

# Thermal stratification hinders gyrotactic micro-organism rising in free-surface turbulence

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Thermal stratification in water bodies influences the exchange of heat, momentum, and chemical species across the air-water interface by modifying the sub-surface turbulence characteristics. Turbulence modifications may in turn prevent small motile algae (phytoplankton, in particular) from reaching the heated surface. We examine how different regimes of stable thermal stratification affect the motion of these microscopic organisms (modelled as gyrotactic self-propelling cells) in a freesurface turbulent channel flow. This archetypal setup mimics an environmentally plausible situation that can be found in lakes and oceans. Results from direct numerical simulations of turbulence coupled with Lagrangian tracking reveal that rising of bottom-heavy self-propelling cells depends strongly on the strength of stratification, especially near the thermocline where high temperature and velocity gradients occur: Here hydrodynamic shear may disrupt directional cell motility and hamper nearsurface accumulation. For all gyrotactic re-orientation times considered in this study (spanning two orders of magnitude), we observe a reduction of the cell rising speed and temporary confinement under the thermocline: If re-orientation is fast, cells eventually trespass the thermocline within the simulated time span; if re-orientation is slow, confinement lasts much longer because cells align in the streamwise direction and their vertical swimming is practically annihilated. Published by AIP Publishing. [http://dx.doi.org/10.1063/1.4983345]

## I. INTRODUCTION

Thermally stratified turbulence is of crucial importance in many environmental and geophysical flows.<sup>28,41</sup> At the air-water interface of large water bodies, stable thermal stratification (i.e., fluid density increasing with depth) is typically established by solar radiation and regulates mixing<sup>33</sup> as well as surface renewal processes produced by turbulent upwashes of fresh water from the bottom boundary layer.<sup>20</sup> For strong enough surface heating, Internal Gravity Waves (IGWs)<sup>9,15,44</sup> may arise due to the instability generated by lumps of denser (cold) fluid being lifted upwards into regions of lighter (warm) fluid by turbulence and subsequently driven downwards by buoyancy. These waves form near the free surface, topping regions of well-mixed turbulence and active bursting phenomena. It has been shown that IGWs correlate well with regions of the flow characterised by large temperature gradients and low mixing (thermoclines)<sup>17,34,38</sup> and can act as a thermal barrier for organic and inorganic matter: At sufficiently high levels of stratification, such a barrier may prevent vertical mixing and trigger spatial accumulation.<sup>18,36,44</sup> Recent studies have demonstrated that the constant warming of oceans and big lakes gradually elevates the thermocline, possibly leading to a reduction in biomass in the upper water layers.<sup>21,31</sup> This is expected to have significant consequences on biogeochemical cycles, climate patterns, and marine ecosystems, which are strongly sensitive to changes in marine biomass

Many phytoplankton species are motile<sup>7,8,12</sup> and, even if their swimming speeds are typically smaller than ambient flow speeds, there is clear evidence that the interplay between motility and fluid turbulence can result in complex and ecologically important phenomena.<sup>6,12</sup> From a modeling viewpoint, phytoplankton cells can be treated as very small particles. However, their motility and degree of anisotropy make modeling more complicated than for small spherical particles (see Ref. 40 for a review on anisotropic particle dynamics in turbulence). In particular, motility can lead to a striking focusing effect known as gyrotaxis when coupled with shear in the form of vertical gradients in horizontal fluid velocity.<sup>12,16</sup> Gyrotaxis is the directed motility of cells arising from the combination of gravitaxis (which stabilizes cell orientation in the vertical direction, typically through bottom heaviness) and destabilisation by the ambient fluid shear. $^{6-8,19,29,30}$  This results in a balance between the gravitational torque due to the uneven density distribution within the cell, which tends to keep the center of

concentration.<sup>1</sup> One important consequence that has been ascribed to stratification (albeit in combination with other convergence mechanisms<sup>7,8</sup>) is the occurrence of intense assemblages of unicellular photosynthetic organisms known as thin layers.<sup>7,8</sup> Thin layers contain high concentrations of marine snow and bacteria, enhance zooplankton growth rates, and are essential for the survival of some fish larvae. Also, many phytoplankton species populating these layers are toxic, and their accumulation can disrupt grazing and enhance zooplankton and fish mortality, while seeding harmful algal blooms at the ocean surface.<sup>7,8</sup>

