Concealed Swarm of Micro-swimmers

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Here we show that micro-swimmers can form a hydrodynamically concealed swarm through synergistic cooperation in suppressing one another’s disturbing flows. We then demonstrate how such a concealed swarm can actively gather around a favorite spot, point toward a target, or track a desired trajectory in space, while minimally disturbing the ambient fluid. Quenching flow signatures and thus shrinking the associated detection region, by swarming in concealed modes, can potentially have a significant impact on trophic transfer rates among a broad range of aquatic organisms.

Remarkable progress has been made toward understanding optimality of mobility-related characteristics of individual swimming organisms, including their energetic expenditure and nutrient uptake [see e.g. 1]. However, swimming organisms nearly always come in groups [2], and favor from a variety of sophisticated communication capabilities, including cell-cell physical interactions and long-range chemical signaling [3]. Yet, little is understood about their potential ability as a group to optimize their ecological traits. Prior observations have already revealed a glimpse of such cooperative behaviors in nature [4-6]. For instance, sperm cells of the wood mouse, *Apodemus sylvaticus*, are observed [6] to undergo an altruistic morphological transformation forming ‘train’-like aggregates, in order to increase their progressive motility. Recently, it has been shown [7] that two interacting micro-swimmers can help each other swim faster through ambient fluid –phenomenon termed as ‘hydrodynamic slingshot effect’. This behavior, which later has been also reported [8] in a similar form for a group of interacting fish, implies that by forming a swarm, swimmers can collaborate to boost each other’s swimming speed and travel faster as a group than single individuals. Now, the more intriguing question is whether by forming a swarm, swimmers are also able to smartly cancel each other’s disturbing flows to the fluid environment. In other words, is it possible to form a stealth swarm with minimally disturbing the ambient fluid?

Importance of the fluid mechanical signals produced by swimmers (i.e. flow signatures induced by swimming organisms to the ambient fluid) in dynamics of prey-predator systems is well appreciated for a broad range of aquatic organisms – from swimming microorganisms to fish. Take for example the Gram-negative *Bdellovibrio bacteriovorus* [9], which is a prototypical predator among motile microorganisms and hunts other bacteria, such as *Escherichia coli*. Recent experiments [10] show that it is, in fact, hydrodynamics rather than chemical clues that lead this predator into regions with high density of prey. Free-living copepods possess highly sensitive fluid-mechanoreceptors capable of detecting disturbing flows as small as 20 µm s$^{-1}$ [11]. These sensors are used by the organism to estimate the distance as well as the size of a nearby predator (prey) to properly trigger escape (catch) behavior, subsequently [12] [13]. Fish are also known to benefit from the flow information provided by their sensory organs (such as lateral lines) to detect a predator’s threatening movements, or conversely, to track down a prey [14]. Therefore, for a wide range of swimming organisms, forming a swarm with minimally disturbing the ambient fluid: (i) will help prey organisms to reduce the risk of predation – by quenching the flow signature that predators use to detect them, and (ii) conversely, helps a swarm of predators to remain stealth while attacking a target prey flock. These can potentially have a significant impact on trophic transfer rates in aquatic environments.

Here, we reveal altruistic behavior of micro-swimmers in formation of a stealth swarm minimally disturbing the surrounding fluid. We call this mode of swarming the concealed mode, which can be achieved when a group of swimmers (actively swimming through an ambient fluid) collaborate to cancel out one another’s disturbing flow. We also present computational evidences and demonstrate how such an active concealed swarm is able to gather around a desired location, point toward a target, or to track an optimal trajectory, whilst minimally disturbing the ambient fluid.

In the most general form, far-field of the flow induced by a micro-swimmer can be well described by the flow of a force dipole [15]. This simple model has been validated and widely used in the literature [see e.g. 2, 16-18]. In modeling a microorganism swimming toward direction $\mathbf{e}$ through an unbounded fluid domain, for instance, the model dipole is composed of the thrust force generated by swimmer’s propulsion mechanism and the viscous drag acting on its body. These forces are exerted in opposite directions (±$f_0 \mathbf{e}$) to the ambient fluid at $x_0 \pm \mathbf{e} l/2$, where $x_0$ is the instantaneous position of the swimmer, and the characteristic length $l$ is on the order of swimmer dimensions. The model dipole [c.f. Fig. [1 a]] is contractile for swimmers with front-mounted flagella (i.e., ‘pullers’ such as C. reinhardtii), and extensile for those with rear-mounted flagella (i.e., ‘pushers’ such as *E. coli*). The associated values of $f_0$ and $l$ can be inferred from experimental measurements. For instance, the values of $f_0 = 0.42$ pN and $l = 1.9$ µm, have been experimentally obtained [18] for *E. coli*, in agreement with resistive force theory [19], and optical trap mea-
measurements \([20]\). We use velocity scale \(U_s = f_0/8\pi\eta l\), length scale \(L_s = l\), and time scale \(T_s = L_s/U_s\), to non-dimensionalize the presented quantities. Dimensionless disturbing flow of a dipolar swimmer can then be expressed as \(\bar{u} = \left[-1 + 3(\bar{r} \cdot \bar{e}/\bar{r})^2\right] c_0 \bar{r}/r^3\) \([19]\), where \(\bar{r} = \bar{x} - \mathbf{x}_0\), for any generic point \(\mathbf{x}\) in space, \(c_0 = +1\) \((-1)\) for pushers (pullers), and the bar signs denote dimensionless quantities.

