ENGINEERING

Confinement, chaotic transport, and trapping of active swimmers in time-periodic flows

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Microorganisms encounter complex unsteady flows, including algal blooms in marine settings, microbial infections in airways, and bioreactors for vaccine and biofuel production. Here, we study the transport of active swimmers in two-dimensional time-periodic flows using Langevin simulations and experiments with swimming bacteria. We find that long-term swimmer transport is controlled by two parameters, the pathlength of the unsteady flow and the normalized swimmer speed. The pathlength nonmonotonically controls swimmer dispersion dynamics, giving rise to three distinct dispersion regimes. Weak flows hinder swimmer transport by confining cells toward flow manifolds. As pathlength increases, chaotic transport along flow manifolds initiates, maximizing the number of unique flow cells traveled. Last, strong flows trap swimmers at the vortex core, suppressing dispersal. Experiments with *Vibrio cholerae* showed qualitative agreement with model dispersion patterns. Our results reveal that nontrivial chaotic transport can arise in simple unsteady flows and suggest a potentially optimal dispersal strategy for microswimmers in nature.

INTRODUCTION

F o a ae b oo s a e s a ve s o s e ce s e e o- c ve ac , sw • c oo • a s s of e co e s e a y f ows a s a a w e a • e of e • sca es, La • e ocea c f ows s c as e e a e- ve e o a ove • c c a o s, co o y ow as • oba co veyo be s, ve e • oba -sca e a s o of ca bo -f x • a e c oo • a s s a e f ow (*1–3*), A s a e sca es, oca f ow • a e s exe fo ces a o q es o c oo • a s s, w c ca a e sw e o y a ove a a s o (*4*) a ea o • • ys ca e o e a o fo fo ass ve a ce s s c as eo ax s (*5, 6*), • y o ax s (*7–9*), a • a e - ce c e o ax s (*10, 11*),

c oo • a s s, , ay a a e o ys a e es, ac- ve y o fy exe a f ows, a a e a va a e of e co • be wee o y a f ow o fo a e a e o ce (*12*), U e q - esce f ow co o s, fo exa e, c osw e s ca a e co ec ve f c a • o o s e f e va y o y- a c e ac o s (*13, 14*), I s e a y e- e o c) f ows, bac- e a sw e s ca a e a e a • e-sca e sca a a s o w e e a c • x • a s a sca es (*15*), T ese se f- ce f ows a f ow o f ca o s ca e a o • • o e es f s co a • ac ve sw e s, c • e a ce B ow a ff - s v y (*16–18*), ac ve f a s o a x • (*19–21*), a , os- s by, wo ex ac o (*22, 23*),

Eve s e s e a f ows ca o fo y a e e ove e of c osw e s (*24–26*), Ex e e ss ow a o e bac e a ca f ac oss s e a e s o of e a e of s e a (*6*), sca e ow-s e a • o s, a beco e a e • -s e a • o s (*24*), o e y o a o a e fo o acc a e o be e e- e f o • o s of ffe e s e a a es (*25*), a ey fo ce as- se b a es ca e " aye s" (*26*), T e be av o of c osw e s co ex f ows s ows eq a y c y a cs b s c ess - e s oo , I b e f ows, fo exa e, • y o ac c sw e s ca c s e s a -sca e a c es (*8, 27*) a • a e • o s of os- ve ve oc y • a e s (*28*), e ca s a o s so o c - b e ce s ow a e o • a e sw e s efe e a y a • w f ow ve oc y (*29*), w e c s e • a ac ess a e • e a y e ce (*30*), I ca o c f ows, s a o s s ow a o - e sw - e s ca be a e o ex e e by e c s a s (*31*), e, Ko- • o ov-A o - ose o (*32*), e e • o e s a e s a sw • s ees, T e a • of a ces e c s a sca e a o a e c o sw e a s o (*33, 34*), I s e a y co vec- o o s, s e c e a c o a y e a o co exc s e • a e s of ac ve a ces (*35*), w e a s e o -Ga ss a ff s o s fo a s o obse va o es (*36*), Rece y, bac e a sw e s a e fo o ex b a • a o • y a cs o o s e a w e e e o a s e a • s co o e by e • (*37, 38*), S y of s e a y f ows o o s e a s owe a bac e a a • a acc a e a o • f ow • o s a ex e e ce a e s ec • (*39*), Des e ece • ess, ow eve , e s e so y- a cs a s a s o of ac ve sw e s s e a y co ex f ows e a oo y e s oo ,

I s co b o , we co c bo La • ev s a o s a bac e a s e s o ex e e s o ves • a e e o • - e a s- o a a • a o y a cs of s oo ac ve sw e s e- e o c f ows co ose of a a ay of vo ces, A o • e s- ace e e e of ow co e e y eve ses se f a y ve cyc e, we f a e a s o of co sw e s s s bs a a y a e e by e e- e o c f ow, T e f ow e e o c y, w e co e o e f ow o oo • y a sw e o y, • ves se o a se es of sw e s e s a • e s w • y o o o o c a s o ef- f c e cy, o fo s e a y f ow co e a s, As • e f ow co o a a e e, w c we e e a e • , ca es e o- o o o c s e s o a • ves se o c ao c sw e y a cs fo sw e s w f xe s ee , A o e a e f ow s e • s, sw e a s o s e e by as c as 10-fo co a e of ee sw • as sw e s a e aw owa e f ow's va- a s c es o a fo s) a fo e bo a es of e

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vo ces. As a e c eases, we obse ve a e a ce e f ow- ce sw e as o ao f ow a fo s as ey ff sve a e. T e be of q e f ow ce s ave e e by e sw e s e so s ax e s e, w e e sw e s a access o e a es be of o e a fo- a s o s e f ow o a . Las , fo ve y s o f ows, cyc ese e ew e vo ex a a as bse of sw e s a s ess s e sa ; vo ex a s so e fo s owe sw e s. O es s evea a e f ow- ce s e so s y o- o o o c w f ows e a s ows s c a a o a s e so ec a s s. A a o ao f ow a fo s a a vo ces obse ve e e ay a e sw e e co e a es, e a e s, a acc a o of s a a oec es. T s co ex co be wee sw e be av o a f ows c- es a y a cs co ea o o a s e sa s a e s a s c bac e a fes y e as o a e s a aa s- a x e v o e s.