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mass below the center of buoyancy, and the hydrodynamic torque exerted by the fluid that surrounds the cell. Gyrotaxis was first observed by showing that phytoplankton cells tend to collect along the centerline of a laminar Poiseuille flow.<sup>19</sup> Subsequent experiments and simulations have demonstrated that gyrotactic plankton can be trapped in horizontal layers in laminar vertical shear.<sup>7,11,32</sup> Only recently it was discovered that plankton accumulation due to gyrotaxis can occur also in synthetic or homogeneous isotropic turbulence.<sup>3,5,22,23,32,39,42</sup> In this situation, the resulting spatial distribution is far from uniform and small-scale densely concentrated clusters with fractal properties are observed.<sup>5,10,23,42</sup> Gradients in plankton concentration typically span a huge range of length scales, from regions covering thousands of kilometres to patchiness occurring at the scale of centimetres.<sup>4,7,37</sup> Recent experiments have shown that gyrotactic trapping<sup>7,8</sup> occurs when vertically migrating cells reach localised areas of the flow where the vertical gradient of horizontal velocity exceeds a critical shear threshold. This causes cells to tumble end over end, disrupting collective upward motions and preventing any equilibrium orientation from being reached.

To the best of our knowledge, the interplay between stable thermal stratification and gyrotaxis in turbulent flows has not been examined in detail yet. Therefore, the physical mechanisms that govern the dynamics of motile aquatic micro-organisms (referred to as swimmers hereinafter) in stratified turbulence are not fully understood, and the possibility of observing trapping phenomena in the presence of strong stratification is not yet assessed. Some studies<sup>15,25</sup> have focused on the effect of thermal stratification and internal gravity waves, yet considering buoyant non-motile organisms. In particular, Hingsamer et al.<sup>15</sup> observed that buoyant phytoplankton species do not or cannot regulate their buoyancy to prevent wave-induced vertical displacements. Lovecchio et al.<sup>25</sup> examined the effect of different regimes of stable stratification on the surface distribution of floaters (small organic particles that, being lighter than water, migrate vertically due to buoyancy): The modification of turbulence due to the thermal stratification was found to influence strongly the settling velocity of floaters in the bulk of the flow. At the surface, stratification effects are also observed on the clustering of the floaters: the filamentary patterns of floaters observed in unstratified turbulence<sup>24</sup> progressively fade away as thermal stratification increases, and the distribution of the floaters remains roughly two-dimensional. Other studies (see Refs. 16, 23, 27, 39, and 42 among others) have considered gyrotaxis, yet only in idealised or simplified flow configurations and in the absence of stratification. For instance, Hoecker-Martínez and Smyth<sup>16</sup> considered a two-dimensional dynamically unstable stratified shear layer (which mimics the surface mixed layer of large water bodies) and found that the resulting pre-turbulent Kelvin-Helmoltz instability is sufficient to enhance the ability of the shear layer to retain gyrotactic organisms. Gyrotactic trapping was also observed by Manela and Frankel<sup>27</sup> in steady homogeneous shear flows and by Thorn and Bearon<sup>39</sup> in synthetic turbulence. More recently, Zhan et al.<sup>42</sup> and De Lillo et al.<sup>23</sup> investigated the same phenomena considering three-dimensional time-dependent homogeneous isotropic turbulence. Compared to laminar and linear shear flows, clustering and patchiness are significantly reduced but still occur in the downwelling regions of the flow.<sup>42</sup> When fluid acceleration is of the same order as gravitational acceleration, however, accumulation phenomena can be enhanced: This condition is unlikely in most marine environments, yet possible under non-homogeneous flow conditions as those encountered in the bottom boundary layer.<sup>23</sup>

