

Low-Reynolds-number swimming at pycnoclines

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Microorganisms play pivotal functions in the trophic dynamics and biogeochemistry of aquatic ecosystems. Their concentrations and activities often peak at localized hotspots, an important example of which are pycnoclines, where water density increases sharply with depth due to gradients in temperature or salinity. At pycnoclines organisms are exposed to different environmental conditions compared to the bulk water column, including reduced turbulence, slow mass transfer, and high particle and predator concentrations. Here we show that, at an even more fundamental level, the density stratification itself can affect microbial ecology at pycnoclines, by quenching the flow signature, increasing the energetic expenditure, and stifling the nutrient uptake of motile organisms. We demonstrate this through numerical simulations of an archetypal low-Reynolds-number swimmer, the “squirmers.” We identify the Richardson number—the ratio of buoyancy forces to viscous forces—as the fundamental parameter that quantifies the effects of stratification. These results demonstrate an unexpected effect of buoyancy on low-Reynolds-number swimming, potentially affecting a broad range of abundant organisms living at pycnoclines in oceans and lakes.

stratified fluid | bio-locomotion

Vertical variations in water density, or “pycnoclines,” occur ubiquitously in aquatic and marine environments (1), due to gradients in temperature (thermoclines) or salinity (haloclines). Pycnoclines can trigger a wide range of environmental and oceanographic processes. In oceans and lakes, intense biological activity and accumulation of organisms and particles are associated with pycnoclines (2, 3). For example, formation of phytoplankton blooms is often correlated with stratification (3), and these blooms can enhance CO₂ sequestration (4) or disrupt water supply systems (5). Stratification can also affect organism migration: Some species of euphausiids do not cross thermoclines (6) and haloclines can act as a barrier to the vertical migration of dinoflagellates (7).

Despite the widespread ecological implications of stratification, its hydrodynamic effects on organisms remain poorly understood. This is partly due to the notion that most organisms are too small to be affected by stratification, because the water density varies on a length scale, $L_\rho = \rho_0/\gamma \sim O(\text{km})$, much larger than the size of the organism, where ρ_0 is a reference density (e.g., 1,000 kg m⁻³) and γ is the vertical gradient in water density [typical values of γ range from $O(0.01)$ kg m⁻⁴ at ocean thermocline (8) to $O(1)$ kg m⁻⁴ in fjords and lakes (2, 3)].

This notion is incorrect. It was recently found that the appropriate length scale to determine whether stratification affects motion is $L = (\mu\kappa/\gamma g)^{1/4}$, where μ is the dynamic viscosity, κ the diffusivity of the stratifying agent, and g the acceleration of gravity (9). [This length scale was earlier derived, in a different context, by List (10)]. Organisms larger than L are affected by stratification. For typical stratifications, L is in the order of a millimeter ($\ll L_\rho$), overturning the idea that the fluid mechanics of small aquatic organisms is unaffected by stratification.

Low-Reynolds-number swimming in homogeneous fluids has been studied for more than half a century (11–13). The smallness of the Reynolds number, $Re = Ua/\nu$, indicates that inertial forces are negligible compared to viscous forces, where a and U are the

size and speed of the swimmer and ν the kinematic viscosity of water. Flow in this regime is often modeled by means of singularity solutions, fundamental solutions of the inertialess momentum equation (Stokes equation) (14). For example, the Stokeslet is the flow field generated by a point force, a first order model of a sinking particle, and the stresslet is the flow resulting from two equal and opposite point forces, such as thrust and drag of low-Reynolds-number swimmers. The linearity of the Stokes equation allows general flow fields to be represented by a superposition of singularity solutions.

To determine how stratification affects low-Reynolds-number flows, one can derive singularity solutions in a stratified fluid (“stratlets”) (9, 10). These solutions reveal the tendency of a stratified fluid to hamper vertical motion, resulting in vortical flows that are absent in homogeneous fluids and in a reduced flow signature associated with point disturbances. However, recent laboratory observations have shown that flows of low-Reynolds-number swimmers can differ substantially from those predicted by the superposition of singularities (15). Furthermore, stratlets are limited to weak stratifications, and their superposition can currently not describe actual swimmers, because the solution that satisfies boundary conditions (the source dipole in homogeneous fluids) remains unknown. Here we present a numerical model that reveals how low-Reynolds-number swimming is affected by stratification.