It is noteworthy that near-field of the flow induced by micro-swimmers can be described more accurately by including an appropriately chosen combination of higher order terms from multipole expansion [see e.g. \([21, 22]\). However, in the present study, we are interested in the span of swimmers’ induced fluid disturbances and their consequent detection region, for which, only far-field of the flow is important. In describing the flow field of a swimmer, the term with lowest rate of spatial decay represents the far-field approximation of the flow. Therefore, here it suffices to take only the leading term (i.e., the force dipole vanishing as \(1/r^2\)) into account, and color higher order terms as insignificant.

To assess optimality of swarming arrangements in stifling disturbing effects, one needs to first quantify the induced fluid disturbances. A measure of distortion caused by the swimmers to the ambient fluid, can be obtained by either: (i) directly computing the Mean Disturbing Flow-magnitude (MDF) over a surrounding ring \(C\) of radius \(R\), i.e. \(\int_C |\bar{u}| ds/(2\pi R)\) – which in fact measures deformation induced by the swimmers on a closed material line, or (ii) computing Area of the Detection Region (ADR), within which, disturbances exceed a predefined threshold. More precisely, the detection region is defined as \(\{\forall \bar{x} | \bar{u}(\bar{x}) \geq \bar{u}_{th}\}\) which is also consistent with previous numerical studies [see e.g. \([23]\). Value of the threshold \((\bar{u}_{th})\) must be tuned based on characteristics of the specific problem of interest. For the system representing a prey swarm, as an example, it can be inferred from experimental observations on sensitivity of the predator’s receptors in sensing flow signatures (c.f. \([14]\)). Among swimming organisms, experimental data are available in more details for copepods [e.g. \([11, 13]\). With their characteristic swimming speed of few \(\text{mm/s}\), it has been reported \([11]\) that copepods can detect disturbing flows as small as \(20,000\ \mu\text{ms}^{-1}\). Therefore, as the velocity scale, \(f_0/8\pi\eta l\), is on the order of swimming speed of the organism, one may choose the normalized disturbing flows of \(\bar{u}_{th} = 0.001\) as the threshold to determine the associated detection region.

We then perform a systematic parametric study on flocks of \(N \geq 2\) swimmers, with the bottom-up approach. Specifically, through numerical modeling and non-linear optimization \([15]\), we develop a general optimization procedure to determine the existence of optimal swarming configurations, and systematically investigate their significance in reducing the swarm’s induced fluid disturbances. As a benchmark, here we consider pusher swimmers (say, \(E. coli\) bacteria) swimming in an infinite two-dimensional fluid domain. Nevertheless, the results will be the same for pullers, and our study can be inherently generalized to a 3D domain.

Note that the objective functions quantifying fluid disturbances (i.e., MDF and ADR) are nonlinear, and subject to constraints (e.g. minimum separation distance between the swimmers). Therefore, in search of the global minima by starting from multiple points, we perform sequential quadratic programming using local gradient-based solvers. The starting points are generated using
the scatter-search mechanism [24], which is a high-level, heuristic, population-based algorithm designed to intelligently search on the problem domain. Its deterministic approach in combining high-quality and diverse members of the population—rather than extensive emphasis on randomization—makes it faster than other similar evolutionary mechanisms such as genetic algorithm [25].

Let us consider simple groups of only two and three swimmers. The relative orientation of the swimmers primarily controls the amount of distortion (measured in terms of MDF/ADR) they induce to the surrounding environment [Fig. 1(b-c)]. Our results reveals that by swimming in optimal orientations, swimmers can reduce induced disturbances by more than 50% [Fig. 1(b)] compared to when they simply swim in schooling orientation (i.e., in the same direction). Note that the computed ADR will vary for different threshold values. However, for a sufficiently large computational domain, dimensionless values of ADR (normalized by ADR of schooling) match for all different threshold values [Fig. 1(b)]. These results also match to those generated through the normalized MDF analysis [Fig. 1(b)]. It bears attention that when two of the swimmers (in a group of three) swim in directions normal to each other, the swarm arrangement will remain optimal regardless of the third one’s swimming direction [c.f. the green dashed line in Fig. 1(c)]. This is due to axisymmetric nature of the disturbing flow induced by two perpendicular dipoles [Fig. 1(b-II)].

For suspensions including a larger number of swimmers, optimal swarm arrangements can be found using the same procedure. A swarm with the optimal arrangement minimally disturbs the ambient fluid, and we call it a concealed swarm, for which reduction in disturbances in terms of MDF (or equivalently shrink of the detection region measured by ADR) exceeds 50% compared to an organized school. As a benchmark, magnitude of the disturbing flow induced by a random suspension of twelve swimmers, and the one induced by the same group arranged into an isotropic organized school are compared in Fig. 2 to that induced by concealed swarms of twelve swimmers. The bottom line for efficiency analysis of configurations in terms of ADR is similar: by forming an optimal arrangement, swimmers can shrink their detection region by more than 50% compared to an organized school. It worth mentioning that the amount of disturbances induced by a flock of swimmers depends also on the minimum separation distance between the agents. Our numerical results show that the role of this factor is more significant for a concealed swarm than for an organized school [Supplementary Notes and Fig. S2]. However, it can still be considered as a minor factor compared to relative orientation of the swimmers.

There exist many situations (for both swimming organisms and artificial micro-swimmers) in which, swimmers form a swarm (i.e., a disordered cohesive gathering) around a desired spot. It can be a swarm of bacteria around a nutrient source [see e.g. 20], or a flock of biological micro-robots performing a localized surgery [see e.g. 27, 28]. It is often highly desired for such an active (yet confined) swarm to remain concealed by minimally disturbing the ambient fluid. This, for instance, keeps the bacterial swarm stealth from the predators, and helps the flock of micro-robots to be non-disturbing toward their host medium. Note that forming a cohesive swarm (as opposed to a random suspension [c.f. Fig. 2]), by itself, is the first constructive step toward reducing distortions. To have the minimal disturbing effects to the surrounding environment, however, arrangement of the swimmers must lie within the optimal region of configurations at every instant of time. The active, yet concealed, swarm presented in Fig. 3 as a benchmark, remains cohesive, keeps itself confined within a finite region of space around the desired spot, and is able to stifle the induced disturbances by up to 50%. This is remarkable as it is equiva-
lent to shrinking the swarm’s detection region by half.