Ex e e s a e e fo e a e ec o a e ca y ve f aye (*15*, *40*, *41*). A e- e o cc e ave s o y o a aco c f aye as ace above a a ay of e- a e a e sw a e a e a o a y (F 1A). T e es Lo e fo ces ve a e- e o c ce a f ow, a e y, **u** *t*) = **u** *t* + *T*), a ss a a y o e e e o e a a e e of e fo c a es (F 1B a f S1); es e of eac vo ex o ce) co es o s o es ac be wee a es ~6.5). We q a fy e ex e e a f ow f e s a ce ac- ve oc e y see F 1B a a e a sa e o s). T e f ow vo c y e a sa e e cf x o s o vo ex ce e) of e f ow; f s ec s ax e ao e s ab e a s ab e) a- fo s a se a a e e bo vo ces a co ec s e y e bo- cf x e o s (*40*, *41*); o a f s a ox a o , ese a fo s a e va a f ows c es a ex e e ce eves of e fo a o o s a). Bac e a s e so ex e e s a e co ce by a as a a o off o esce y abe e bac e as s e so a ece e of a vo ex ce . T es s e so s e a owe o s- ese e f ow a c a ace e s a ea ays s see a e- a sa e o s). A ex e e s a e e fo e a Rey o s be s, *Re* = *UI*/ν, a f o 0.1 o 10, w e e sf e s y, *U* s ea f ow ve oc y, *l* = *L*/2 s e q a e -ce e of e vo ex a ay, a v s e a c v scos y. T e- e o c f ow w a ys ace fo c s ow o o ce c ao c x of ass ve sca a s eve a a ow Rey o s be w e e- e a f ow s ab es a e abse (*40*, *41*). F ow c a ace s cs ca be a se by e e e y va y e ose c e a fe- q e cy. Las , we ef e *p* = /4π²*f*, w c we e e f ow a- e . T e a e e *p* s a o e so a a a e e a c a ace es e e- e o c f ow a as bee s ow o o- a e x ass ve sys e s (*40*).

T e o e f ow sys e es a o co sss of a wo- e so a 2D) Tay o -G ee vo ex a ay a s e o c s ace a e f S1). S a o e ex e e a f ow, eac vo ex occ es a q a e -ce w a e of *l* = 6.5 a o a es o os e ec o o s e a e e bo s ac ec- e boa a e . T es ea f c o of e f ow osc a ess so- a y ew f eq e cy *f*, e o *T*, a a e *Ul*/π. S oc as cs a o s of 10⁴ ac ve sw e s a e co ce fo eac f ow co o w e e e a s a o a ff so s o e e as a o W e e ocesses. T e ac ve sw e s a e o e e as o e ac , s oo -sw ax sy e ce so s a ove w ve oc y u_s a eo e e f ow a e s acco o effe y's y a cs (*42*) w o o a o a a ff s v y ess s a e o e w se. We o e a o a o a eo e a o s of e wea fo fas -sw bac e a a s o es), sw es a ac - a - be e av o o ave a e c e o ax s s a a - ways (*43*), a sy e c a s- a ce sw es (*44*). Va a o s sw s ee a e o es o a e as u_sT/l o ef ec e sw e o y a f ow e o . T e e sw e ve oc y s e s os o of e e y f ow a e sc sw ve oc y see a e a sa e o s).

RESULTS

Emergence of distinct swimmer transport patterns is universally controlled by the flow pathlength

We ba w s e so a e s of e G a - a ve bac e *Vibrio cholerae* e f ow ce a a s see F 1C a a e as a e o s) a ffe e f ow f eq e cy a ea vo c y, *V. cholerae*, e ca sa ve a e fo e y co a o s sease c o e a, s a aq a c- we a e a e co es s ea y f ows a e. T e a so o a s e so of *V. cholerae* s ea y f ows ay affec sease as sso a a e v o e s. T e sw s ee of s fa e a e sw e a es fo 40 o 80 /s (*45*, *46*). U ex ec e y, w e e f ow s ace e a ways eve ses se f as e e o fo a f ow co o s, e ove a a so a e s of ac ve sw es e a e y ffe- e . We se e f ow a e *p* o esc be e f ow co o s fo easo s a w be c ea a e sec o s. A *p* = 7, e s e so a e s of e f o esce y abe e bac e a F 1C) s ows o a a o ao f ow a fo s. A ve y a e s, owe e , s o a of e bac e a e vo ex co es occ s F 1D).

To eve a e ec a s e y e s e so a e sob- se ve *V. cholerae*, we co c La ev s a o s vo ex a ay s a o a se e ex e e s f S1). I e o e e- e o c f ow, vo c y s ax a a e cf x e o s, w e e as f ow a fo s vo ex bo a es) co ec y e- bo cf x e o s F 1E). We ba by ves a e ove a a so eff c cy of ac ve sw e s. T e oa s o cove e ey a a e es co o o -e sw e s e so . Sw e a so sca ace e by e e se be-ave a e o -e ea sq a e s ace e s SDs) o a e by e s e of e vo ex *l*. T e q a y SD/*l*² s co e fo *t* = 2000 s, as ff ce y o e fo e SD o eac a s a sca y s a o a y so e f S2). We f s s ow SD/*l*² as a f c o of f ow vo c y 0.1 o 100 s⁻¹) a osc a o f eq e cy *f* 0.1 o 10 H , as e se of F 1F. Res s ca e a e va a o SD w ss so y sca e e fo ff e e f ow f eq e ces *f* a a e co s a so occ a ffe e va es. Howeve , w e o e a as e a o of ese wo a a e es, a e y, e a- e *p* = /4π²*f*, e a a co a se o a s e as e c ve F 1F). T e a e e eas es e ax a a s ace- e ex e e ce by a ass ve f a ce a f ow cyc e a a ses fo e o e so a ove eq a o Eqs. 4a o 4). S a y, esca e e va a o s e SD sca ex o e *n* as a f c o of F 1G, se) a so co a se w e o e a a s a e p F 1G). He ce, e a a s ace e cyc e co os e ove a s e a e a e of sw e a so .

Flow pathlength nonmonotonically controls four swimmer dispersion regimes

As e co o a a ee p c eases, we f s c a es of ac ve sw e a so w ◂ y o o o c c a◂ es s e so eff c e cy, Fo e owes fow s e◂ s p < 0.5), e sw e s be ave esse a y as "f ee sw e s." T es obosco c SD/l² s e e e of p a e 0, F◂ , 1F), a e SD sca ◂ ex o e s co s a a n = 2 a e 0, F◂ , 1G). He ce, fo p < 0.5, e wea osc a o y fow s ff c e o a e e ba s c f ee-sw ◂ a e of c oo◂ a s s. As p c eases 0.5 ≲ p < 2), owe e , we obse ve a as c e c o sw e a s-o SD by a ox a e y o e o e of a e a e I, F◂ , 1F). Co c e y, e s obosco c SD sca ◂ ex o e n ec eases o a ox a e y 1.2, ca ◂ a a s o fo ba s c o ea y ff s ve a s o be av o a e I, F◂ , 1G). We c a-ac e e s a s o a e as" a fo co f e e "a e I) fo ea so s esc be be ow. As p f e c eases 2 < p ≲ 5), e e SD eve ses a c eases s a y by ea y a o e of a e a e II, F◂ , 1F). U ex ec e y, e SD sca ◂ ex o e n e a s c ose o 1.0 a e II, F◂ , 1G), ca ◂ a q e ec a s off ow-e abe a so a s e y ff s ve a e. We c a ac e e s a so a e as" a fo af-f c ◂ " a e II). Las , a ve y ◂ p (p > 5) o ve y a ea◂ a s ace e e cyc e, e SD ec eases a a , w e sw e a so e a s ff s ve a e III, F◂ , 1, F a G). We c a-ac e e s a so a e as "vo ex a ◂ ." T ee e ce of ese s c a so a es occ s fo a a◂ e of sw e as ec a os f◂ , S3) a o a o a ff s v es f◂ , S4). T ese es s ca e a c eas◂ e fow s e◂ va a e◂ p e ab es e se s ve co o of fow- ce sw e s e so a o o o o c fas o .