A Squirmer in a Stratified Fluid

The squirmer (16) is an archetypal model for studies of low-Reynolds-number swimming because of the balance of tractability and realism. It consists of a spherical cell that swims using wave-like deformations of its surface (16), approximating ciliates moving by synchronized beating of cilia on their surface (17) or colonies of flagellates such as *Volvox* (18). The squirmer model has been used among others to study hydrodynamic interactions among cells (19), mixing by microbial swimmers (20), and locomotion in complex fluids (21).

Here we study a squirmer of radius a swimming downward in a stratified fluid. To model propulsion, we neglect small radial displacements of the cilia (21) and prescribe a tangential velocity on the swimmer’s surface (17),

$$u_\theta = B_1 \sin \theta + \frac{B_2}{2} \sin 2\theta, \quad [1]$$

where θ is the orientation measured from the swimming direction. We consider u_θ to be independent of time, thus modeling the mean motion of the swimmer over one ciliary beating period. In a homogeneous fluid, the constant B_1 sets the swimming speed, $U = 2B_1/3$, while B_2 determines the stress field around the swimmer (17). Changing the sign of $\beta = B_2/B_1$ captures two general swimmer typologies: For $\beta > 0$, thrust is generated in front of the body and the squirmer models a class of organisms called

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“pullers” (e.g., biflagellated algae such as *Chlamydomonas*); for $\beta < 0$, thrust is generated behind the body and the squirmer models “pushers” (e.g., spermatozoa). Pullers drag fluid from front and back toward their body, expelling it from the sides; pushers do the opposite. $\beta = B_2/B_1$ scales with $a\omega/U$ where ω is the vorticity generated by the organism. Thus, knowledge of $a\omega/U$ allows one to map a real organism onto its corresponding squirmer model. For example, for copepods $a\omega/U$ is of order unity (22).

Two physical effects distinguish the fluid dynamics of a swimmer in a stratified fluid from that in a homogeneous fluid: the variation of buoyancy over depth, due to the change in fluid density, and the diffusion of the stratifying agent. These two effects are captured by two dimensionless numbers that, together with the Reynolds number, control the flow. The Prandtl number determines the ratio of the diffusivity of momentum, ν , to the diffusivity of the stratifying agent, κ . For salt stratifications $Pr \approx 700$; for temperature stratifications $Pr \approx 7$. Diffusion of the stratifying agent is important because it prevents the extreme compression of isopycnals (surfaces of constant density) as particles or organisms traverse them (23, 24). Here we focus on $Pr = 700$.

The effect of buoyancy is often quantified by means of the Froude number (23, 25, 26), $Fr = U/(Na)$, where $N = \sqrt{\gamma g/\rho_0}$ is the Brunt-Väisälä frequency, the natural frequency of oscillation of a vertically displaced particle in a stratified fluid, and $\gamma = -d\rho/dz$ is the background density gradient. However, Fr measures the relative importance of inertial and buoyancy forces, whereas in the inertialess world of microorganisms it is more appropriate to compare viscous and buoyancy forces. This can be done by means of the viscous Richardson number, $Ri = a^3 N^2 / (\nu U)$, related to Fr and Re by $Ri = Re/Fr^2$ (27). Experimental and numerical results for settling particles have shown that Ri is the appropriate parameter to quantify the effects of stratification at low Reynolds numbers (27).

The fluid is assumed to be linearly stratified ($\gamma = \text{constant}$), a good approximation of natural stratifications at centimeter scales. The equations governing the fluid motion are

$$\nabla \cdot \mathbf{u} = 0, \quad [2]$$

$$\rho \frac{\partial \mathbf{u}}{\partial t} + \rho \mathbf{u} \cdot \nabla \mathbf{u} = -\nabla p + \mu \nabla^2 \mathbf{u} + \rho \mathbf{g}, \quad [3]$$

$$\frac{\partial \rho}{\partial t} + \mathbf{u} \cdot \nabla \rho = \kappa \nabla^2 \rho, \quad [4]$$

where $\mathbf{u} = (u, v, w)$ is the velocity field, t is time, p is the pressure, ρ is the fluid density, $\mathbf{g} = -g\hat{\mathbf{k}}$ is the acceleration of gravity, and $\hat{\mathbf{k}}$ is the vertical unit vector, positive upward. The first equation states that the fluid is incompressible. The second equation expresses conservation of momentum, under the assumption that changes in fluid density only affect the body force $\rho \mathbf{g}$ (Boussinesq approximation). The last equation describes how fluid density changes due to advection and diffusion of the stratifying agent. Eqs. 2–4 are solved using a finite volume method, prescribing zero radial velocity and tangential velocity u_θ (Eq. 1) at the swimmer’s surface.