Dynamics of such an active concealed swarm can be described as follows: (i) swimmers forming the swarm get into an optimal arrangement causing minimal fluid disturbances; (ii) each swimmer then swims steadily forward for a while (say, \( \tau_r \)) toward the assigned directions (‘run’); (iii) swimmers reorient quickly into a new optimal arrangement (‘tumble’), and then (iv) they start running once again toward the newly assigned directions. This sequence of events occur in turn repeatedly [Fig. 3 and Movie S1]. Note that each individual swimmer represents a version of the so-called run-and-tumble behavior. Parameters including swimming speed and frequency of tumbling events (\( \tau^{-1} \)) can be tuned according to the system of interest [15]. Among swimming microorganisms, E. coli bacteria are known as paradigms of the run-and-tumble behavior [29]. Recent observations [30] reveal that even C. reinhardtii cells swim in a version of run-and-tumble locomotion. On the other hand, realization of the smart form of run-and-tumble mechanism also seems feasible in the context of artificial and model micro-swimmers. The recently proposed Quadroar swimmer [31, 32], for instance, propels on straight lines (runs), and can perform full 3D reorientation (tumbling) maneuvers [33].

Through altruistic collaborations, micro-swimmers also can form a concealed swarm while traveling toward a target point or tracking a desired trajectory in space. The objective function \( Z \), to be minimized by the swarm through cooperation of the swimmers during each run, must now represent a measure for both the overall disturbances induced by the swimmers and their distances from the target point (or from the desired trajectory).

\[
Z = \epsilon \times \text{MDF} + (1 - \epsilon) \times \text{RMS},
\]

where RMS stands for the normalized root mean squared of swimmers’ distances from the target point, MDF quantifies the overall induced disturbances, and \( \epsilon \in [0,1] \) is the detuning parameter determining the importance of concealing versus travel time [15].

We show sample flocks of micro-swimmers traveling from point \( A \) toward a target point \( B \) in Fig. 4(a-b). These traveling swarms may represent: (i) flocks of micro-robots traveling toward a target point while controlled to be fast/concealed (tuned by \( \epsilon \)); (ii) flocks of motile microorganisms swimming under influence of an external gradient from \( A \) to \( B \), e.g. in chemotaxis [34], (the intensity of which being tuned by \( 1 - \epsilon \)); or (iii) a swarm of predators attacking a target prey flock at \( B \) in stealth versus fast modes (tuned by \( \epsilon \)).

Figure 4. A controlled flock of micro-swimmers traveling from point \( A \) toward the target point \( B \). (a): Comparison between trajectories of the fastest traveling swarm (travel time \( = 130T_s \)) with no concealing (\( \epsilon = 0 \)) denoted by dashed thin lines, and a traveling swarm with highest possible concealing efficiency (MDF = 49.7%) and no constraint on preferred direction (\( \epsilon = 1 \)) denoted by solid thick lines. The latter never reaches the target [Movie S2]. (b): Snapshots of the optimal concealed traveling swarm (\( \epsilon = 0.5 \)) having the most possible concealing efficiency in the cost of only 23% increase in the travel time [Movie S3]. Blue, green, and red thick (thin) solid (dashed) lines represent trajectories of the swimmers after \( 50T_s \) (160\( T_s \)). Instantaneous arrangement of the swimmers at \( t = 50T_s \) is schematically shown in a magnified view as inset (I) and is compared to the arrangement of an organized school (II) with MDF of about 100%. Dashed circles in each panel represent sample surrounding rings over which one may compute the MDF.

We define:

\[
Z = \epsilon \times \text{MDF} + (1 - \epsilon) \times \text{RMS},
\]

Note that \( \epsilon = 0 \) corresponds to the fastest traveling swarm, which moves on a straight line in homogeneous environments, but represents no concealing effect on swimmers’ disturbances. On the other extreme, i.e. for \( \epsilon = 1 \), the swarm will have the highest concealing efficiency (MDF = 49.7%), but never reaches the target [Fig. 4(a) and Movie S2].

Trade-off between the travel time and the overall efficiency of concealing is demonstrated with more details.
Figure 5. Fluid disturbances (in terms of MDF) induced by traveling swarms controlled with various tuning parameters $\epsilon$, during the trip from $A$ to $B$ [c.f. Fig. 4]. The terminal time, at which the swarm reaches the target point $B$, is denoted in each case by an asterisk. Note that the swarm corresponding to the extreme case of $\epsilon = 1$, never reaches the target.

The induced fluid disturbances are monitored during the trip from $A$ to $B$ for traveling swarms controlled with various values of $\epsilon$. As $\epsilon \to 0$ ($\to 1$), the swarm will be faster (slower), i.e. the travel time decreases (increases), but will induce more (less) disturbances to the ambient fluid. It is remarkable that swarm-ing in a concealed mode, with more than 50% reduction in disturbances, may cost only 23% increase in the trip duration compared to the fastest possible trip [Fig. 4(b), Movie S3]. This is equivalent to 50% shrink in detection region of the swarm throughout the trip from $A$ to $B$.

Additionally, an example of a concealed swarm of micro-swimmers tracking a desired trajectory through a non-uniform environment is discussed in Supplementary Notes [see Fig. S3 and Movie S4].