Distinct dispersion patterns underlie different swimmer transport regimes

ex , we ex o e sw e s e so y a cs a a e s - e y◂ e o o o o c va a o s o◂ -e a so . T es a a s b o a co es o◂ sw e o e a os ob a e fo e ca s a o s a es ow F◂ , 2 A o L)

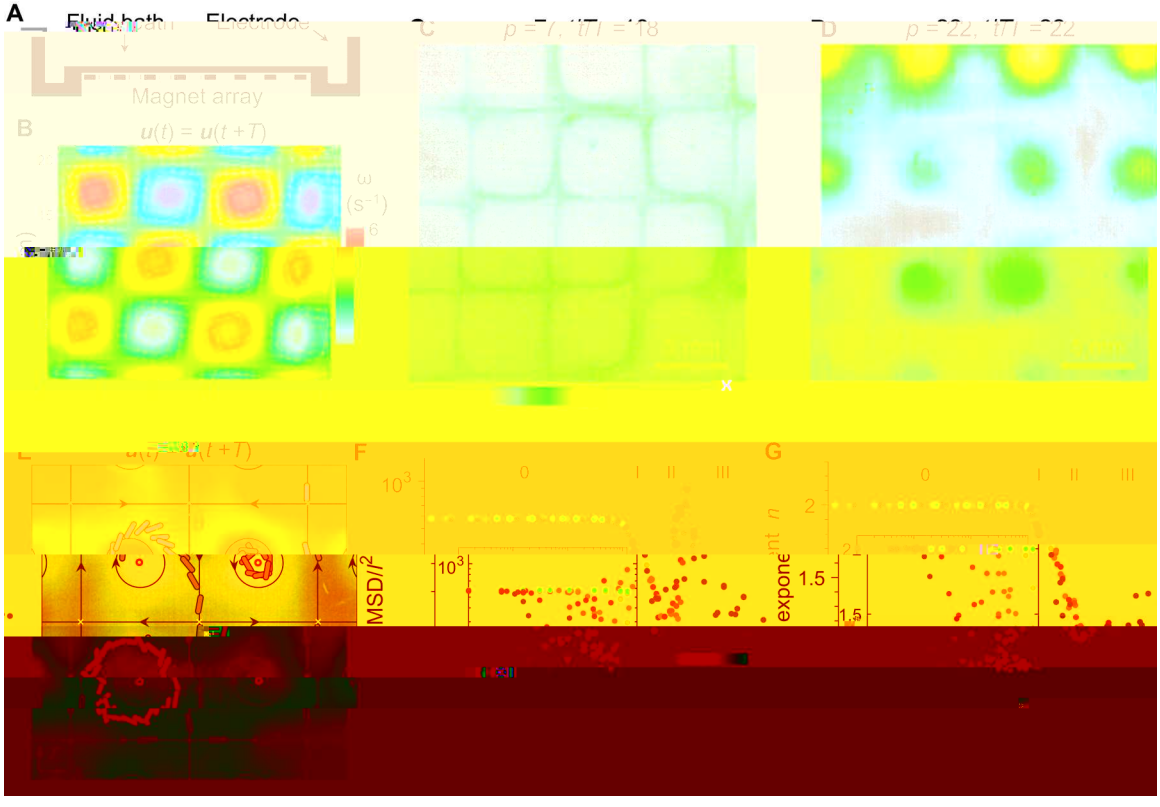

Fig. 1. Dispersion patterns of active bacteria and long-term swimmer transport from the Langevin model reveal distinct dispersion regimes mediated by the time-periodic flow. (**A**) Schematic of the periodic flow cell apparatus used in the experiments. (**B**) Flow vorticity and velocity vectors in the experimental flow cell, obtained by particle tracking velocimetry. (**C** and **D**) Cell distribution patterns in bacteria dispersion experiments using *V. cholerae* labeled with green fluorescent protein (GFP) at (C) pathlength p = 7 and time t/T = 18 in the manifold trafficking regime and (D) pathlength p = 20 and time t/T = 2 in the vortex trapping regime. Colors indicate GFP intensity. a.u., arbitrary units. (**E**) Schematic of active swimmer transport in the time-periodic flow. Black arrows indicate directions of vortices and flow manifolds, which connect hyperbolic fixed points (white crosses). Fluorescent bacterial swimmers (green) are allowed to disperse under time-periodic flow. As flow pathlength increases, a subset of swimmers spiral outward the initial vortex and participate in chaotic transport along flow manifolds (blue, regime II). At high pathlength, increasing numbers of swimmers are trapped (red, regime III) near elliptic points (red circles). Swimmer orientation is indicated by the angle θ. (**F**) Ensemble-averaged stroboscopic MSDs of active swimmers as a function of flow pathlength p for various flow frequencies f and flow peak vorticities at time t = 2000 s, normalized by the flow quarter-cell length l^2 for u_s = 80 m/s. Inset: Identical MSD plotted against . (**G**) The corresponding MSD scaling exponent n. Inset: Identical exponent n plotted against . The designations 0, I, II, and III in (F) and (G) indicate transport regimes.

a va o s es e s e s o ocess fo eac of e a s-
o es esc be above, Befo e e o se of e a fo co -
f e e e e I, $p = 0.5$), w e e sw e SD b s o
ev a e f o a of e f ee-sw case, we f a sw e s
o a a e a a y o wa f o e see q a e -ce F , 2, A
o C, a ov e S1); sw e s s ow o ff s ve a o o o ,
eav e a q a e -ce evo

