{4\pi (1-G(1-2\sin^2\varphi))}. \tag{S30}
\]

This density has two maxima, at \( \varphi_+ = 0 \) and \( \varphi_+ = \pi \), and two minima at \( \varphi_- = \pm \pi/2 \), resulting in a density range \( \rho_\varphi(\varphi_-) \leq \rho_\varphi \leq \rho_\varphi(\varphi_+) \) with \( \rho_\varphi(\varphi_\pm) = (4\pi)^{-1} [(1+G)/(1-G)]^{1/2}. \)

In order to derive the full density \( \rho_e(\theta, \varphi) \), we use an alternative scheme to solve the continuity equation, inspired by the method of characteristics. Effectively, an ordinary differential equation (ODE) and a system of ODEs are solved instead of one partial differential equation (PDE). The dynamics of \( \epsilon \) correspond to a flow \( w(\epsilon) \) on the unit sphere. The continuity equation for a density \( \rho_e(\epsilon, t) \) in an arbitrary flow field \( w(\epsilon, t) \) reads

\[
\partial_t \rho_e(\epsilon, t) = -\nabla \cdot [\rho_e(\epsilon, t)w(\epsilon, t)] \tag{S31}
\]

Instead of solving directly for the density \( \rho_e(\epsilon, t) \) in the laboratory frame, we can first solve for the density \( \tilde{\rho}_e(t; \epsilon_0) \) in a co-moving frame

\[
\tilde{\rho}_e(\epsilon, t) = \tilde{\rho}_e(t; \tilde{\epsilon}(-t, \epsilon)) \tag{S32}
\]

where \( \tilde{\epsilon}(t; \epsilon_0) \) is the trajectory starting at \( \tilde{\epsilon}(0; \epsilon_0) = \epsilon_0 \) and following the flow \( \tilde{\epsilon} = w(\tilde{\epsilon}, t) \). We obtain \( \tilde{\rho}_e(t; \epsilon_0) \) from the rewritten continuity equation

\[
\dot{\tilde{\rho}}_e(t; \epsilon_0) = -\tilde{\rho}_e(t; \epsilon_0) \nabla \cdot w(\epsilon(t; \epsilon_0), t). \tag{S33}
\]

Applying this scheme to Eq. (S25) with flow \( w(\theta, \varphi) = \delta\theta_0 + \sin \varphi \dot{\varphi}_e \) on the unit sphere and using the solutions \( \theta(t), \varphi(t) \) from Eqs. (S26,S29) yields

\[
\tilde{\rho}_e(t; \theta_0, \varphi_0) = C_0(\theta_0, \varphi_0) \left[ \cos^2(\theta_0)/(1+G \cos[2\Psi(0)]) + (1+G \cos[2\Psi(t)]) \right]^{1/2}, \tag{S34}
\]

where the pre-factor \( C_0(\theta_0, \varphi_0) \) is defined by the initial conditions. For our simulations, we use an initially uniform distribution such that \( \tilde{\rho}_e(0, \theta_0, \varphi_0) = (4\pi)^{-1}. \)

Switching notation to \( \tilde{\theta}(t, \theta_0, \varphi_0) = \theta(t) \) and \( \tilde{\varphi}(t, \varphi_0) = \varphi(t) \), the density \( \rho_e \) follows

\[
\rho_e(\theta, \varphi, t) = \delta(\tilde{\theta}(t, \theta_0, \varphi_0)) \delta(\tilde{\varphi}(t, \varphi_0)) \tag{S35}
\]

While \( \rho_e \) is periodic in time with period \( T \) by Eq. (S28), we can compute a time-average over one period, starting with a uniform distribution of directions \( \epsilon \) at \( t = 0 \). The time-averaged density displays a maximum at the axis of flow \( \epsilon = \pm \epsilon_e \) and a minimum at the shear axis \( \epsilon = \pm \epsilon_y \). These extrema vanish for a sphere \( (G = 0) \) and become more pronounced with increasing \( G \).