In this letter, we demonstrated how micro-swimmers can form a stealth swarm and collaborate to minimize their overall fluid disturbances. Such a concealed swarm can actively confine itself to a specific region gathering around a desired spot, point toward a target, or track a prescribed desired trajectory. These findings provide a road map to control and lead a swarm of interacting micro-robots from point $A$ to $B$, while they collaborate to minimally disturb their host medium. Also, provide insights into dynamics of prey-predator systems. Stifling the induced disturbances will help an active swarm of prey swimmers gathered around a favorite spot (say, a nutrient source) to lower their detectability and thus predation risk by shrinking their detection region. Quenching flow signatures induced by a traveling swarm, on the other hand, may help a swarm of predators to remain concealed while attacking a target prey flock.

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I. DETAILED MATHEMATICAL FORMULATION

Dynamics of the incompressible flow around swimming organisms is governed by Navier-Stokes equations:

\[
\frac{D\mathbf{u}}{Dt} = -\nabla P + \eta \nabla^2 \mathbf{u} + \mathbf{F}, \quad \nabla \cdot \mathbf{u} = 0,
\]

(2)

where \( \rho \) and \( \eta \) are density and dynamic viscosity of the ambient fluid, \( P \) is the pressure field, \( \mathbf{u} \) is the velocity field, and \( \mathbf{F} \) is the external body force per unit volume. The relative importance of inertial to viscous effects is represented by the Reynolds number, \( \text{Re} = \rho U L / \eta \), where \( U \) and \( L \) denote characteristic velocity and length, respectively. For microorganisms swimming in water (\( \rho \approx 10^3 \) kg/m\(^3\) and \( \eta \approx 10^{-3} \) Pa.s) the corresponding Reynolds number is always very small (i.e., Re \( \ll 1 \)). Let us, for instance, take a look at two of the most common examples. A typical bacteria, such as E. coli, with length of 1-10 \( \mu \text{m} \) and swimming speed of \( \sim 10 \) \( \mu \text{m/s} \) [19] has the Reynolds number of \( \sim 10^{-4} \) when swimming in water. For green alga Chlamydomonas reinhardtii with characteristic length \( L \approx 10 \) \( \mu \text{m} \) and swimming speed \( U \sim 100 \) \( \mu \text{m/s} \) [25], the Reynolds number is \( \text{Re} \sim 10^{-3} \).

Therefore, it is appropriate to study micro-swimmers in the context of low Reynolds number regimes (Re \( \ll 1 \)), where the fluid inertia is negligibly small compared to the fluid viscosity, and the viscous diffusion dominates fluid transport. The Navier-Stokes equation of motion will then simplify to the Stokes equation:

\[
\nabla P = \eta \nabla^2 \mathbf{u} + \mathbf{F}, \quad \nabla \cdot \mathbf{u} = 0.
\]

(3)

In Stokes regime, self-propelled buoyant micro-swimmers exert no net force and no net torque to the ambient fluid. Flagellated microorganisms, for instance, use their flagella – flexible external appendages – to generate a net thrust, and propel themselves through ambient fluids. This propulsive force – generated mainly owing to the drag anisotropy of slender filaments in Stokes regime [30] – is, however, balanced by the drag force acting on the cell body (c.f. Fig. S1).

Hence, in the most general form, far-field of the flow induced by a micro-swimmer can be well described by the flow of a force dipole [2]. To be more precise, by the flow of a force dipole composed of the thrust force generated by swimmer’s propulsion mechanism, and the viscous drag acting on its body. This simple model has been validated and widely used in the literature [see e.g. 2, 16, 17]. In the case of E. coli bacteria, for example, the validity of this model has been further confirmed by comparing it to the flow field experimentally measured around an individual swimming cell [18]. Note that the model dipole is contractile for swimmers with front-mounted flagella (i.e., ‘pullers’ such as C. reinhardtii), and extensile for those with rear-mounted flagella (i.e., ‘pushers’ such as E. coli). Schematic representations of the force dipoles generated by archetypal puller and pusher swimming microorganisms, as well as direction of the induced flow fields are shown in Fig. S1.

Let us consider a model microorganism swimming toward direction \( \mathbf{e} \) through an unbounded fluid domain. Disturbing flow of the swimmer can be modeled as the flow of a force dipole located at instantaneous position of the swimmer (\( \mathbf{x}_p \)). Thrust and drag forces of equal magnitude are exerted in opposite directions (\( \pm f \mathbf{e} \)) to the ambient fluid at \( \mathbf{x}_0 \pm \mathbf{e} l/2 \), where the characteristic length \( l \) is on the order of swimmer dimensions. For each point force \( \mathbf{f} \) exerted at point \( \mathbf{x}_p \) in an infinite fluid domain, the governing equation will turn into:

\[
\nabla P = \eta \nabla^2 \mathbf{u} + \mathbf{f} \delta(\mathbf{x} - \mathbf{x}_p), \quad \nabla \cdot \mathbf{u} = 0.
\]

(4)

where \( \delta(\mathbf{r}) \) is the Dirac delta function. [4] can be analytically solved in several ways [see e.g. 37], and the resultant velocity field is known as Stokeslet:

\[
\mathbf{u}_S(\mathbf{r}_p,t) = \frac{f}{8\pi \eta} \left( \frac{I}{r_p^3} + \frac{r_p r_p}{r_p^3} \right) \equiv \mathbf{G} \cdot \mathbf{f},
\]

(5)

where \( \mathbf{r}_p = \mathbf{x} - \mathbf{x}_p \), and \( \mathbf{G} \) is the corresponding Green’s function, known as the Oseen tensor. A complete set of singularities in Stokes regime, can then be easily found by taking derivative [c.f. 37] of the fundamental solution presented in [5]. Taking one derivative provides the force-dipole solution, decaying as \( 1/r^2 \), and the second derivative results in the source-dipole and force-quadrupole solutions, decaying as \( 1/r^3 \), and so forth. In describing the flow field of a swimmer, the one with lowest rate of spatial decay represents the far-field approximation of the flow. It is noteworthy that near-field of the flow induced
by micro-swimmers can be described more accurately by including an appropriately chosen combination of higher order terms [e.g. 21]. However, in the present study, we are interested in the span of swimmers’ induced fluid disturbances and their consequent detection region, for which, only far-field of the flow is important. In describing the flow field of a swimmer, the term with lowest rate of spatial decay represents the far-field approximation of the flow. Therefore, here it suffices to take only the leading term (i.e., the force dipole vanishing as $1/r^2$) into account, and color higher order terms as insignificant.