In an effort to advance the current understanding of how gyrotactic swimmers propel themselves through a thermally stratified fluid, in this paper we investigate their dynamics in the presence of thermocline for the reference case of turbulent open channel flows. In particular, we want to quantify the effect of stratification on the vertical migration of swimmers at varying gyrotaxis (covering a wide range of re-orientation times) and at self-propelling speeds that are typical of the most common phytoplankton species. To this aim, we use Direct Numerical Simulation (DNS) and Lagrangian Particle Tracking (LPT), modeling swimmers as massless pointwise spheres advected by the local fluid velocity while moving with constant self-propelling speed in the direction of their orientation vector. We analyze the effect of different stratification strengths on surfacing and clustering of the swimmers. We perform this analysis considering swimmers with different bottom-heaviness because this is known to drive different spatial cell distributions and possibly determine the success of different species in processes like the competition for nutrients and sexual reproduction.<sup>2,6</sup> In the present flow configuration, stable stratification is obtained imposing a constant heat flux at the free surface and an adiabatic condition at the bottom wall. The paper is organized as follows: The problem statement, the governing equations, and the numerical methodology used for the simulations are presented in Sec. II; Sec. III is devoted to the analysis and discussion of concentration and orientation statistics, which are used to examine the occurrence of temporary confinement under the thermocline for both short and long re-orientation times. Finally, concluding remarks are made in Sec. IV.

### **II. PHYSICAL PROBLEM AND METHODOLOGY**

The physical problem considered in this study is the dispersion of gyrotactic swimmers in a thermally stratified turbulent flow in an open channel with a flat undeformable free surface (free-surface turbulence). The effect of imposing a flat free surface does not alter significantly the strength of the IGW, since the elevation of surface waves is roughly one order of magnitude smaller than the thickness of the IGW. In addition, it has been shown that light particles moving at the deformed free surface of a turbulent flow are subject to clustering mechanisms that come from the horizontal divergence in the surface and induce a compressible effect similar to the one observed for the flat surface.<sup>14,24–26</sup> The reference geometry consists of two horizontal (infinite) flat parallel walls, with the x-, y-, and z-axis of the coordinate system pointing in the streamwise, spanwise, and wall-normal directions. Indicating with hthe channel height, the size of the channel is  $2\pi h \times \pi h \times h$  in x, y, and z, respectively. Conservation of mass, momentum, and energy for an incompressible, Newtonian fluid and under the Boussinesq approximation is described by the following set of three-dimensional time-dependent equations, written in dimensionless vector form as

$$\nabla \cdot \mathbf{u} = 0 , \qquad (1)$$

$$\frac{\partial \mathbf{u}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{u} = \frac{1}{Re_{\tau}} \nabla^2 \mathbf{u} - \nabla p + \frac{Gr}{Re_{\tau}^2} \theta \mathbf{k} + \boldsymbol{\delta}_p, \qquad (2)$$

$$\frac{\partial \theta}{\partial t} + \mathbf{u} \cdot \nabla \theta = \frac{1}{Re_{\tau}Pr} \nabla^2 \theta - \beta_T, \qquad (3)$$

where  $\mathbf{u} = (u_x, u_y, u_z)$  is the fluid velocity, p is the fluctuating pressure,  $\delta_p = (1, 0, 0)$  is the mean pressure gradient imposed to drive the flow in the streamwise direction,  $\theta$  is the fluid temperature, and  $\mathbf{k} = (0, 0, 1)$  is a unit vector introduced to compute the buoyancy term only in the wall-normal direction. Variables are made dimensionless using the half channel height, h, the friction velocity,  $u_\tau = \sqrt{\tau_w/\rho}$ , with  $\tau_w$  the shear stress at the wall and  $\rho$  the fluid density, and the absolute value of the imposed free surface heating,  $\partial \theta / \partial z|_s$ , as reference quantities. For the fluid velocity, no-slip (respectively, no-stress) boundary conditions are enforced at the bottom wall (respectively, free surface); for the fluid temperature, a constant heat flux (respectively, adiabatic condition) is enforced at the free surface (respectively, bottom wall),

At the wall 
$$(z = 0)$$
,  $u_x = u_y = u_z = 0$ ,  $\frac{\partial \theta}{\partial z} = 0$ , (4)

at the free-surface 
$$(z = h)$$
,  $\frac{\partial u_x}{\partial z} = \frac{\partial u_y}{\partial z} = u_z = 0$ ,  $\frac{\partial \theta}{\partial z} = 1$ .