While the above results are derived for the case of a suspended particle, numerical simulations show that they also approximately apply to the centerline \( r_c(t) \) of a helical swimmer with helix axis \( h \) (without chemotaxis) if we use an effective aspect ratio \( \gamma_{\text{eff}} \). Specifically, the dynamics of the helix axis \( h \) resembles the above solutions with a smaller aspect ratio \( 1 \leq \gamma_{\text{eff}} \leq \gamma \). This approximation is valid for small times \( t \) and at small \( \alpha \), i.e., as long as the helix period is much smaller than the period \( T(\gamma) \). For instance, we fit \( \gamma_{\text{eff}} = 1.3 \pm 0.1 \) \( (G_{\text{eff}} = 0.26) \) for the sea urchin helix parameters and \( \gamma = 5 \) \( (G = 0.92) \). This effective parameter is a result of averaging the instantaneous co-rotation for the swimming direction \( e_1 \) with parameter \( G \) over one period of helical swimming. Generally, \( \gamma_{\text{eff}} \) depends on the angle between \( h \) and \( e_1 \). For larger \( \alpha \), complicated behavior of \( h \) is observed with limit cycles and stable fixed points, which is consistent with recent results for Jeffrey equation in perturbed shear flow [68]. We use the value \( \gamma_{\text{eff}} \) in all simulations to determine the periodic boundary conditions at the boundary of the simulation domain.

G. Choice of parameters

Parameters used throughout the three simulation scenarios (Arabacia punctuala for Figs. 1B, 2, S4, Strongylocentrotus purpuratus from Refs. [18, 29, 30, 69] for Figs. 4, S3, S2, Halioctis rufescens from Refs. [13, 14] for Figs. 3, S1) are listed in Tab. I and discussed in the following.

Mean path curvature \( \kappa_0 = 0.065 \mu m^{-1} \) and mean path torsion \( \tau_0 = 0.067 \mu m^{-1} \) of the helical paths are set according to three-dimensional tracking of A. punctuala sperm cells [11]. Three-dimensional tracking for S. purpuratus give similar values [4], though with larger error intervals. Moreover, the sperm morphology for A. punctuala [11, 45], S. purpuratus [70], and H. rufescens [71] is similar, which justifies the use of the same helix parameters for all three species. Likewise, the effective aspect ratio \( \gamma = 5 \) between major and minor axis of a sperm cell, i.e., length of flagellum divided by typical beat amplitude, suggested for H. rufescens [13] is employed for all three species in the Jeffrey equation Eq. (S8). We observe that simulation results are largely independent of the precise value of \( \gamma \). The signaling time-scale \( \mu = 1/(v_0 \sqrt{\kappa^2 + \tau^2}) \) is chosen to ensure the optimal phase-lag between concentration input \( c(r(t)) \) and motor response \( a(t) \) [10, 72], see Eq. (S7), consistent with experimental observations [11]. For all three species, the gain factor is set as \( \rho = 5 \), corresponding to the mean of the values used in Ref. [45]. This value reproduces typical bending rates of helical swimming paths as observed in experiments [11]. The threshold of sensory adaption \( c_0 = 10 \) Pm is chosen as suggested in Ref. [16]. At the concentration \( c_0 \), about 20 chemoattractant molecules would diffuse to a sperm cell during one helical turn. Note that sea urchin sperm cells respond to single chemoattract-
tant molecules [73]; the change in intra-cellular calcium concentration caused by the binding of chemoattractant molecules as function of stimulus strength becomes sub-linear already for chemoattractant concentrations on the order of $c_h$ [16]. For *A. punctuala*, other parameters were also tested, i.e., $\rho = 2$ and $c_b = 1$ pM, which yielded qualitatively similar simulation results and again agreement of theory and simulations. Note that the experimental protocol used in Ref. [14] for *H. rufescens* results in a substantial background concentration of chemoattractant, which we estimate as $c_{bg} \sim 4$ nM (experiments are conducted 10–30 min after spawning at a high density of eggs $\rho_{egg} = 10^3$ ml$^{-1}$ with the known release rate $Q = 0.18$ fmol min$^{-1}$ of chemoattractant [3]). According to our theory, such a background concentration causes effectively a higher sensitivity threshold $c_{h,eff} = c_h + c_{bg}$ (see SI E), which may be the reason for the higher behavioral threshold 300 pM observed in Ref. [14]. In the case of *S. purpuratus*, we estimate an even higher background concentration, $c_{bg} \sim 500 - 4000$ nM, which renders chemotaxis ineffective. For this estimate, we use that experiments were conducted 1–8 h after spawning at a high egg density $\rho_{egg} = 1.5 \cdot 10^4$ ml$^{-1}$ [18, 69] and assume a release rate $Q = 0.46$ fmol min$^{-1}$ of chemoattractant as for *A. punctuala* [16].