The induced flow field of a model force dipole, $\pm f_0 e$, located at instantaneous position of the swimmer (i.e., $x_0$), can be mathematically expressed as [2]:

$$u_{DS} = \frac{\mathcal{D}}{8\pi\eta} r^3 \left[ -1 + 3 \left( \frac{r \cdot e}{r} \right)^2 \right] r,$$

where $r = x - x_0$, for any generic point $x$ in space. Dipole strength, $\mathcal{D} \approx f_0 l$, has a positive (negative) sign for pusher (puller) swimmers and its value can be inferred from experimental measurements. For instance, the values of $f_0 = 0.42$ pN and $l = 1.9$ $\mu$m, have been experimentally obtained [18] for E. coli, in agreement with resistive force theory [19], and optical trap measurements [20]. One may then use $f_0$, $l$, and $\eta$ to make the problem dimensionless and come up with velocity scale $U_s = f_0 / 8\pi\eta l$, length scale $L_s = l$, and time scale $T_s = L_s / U_s$. Therefore, dimensionless disturbing flow of a dipolar model swimmer reads as:

$$\bar{u}_{DS} = \frac{c_0}{r^3} \left[ -1 + 3 \left( \frac{\bar{r} \cdot e}{r} \right)^2 \right] \bar{r},$$

where $\bar{r} = x - x_0$, for any generic point $x$ in space, $c_0 = +1$ ($c_0 = -1$) for pushers (pullers), and the bar signs denote dimensionless quantities. Flow field induced by an extensile force dipole (i.e., that of a pusher swimmer, say E. coli) oriented along the horizontal direction is demonstrated, as a benchmark, in Fig. 1(b). Color shading represents the magnitude, and black arrows show direction of the flow. Inward and outward flows are separated by $y = \pm \sqrt{2} \bar{x}$ white dashed lines [2].

II. ILLUSTRATION OF SYSTEM DYNAMICS AND PARAMETER SETUP

In a swarm of $N$ swimmers, each individual swimmer represents a version of the so-called run-and-tumble behavior. Dynamics of such an active swimmer can be described as follows: (i) swimmers forming the swarm get into an arrangement (that is an optimal arrangement causing minimal fluid disturbances in the case of a concealed swarm); (ii) each swimmer then swims steadily forward for a while (say, $\tau_r$) toward the assigned directions (‘run’); (iii) swimmers reorient quickly into a new (optimal) arrangement (‘tumble’), and then (iv) they start running once again toward the newly assigned directions. This sequence of events occur in turn repeatedly [see e.g. Fig. 3 in the main text and Movie S1].

Parameters including swimming speed of the swimmers and frequency of the tumbling events can be tuned according to the system of interest. To represent swimming microorganisms, for instance, these tuning parameters can be picked according to the values already available in the literature. In case of E. coli bacteria, for instance: the swimming speed is $\sim 25 - 35$ $\mu$m$^{-1}$ [19], and the mean duration ($\tau_r$) of the run phase, which in turn determines frequency of the tumblings, is $\sim 1$ $s$. Note that the run time ($\tau_r$) may vary spatiotemporally due to various external field gradients This in fact enables swimming cells to bias toward a favorable direction; say in chemotaxis [34]. However, one can generally assume frequency of the tumbling events ($\tau_t^{-1}$) to be constant in homogeneous environments. Inspired by the behavior of swimming microorganisms, we also consider the tumblings to be in-place, abrupt reorientations. Notably, for a swimming E. coli, it is observed that tumbling is either abrupt or takes only tenths of a second (with the mean duration of $\sim 0.1$ s), and those happening instantaneously are most probable to occur [38]. Moreover, one may put a bound for the angle between pre- and post-tumbling swimming directions of each swimmer’s motion. Such an upper/lower bound can be picked according to the observed behavior of motile cells. For instance, inspired by the observed behavior of E. coli bacteria, the value of $90^\circ$ has been set as the upper bound for the angle between pre- and post-tumbling directions of swimmers forming the active swarm presented in Fig. 3 of the main text. Note that although tumbling events seem to be stochastic for E. coli, the swimming directions of two successive runs are, in fact, correlated. Specifically, the average change of direction (mean value $\pm$ standard deviation) during a single tumble has been reported as $\sim 58^\circ \pm 40^\circ$ [38].

III. QUANTIFYING INDUCED DISTURBANCES: COMPUTING MDF AND ADR

In order to quantify swarm’s induced fluid disturbances – to be used in assessing optimality of various swarming arrangements in stifling disturbing effects – the following measures have been proposed in the main text. Here we provide more details on how to compute them.