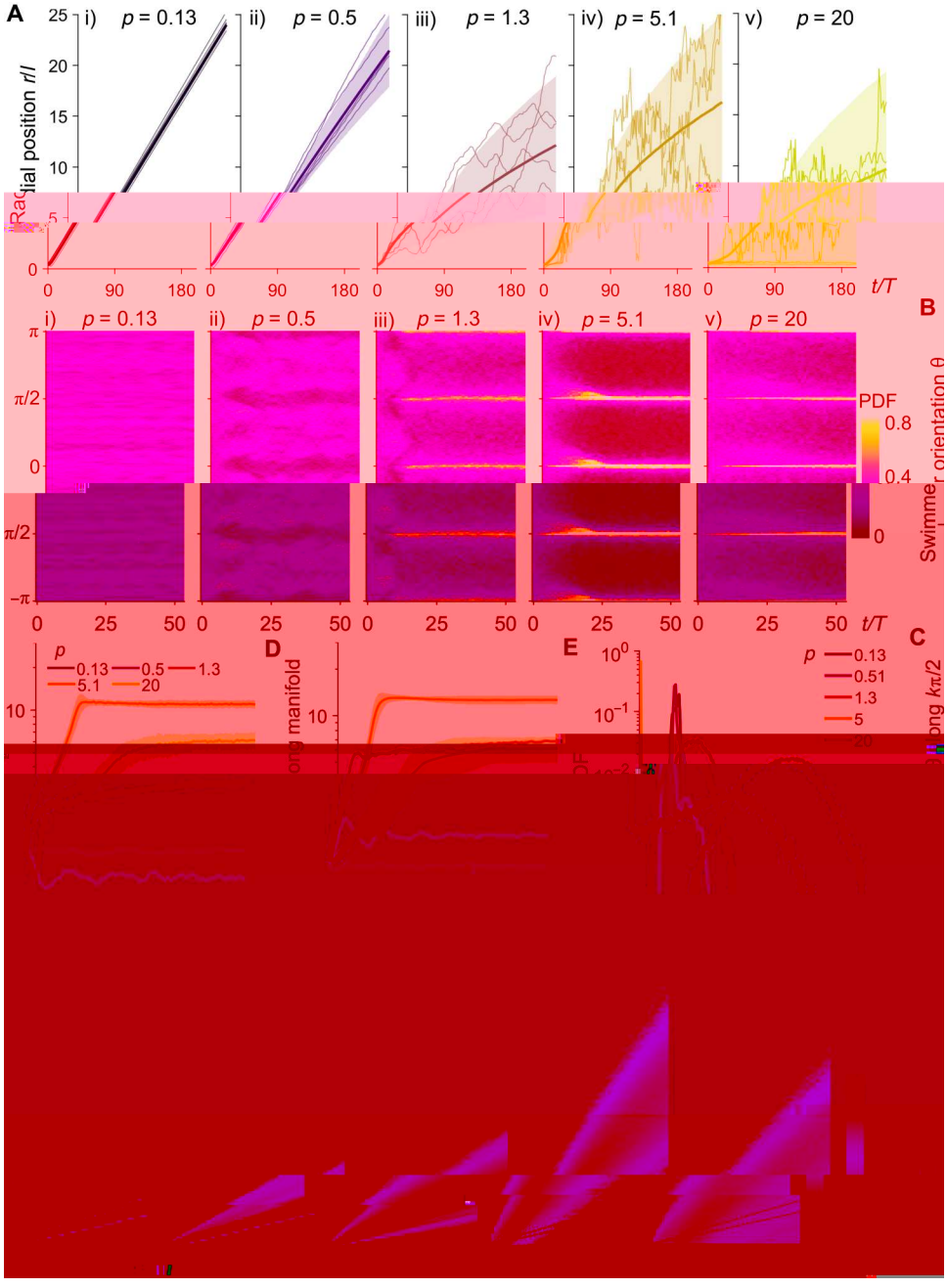

Fig. 3. Swimmer radial spreading, swimming orientation bias, aggregation toward flow manifolds, and unique flow cells traveled are nonmonotonically controlled by the flow pathlength

f ow a fo s , F 3B) I e a fo aff c e a e $p = 5.1$), e o a o a a s ace e c eases co a e o a a $p = 1.3$ v, F 3A) acco a ce w e c ease SD va es F 1B) T e v a sw e a ec o es osc a e w a e a es a s o e e sca e, a sw e a e - e a o a fo s s ax e v, F 3B) Las , e vo ex a a e $p = 20$), e o a o ea s ace e s e ce o ce a a v, F 3A) I v a sw e a ec o es co e o ex b a e c ao c ev a o s fo e o a o ea , w e a s bse of sw e s beco e a e e a q a e -ce T e a e a o fow a fo s s wea e e co - a e o a a $p = 5.1$ v, F 3B)

To q a fy e e evo o of sw e a e w fow a fo s, we co e e b as of obab y e s y f c o PDF) of θ a o $k\pi/2$ as a f c o of p see F 3C a a e as a e o s) T e b as s ef e as e PDF o a e by a of a a o fo s b o W e o o e a o a b as occ s e f ee-sw a e $p = 0.13$), we f wea sw e e- e o f o a fo s a e o se of f ow- ce a s o ; o e a e PDF b as fa s be ow 1 fo $p = 0.5$ As e f ow s e f e c eases o $p = 5.1$, sw e s beco e c eas y a e w f ow a fo s, eac a o e of a e - c ease e obab y b as befo e a e y ec eas a e ax $p = 20$ Sw e a a o y a cs s ow s a e s F 3D) Sw a ces beco e c eas y a a e owa f ow a fo s as p c eases, eac a o e of a - e c ease obab y a $p = 5.1$ befo e ec eas a $p = 20$ e o a a e vo ex co e Ove a , we f a e e e - s c- o-c ao c a s o v a ce a ec o es e - es e f ow- ce e a ce e s a s o a e o a o eve T e co ec ve co ve e ce owa a a e w fow a fo s e ab es bseq e c ao c aff c by e e- e o - c f ow

An optimal dispersion regime occurs at intermediate pathlengths

F ow- ce a s o ca f e ce e ab y of c oo a s s o ex o e e f ow o a a fo a e fo e s T e ab y o cove a e f ow a o s o vo es) s co c ve o e access, w e eas a es s a e e e o He e, we q a fy s be av o by o o e s a s cs of q e q a e -ce s ave e by e sw e s s e s o as a f c- o of f ow a e p F 3E) I e f ee-sw a e $p = 0.13$, e PDF s b o s ows a a ow ea a o a s a se of q a e -ce s T ese q a e -ce s oca e a o e sw e a ec o y, as s ow by e ea c ease e be of q e q a e -ce s ave e w e , F 3F) As f ow- ce a s o co e ces $0.51 < p < 5$), e s b o of q e q a e -ce s ave e w e s a s f s o e va es F 3E) T s es ca es a sw e s a e c eas y ab e o ex o e a a e se of vo ex ce s as p c eases I a o , e e eve o e of e s a s cs c eas y fo ows a sq a e- oo e a o s o v, F 3F), co s s e w e ff s ve a e of e f ow- ce a s o T s e a ce e effec s ax e a $p = 5.1$ e a fo aff c a e F 3, E a F, v)

sw e s $u_sT/l = 0.18$ o 0.25; F 4B) ss o y e e by e fow e ave of ee sw T ese es ss ow a sow-sw - coo a s ay ex o e- e o c fows o ac eve eff ce s e so eve w o a e e e y ex e es o o y.

Swimming speed affects dispersion rate but not the patterns in the manifold confinement regime

Fo s oo sw e s q esce fow e, f ee sw), a c ease sw s ee ea y e ces e ave e- q e fo a ve s ace e He e, we ex o e w e e s c ea sca os e fow- ce a so es To s e , we o o es a s cs of e q eq a e -ce s ave e a va o s es a sw s ee s I e a fo co f e e e $p = 1.3$) w e e e co a so s ax a, we f a, fo a f xe e e va e, $t/T = 11$), fas e sw e s ave se a a e be of fow ce s F 4C, se) We ca f e co a se a e c ves o a e ca s b o v a a s ee -co e sa e e, u_st/l F 4C), s es a e a fo co f e e e, e e ee e o eac a ve eve of se so s y e ces ea y fo fas sw e s T e co a se o a ve sa c ve s a so obse ve fo e sw e a e a a e a o owa fow a fo s f S5) F e o e, by ea y co e sa- ew sw s ee , s c a u_st/l s co s a , we f a sw e s e so a e ss e ose w o e a o e f S6, A o H) T e s e so a e s fo $u_sT/l = 0.06$ e f s ow f S6, A o D) a e eq va e o a a e ca sca e es e seco ow f S6, E o H) fo ffe e e sw s ee s We ca co c e a w e sw e s ee co os e a e of se- so , s ee a a e y oes o a e e s e so a e o e y- a cs e a fo co f e e e e