For the swimming speed $v_0$ of sperm cells along helical paths for both sea urchin species, we use the measured value $v_0 = 200$ $\mu$m s$^{-1}$ from Ref. [11]. Note that some experiments effectively measure the net swimming speed along the helix axis $v_h = v_0 t_0 / \sqrt{r_0^2 + z_0^2}$, which is smaller than $v_0$. For *H. rufescens*, we use the speed $v_0$ measured during the same experiment [14]. Note that this experiment also indicated chemokinesis, i.e., higher swimming speeds at elevated chemoattractant concentration, an effect which we neglect here for simplicity.

For *A. punctuala*, we use the diffusion coefficient $D = 239$ $\mu$m$^2$s$^{-1}$ and release rate $Q = 0.46$ fmol min$^{-1}$ of chemoattractant [16]. For this simulation, we assume a low egg density $\rho_{egg} = 10^{-3}$ ml$^{-1}$, which yields the radius $r_{max} = 6 \cdot 10^4$ $\mu$m of the outer boundary centered around the egg according to $\rho_{egg} = (4\pi r_{max}^3 / 3)^{-1}$. For this reference case, the filament is completely included inside the simulation domain for all considered shear rates $\alpha$. The exposure time $t_{max} = 360$ s is chosen comparable to the experiment in Ref. [18], where $t_{max} = 120$ s. For comparison with the experiments with *S. purpuratus* and *H. rufescens*, the radius $r_{max}$ is computed directly from the stated egg density $\rho_{egg} = (4\pi r_{max}^3 / 3)^{-1}$. From the 5 vol% solution with $w_{egg} = 40 - 55$ $\mu$m [69, pg. 161], we infer a range $\rho_{egg} = 0.9 - 3.4 \cdot 10^4$ ml$^{-1}$ for the experiments with *S. purpuratus*. This estimate already takes into account that, according to the experimental protocol, the above egg solution is mixed 9 : 1 with sperm solution [18, 69]. Likewise, from the range of sperm densities $\rho_{sperm} = 1.9 - 3.1 \cdot 10^6$ ml$^{-1}$ in Ref. [18, Fig.4] and the estimate $\rho_{sperm} = 4 \cdot 10^6$ ml$^{-1}$ in Ref. [69, pg. 59], both before 9 : 1-dilution, we infer a final concentration $\rho_{sperm} = 3.9 \cdot 10^5$ ml$^{-1}$. We use the kinematic viscosity $\nu = 10^{-6}$ m$^2$s$^{-1}$ of sea water at room temperature.

H. Numerical Simulation

The equations of motion are integrated using an Euler scheme with fixed time step $dt$. For all time integrations, a time step $dt = 10^{-3}$ s is used. Integration with smaller $dt = 10^{-4}$ s for some test cases gave consistent results. The number $N_{sperm}$ of sperm cells simulated in each case is $10^5$, except for *S. purpuratus*, where $N_{sperm} = 10^4$ is used.

The concentration field is computed from Lagrangian particle tracking with Euler-Maruyama method for the Fokker-Planck equation

$$\partial_t c = - \nabla \cdot \mathbf{v}_{ext} + D \Delta c$$

with $\mathbf{v}_{ext}$ from Eq. (S1). For this, we used $4 \cdot 10^6$ test particles, which corresponds effectively to $1.6 \cdot 10^7$ particles by exploiting symmetries of the flow field. Concentrations are evaluated on a uniform three-dimensional grid and then interpolated by a spline interpolation of order 3. The rapid convergence to a near-steady state allows to use a static concentration field corresponding to exposure time $t_{max}$ for each simulation. We checked for test cases that full simulations with time-varying concentration field do not yield different results. The concentration is evaluated on a cubic $50 \times 50 \times 50$ grid spanning in each dimension from $-r_{max}$ to $r_{max}$.