A measure of distortion caused by the swimmers to the ambient fluid can be obtained by directly computing the Mean Disturbing Flow-magnitude (MDF) over a surrounding ring, i.e.

$$\text{MDF} = \frac{1}{2\pi R} \int_{C(R)} |\bar{u}| \, ds,$$

where $|\bar{u}|$ is the magnitude of the mean disturbing flow.
where $ds$ is the differential length along the surrounding ring of radius $R$, denoted by $C(R)$, and $\overline{u}$ is the overall dimensionless flow field induced by the swarm—that is the superposition of flow fields induced by individual swimmers forming the swarm [c.f. Eq. 6]. To compute Eq. (5) numerically, the surrounding ring is first discretized to 300 equally spaced mesh points. Magnitude of the induced flow field is then computed at each point and averaged over the entire ring. Note that the computed value of MDF in fact measures deformation induced by the swarm on a closed material line.

Alternatively, to quantify induced disturbances, one may compute Area of the Detection Region (ADR), as the area of a region within which induced flow field exceed a predefined threshold. More precisely, the detection region, $\mathcal{R}$, is defined as

$$\mathcal{R} = \{ \forall x | \overline{u}(x) \geq \overline{u}_{th} \},$$

which is also consistent with previous numerical studies [see e.g. 23]. Value of the threshold ($\overline{u}_{th}$) must be tuned based on characteristics of the specific problem of interest. For the system representing a prey swarm, as an example, it can be inferred from experimental observations on sensitivity of the predator’s receptors in sensing flow signatures. Among swimming organisms, experimental data are available in more details for copepods [e.g. 11–13]. With their characteristic swimming speed of few mm/s, it has been reported [11] that copepods can detect disturbing flows as small as $20 \mu m/s$. Therefore, as the velocity scale, $f_0/8\pi\eta l$, is on the order of swimming speed of the organism, one may choose the normalized disturbing flows of $\overline{u}_{th} = 0.001$ as the threshold to determine the associated detection region.

Note that the computed values of ADR will vary for different chosen thresholds. However, for a sufficiently large computational domain, dimensionless values of ADR (i.e. when normalized by ADR of the schooling orientation) match for all different threshold values. This has also been confirmed with our computational results [see Fig. 1b in the main text]. Similar argument can be made regarding MDF versus ADR as follows. Although defined independently, and are different in values, the bottom line of the analysis will be the same (see e.g. Fig.1b of the main text) for both MDF and ADR, once we normalize each of them with their corresponding values for the reference case (i.e. the case of aligned swimmers swimming in the same direction). This is due to the fact that in the normalized form, they both represent how does the distortion induced by a specific swarm compare to that of a swarm arranged into schooling orientation (where all the swimmers swim in the same direction).

### IV. OPTIMIZATION METHODS

At every instant of time, the optimal arrangement of the swarm, minimally disturbing the ambient fluid, is computed via nonlinear optimization of the objective function quantifying fluid disturbances (i.e., either MDF or ADR). These objective functions are nonlinear and sometimes subject to constraints (e.g. minimum separation distance between the swimmers). Therefore, in search of the global minima by starting from multiple points, we perform sequential quadratic programming using local gradient-based solvers (such as fmincon). Note that merely applying gradient-based solvers will only find local optima depending on the starting point. To avoid this, the starting points are generated using a scatter-search mechanism [24], which is a high-level, heuristic, population-based algorithm designed to intelligently search on the problem domain. Its deterministic approach in combining high-quality and diverse members of the population—which rather than extensive emphasis on randomization—makes it faster than other similar evolutionary mechanisms such as genetic algorithm [25].

To make sure about the robustness of our optimization results, we also tested our numerical experiments using other popular schemes such as the Particle Swarm [39] and Genetic Algorithms [40]. It is noteworthy to mention that in a swarm of $N$ swimmers, as discussed in the main text, there exist a range of optimal arrangements, the so-called optimal region of configurations, with minimal disturbing effects to the ambient fluid. For flocks of two and three swimmers, for instance, the optimal region of configuration will be different in each run. However, the obtained concealing efficiency is the same for all resultant arrangements (as the all lie within the optimal region), and is in agreement with the presented results obtained through our optimization method.

### V. SWARM ARRANGEMENT VS. SEPARATION DISTANCE BETWEEN SWIMMERS

As discussed in the main text, orientations of the swimmers forming a swarm primarily determines the amount of induced disturbances. As a benchmark, let us consider a flock of twelve swimmers. Magnitude of the induced flow field by the flock is represented in Fig. S2 when swimmers: (i) arrange into isotropic positions but all orient in the same direction (as an organized school) with minimum separation of $10L_s$ and $20L_s$ (panels a-b); or (ii) arrange into isotropic positions and orientations with minimum separation of $10L_s$ and $20L_s$ (panels c-d).

Note that the effect of separation between swimmers
becomes more important for a concealed swarm (compare panels a-b with c-d in Fig. S2). However, is still a minor factor compared to orientation of the swimmers.

VI. TRAJECTORY TRACKING THROUGH A NON-UNIFORM ENVIRONMENT

There exist many situations, for both biological micro-robots and swimming microorganisms, in which they travel through a non-uniform environment. Examples include fluids at the interface of different organs inside the human body with distinct viscosities, or those in vicinity of a mucus zone \(^{41}\). Depending on their propulsion mechanism, motile microorganisms experience different energy expenditures, and thus distinct swimming speeds, while traveling in regions with different rheological properties \cite{42,47}.