Swimmers engage in chaotic escape spirals with exponential scaling in time before trafficking along manifolds

T es e ea sca be wee sw s ee a e a e of s e so b ea s ow fo s o e fows $p \geq 5$) We f s o o e e eve o e of e s b o of sw e o e- so a sa ce o fow a fo s, $d = \cos 2\pi x/L) \cos 2\pi y/L)$, w e e $d = 1$ a e vo ex co e a $d = 0$ a e bo a es be wee q a e -ce s see a e as a e os) I e a fo aff c e ew e e sw e a so s ax a ye a ce $p = 5.1$; F 5A), we f a fo sw s ee s u_sT/l) a fo 0.015 o 0.18, os sw es co ve e owa fow a fo s as d ec eases o e o; a s, ac ve sw es a ea ace o e sab e fow a fo s, T e a e of co ve e ce s ex o e a e fo a sw s ee s o v, F 5A) T e oca ea e PDF eac es e o a ac ca e t_c , F 5A) af e w c e s b o eac es as a o a y s a e w e e os sw es a e o fow a fo s, T e ex o e a sca es as ow ow e a e of co ve e ce as sw es a oac fow a fo s, T e c a ac e s c e τ of e ex o e a co ve e ce owa fow a fo s, ex t/τ), ca be obse ve e PDF b as F 5B) As sw s ee c eases, ec a ac e s c esca e τ a e c ca e t_c c ease ea y w l/u_s F 5B, se) S ce s ow sw es $u_sT/l = 0.015$) e a es a o es- a o , e SD sca ex o e s a ox a e y 2 ba s c be- av o) e aff c e We o e a a a ea va e PDF b as s eac e a s e e e of sw s ee , w e e a ox a e y 10% of e sw es e a o s e of fow a fo s f S7)

We ex o e e o of e ex o e a a a o occ s owa fow a fo s, I e va case of f ee sw q esce fow, sw e a va a fow a fo s s ea e fo s oo sw es a y e vo ex e o f S8) a ec ca e, t_c a, f a va o fow), s eq a o l/u_s o e e o eac $d = 0$ v as a a e co es t_c a, f se , F 5B) He ce, sw es e a fo aff c e s s ay a o a fow- ce y a cs ea o e ex o e a sow- ow To e os a e s be av o , we o es obosco c sw e a e co es co o e by e s e w be w a o e e c o of e vo ex see a e as a e os) fo bo e f ee-sw $p = 0.13$; F 5C) a e a fo aff c $p = 5.1$; F 5D) es I e $p = 0.13$ case, sw e a e co es a es a w a w a o e vo ex ce e befo e eac fow a fo s F 5C) I e $p = 5.1$ case, owe e , as bse of sw e a e co ess a e es a o e vo ex ce e as ey a oac fow a fo s F 5D) T e as c c ease w , w c s abse ea e e c o , ea s o e ex o e a sow ow co ve e ce

T e co os a ve se o es a esca e owa e fow a fo s a e ow ex o e To se , we co e e e- se be-ave a e a e co y w <w> befo e eac fow a- fo s fo sw es w ffe e a s a ces d_0 a a o e a o a es ea ve o oca s ea e a e e $\phi_0 = \theta - \theta_s$ a $t = 0$ F 5E) T es co ve o of ϕ ss c a e o ca es a e w e oca s ea e, a ave ca es a e owa e fow a fo s, a os ve ca es a e owa ee c o s see a e as a e os) T s a a- e e s ace a ows s o ec y o o sw es a a s b- o e a ve of fow a fo s a e sw e 's e ec y o a oac o avo s c fows s c es We f a sw es a a e a y ea fow a fo s $d_0 \lesssim 0.2$ b sw owa e e c o $\phi_0 < 0$) o a a e o s ea e $\phi_0 \approx 0$) ave w , By co as , sw es a a e a y ea e vo ex co e $d_0 \gtrsim 0.5$) o a sw o wa $\phi_0 > 0$) ave ow w , Ty ca a e co es e x, y) a e fo sw es a a y sw away fo e e c o , a a e o es ea e, a owa e e c o f S9) a e co sse w ese sw es a a co o s, U ex ec e y, sw s ee va- a o s o o a e a e co y w esca e, Fas sw- es o o ex e e ce ess w ea ve o s ow sw es, a e o a o s b o of a e co y w w befo e eac fow a fo s s e e e of sw s ee F 5F) Ra e, e c ease fow s e e es ea- c ease <w> a ca es e ee of w a w occ e a fo aff c e F 5F, se)

Faster swimming facilitates escape from chaotic limit cycles in the vortex trapping regime

To obe e ec a s e y vo ex a fo s o fows, we o o es w e ce fa e e a a e e s ace of (d, ϕ) o s a ce o fow a fo s a ea a ev a o fo oca s ea es T es w e s b o a o es fo $p = 20$ eve as e e e e ece of ee a sa s eac ce e e a o $\phi = 0$ b s a ffe e d va es F 5G) S obosco c sw e a e co y eac o s ays ac ao c cyc e a we s a fxe d va es a ea $\phi \approx 0$ a w e