Self-propelled microorganisms are force-free: Thrust balances drag and gravity because inertia is negligible. Thus, the total force on the swimmer, $F_D = \int_S \mathbf{n} \cdot (-p\mathbf{I} + \boldsymbol{\tau})dS - Mg\hat{\mathbf{k}}$, must be zero, where $\boldsymbol{\tau} = \mu(\nabla \mathbf{u} + \nabla \mathbf{u}^T)$ is the viscous stress, \mathbf{n} is the unit normal vector, \mathbf{I} is the identity matrix, and S , V , and M are the surface, volume, and mass of the swimmer, respectively. For a neutrally buoyant swimmer $Mg = \rho(0)gV$, where $\rho(0)$ is the instantaneous background density at the center of the swimmer. For a given value of $\beta = B_2/B_1$, we computed F_D for three values of B_1 and interpolated to find the value of B_1 for which $F_D = 0$ (21). A simulation for that value of B_1 was performed to confirm that the total force on the swimmer was below a prescribed tolerance ($F_D/(6\pi\mu aU) < 10^{-2}$).

Results and Discussion

Results reveal that density gradients encountered by organisms at pycnoclines can have a major effect on their flow field, energy expenditure, and nutrient uptake. We performed simulations for pushers and pullers in a linearly salt-stratified fluid ($Pr = 700$) at Reynolds numbers comprised between 0.05 and 0.5 and a range of Richardson numbers. It should be noted that the Stokes solution for a squirmer in a homogeneous fluid, given by Blake (17), is used to normalize all the results. The speed of swimmers in a stratified fluid, U , relative to that in a homogeneous fluid, U_H , shows that stratification can markedly slow down swimmers (Fig. 1). The reduction in speed can exceed 50% at $Ri > 3$ (Fig. 1A).

For a pusher, results for different Re values collapse when swimming speed is plotted against Ri , indicating that the Richardson number is the fundamental parameter describing the decrease in speed caused by stratification at low Ri , as found previously for particles settling at low Reynolds numbers (27). In contrast, for a puller the effect of stratification can depend on the Reynolds number (Fig. 1B). At $Re = 0.5$, swimming speeds are again lower than in the homogeneous case and the speed reduction can be large even when buoyancy forces are weak: for example, speed is reduced by 14% at $Ri = 0.05$. However, at smaller Reynolds numbers swimming speeds are enhanced by stratification.

A pusher’s decrease in speed with increasing stratification can be understood by considering how the swimmer perturbs the density stratification. This is shown by the isopycnals, $(\rho - \rho(0))/(a\gamma)$ (Fig. 2A–D). As the pusher swims down, it entrains lower-density fluid from upper layers. This entrainment is due to viscosity and is akin to that of a sinking particle but considerably stronger because the flow field due to the pusher includes a region of closed streamlines in front, which traps lighter fluid. This process creates a region of light fluid in front of the swimmer, which is not observed for settling particles (27), and a tail of perturbed isopycnals behind it. “Pushing down” this blob of light fluid increases the drag on the swimmer, reducing its speed. Streamlines reveal that the blob of light fluid is in motion and forms a toroidal eddy of size comparable to the swimmer (Fig. 2A–C). Above the swimmer, the isopycnals’ return to their neutral buoyancy height generates fluid motion directed away from the organism. This ejection of isopycnals is also observed for settling particles (27, 28) but is here again enhanced by propulsion.