Periodic boundary conditions are applied in x and y for both velocity and temperature. Note that surface heating generates a negative temperature difference between the bottom and the top regions of the channel, thus causing a stable buoyancy effect (the gravitational acceleration g acting downward along the wall-normal direction). The dimensionless Reynolds, Grashof, and Prandtl numbers are defined as

$$Re_{\tau} = \frac{u_{\tau}h}{v}, \quad Gr = \frac{g\beta h^4}{v^2} \frac{\partial \theta}{\partial z}\Big|_s, \quad Pr = \frac{\mu c_p}{\lambda},$$
 (6)

where  $\mu$  and  $\nu$  are the dynamic and the kinematic fluid viscosity,  $\beta$  is the thermal expansion coefficient,  $c_p$  is the specific heat, and  $\lambda$  is the thermal conductivity of the fluid. Note that, for the specific flow configuration considered here (open channel flow with constant surface heating), we can assume  $\beta_T = (Re_\tau Pr)^{-1}$  in Eq. (3). Further details on this assumption are discussed in Ref. 25.

Eqs. (1)–(3) are discretized using a pseudospectral method based on transforming the field variables into the wavenumber space, through a Fourier representation for the periodic (homogeneous) directions x and y and a Chebyshev representation for the wall-normal (non-homogeneous) direction z. A two-level explicit Adams-Bashforth scheme for the non-linear terms and an implicit Crank-Nicolson method for the viscous terms are employed for the time advancement. As commonly done in pseudospectral methods, the convective non-linear terms are first computed in the physical space and then transformed in the wavenumber space using a de-aliasing procedure based on the 2/3-rule; derivatives are evaluated directly in the wavenumber space to maintain spectral accuracy. Further details can be found in Refs. 35, 43, and 44. Individual swimmers are modelled as spherical, massless, and pointwise particles whose position  $\mathbf{x}_p$  evolves in time according to the following equation:

$$\dot{\mathbf{x}}_p(t) = \mathbf{u}_{@p}(\mathbf{x}_p) + v_s \mathbf{p},\tag{7}$$

where  $v_s$  is the (constant) swimming speed,  $\mathbf{u}_{@p}(\mathbf{x})$  the velocity of fluid in the position of swimmer, and  $\mathbf{p}$  defines the spatial orientation of the swimmer. The orientation vector  $\mathbf{p}$  evolves in time according to the response of the swimmer to the biasing torques acting upon it: The viscous torque on the swimmer body, caused by the local shear, and the gyrotactic torque, arising from bottom heaviness<sup>30</sup> (see Fig. 1). The orientation rate is computed from the following equation:

$$\frac{d\mathbf{p}}{dt} = \frac{1}{2B} \left[ \mathbf{k} - (\mathbf{k} \cdot \mathbf{p})\mathbf{p} \right] + \frac{1}{2} \omega_{@p} \wedge \mathbf{p}, \tag{8}$$

where  $\mathbf{k} = (0, 0, 1)$  is a unit vector pointing upward in the vertical direction,  $\omega_{@p}$  is the fluid vorticity at the swimmer's position, and B is the characteristic time a perturbed gyrotactic swimmer takes to return to the vertical orientation when  $\omega = 0$ . Such a re-orientation time can be computed as  $B = \mu \alpha_{\perp} / (2 \mathcal{H} \rho g)$ , where  $\alpha_{\perp}$  is the dimensionless resistance coefficient for rotation about an axis perpendicular to **p** and  $\mathcal{H}$  is the center-of-mass offset relative to the center of buoyancy (located at point b in Fig. 1). The first term on the right-hand side of Eq. (8) represents the tendency of a swimmer to remain aligned with the vertical direction due to bottom-heaviness, while the second term represents the tendency of fluid vorticity to overturn the swimmer through a viscous torque. The time evolution of swimmer's position and orientation was computed upon time integration of the non-dimensional form of Eqs. (7) and (8), which read as