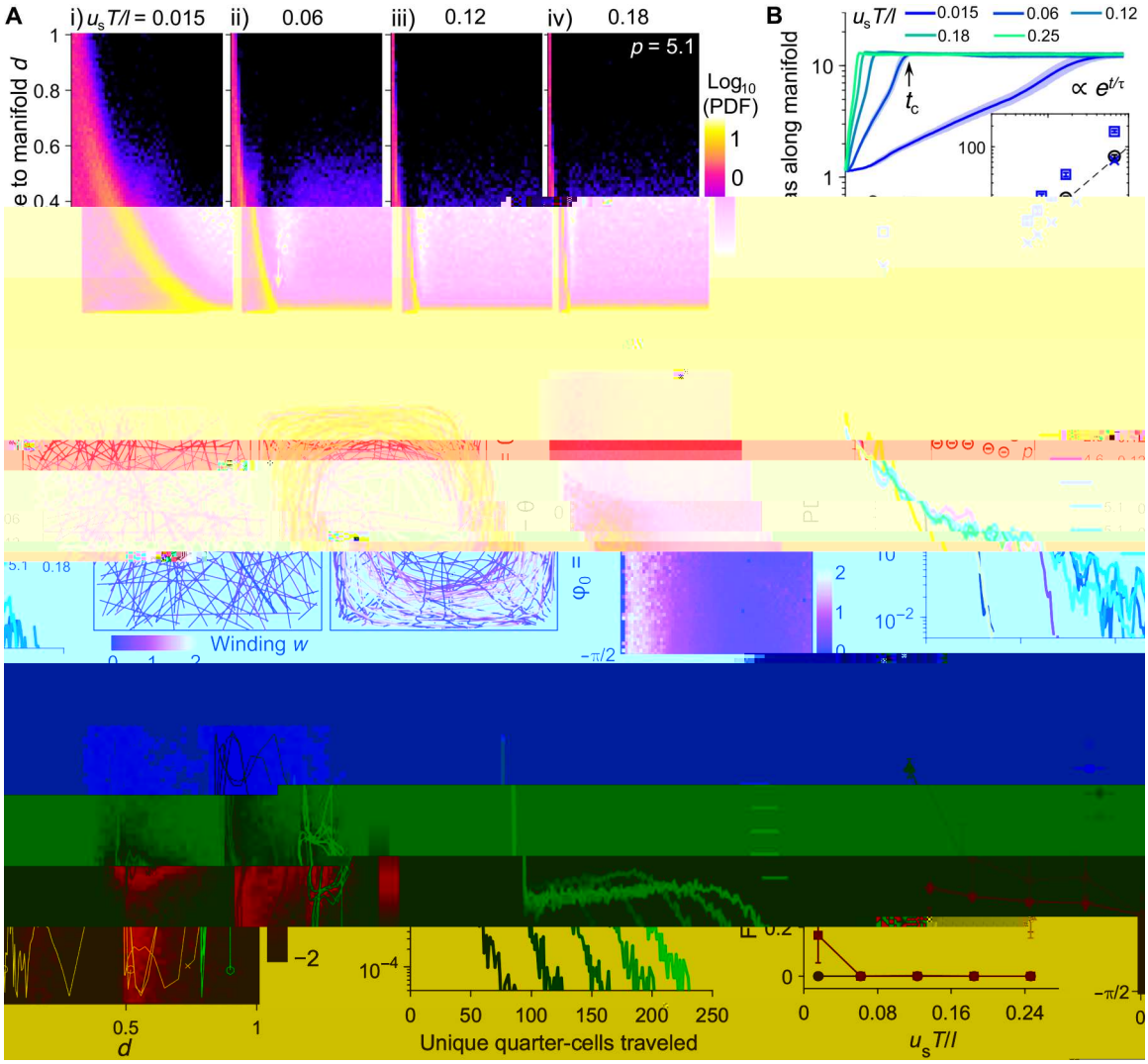

Fig. 5. Effect of swimming speed on transport dynamics in the manifold trafficking and vortex trapping regimes. (**A**) PDF distribution of swimmer distance to flow manifolds d, in the manifold trafficking regime p = 5.1, for (i) u_sT/l = 0.015, (ii) u_sT/l = 0.06, (iii) u_sT/l = 0.12, and (iv) u_sT/l = 0.18. White arrow indicates the critical time t_c to reach flow manifolds. (**B**) PDF bias of swimmer aggregation toward flow manifolds for various values of u_sT/l. Black arrow indicates the critical time t_c. Inset: Normalized τ/T of the exponential growth, the critical time t_c/T, and the critical time of arrival without flow t_c/T a.n.f., versus inverse scaled swimming speed l/u_sT. Dashed line: The abscissa is equal to the ordinate. (**C** and **D**) Swimmer trajectories before reaching flow manifolds u_sT/l = 0.12 for (C) p = 0.13 and (D) p = 5.1. Colors indicate trajectory winding w. (**E**) Population-averaged winding <w> before reaching flow manifolds, in the space of swimmer initial distances to flow manifolds, d_0, and orientations relative

s ea es) fo ex e e es, T ese sw e s s ay w e c ao c s a w o e e a e a s o ba e s a c ca d va es) o e bo e o s, Howeve , occas o a y, ese sw e s e o a e exc s o s d a ev a o s f o a e - e w e f ow, T e c ao c s obosco c sw e a ec o es e x, y) s ace a e s ow f S10, We o e a sw e s a a e a y ea f ow a fo s a a e sw away f o e e c o o o e a e, T ey o e e ess a c a e e f ow-e ab e aff c a ex o e a a e be of f ow ce s F 5H),

Las , fas e sw e s ave s f ca a s o a va a es ove s ow sw e s e vo ex a e F s, a c ease sw s ee a p = 20 es s a a e be of f ow ce s ave e F 5H) w e e o a o - eve s e s o <n_q> sca es w e sq a e oo of e sw s ee F 5H, se), Seco , fas e sw e s a e a so be e a esca vo ex a a s owe sw e s F 5I), P ase a a s fo e f ow- ce sw e a s o a a as f c o s of bo sw s ee a f ow a e a es a e f S11, He ce, e s o es e- e o c f ow, sw e s a e oc e

e a◂ e a se a a o fo fow a fo sa o b c ao c cyc es. Fas e sw e s, owe e , ca esca e fow- ce a ◂ a co e o ex o e e fow o a .

DISCUSSION

c oo◂ a s sof e e co e sea y fows bo a e a s a a ca a o s. T e co ◂ be wee o ya fows c ca o e s e so , e o co , a ove a s v va of - c osw e s. I ocea s, ve s, a b o eac o s, sea y fows w s o◂ oca ve oc y◂ a e s a e ese ac oss a a e a◂ e of esca es a e◂ sca es. W e sw e a s o as bee exe s ve ys e sea y fows of vo ex a co vec- o o a ays, e e, we ex o e ec ao ca o o o o c a s o of c osw e s v a a o e e- e o c x◂ fow s◂ bo La◂ ev s a o s a bac e a s e s o ex- e e s. Two o e s o a a a e e s co o e ac ve sw e a s o e sea y fow, a ey, e a e◂ , w c se s e a e of e bac◂ o fow, a o e s o a sw ◂ s ee e a ve o e fow. Fo fxe -s ee sw e s w a B ow a effec s, c eas◂ e a e◂ a a- e- eve a e ee s c fow-e abe a s o e s w o aby ffe e s e so y a cs. A o e a e fows e◂ ea ve o sw ◂ , e sw e s a e c eas◂ y a ace owa e bo a es of e fow ce s, ea ◂ o a a e e c- o SD a s o◂ wea e ◂ of ba s c sw ◂ . As a - e◂ f e c eases, a s c fow- ce a s o e e◂ es a a y s e ses sw e s ac ao c a e y ff s ve fas o a o◂ a s fo e by vo ex bo a es. To a c a e e c ao c affc ◂ a o◂ vo ex bo a es, owe e , a s bse of sw e s ee o esca e e vo ex v a ex o e a s as a a e ve sa fo sw e s, fas o s ow. Fac a e by e c ao c a s o a o◂ fow a fo s, e be of q e fow ce s ave se by sw e s ◂ s e so s ax e , ea ◂ o e a◂ es ex os e o o e a fo a ◂ ◂ o s e fow o a . S c e a ce e s o o ex e e f e y, owe e , as f e c eases fow s e◂ es e fa e of sw e s o esca e e vo ex. I sea , sw e s a e oc e c ao c cyc es w e vo ex. T e o a s e so e e◂ es e o e co e o be wee e c ao c a s o a e vo ex bo a es a e s o◂ eo e a o a a ◂ a e vo ex co e. Fas e sw e s s a ess ve y ove co e fow- ce a ◂ a a a eff c e s e so s fow a e. O es s s ow a, a o◂ e sw e s ace e e o fow a o e s f y eve se a y◂ ve cyc e, e- e o c fows ca s f a e a y a e e a s o o co e a s- e so of e sw e v a e o ea a c ao c co ◂ be wee fow e sca e, ve oc y, a sw e o y.