Isopycnals reveal that the slower swimming speeds at higher Richardson numbers can arise due to two effects (recall that $Ri = Re/Fr^2$): an increase in the stratification (lower Fr) or an increase in the swimmer’s inertia (higher Re). Stronger stratification (compare Fig. 2A and B) more rapidly restores isopycnals to their neutral buoyancy height and more effectively opposes the vertical motion of the organism. Larger inertia (compare Fig. 2C and A) causes the swimmer to entrain lighter fluid into

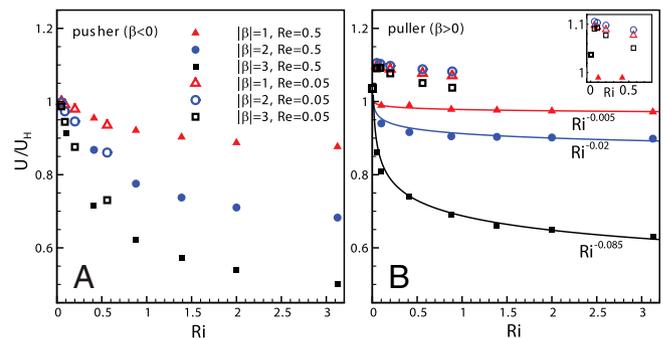


Fig. 1. Stratification can significantly affect the swimming speed of microorganisms. The speed of a squirmer in a stratified fluid, U , normalized by the speed in a homogeneous fluid (Blake’s solution), U_H , is plotted as a function of the Richardson number Ri for (A) a pusher squirmer and (B) a puller squirmer.