$$\frac{d\mathbf{x}_{@p}^{*}}{dt^{+}} = \mathbf{u}_{@p}^{+}(\mathbf{x}_{@p}^{+}) + \Phi \mathbf{p}, \tag{9}$$

$$\frac{d\mathbf{p}}{dt^{+}} = \Psi \left[ \mathbf{k} - (\mathbf{k} \cdot \mathbf{p})\mathbf{p} \right] + \frac{1}{2}\omega_{@p}^{+} \wedge \mathbf{p}, \qquad (10)$$

where time, length, and velocity were made dimensionless using  $u_{\tau}$  and v. The key parameters in Eqs. (9) and (10)



FIG. 1. Gyrotactic micro-organisms swim with velocity  $v_s$  in the direction given by the orientation vector **p**, set by a balance of torques: The torque due to cell asymmetry (bottom heaviness:  $\mathbf{T}_{grav}$ ), which tends to align the cell to its preferential orientation along the vertical direction **k**, and the torque due to flow ( $\mathbf{T}_{visc}$ ), which tends to rotate the cell according to the local velocity gradients.

are the swimming number  $\Phi = v_s/u_\tau$  and the stability number  $\Psi = \frac{1}{2B} \frac{v}{u^2}$ , which parameterises the importance of vortical overturning with respect to directional swimming. Time integration exploits a fourth-order Adams-Bashforth scheme, starting from a two-dimensional random distribution (in both space and orientation) of 10<sup>6</sup> Lagrangian swimmers at the centerplane of the channel. Swimmers are tracked using a point-particle approach, justified by the sub-Kolmogorov size typical of aquatic micro-organisms, and are injected into the flow at a concentration low enough to consider dilute conditions: the effect of the swimmers on turbulence is neglected (one-way coupling) as well as collisions between swimmers. Periodic boundary conditions are imposed on swimmers moving outside the computational domain in the horizontal (homogeneous) directions. In the wall-normal direction, the swimmers rebound elastically at both boundaries. The fluid velocity and vorticity at the instantaneous location of the swimmer is obtained through interpolation based on 6th-order Lagrange polynomials.

An extensive campaign of direct numerical simulations, summarized in Table I, was performed to investigate the role of stratification on the motion of the swimmers. All simulations were run at a reference Prandtl number Pr = 5 and a Reynolds number  $Re_{\tau} = 171$ , with spatial a grid resolution of  $128 \times 128 \times 257$  points in the streamwise, spanwise, and vertical directions, respectively.<sup>43</sup> The dimensionless time step used to integrate the governing equations is  $dt \cdot u_{\tau}/h = 2 \cdot 10^{-4}$ . Three different values of the Grashof number are considered in this study: Gr = 0,  $Gr = 3.02 \cdot 10^5$ , and  $Gr = 9.15 \cdot 10^5$ , yielding shear Richardson numbers  $Ri_{\tau} = 0$ ,  $Ri_{\tau} = 165$ , and  $Ri_{\tau} = 500$ , respectively. The shear Richardson number,  $Ri_{\tau} = Gr/Re_{\tau}^2$ , measures the importance of fluid buoyancy compared to fluid inertia. Note that Gr is changed by changing the temperature gradient at the free surface.<sup>25</sup> For each value of  $Ri_{\tau}$ , we considered a fixed value of the swimming number ( $\Phi = 0.048$ ), corresponding to a dimensional swimming velocity  $v_s = 100 \ \mu m/s$ typical of Chlamydomonas augustae cells,<sup>3,5</sup> but three different values of the stability number ( $\Psi_H = 1.13$ ,  $\Psi_I = 0.113$ ,  $\Psi_L = 0.0113$ ), corresponding to B = 0.054, 0.54 and 5.4 s, respectively: These values fall within the typical range of motile phytoplankton species  $(0.1 \ s < B < 10 \ s)$ . We remark here that, in the present flow configuration, the Kolmogorov time scale varies from  $\tau_{K,min}^+ \simeq 2$  at the wall to  $\tau_{K,max}^+ \simeq 13$ at the free surface.<sup>24</sup> Therefore, the selected values of the

TABLE I. Summary of the simulation parameters.