The implementation of an unsteady shear flow for a shear rate $\alpha$ used as illustration in Fig. 1A is inspired by Ref. [23]: We use the flow field $\mathbf{v}_{ext}(r, t) = 0(r, t) = \alpha(r, t) \left[ \mathbf{r} \cdot \mathbf{e}_y'(t) \right] \mathbf{e}_y'(t)$, where the shear axis $\mathbf{e}_y'(t)$ and the flow axis $\mathbf{e}_y'(t)$ are subject to a three-dimensional random walk on the unit sphere with rotational diffusion coefficient $D_{rot} = \pi \alpha$. The shear rate profile is given by $\alpha(r, t) = \sqrt{2} \alpha \sin(2\pi t / T_\alpha) h(r)$. The shear rate $\alpha(r, t)$ decays as $h(r)$ with distance $r$ away from the center. This decay $h(r)$ mimics the decay of velocity from the center of a vortex. We use the decay of an Lamb-Oseen vortex

$$h(r) = \left( \frac{r_{core}}{r} \right)^2 \left( 1 - \exp \left[ - \left( \frac{r}{r_{core}} \right)^2 \right] \right),$$

employing the Burger radius $r_B$ of a Burger vortex as core radius $r_{core} = r_B$, where $r_B = K \eta_{col} \approx K \eta_0 / \pi$ with $K = 7.1$ [19, 35, 36]. The shear rate $\alpha(r, t)$ oscillates in time with root-mean-square amplitude $\sqrt{\frac{1}{T_\alpha} \int_0^{T_\alpha} dt' \alpha'(r, t)^2} = h(r) \alpha$ and period $T_\alpha = \frac{r_{core}^2}{2} \frac{\eta_{col}}{K \pi}$, corresponding to the time scale of decay of a Burger vortex.
| Parameter | Sea urchin [11] | Sea urchin [18, 29, 30, 69] | Red abalone [13, 14] |
|-----------|----------------|-----------------------------|---------------------|
|            | (A. punctula) | (S. purpuratus) | (H. rufescens) |
| Figs. 1, 2, S4 | Figs. 4, S3, S2 | Figs. 3, S1 |
| path curvature | \( \kappa_0 [\mu m^{-1}] \) | 0.065 | 0.067 |
| path torsion | \( \tau_0 [\mu m^{-1}] \) | 0.067 | |
| helix radius | \( r_0 [\mu m] \) | \( \kappa_0/ (\kappa_0^2 + \tau_0^2) \approx 7 \) | |
| gain factor | \( \rho \) | 5 | 5 |
| threshold of sensory adaption | \( c_b [pM] \) | 10 | |
| signaling time-scale | \( \mu [s] \) | \( (\sqrt{\kappa_0^2 + \tau_0^2})^{-1} \) | 5 |
| sperm aspect ratio | \( \gamma \) | 200 | 42 |
| swimming speed | \( v_0 [\mu m s^{-1}] \) | 200 | 42 |
| net speed along helix axis | \( v_h [\mu m s^{-1}] \) | 145 | 30 |
| chemoattractant release rate | \( Q [fmol min^{-1}] \) | 0.46 | 0.18 |
| diffusion coefficient | \( D [\mu m^2 s^{-1}] \) | 239 | 660 |
| egg radius | \( r_{egg} [\mu m] \) | 100 | 108 |
| egg density | \( \rho_{egg} [ml^{-1}] \) | \( 10^{-3} \) | \( 1.5 \cdot 10^4 \) |
| boundary radius | \( r_{max} [\mu m] \) | \( 6 \cdot 10^4 \) | 240 |
| sperm density | \( \rho_{sperm} [ml^{-1}] \) | - | \( 3.9 \cdot 10^5 \) |
| exposure time | \( t_{max} [s] \) | 360 | 120 |
| background concentration | \( c_{bg} [nM] \) | - | \( 500 - 4000 \) |
| fertilizability (fit) | \( p_f \) | - | 10% |
|                 |                 |                 | 60% |

TABLE I. List of parameters used or obtained for the three scenarios. See text for discussion and further parameters.