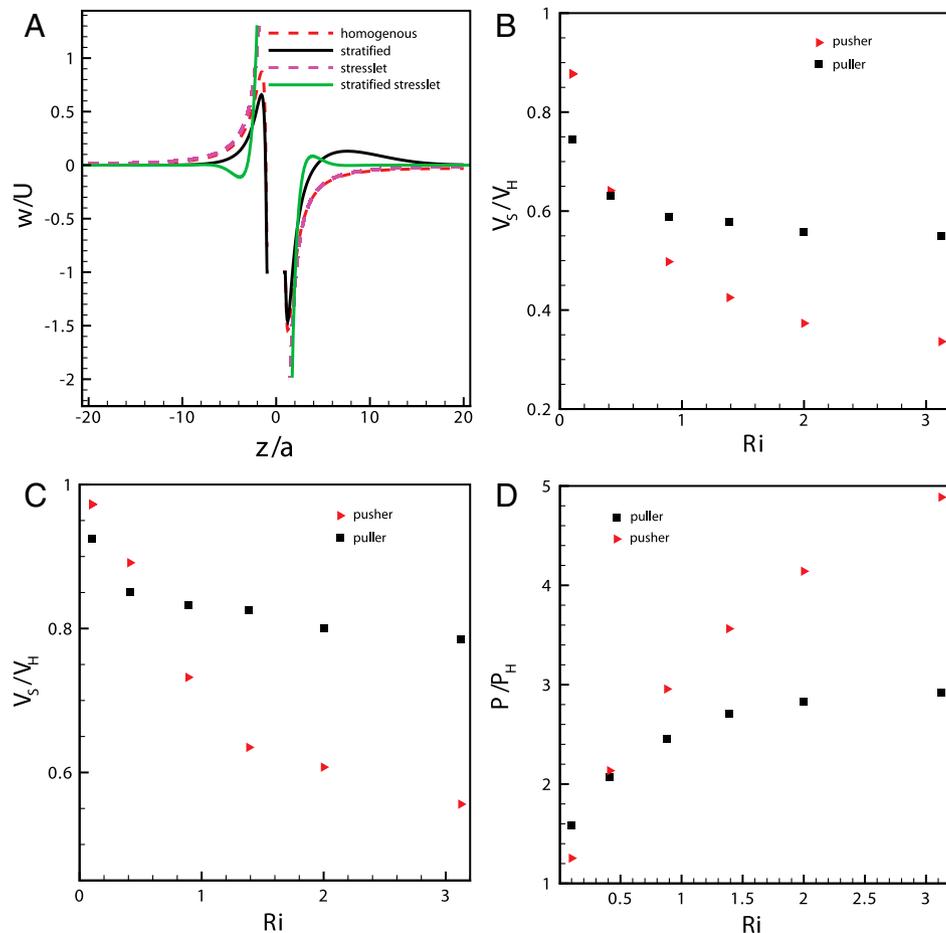


Fig. 3. Stratification affects the flow signature and energetic expenditure of swimmers. (A) The vertical flow velocity, w , induced by the motion of a puller squirmer, along the vertical axis through the center of the squirmer, normalized by the swimming speed U ($Re = 0.05$, $Ri = 0.2$, $\beta = 3$). The cases of a squirmer swimming at the same speed in a homogeneous fluid, of a stresslet in a homogeneous fluid and of a stresslet in a stratified fluid (9) are shown for comparison. The strength of the stresslet is $4\pi\mu B_2 a^2$. Note that the stratified stresslet cannot quantitatively predict the flow field, due to the nonlinearity in the advection-diffusion equation and the no-flux boundary condition at the swimmer surface. (B and C) The detection volume V in a stratified fluid is smaller than that in a homogeneous fluid, V_H , for both pushers and pullers ($Re = 0.5$, $|\beta| = 3$), whether detection volume is computed based on absolute flow speed (B) or magnitude of the shear rate (C). The same values of B_1 are used for the squirmer in homogenous and stratified fluids in B and C. (D) The energetic expenditure of swimming, P , increases dramatically with Richardson number, relative to that in a homogeneous fluid, P_H , for both pushers and pullers ($Re = 0.5$, $|\beta| = 3$).

nitude of either flow velocity, $|\mathbf{u} - U\hat{\mathbf{k}}|$, or shear rate, $(2\mathbf{D}:\mathbf{D})^{1/2}$, where \mathbf{D} is the rate of strain tensor. Using velocity and a threshold of $0.2B_1$, the detection volume in a stratified fluid, V , can be 60% smaller than in a homogeneous fluid, V_H (Fig. 3B). Furthermore, pushers are slightly more stealthy than pullers. Using shear rate and a threshold of $0.1B_1/a$, V can be 45% smaller than V_H (Fig. 3C). Because foraging rates of predators that detect prey based on hydromechanical signals are proportional to detection volumes (29), we suggest that stratification can reduce trophic transfer rates among aquatic organisms.

A primary fitness cost of motility is the energy expenditure associated with swimming. A swimmer in a stratified fluid, in addition to overcoming viscous forces, spends energy in mixing (i.e., in increasing the potential energy of the ambient fluid). The energy expended by the swimmer can be computed as (30) $P = -\int_S \mathbf{n} \cdot (-p\mathbf{I} + \boldsymbol{\tau}) \cdot \mathbf{u} dS$. By increasing the resistance to motion (Fig. 1), stratification augments the energy necessary for swimming at a given speed (Fig. 3D). In the regime investigated here, this increase is up to 300% for pullers and 500% for pushers.

An important benefit of motility is that it can enhance foraging. We find that stratification can markedly affect uptake by altering the nutrient concentration around a swimmer. We compute the nutrient concentration, C , by solving the advection-diffusion equation

$$\frac{\partial C}{\partial t} + \mathbf{u} \cdot \nabla C = \kappa_N \nabla^2 C, \quad [5]$$

where κ_N is the nutrient diffusion coefficient. For low-molecular-weight nutrients, such as many sugars and amino acids, $\kappa_N \approx 10^{-9} \text{ m}^2 \text{ s}^{-1}$, whereas larger molecules, including refractory organic matter, diffuse considerably more slowly ($\kappa_N \approx 10^{-12} \text{ m}^2 \text{ s}^{-1}$)

(31). The swimmer is assumed to be perfectly absorbing [i.e., uptake is diffusion-limited ($C = 0$ at the swimmer surface)], while far from the swimmer the concentration is unperturbed ($C = C_\infty$).

Nutrients reach the swimmer by molecular diffusion and advection by the flow. The relative importance of advection and diffusion can be estimated with the Peclet number, $Pe = Ua/\kappa_N$, and quantified with the Sherwood number, $Sh = -\int_S \mathbf{n} \cdot \nabla C dS / (4\pi a C_\infty)$, which represents the ratio of the total nutrient uptake to the nutrient uptake by diffusion alone (i.e., for a still organism). For very small organisms ($\approx 1\text{--}10 \mu\text{m}$), such as bacteria, foraging on small-molecular-weight solutes, $Pe \ll 1$ and $Sh \approx 1$: The action of swimming does not increase uptake, and motility serves primarily to move toward regions of higher resource concentration (31). In contrast, in somewhat larger organisms ($>50\text{--}100 \mu\text{m}$) swimming can enhance uptake ($Sh > 1$) by thinning the concentration boundary layer around the organism (31).