Simulation	Ψ	$Re_{\tau}$	$Ri_{\tau}$	Φ
S1.1	0.0113			
S1.2	0.113	171	0	0.048
S1.3	1.13			
S2.1	0.0113			
S2.2	0.113	171	165	0.048
\$2.3	1.13			
\$3.1	0.0113			
S3.2	0.113	171	500	0.048
\$3.3	1.13			

stability number  $\Psi$  correspond to three different physical instances. For a small value of the stability number, we have  $\Psi_L \cdot \tau^+_{K,max} \sim \mathcal{O}(10^{-1})$ , representing the case in which the time scale of gravitaxis (i.e., the time the swimmer takes to reorient along the vertical direction) is large compared to the time scale of turbulence at the free surface. This implies that the dynamics of swimmers is primarily controlled by the external action of turbulence rather than by the re-orientation time of the swimmers. For a large value of the stability number, we have  $\Psi_H \cdot \tau^+_{K,max} \sim \mathcal{O}(10)$ , representing the case in which the time scale of gravitaxis is small compared to the time scale of turbulent eddies at the surface. This implies that swimmers' dynamics is likely controlled by their re-orientation time. For the intermediate value of the stability number, we have  $\Psi_I \cdot \tau^+_{K,max} \sim \mathcal{O}(1)$ : This latter instance represents the situation in which the two time scales are comparable, and the motion of the swimmers results from the competition between small-scale turbulence and gravitaxis. We remark here that, in the present flow, the quantity  $\Psi \cdot \tau_K^+$  changes with the distance from the free surface. This implies that also the relative importance of small-scale turbulence and gravitaxis changes along the vertical direction, thus adding a source of anisotropicity to plankton rising.

### **III. RESULTS AND DISCUSSION**

#### A. Stably stratified free surface turbulence

Stratified flows can sustain a variety of wavy motions that have no counterpart in unstratified flows and are therefore expected to affect the migration of the gyrotactic swimmers towards the free surface, where they can receive the sunlight and activate photosynthesis. This is explicitly shown in Fig. 2 through the use of temperature contours on a vertical x-z plane. The flow is driven from left to right by the imposed pressure gradient. Temperature, which is a transported scalar (albeit active), reproduces faithfully the structure of the flow below the free surface. Fig. 2(a) refers to the case Ri = 0, Fig. 2(b)refers to the case Ri = 165, whereas Fig. 2(c) refers to the case Ri = 500. The main mechanism driving wave formation is the suppression of vertical motions by buoyancy. This mechanism acts to restore the position of a fluid parcel whenever it is displaced vertically by the velocity fluctuations.<sup>17,34,44</sup> In the case of strong stratification (Fig. 2(c)), e.g., near the thermocline in our simulations, the fluid parcel can undergo inertial overshoot: When this happens, the parcel starts oscillating about the initial position and internal gravity waves form<sup>44</sup> (red wavy region close to the free surface in Figs. 2(b) and 2(c)). The extension and the persistence of internal gravity waves are apparent, in particular for large  $Ri_{\tau}$ .

We start our statistical description of the flow by considering the mean temperature distribution. The behavior of the normalized mean temperature profile  $\langle (\theta - \theta_s)/\Delta\theta \rangle$ , with  $\theta_s$  the surface temperature and  $\Delta\theta$  the top-to-bottom temperature difference, is shown in Fig. 3(a) as a function of  $z^+$ . Brackets indicate time and space average. The averaging procedure is the same as that adopted in Ref. 25 and is based on snapshots of the velocity field separated in time exceeding the correlation time and in space exceeding the integral scale. We clearly notice that the mean temperature profile has



FIG. 2. Contour maps of the temperature field on a x-z plane for simulation at  $Ri_{\tau} = 0$  (panel (a)),  $Ri_{\tau} = 165$  (panel (b)), and  $Ri_{\tau} = 500$  (panel (c)).

a two-layer structure: a thick bottom layer across which the temperature changes mildly ( $z^+ > 40$  in Fig. 3(a)) and a thin top layer close to the interface where large temperature variations are observed ( $z^+ < 40$  in Fig. 3(a)). While the bottom layer ( $z^+ < 40$ ) defines the extension of the well-mixed temperature region (typically characterized by active turbulence), the top layer  $z^+ > 40$  defines the extension of a low mixing region called the thermocline and dominated by internal gravity waves. Note that the thickness of the thermocline increases for increasing  $Ri_{\tau}$ .