[1] Miller RL (1985) Sperm chemo-orientation in the metazoa. Biol. Fertil. 2:275–337.
[2] Eisenbach M, Giojalas LC (2006) Sperm guidance in mammals: an unpaved road to the egg. Nat. Rev. Mol. Cell Biol. 7(4):276–285.
[3] Riffell JA, Krug PJ, Zimmer RK (2004) The ecological and evolutionary consequences of sperm chemoattraction. Proc. Natl. Acad. Sci. USA 101(13):4501–4506.
[4] Corkidi G, Taboada B, Wood CD, Guerrero A, Darszon A (2008) Tracking sperm in three-dimensions. Biochem. Biophys. Res. Commun. 373(1):125–129.
[5] Kaupp UB (2012) 100 years of sperm chemotaxis. J. Gen. Physiol. 140(6):583–586.
[6] Serro EA, Pearson G, Kautsky K, Brawley SH (1996) Successful external fertilization in turbulent environments. Proc. Natl. Acad. Sci. USA 93(11):5286–5290.
[7] Gordon R, Brawley SH (2004) Effects of water motion on propagule release from algae with complex life histories. Mar. Biol. 145(1):21–29.
[8] Levitan DR (1993) The importance of sperm limitation to the evolution of egg size in marine invertebrates. Am. Nat. 141(4):517–536.
[9] Cresshaw HC (1996) A new look at locomotion in microorganisms: Rotating and translating. Integr. Comp. Biol. 36(6):608–618.
[10] Friedrich BM, Jülicher F (2007) Chemotaxis of sperm cells. Proc. Natl. Acad. Sci. USA 104(33):13256–13261.
[11] Jikeli JF, et al. (2015) Sperm navigation along helical paths in 3D chemoattractant landscapes. Nat. Commun. 6:7985.
[12] Eisenbach M (1999) Sperm chemotaxis. Rev. Reprod. 4(1):56–66.
[13] Riffell JA, Zimmer RK (2007) Sex and flow: the consequences of fluid shear for sperm–egg interactions. J. Exp. Biol. 210(20):3644–3660.
[14] Zimmer RK, Riffell JA (2011) Sperm chemotaxis, fluid shear, and the evolution of sexual reproduction. Proc. Natl. Acad. Sci. USA 108(32):13200–13205.
[15] Taylor JR, Stocker R (2012) Trade-offs of chemotactic foraging in turbulent water. Science 338(6107):675–679.
[16] Kashikar ND, et al. (2012) Temporal sampling, resetting, and adaptation orchestrate gradient sensing in sperm. J. Cell Biol. 198(6):1075–1091.
[17] Crimaldi JP, Zimmer RK (2014) The physics of broadcast spawning in benthic invertebrates. Annu. Rev. Mar. Sci. 6:141–165.
[18] Mead KS, Denny MW (1995) The effects of hydrodynamic shear stress on fertilization and early development of the purple sea urchin Strongylocentrotus purpuratus. Biol. Bull. 188(1):46–56.
[19] Jumars PA, Trowbridge JH, Boss E, Karp-Boss L (1989) Turbulence-plankton interactions: A new cartoon. Mar. Ecol. Prog. Ser. 46(1):327–337.
[20] Denny, Shibata MF (1989) Consequences of fluid shear for sperm–egg interactions. J. Exp. Biol. 210(20):3644–3660.
[21] Lazier JRN, Mann KH (1989) Turbulence and the diffusive layers around small organisms. Deep-Sea Res. 36(11):1721–1733.
[22] Bell AF, Crimaldi JP (2015) Effect of steady and unsteady flow on chemoattractant plume formation and sperm taxis. J. Marine Syst. 148:236–248.
[23] Xu H, et al. (2018) Sperm-hybrid micromotor for targeted drug delivery. ACS Nano 12(1):327–337.
[25] Vogel H, Czihak G, Chang P, Wolf W (1982) Fertilization kinetics of sea urchin eggs. *Math. Biosci.* 58(2):189–216.