Stratification can markedly alter uptake by distorting the nutrient field around swimmers. A first comparison can be made between organisms that swim at the same speed in homogeneous and stratified fluids. Both pushers and pullers display a thinner concentration boundary layer and a considerable reduction in nutrient-deplete regions around the swimmers, compared to the homogeneous case (Fig. 4A and B). This difference results primarily from the larger tangential surface movements required by swimmers in a stratified fluid to achieve the same swimming speed as in a homogeneous fluid, which more effectively renews the water in contact with the swimmer. This increased stirring enhances uptake and results in larger Sherwood numbers in stratified fluids, Sh , compared to homogeneous fluids, Sh_H (Fig. 4C and D). Interestingly, however, stratification does not change the fundamental scaling of Sh with Pe and our results confirm the $Sh \sim Pe^{1/2}$ dependence (Fig. 4E) previously obtained for a squir-

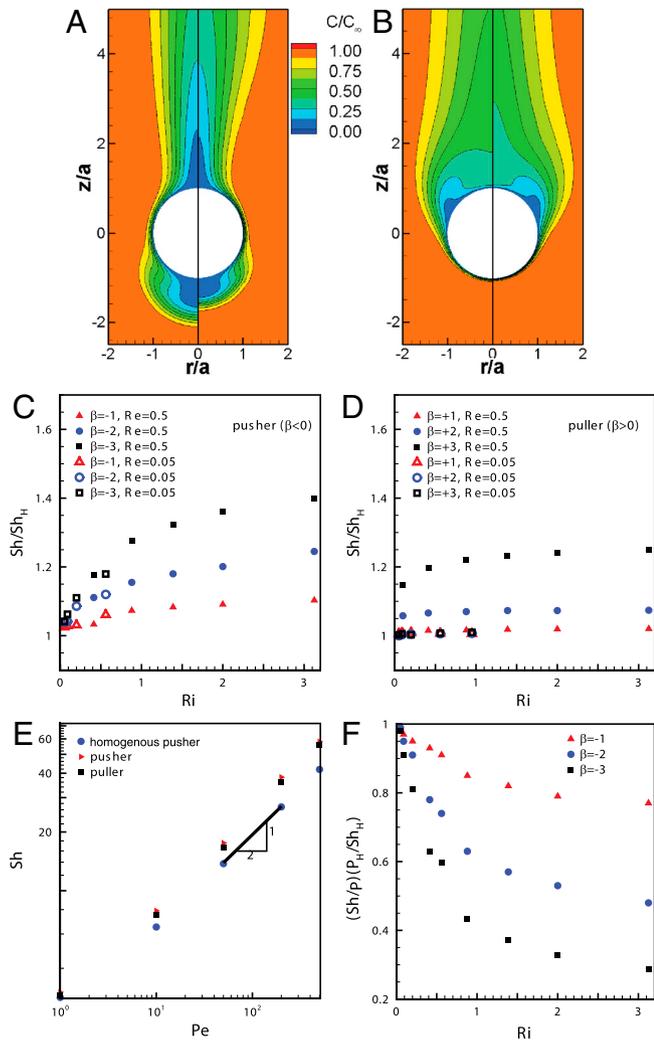


Fig. 4. Stratification changes the concentration field around a swimmer and hence its nutrient uptake. (A and B) Nutrient concentration field around a swimmer, for (A) a pusher and (B) a puller. The left and right halves of each panel show the concentration field in a homogeneous and in a stratified fluid, respectively. Parameter values are $Re = 0.5$, $Ri = 0.89$, $|\beta| = 3$ and $Pe = 50$. (C and D) For equal swimming speed, nutrient uptake increases with stratification, as shown by the increase of Sh with Ri for both (C) a pusher and (D) a puller. The Sherwood number was normalized by the homogeneous case, Sh_H . (E) The scaling of Sh with Pe is unaffected by stratification. (F) The enhancement in nutrient uptake per unit energy expended in swimming, Sh/P , compared to the homogeneous case, Sh_H/P_H , decreases with increasing stratification.

mer in a homogeneous fluid (32). Thus, Sh in a stratified fluid is a constant multiple of Sh_H , irrespective of Pe . For $Re = 0.5$, $Ri = 0.89$ and $\beta = -3$, $Sh/Sh_H \sim 1.3$, thus the uptake enhancement is about 30% larger in a stratified fluid.