Let us consider a simple example of two side-by-side regions, through which the swimming costs are different for swimmers –say, the interface between two distinct liquids. Here the swarm has to travel from point \(\mathcal{A}\), in region I, to point \(\mathcal{B}\), within region II. We set the starting point, \(\mathcal{A}\), as the origin of reference frame. Note that once the swimming cost \(C(x, y)\) is known for every point \((x, y)\) in space, the swimming speed of swimmers is taken as \(1/C(x, y)\), accordingly. Here, the swimming cost, normalized by \(U_s^{-1}\), is assumed to be \(C(x, y) = 1\) and \(2\), for regions I and II, respectively (Fig. S3). By solving the normalized eikonal equation,

\[
|\nabla \bar{T}| = \tilde{C}(\bar{x}, \bar{y}),
\]

using a fast marching level-set method \cite{48,49}, one can find \(\bar{T}(\bar{x}, \bar{y})\), which is the minimum cost (i.e., the least required time) of reaching to any arbitrary point \((\bar{x}, \bar{y})\) in space. The bar signs denote dimensionless quantities, and the value of \(\bar{T}\) is normalized by the time scale \(T_s = L_s/U_s\). Tracing back from point \(\mathcal{B}\) to \(\mathcal{A}\), while always moving normal to the isolines of \(\bar{T}\) (see Fig. S3), will then provide the optimal path \cite{49}.

Figure S2. (a)-(b) Flow disturbance induced by twelve schooling swimmers arranged into isotropic positions with minimum distance 10\(L_s\) and 20\(L_s\) between them. (c)-(d) Flow disturbance induced by swarms of twelve swimmers forming isotropic arrangement (i.e., positions and orientations) with minimum distance 10\(L_s\) and 20\(L_s\) between them. Color shading represents the flow magnitude, and MDF is computed over the black dotted ring. The scale bar is 40\(L_s\).

Figure S3. A concealed swarm of three swimmers tracking the optimal trajectory in a non-uniform environment from point \(\mathcal{A}\) to the target point \(\mathcal{B}\) (see Movie S4). Detection region of the swimmers is significantly stifled, such that reduction in ADR exceeds 50% during the trip. This also means a minimal disturbance to the ambient fluid with 50.4% reduction in MDF. Total time taken for the swimmers to reach the target point is \(210T_s\). The optimal path is shown by a black dashed line, and trajectories of the swimmers are shown by blue, red and green solid lines. The inset represents a specific moment (the location of which is marked by a dashed circle) from the trip, and schematics demonstrate arrangement of the swimmers at this moment. The normalized swimming cost is \(\bar{C}(x, y) = 1\) for \(x/l < 50\), and \(\bar{C}(x, y) = 2\) for \(x/l \geq 50\). Isolines correspond to \(\bar{T}(x, y)\): the minimum time required to reach any point \((x, y)\), starting from point \(\mathcal{A}\).

Now using the objective function \((Z)\) which also includes root mean squared (RMS) of swimmers’ distance from the optimal path, one can make the concealed swarm to track the desired trajectory.
A concealed swarm of three swimmers is represented in Fig. S3 while tracking an optimal trajectory in a non-uniform environment from point $A$ to the target point $B$. Note that in the cost of only 30% increase in the travel time, detection region of the swarm is significantly stifled, such that reduction in ADR exceeds 50% during the trip. This is also equivalent to minimally disturbing the ambient fluid with 50.4% reduction in MDF.

**VII. EXPANSION OF A CONCEALED SWARM**

It is desired for individual swimmers to form a group and collaborate to cancel out each others disturbing effects to the surrounding fluid. Our results further reveal that a traveling concealed swarm can attract nonmember individual swimmers (those swimming in its vicinity), then expand and re-form into a new larger swarm. To provide further insight, the simplest example is demonstrated in Fig. S4 via successive snapshots (a)-(e). It is shown how a single traveling swimmer joins an existing concealed swarm of two swimmers, and together, they form a new concealed swarm of three swimmers. Note that the only imposed constraint on the motion of swimmers is the upward swimming (c.f. gravitaxis). Relaxing this constraint will simply result in a quasi-random walk of the swarm with no preferred direction.

![Figure S4. Snapshots of a single traveling swimmer joining a concealed swarm to minimize the overall disturbing flow. (a)-(b) There is a mutual desire to bring the single swimmer into the swarm. (c)-(d) Members trying to hammer out an optimal swarm arrangement with the new member just joined the group. (e) A concealed swarm of three swimmers is formed with more than 50% reduction in MDF.](image)

**VIII. SIMILAR OBSERVATIONS ON THE BEHAVIOR OF SWIMMING ORGANISMS**

Fish aggregates are widespread, but such collective behaviors are not always synchronous or polarized – as in the well known schooling behavior [50]. They may just form an interactive group and stay together in a loose and non-synchronized way – this is often called shoaling [51]. For instance, some species such as goldfish (Carassius auratus) or surgeonfish are known to spend most of their lives in shoaling [51], sometimes in a way that each seem to be swimming independently while still forming a social group by staying close together. These kinds of shoaling is believed to reduce predation rate, but this is often attributed to the mobbing effect [c.f. 52]. However, the resultant lower predation rate may also have hydrodynamic reasoning, as these collective behaviors are, in fact, reminiscent of our optimal idle and traveling swarms which minimally disturb the ambient fluid. Specifically, individuals seem to be swimming in independent directions with low polarity (as opposed to schooling configuration) while remaining cohesive (i.e. staying close together). Note that lowering induced disturbances for a prey swarm means a lower detection region, and hence a lower predation rate.

Moreover, recent field observations counter-intuitively reveal that for small marine predators (specifically, Eudystyptula minor), the hunting success rate in attacking a prey flock is less when predators appear in schools with their conspecifics [53]. This observation in its spirit is similar to the bottom line of our comparison between various swarm arrangements in terms of their induced fluid disturbances (see e.g. Fig. 2 in the main text). Specifically, as pointed out in the main article, the organized schools are not efficient in stifling their flow signatures. Therefore, predators forming an organized school will have a larger detection region, higher detectability, and thus lower hunting success. It is noteworthy to mention that a detailed discussion on the importance of fluid mechanical signals produced by swimmers (i.e. flow disturbances induced by swimming organisms to the ambient fluid) in dynamics of prey-predator systems across a broad range of aquatic organisms – from swimming microorganisms to fish – is presented in the main text.