[26] Levitan DR, Sewell MA, Chia FS (1991) Kinetics of fertilization in the sea urchin *Strongylocentrotus franciscanus*: Interaction of gamete dilution, age, and contact time. *Biol. Bull.* 181(3):371–378.

[27] Styan CA (1998) Polyspermy, egg size, and the fertilization kinetics of free-spawning marine invertebrates. *Am. Nat.* 152(2):290–297.

[28] Millar RB, Anderson MJ (2003) The kinetics of monospermic and polyspermic fertilization in free-spawning marine invertebrates. *J. Theor. Biol.* 224(1):79–85.

[29] Gaylord B (2008) Hydrodynamic context for considering turbulence impacts on external fertilization. *Biol. Bull.* 214(3):315–318.

[30] Denny MW, Nelson EK, Mead KS (2002) Revised estimates of the effects of turbulence on fertilization in the purple sea urchin, *Strongylocentrotus purpuratus*. *Biol. Bull.* 203(3):275–277.

[31] Kolmogorov A (1941) The local structure of turbulence in an incompressible viscous fluid for very large Reynolds’ numbers. *Akademiia Nauk SSSR Doklady* 30:301–305.

[32] Kolmogorov AN (1962) A refinement of previous hypotheses concerning the local structure of turbulence in a viscous incompressible fluid at high Reynolds number. *J. Fluid Mech.* 13(1):82–85.

[33] Shraiman BI, Siggia ED (2000) Scalar turbulence. *Nature* 405(6787):639–646.

[34] Aref H, et al. (2017) Frontiers of chaotic advection. *Rev. Mod. Phys.* 89(2):025007.

[35] Hatakeyama N, Kambe T (1997) Statistical laws of random strained vortices in turbulence. *Phys. Rev. Lett.* 79(7):1257–1260.

[36] Webster DR, Young DL (2015) A laboratory realization of the Burgers’ vortex cartoon of turbulence-plankton interactions. *Limnol. Oceanogr.: Methods* 13(2):92–102.

[37] Bentkamp L, Lalescu CC, Wilczek M (2019) Persistent accelerations disentangle Lagrangian turbulence. *Nat. Commun.* 10(1):1–8.

[38] O’Malley S, Bees MA (2012) The orientation of swimming biflagellates in shear flows. *Bull. Math. Biol.* 74(1):232–255.

[39] Marcos H, Fu HC, Powers TR, Stocker R (2012) Bacterial rheotaxis. *Proc. Natl. Acad. Sci. USA* 109(13):4780–4785.

[40] Kumar M, Ardekani AM (2019) Effect of external shear flow on sperm motility. *Soft Matter* 15(31):6269–6277.

[41] Klindt GS, Rulof C, Wagner C, Friedrich BM (2016) Load response of the flagellar beat. *Phys. Rev. Lett.* 117(25):258101.

[42] Celani A, Vergassola M (2010) Bacterial strategies for chemotaxis response. *Proc. Natl. Acad. Sci. USA* 107(4):1391–1396.

[43] Brumlery DR, et al. (2019) Bacteria push the limits of chemotactic precision to navigate dynamic chemical gradients. *Proc. Natl. Acad. Sci. USA* 116(22):10792–10797.

[44] Berg HC, Purcell EM (1977) Physics of chemoreception. *Biophysical Journal* 20(2):193–219.

[45] Kromer JA, Märcker S, Lange S, Baier C, Friedrich BM (2018) Decision making improves sperm chemotaxis in the presence of noise. *PLoS Comput. Biol.* 14(4):e1006109.

[46] Luchsinger RH, Bergersen B, Mitchell JG (1999) Bacterial swimming strategies and turbulence. *Biophys. J.* 77(5):2377–2386.