Does the increase in uptake justify the extra energetic investment of swimming at pycnoclines? We find that this is not the case. We quantified the increase in nutrient uptake per unit energy expended, or Sh/P , and normalized this by the homogeneous case, Sh_H/P_H (Fig. 4F). For all values of β , we find that $Sh/P < Sh_H/P_H$. Furthermore, Sh/P decreases with increasing Ri : The additional investment for motility in a stratified fluid gives diminishing returns in terms of uptake. Taken together, these results suggest that swimming at pycnoclines is a trade-off between a decreased foraging efficiency and a smaller risk of predation. Importantly, however, decreased foraging efficiency might frequently be offset by an increase in nutrient resources, caused by the accumulation of organisms and particles at pycnoclines.

The simulations reported here apply to a neutrally buoyant squirmer—that is, one whose mean density is equal to that of the ambient fluid at the height of the squirmer's center. Real situations include the more general case in which the squirmer has a net buoyancy. Then, the squirmer velocity is no longer constant but experiences a deceleration or acceleration. Here, we calculate the deceleration, a_c , of a constant-mass squirmer as it swims, vertically downward, through its depth of neutral buoyancy. To compute the deceleration, we apply the same technique described above so that the force balance is satisfied at each instant. This calculation reveals that the deceleration of a squirmer with $Re = 0.5$, $Ri = 0.005$, and $\gamma a/\rho = 3 \times 10^{-5}$ is $a_c a/U^2 \sim 10^{-3}$. Therefore, changes in speed are small compared to the swimming speed at the neutral buoyancy depth, as long as $\gamma a/\rho$ is small ($< 10^{-5}$). We note that this calculation simply suggests that accelerations in the vicinity of the neutral buoyancy depth are small, whereas the full computation of the trajectory of a squirmer as it passes through its level of neutral buoyancy entails considerable added complexity, because of the need to solve a moving boundary problem.

These results reinforce the notion that flow effects on small aquatic organisms are strongly size-dependent. The smallest organisms, such as bacteria (approximately $1 \mu\text{m}$), are often not affected by flow: Inertial forces do not alter their motion ($Re \ll 1$), transport by advection does not increase their uptake ($Pe \ll 1$; $Sh = 1$), and stratification does not influence the flow associated with their propulsion ($Ri \ll 1$). Somewhat larger organisms, including many phytoplankton and small protists (approximately $10\text{--}100 \mu\text{m}$), are also not affected by inertia, but the flow generated by their motion, or the motion of their appendages, can increase nutrient uptake (33). These organisms, however, are likely too small to be influenced by natural stratifications. In contrast, organisms one order of magnitude larger, such as copepods, amphipoda, and mollusc larvae, can be affected by stratification (9). Organisms in this size range are frequently motile and the effect of the physical environment on propulsion and uptake could have direct fitness consequences. Our results suggest that fitness at pycnoclines can be curtailed by increased propulsion cost and decreased nutrient uptake. A 2.1-mm organism swimming at $230 \mu\text{s}^{-1}$ and $\beta = -3$ in a $\gamma = 1 \text{ kg m}^{-4}$ stratification spends 100% more energy than in a homogeneous fluid and takes up 40% less nutrients per unit energy. Conversely, stratification can favor fitness by reducing the flow signatures that predators use to detect prey. For example, copepods can detect shear rates of $1\text{--}50 \text{ s}^{-1}$ (34). For a threshold of $0.1B_1/a \sim O(1 \text{ s}^{-1})$, their detection volume can be reduced as much as 45%, suggesting that pycnoclines can act as refugia, for example for smaller copepods from larger copepods.

Interestingly, the effect of stratification is sensitive to changes in Re for pullers but not pushers, even in an essentially noninertial world. For downward swimming organisms, we found that stratification can increase the swimming speed of a puller but not a pusher, and the behavior is the same for upward swimmers. The distinction between pushers and pullers has been emphasized in a number of contexts: pushers cause greater mixing (35) and decrease the viscosity of dense suspensions (36), whereas pullers increase the viscosity (37). The difference between pullers and pushers in stratified fluids cannot be predicted from singularity solutions (9) but instead arises from the nonlinearity of the governing equations, due to the advection of the stratifying agent. This effect cannot be neglected for millimeter- to centimeter-sized organisms, for which the swimmer's Peclet number $Pe_s \geq 1$, where $Pe_s = RePr$. This highlights the importance of a numerical solution, as pursued here, or of direct experiments, of the kind performed recently in homogeneous fluids (15).