T e wo o e s o a co o a a e e s ay be◂ e e a beyo e s ec f cs of e fow sys e e e o e sco e ac ve a e a s o s ea y fows fo s oo sw e s w a a◂ e of s a es, s ee s, a o a o a ff s v es. O es s w be es ec a y e eva fo sy e c ac ve co o s s c as a s- e a c es ac ◂ e e o a o a ff s v y, fas sw e s w e e o a o a eo e a o s wea co a e o ba- s c sw ◂ , a bac e a s ec es a o o a be, s c ass oo -sw ◂ *Bacillus subtilis* a c e o axs a s s c as Δ*cheY* a s fo *Escherichia coli* a Δ*cheY3* a s *V. cholerae* (*43*).

We o e seve a a o s fo ec e s y. We o o co- s e sw e s w f eq e eo e a o s. Seco , o o e ea s sw e s as o a ces a o o oca y o fy e ose fow. T e efo e, we ca o acc a e y ca e e a s o be av o of ex e e y e se c ob a s s e s o s, w e e se c - e ac o s, f e s e effec , a fee bac o e fow a e o- o ce . I ◂ o s of s a ve oc y◂ a e , s c as y e bo c o s a fow a fo s, as a va a o sw e os o e o e◂ co ea o s bs a a va a o s sw e a- ec o y. Las , ex e e a y oba ◂ ◂ - e so o o◂ - e SD a SD sca ◂ ex o e s fo c o e e -s e bac e a ove ce e e -s e fow ce s, es ec a y e s o◂ ose fow◂ a e s, e ese s as bs a a ca a e◂ e, w c we see o a ess f e wo s.

We y o es e a co f e e a fow a fo sa o e a e fows a a ◂ e vo ex co es as o◂ fows fo ex e e es ay ea o c ease sw e e co e a es, e e◂ e ◂ a e s e sa c e oa ac a s, a oca acc a- o of q o -se s◂ s a ◂ o ec es a a se ◂ s. A- e a o s ese bo ◂ ca s e e e by e e- e o c fow ay ave s◂ f ca ca o s ca ◂ as o s co ba fes y es a s v va s a ◂ e s. Fow- ce s e so s os ev e fo s ow sw e s co a e of ee sw ◂ q esce fow. He ce, by ca ef se ec o a co o off ows c- ea a e◂ , o eca ev se a o a as o s a◂ y o ax e co be e s e so e- e o c fow sys e s s c as x◂ bo eac o s, es ec a y fo sw e s w e o y. F e o e, by ex o ◂ e vo ex a ◂ ◂ ea ◂ a- e◂ , w e e fas e sw e s esca e e a fow ce c q ce a s ow sw e s, o e co es◂ abe ev ces o efe e a y so sw e s by s ee . O es so e o ea co ◂ be wee fows c e, e e o c y, a sw e a s o co a so ave ca o s fo e fes y e a s o s a fa es of s a a e o◂ a s s.

MATERIALS AND METHODS

Langevin simulation

A e- e o c 2D Tay o -G ee vo ex y e of fow s se e La◂ ev s a o . I e x,y) a e, es ea f c o ψ of e fow s

$$\psi = \frac{UL}{2\pi}\cos(2\pi ft)\cos(2\pi x/L)\cos(2\pi y/L) \quad (1)$$

w e e U s e a fow ve oc y a fow a fo s, f s e feq e cy of e fow, $L = 2l$ s e wave e◂ of e e o c fow ce a co sss of fo q a e -ce s, a $l = 6.5$ s e w of e q a e -ce . T e ea vo c y a vo ex co es s $= 2\pi U/l$. T e ve- oc y fe s e $\boldsymbol{u} = <\psi_y, -\psi_x>$, w e e x, y s bsc e o e a a ffe e a o . I a o , we ef e a o e so a fow a e◂ a a e e $p = UT/2\pi l = /4\pi^2 f$, w c s e ax a a◂ e swe by e fow ea e vo ex co o e a cyc e, o a e by a f c ce. T e o e so a a e◂ sa ◂ e e a fea e of e e- e o c fow.

We o e e sw e s as ac ve e so s ov◂ a o◂ e a o ax s (*31*, *47*), w ose o e a o a◂ ew $+x$ ax s s ve by θ. T e as ec a o of e sw e s y $\gamma = 5$ fo *V. cholerae* ess o e w se s a e) a e eo e y a a e e $= \gamma^2 - 1)/\gamma^2 + 1)$. T e sw ◂ s ee s u_s $u_s = 80$◂ /s fo *V. cholerae* ess

o e w se s a e). T e sw e s a e a vec e by e f ow f e a eo e e by es ea a o a o a f ow a e s

$$d\mathbf{q} = \left[\frac{\nabla \boldsymbol{u} - \nabla \boldsymbol{u}^{\mathrm{T}}}{2} + \alpha \frac{\nabla \boldsymbol{u} + \nabla \boldsymbol{u}^{\mathrm{T}}}{2} \cdot (\mathbf{I} - \mathbf{q} \otimes \mathbf{q})\right] \mathbf{q}\, dt \qquad (2a)$$

$$d\mathbf{x} = (\mathbf{u} + u_s \mathbf{q})dt + \sigma_s d\mathbf{W} \qquad (2b)$$

w e e **q** s e ec o of e sw e , $\mathbf{x} = \langle x, y \rangle$ s e os o vec o of e sw e , $\nabla \boldsymbol{u}$ s e f ow vo c y e so , $\mathbf{W} = \langle W_x, W_y \rangle$ s e W e e o se, a W_x, W_y e ese e s oc as c W e e o se e co es o va ab es. We c e a s a o a f- f s o a e a x, y ec o s w e e e W e e o se fo ows a G a ss a s b o w SD σ_s. o e a e a s a o a ff - s o e o B ow a o o s $D_0 = \sigma_s^2/n_s$, w e e $n_s = 2$ s e - e s o of e sys e a s es a e by e S o es-E s e e a o w e eo e ca y ave a e sw e e s o s e- so 1.7 e a 0.3 w) fo s c y. T s a o s o $D_0 = 4.0 \times 10^{-13}$ ^{2}/s wa e - e v scos es. We o e a e eve of s ace e e o B ow a o o s c ess a a of sw e o y fo o e sw e s. We co o- a e f e sw e o a o a ff s v y, as ve by $D = \sigma^2$ a W_θ. Ex esse e s of e f ow s ea f c o , eo e a o a e θ a os o x, y of e sw e a e ove e by

$$d\theta = \left[-\frac{\psi_{xx} + \psi_{yy}}{2} + \alpha \left(\frac{\psi_{yy} - \psi_{xx}}{2} \cos 2\theta - \psi_{xy} \sin 2\theta\right)\right] dt + \sigma\, dW_\theta \qquad (3a)$$

$$dx = (\psi_y + u_s \cos\theta)dt + \sigma_s dW_x \qquad (3b)$$

$$dy = (-\psi_x + u_s \sin\theta)dt + \sigma_s dW_y \qquad (3c)$$

T e s a a o a of e s a o s bo e . Fo eac e ca e of a se of f ow co o s, 10^4 sw e s a e a y see e fo y a a o y e q a e -ce fo $x/l = -0.5$ o 0.5 a $y/l = -0.5$ o 0.5 w a o sw - ec o s. T ee e ca es a e co c e fo eac se of f ow co - o s. A seco -o e R e-K a sc e e s se w a a c se of 10^{-4} s o a f a e of $t_f = 2000$ s. T e a c se s ee e by e e ca e o s ace e s fo ass ve o ff s ve a c es e f ow.