[47] Loecei JT, Pedley TJ (2009) Run and tumble chemotaxis in a shear flow: The effect of temporal comparisons, persistence, rotational diffusion, and cell shape. *Bull. Math. Biol.* 71(5):1089–1116.

[48] Stocker R (2012) Marine microbes see a sea of gradients. *Science* 338(6107):628–633.

[49] Kiørboe T, Saiz T (1995) Planktivorous feeding in calm and turbulent environments, with emphasis on copepods. *Mar. Ecol. Prog. Ser.* 122:135–145.

[50] Breier RE, Lalescu CC, Waas D, Wilczek M, Mazza MG (2018) Emergence of phytoplankton patchiness at small scales in mild turbulence. *Proc. Natl. Acad. Sci. USA* 115(48):12112–12117.

[51] Lombard F, Koski M, Kiørboe T (2013) Copepods use chemical trails to find sinking marine snow aggregates. *Limnol. Oceanogr.* 58(1):185–192.

[52] Suarez SS, Pacey AA (2006) Sperm transport in the female reproductive tract. *Hum. Reprod. Update* 12(1):23–37.

[53] Gaffney E, Gadilha H, Smith D, Blake J, Kirkman-Brown J (2011) Mammalian sperm motility: Observation and theory. *Annu. Rev. Fluid Mech.* 43(1):501–528.

[54] Miki K, Clapham D (2013) Rheotaxis guides mammalian sperm. *Current Biology* 23(6):443–452.

[55] Kantsler V, Dunkel J, Blayney M, Goldstein RE (2014) Rheotaxis facilitates upstream navigation of mammalian sperm cells. *eLife* 3:e02403.

[56] Hein AM, Carrara F, Brumley DR, Stocker R, Levin SA (2016) Natural search algorithms as a bridge between organisms, evolution, and ecology. *Proc. Natl. Acad. Sci. USA* 113(34):9413–9420.

[57] Lancia F, et al. (2019) Reorientation behavior in the helical motility of light-responsive spiral droplets. *Nat. Commun.* 10(1):1–8.

[58] Vergassola M, Villermaux E, Shraiman BI (2007) ‘Infotaxis’ as a strategy for searching without gradients. *Nature* 445(7126):406–409.

[59] Mikulencak DR, Morris JF (2004) Stationary shear flow around fixed and free bodies at finite Reynolds number. *J. Fluid Mech.* 520:215–242.

[60] Friedrich BM, Jülicher F (2009) Steering chiral swimmers immersed in a viscous fluid. *Proc. R. Soc. Lon. A* 465(2102):1339–1365.

[61] Pedley TJ, Kessler JO (1992) Hydrodynamic phenomena in suspensions of swimming microorganisms. *Annu. Rev. Fluid Mech.* 24(1):313–358.

[62] Frankel NA, Acrivos A (1968) Heat and mass transfer from small spheres and cylinders freely suspended in shear flow. *Phys. Fluids* 11(9):1913–1918.

[63] Elrick DE (1962) Source functions for diffusion in uniform shear flow. *Aust. J. Phys.* 15(3):283–288.

[64] Zottl A, Stark H (2013) Periodic and quasiperiodic motion of an elongated microswimmer in Poiseuille flow. *Eur. Phys. J. E* 36(1):4.
[68] Słomka J, Alcolombri U, Secchi E, Stocker R, Fernandez VI (2019) Encounter rates between bacteria and small sinking particles. arXiv:1908.08376 [physics].

[69] Mead KS (1996) Ph.D. thesis (Stanford University).

[70] Alvarez L, et al. (2012) The rate of change in $\text{Ca}^{2+}$ concentration controls sperm chemotaxis. J. Cell Biol. 196(5):653–663.

[71] Horst Gvd, Bennett M, Bishop JDD (2018) CASA in invertebrates. Reproduction Fertility and Development 30(6):907–918.

[72] Friedrich BM (2008) Ph.D. thesis (TU Dresden).

[73] Pichlo M, et al. (2014) High density and ligand affinity confer ultrasensitive signal detection by a guanylyl cyclase chemoreceptor. J. Cell Biol. 206(4):541–557.