**IX. POTENTIAL APPLICATIONS IN THE REALM OF BIOLOGICAL MICRO-ROBOTS**

Two major potential applications of realizing a concealed swarm, subject of the present letter, in the context of biological micro-robots are: (i) stealth remote sensing [27] where the active tagged agents must minimally disturb the dynamics of their host medium while performing the task; and (ii) antibacterial activity of biological micro-robots. It is a well-known natural process that bacterial flocks form in search of nutrients [54]. Any flow in the background fluid can redistribute nutrients, and therefore, guide the bacterial flock. Moreover, some bacteria use their flagella as sensory organelles [52] that respond to the flow around the organism. A concealed
intrusion to bacterial colonies is thus possible if the swimmers minimally disturb the background fluid.

X. OTHER NOTES

A note on two-swimmer disturbing effects

Due to the dipolar nature of the flow induced by each swimmer, the plot of disturbances caused by two swimmers versus the relative angle between their orientations (presented in Fig. 1-b of the main text) has a symmetric shape. The resultant inversed plateau-shape of the first half of the diagram, which corresponds to the case of two co-swimming swimmers (i.e. those with \( \alpha \leq 90^\circ \) between the swimmers), can be explained as follows. Angular size of the sectors corresponding to inward and outward flows in the flow field of each swimmer (c.f. Fig. 1-b) are \( \theta_{in} \approx 70.5^\circ \) and \( \theta_{out} \approx 109.5^\circ \), respectively. When two swimmers orient normal to each other, inward flow of each swimmer is fully effective in canceling out outward flow of the other one. Thus, their disturbance-canceling effect is maximal on each other. This argument will still be valid for relative angles of \( 90^\circ \pm \delta \theta/2 \), where \( \delta \theta = \theta_{out} - \theta_{in} \). This simply results in a range of optimal relative angles, i.e. \( \alpha \in [70.5^\circ, 90^\circ] \).

A note on objective function of a traveling swarm

Through altruistic collaborations, micro-swimmers also can form a concealed swarm while traveling toward a target point or track a desired trajectory in space. In the context of motile organisms, this means that a flock of swimming cells can remain stealth: (i) while traveling under the influence of gradient in an external field (‘trajectory tracking’), say e.g. in chemotaxis [34]; or (ii) while attacking a prey swarm (‘target pointing’). We define the objective function \( Z \), to be minimized by the swarm through collaboration of the swimmers during each running phase, to account for both the overall disturbances induced by the swimmers, and their distances from the target point (or from the desired trajectory), i.e.:

\[
Z = \epsilon \times \text{MDF} + (1 - \epsilon) \times \text{RMS}, \tag{11}
\]

where RMS stands for the normalized root mean squared of swimmers’ distances from the target point (or desired trajectory), MDF quantifies the overall disturbances induced by the swim, and \( \epsilon \in [0, 1] \) is the detuning parameter determining the importance of concealing versus travel time. One may, alternatively, choose coefficients \( \xi \) and \( \zeta \) for MDF and RMS in (11), respectively. However, optimization of the system will then only depend on the ratio \( \xi/\zeta \) of such coefficients. This is due to the fact that any arrangement leading to minimal \( Z \) also provides a minimum point of \( c_0 Z \), for any arbitrary constant \( c_0 \). Thus, the complete parameter space \( (\xi, \zeta) \) can be equivalently covered using only one detuning variable, i.e. \( \epsilon \). In fact, the ratio \( \epsilon/(1 - \epsilon) \) covers the whole span of \([0, \infty)\) when \( \epsilon \in [0, 1] \).

XI. SUPPLEMENTARY MOVIES

Movie S1

An active concealed swarm of ten swimmers. Each swimmer represents the run-and-tumble dynamics with \( \tau_r = 5T_s \). Note that although the swarm is active, it keeps its arrangement within the optimal region. This results in stifling the induced fluid disturbances by up to 50%. The instantaneous positions of the swimmers are denoted by colored circles, gray lines represent trajectories over time, and the normalized MDF is computed over the dashed ring.

Movie S2

A traveling flock of micro-swimmers starting from point \( A \) with the intention to reach the target point \( B \). The traveling swarm is controlled by \( \epsilon = 1 \), and has highest possible concealing efficiency (MDF = 49.7%). But no constraint on preferred direction. Thus never reaches the target. Trajectories of the swimmers are shown by blue, green, and red solid lines. The dashed circle represents a sample surrounding ring over which one may compute the MDF.

Movie S3

A traveling flock of micro-swimmers starting from point \( A \) with the intention to reach the target point \( B \). The traveling swarm is controlled most optimally by \( \epsilon = 0.5 \). It reaches the target in the cost of only 23% increase in the travel time, having the most possible concealing efficiency (MDF = 49.7%). Trajectories of the swimmers are shown by blue, green, and red solid lines. The dashed circle represents a sample surrounding ring over which one may compute the MDF.

Movie S4

A concealed swarm of three swimmers tracking the optimal trajectory in a non-uniform environment from point \( A \) to the target point \( B \). Detection region of the swimmers is significantly stifled, such that reduction in ADR exceeds 50% during the trip. The optimal path is shown by a black dashed line, and trajectories of the swimmers
are shown by colored solid lines. The normalized swimming cost is $C(x, y) = 1$ for $x/l < 50$, and $C(x, y) = 2$ for $x/l \geq 50$. Isolines correspond to $T(x, y)$: the minimum time required to reach any point $(x, y)$, starting from $x$.

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