By ef $\tilde{x} = x/l$; $\tilde{y} = y/l$; $\tilde{t} = t/T$; $\tilde{\psi} = \psi T/l^2$; $\tilde{u}_s = u_s T/l$; a $\tilde{\sigma}_s = \sigma_s/l$, e ove eq a o ca be o e- s o a as

$$\tilde{\psi} = 2p \cos(2\pi \tilde{t}) \cos(\pi \tilde{x}) \cos(\pi \tilde{y}) \qquad (4a)$$

$$d\theta = \left[-\frac{\tilde{\psi}_{\tilde{x}\tilde{x}} + \tilde{\psi}_{\tilde{y}\tilde{y}}}{2} + \alpha \left(\frac{\tilde{\psi}_{\tilde{y}\tilde{y}} - \tilde{\psi}_{\tilde{x}\tilde{x}}}{2} \cos 2\theta - \tilde{\psi}_{\tilde{x}\tilde{y}} \sin 2\theta\right)\right] dt + \sigma\, dW_\theta \qquad (4b)$$

$$d\tilde{x} = (\tilde{\psi}_{\tilde{y}} + \tilde{u}_s \cos\theta)dt + \tilde{\sigma}_s dW_x \qquad (4c)$$

$$d\tilde{y} = (-\tilde{\psi}_{\tilde{x}} + \tilde{u}_s \sin\theta)dt + \tilde{\sigma}_s dW_y \qquad (4d)$$

w e e sw e a s o y a cs a e co o e by a e p a o e s o a sw s ee $\tilde{u}_s$. We o e a e of $p \to 0$, sw o a es, w e eas fo $p \gg \tilde{u}_s$, e effec of sw w o a e o y o s w e e $\tilde{\psi}_{\tilde{x}}$ a $\tilde{\psi}_{\tilde{y}}$ a e s a , e., ea e vo ex co e a q esce e ases. T e bo a y of ese o s w e e o e co e o be wee f ow p a sw $\tilde{u}_s$.

Swimmer statistics

Lo - e SDs a e co e by e se b e ave e SDs fo a sw e s a e f a e $t_f = 2000$ s o $200T$. T e o - e SD sca ex o e n s co e by a owe - aw eas - sq a e f f o $t/T = 50$ o 200. T e o e s o a s a ce o f ow a fo s s ef e by $d = \cos(2\pi x/L) \cos(2\pi y/L)$ a s 1 a e vo ex co e a 0 a f ow a fo s, e., bo a es be wee q a e -ce s. T e PDF b as a o f ow a fo s s co e as fo ows: A a ve e, e sw e obab y fo $d < 0.03$ s eva a e a o a by e obab y fo $d < 0.03$ f a sw - e s we e fo y s b e s ace. T e PDF b as a o $k\pi/2$ s ef e s a y w e e e obab y of sw e o e a o s a e w f ow a fo s o f a s w $|\theta - k\pi/2| \leq 0.035$, $k = \pm 2, \pm 1$, a 0, a s o a by a f a sw e o e - a o s a e fo y s b e . T e a ec o y w be befo e eac f ow a fo s W s ca c a e as e e a e a- ve se a o ee c o of e see f ow ce , f o $t = 0$ o e e w e e sw e eac es $d < 0.03$, o a by e f c c e 2π. T e w be s s e ; e., c oc w se o co - e c oc w se w a es a e o ffe e a e . Po a o -ave - a e w s e o e as <w>. Sw e o e a o ea ve o e a e of e oca f ow s ea es s ef e as e ac e a e fo e be wee e sw e o e a o vec o a e a e e, $\phi = \theta - \theta_s$, a s offse o e a e $-\pi/2 \leq \phi \leq \pi/2$. T e a e of es ea e a e s $\theta_s = \mathrm{atan2}(-\psi_x, \psi_y)$. T e s co ve o of φ s s c a o ca es a e w e oca s ea e, a ve ca es a e owa f ow a - fo s, a os ve ca es a e owa ee c o s.

Bacterial strain and suspension preparation

We se e co a-s a e G a - a ve bac e *V. cholerae* as e ac ve sw e e bac e a s e s o ex e e s. T e *V. cholerae* s a se (C6706, LZV918) s efec ve v e ce (Δ*tcpA*) a co s ve y o ces ee f o esce o e . Bac e a we e ow ove a 37°C w s a LB e s e e e w s e o yc (30 /). *V. cholerae* ce s we e co ec e by ce f a o a es s e e a eo a vo e os a e-b ffe e sa e (PBS; 1×) befo e se ex e e s.

Flow cell apparatus

T e ex e e a f ow ce a a a s co s s s of a e o c a ay of e a e a es, a a e w a e a o a y o f a 10 c 5~q;q esf KaG s;;q sK sK ;q;q G sO/vq;q s sK sG sO a f-0

H T s Lo e bo y fo ce, ce by e co b a o of e s a a y o e e a ay of a e s a e- e e e c e , ves e s a a y a e o a y e o c vo ces Ty ca ea f ow ve oc es U a e f o 0 02 o 2 /s T e Rey o s be of e f ow, ef e by $Re = Ul/\nu$, base o q a e -ce w l a f e a c v scos y ν, a es f o 0 1 o 10 T e Pec e be , ef e by $Pe = Ul/D_0$, s a e a 10^5 e a co o s T e ex e e a f ow f e a vo c y a e s a o ose of e o e e- e o c Tay o - ee vo ex e s - a o s f S1)

Bacterial dispersion experiments

A e b of e ex e e , f e f ow ce a a a s e a s q esce A o a of 50 of e f o esce bac e a s s- e s o s a e o e ce e vo ex of e f ow c a be v a a a s ace e e e I e a e y af e a o , e vo a e ac oss e f ow ce a a a s s ac va e T e ca e a a es a a o of a ox a e y 2 5 c × 2 5 c a e ce e of e c a be a 30 f s T e f ow c a be s a e by a se es of -e o e s ace above 470- ea e ss o wave e) A ba e f e 530- ea ba ass f e) s ace f o of e ca e a o exc e exc a o T e f o esce e s y, w c co e a es w bac e a ce e s y, s eco e fo eac xe oca o T e a o of eac ex e e s a o 10

Particle tracking velocimetry

To c a ac e e f ow, we s e se 39 o ys y e e a c es o e s face of e f T e a c e os o s a e a e s a co e e a y e a -ox e se co c o ca e a IO I s es, F a e 4 180) o e a a 30 f s To co e f ow ve oc y a - e s, s obosco c-ave a e ve oc y f e s, ob a e by ave a a c es a e ca ases 60,000 a a o s e ase), a e se Pa c e ac a o s base o 48) a e se o ac ace a c e ce o s B ef y, e a c e fea es we e ex e f e s a oca ea f e w f e c e o , s c as ea e s y, o a e s y, a s of y a o , a as ec a o T e ce o s of e a c es we e ef e s a ss a T e ;q fK s K0ce Ka sO065K6q06W/q;eKKs bes O0G/0WOs;06sK/q; sO0OO6vq;q T e s+0;;WWWWq0vW6+q;q sKof s0;66WWq

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