In natural waters, turbulence might interfere with stratification effects. The strongest velocity gradients due to turbulence occur at a length scale of $(10\text{--}50)L_K$, where L_K is the Kolmogorov scale,

$L_K = (\nu^3/\epsilon)^{1/4}$, and ϵ is the turbulent dissipation rate (38). For $\epsilon = 10^{-8}$ W/kg, this corresponds to 32–158 mm. As the length scales of scalar gradients are a factor of $Pr^{1/2}$ smaller than those of velocity gradients, the scale at which turbulence might affect the flow field around a swimmer is 1–6 mm for a salt stratification and 10–60 mm for a temperature stratification. These scales are even larger in weaker turbulence conditions, often reported in inlets (39), lakes, and reservoirs (40). Additionally, turbulence is a highly intermittent process (38), with mean dissipation rates resulting from rare bursts that interrupt long periods of quiescent conditions. Therefore, we expect turbulence to destroy the flow field generated by a swimming, millimeter-sized organism only occasionally.

Optimality in the propulsion mechanics of microorganisms has received much attention. For example, the undulatory stroke and the breaststroke of biflagellated green algae both represent local optima for swimming efficiency, and the latter further optimizes nutrient uptake (33). Mathematical models have also shown that the spermatozoa of some invertebrates achieve the fastest swimming for a given energetic expenditure at a flagellar wavelength close to that observed in nature (41). We similarly expect that aquatic organisms optimize propulsion when swimming at pycnoclines. By decreasing the nutrient uptake gain per energy invested in motility, while simultaneously providing refuge from predators, stratification might place strong selective pressure on motility.

As we dive deeper into the world of motile microorganisms, we are beginning to gain an appreciation for how their physico-chemical environment influences their movement behavior. Here we have shown that a frequent feature of the physical environment—density stratification—can have direct ecological consequences on motility-related traits, including energetic expenditure, nutrient uptake, and the risk of predation. These aspects must be con-

sidered when the trade-offs that determine the fitness advantage of motility in the microbial world are evaluated.

Materials and Methods

Eqs. 2–4 are solved in a frame of reference moving with the squirmer. This is computationally advantageous because the flow field around a stationary swimmer can be calculated using a fixed boundary-fitted grid. On the upstream boundary, a uniform velocity, U , is imposed. The upstream density increases as $\rho = \rho_0 + \gamma U t$ as the squirmer swims downward into heavier fluid with velocity U . On the downstream boundary, the exit boundary condition is imposed, $\frac{\partial u}{\partial z} = 0$, and the density gradient is specified as $\frac{\partial \rho}{\partial z} = -\gamma$ to have a linear background density gradient. The flow field generated by the squirmer is assumed to be axisymmetric. The surface of the squirmer is assumed to be impermeable to both flow and the stratifying agent (here, salt). Thus, $\mathbf{n} \cdot \nabla \rho = 0$ on the swimmer's surface. The simulations are done for a squirmer with $a = 200 \mu\text{m}$, $U = 250 \mu\text{m/s}$, $g = 9.8 \text{ m/s}^2$, $\rho_0 = 998 \text{ kg/m}^3$; other parameters are adjusted to obtain reported dimensionless parameters.

The governing equations are solved using a finite-volume method and a projection scheme with a collocated grid. The Crank–Nicolson and second-order central difference schemes are used for time and space discretization, respectively. We implement diagonal lower-upper triangular factorization (DILU) preconditioner to solve for the pressure changes through time. We used an $80 \times 40 \times 40$ rectangular domain and a body-fitted grid with a large concentration of grid points near the surface of the swimmer and a smallest grid size of $O(10^{-4} a)$, which ensures that the velocity and density boundary layers are resolved. We have verified the mesh-, domain-, and time-step-independency of our results to within an error smaller than 3%. The solver was benchmarked against literature results: (i) the drag on a sphere in a viscous stratified fluid was compared with the results of ref. 27 for a broad range of Richardson numbers ($10^{-3} < Ri < 2$); and (ii) the flow field of a squirmer in a homogenous Stokes flow was contrasted with Blake's analytical solution (17). In all cases, numerical results were within 1% of literature results.

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