Next, we consider how the thermocline and the internal waves it generates influence the mean flow field in free-surface turbulence. In Fig. 3(a) the mean streamwise velocity profile  $\langle u_x^+ \rangle$  (in wall units) is shown for the three regimes of stratification as a function of the wall-normal coordinate  $z^+$ . Since our simulations are run keeping the driving pressure gradient constant, the slope of the velocity profile at the bottom wall is invariant among the different simulations. For increasing stratification, however, two different regions can be observed:

a turbulent region near the bottom wall ( $z^+ > 85$  for  $Ri_{\tau} = 500$ ), where mean turbulence properties are not significantly affected by stratification, and a buoyancy-affected region near the free surface ( $z^+ < 85$  for  $Ri_\tau = 500$ ), where stratification induces an increase of the flow velocity (and hence of mass flow rate). This increase becomes more evident at higher  $Ri_{\tau}$  and is due to a reduction of the wall-normal momentum transport and, in particular, of the wall shear stress.<sup>25</sup> In Fig. 3(c) we show the mean shear,  $\langle \partial_7 u^+ \rangle$ , at varying stratification levels. The filled circles in the inset of Fig. 3(c) indicate the point where  $\langle \partial_{\tau} u^+ \rangle$ reaches the maximum value in the upper portion of the domain: This point is located at  $z^+ \simeq 15$  (respectively, 26) wall units below the surface at  $Ri_{\tau} = 165$  (respectively,  $Ri_{\tau} = 500$ ). The gray rectangles highlight the region where the value of  $\langle \partial_z u^+ \rangle$ is at least 30% higher than the centerline value measured at  $z^+ \simeq 85$  (referred to as the higher-than-mean shear region hereinafter). As shown by Ref. 25, temperature variations around the  $\langle \partial_z u^+ \rangle$  peak are strong enough to form internal gravity waves.



FIG. 3. Mean fluid temperature (a), mean streamwise fluid velocity (b) and mean vertical fluid shear (c) in stably stratified free-surface turbulence at  $Ri_{\tau} = 0$  (solid line),  $Ri_{\tau} = 165$  (dashed line), and  $Ri_{\tau} = 500$  (dotted line). The filled circles in panel (c) highlight the location of maximum mean shear generated by stratification, while the gray rectangles visualise the vertical extent of the sub-surface region where  $\langle \partial_z u^+ \rangle$ is at least 30% higher than the centerline value (measured at  $z^+ \approx 85$ ).

#### B. Micro-organism orientation and rising fluxes

As discussed in the Introduction, swimmers can be significantly destabilized in regions of strong velocity and temperature gradients. To examine how such destabilisation may affect the capability of swimmers to trespass the thermocline, Lagrangian tracking was performed releasing cells midway between the bottom wall and the free surface (z/h = 0.5)with random initial orientation. The resulting time evolution of swimmer concentration, C(z, t), along the vertical direction is shown in Fig. 4 for all cases simulated in the  $(Ri_{\tau},$  $\Psi$ ) parameter space: Each column in Fig. 4 corresponds to a specific strength of stratification and each row to a specific strength of gyrotaxis. The concentration C(z, t) represents a volumetric number density and has been obtained by coarsegraining the instantaneous vertical position of the swimmers on horizontal fluid slabs: The colormap is such that green (respectively, blue) indicates a high (respectively, low) concentration of swimmers; the black line in each panel represents the vertical coordinate of the center of mass of the swimmers' distribution,  $z_{CM} = \frac{1}{N} \sum_{j=1}^{N} z_j(t)$ , where N is the total number of swimmers and  $z_j(t)$  is the vertical position of the *j*th swimmer at time t. The white lines in each panel represent the positive standard deviation,  $\sigma^+ = \sqrt{\frac{1}{N} \sum_{j=1}^{N} \left[ z_j^+(t) - z_{CM} \right]^2}$ , and the negative standard deviation,  $\sigma^- = \sqrt{\frac{1}{N} \sum_{j=1}^{N} \left[ z_j^-(t) - z_{CM} \right]^2}$ , of the distribution around the center of mass, with  $z_i^+(t)$  (respectively,  $z_i^{-}(t)$ ) the position of swimmers having a vertical coordinate larger (respectively, smaller) than  $z_{CM}$ .

In the absence of stratification (panels (a), (d), and (g) in Fig. 4), swimmers eventually reach the surface regardless of their vertical stability and concentration in the upper part of the domain steadily increases in time. Clearly, surfacing is quicker for swimmers with a higher vertical stability (stronger gyrotaxis due to predominant gravitaxis). The situation is different in the presence of stratification, especially at a high enough Richardson number (e.g.,  $Ri_{\tau} = 500$ , panels

(c), (f), and (i) in Fig. 4). Surfacing of swimmers with low or intermediate gyrotaxis is inhibited and a more uniform spatial distribution is attained. A sub-surface layer depleted of swimmers is clearly visible in Figs. 4(c) and 4(f): This layer develops around the local maximum of mean shear highlighted in the inset of Fig. 3(b). Only in the  $\Psi_H$  case (Fig. 4(i)), the accumulation at the surface from time  $t^+ \simeq 1500$  onwards is observed.

To corroborate these qualitative observations, in Fig. 5 the instantaneous wall-normal concentration profiles computed at fixed stratification and varying gyrotaxis are presented. The unstratified-flow case in panel (a) is shown as reference. The horizontal line in panels (b) and (c) represents the location of maximum mean shear already shown in Fig. 3, whereas the gray areas correspond to regions of higher-than-mean shear. Results refer to the last time step of the simulation ( $t^+ \approx 2000$ ) and demonstrate that the flow region below the free surface becomes more and more depleted of swimmers as stratification levels increase. At  $Ri_{\tau} = 165$ , only swimmers with intermediate or high gyrotaxis exhibit a vertical stability sufficient to accumulate at the free surface. In all cases, however, a significant decrease of concentration is found precisely in the region of the thermocline. This correlation is even more evident at  $Ri_{\tau} = 500$  (Fig. 5(c)): Accumulation is prohibited for all re-orientation times considered in this study, and the vertical extent of the depletion layer increases as  $\Psi$  decreases. This is an obvious effect of the mean shear and becomes more evident when swimmers react slowly to external fluid velocity fluctuations and gradients.

A general conclusion that can be drawn from Fig. 5 is that, differently from the case of unstratified steady shear flows or homogeneous isotropic turbulent flows,<sup>7,10,11,16,23,27,32,39,42</sup> no gyrotactic trapping occurs and local peaks of concentration do not develop within the thermocline. This happens because our simulations mimic as close as possible a real physical environment (with stratification levels typical of temperate or tropical regions<sup>41</sup>): In this case, the characteristic time scale of turbulent advection along the vertical direction is much shorter



FIG. 4. Time evolution of swimmer concentration along the vertical direction,  $C(z, t)/C_0$ , with  $C_0 = C(z, t = 0)$ . Concentration was computed by coarsegraining the instantaneous vertical position of the swimmers starting from a two-dimensional random distribution at the channel centerplane (z/h = 0.5) and a random distribution of orientations. Rows (a)-(c) swimmers with low gvrotaxis,  $\Psi_L$ , (d)–(f) swimmers with intermediate gyrotaxis,  $\Psi_I$ , (g)-(i) swimmers with high gyrotaxis,  $\Psi_H$ . Columns: (a), (d), and (g) low stratification,  $Ri_{\tau}$ = 0; (b), (e), and (h) intermediate stratification,  $Ri_{\tau} = 165$ ; (c), (f), and (i) high stratification,  $Ri_{\tau} = 500$ . The black line in each panel represents the center of mass  $z_{CM}(t)$  of the distribution and the white lines represent the standard deviation above and below  $z_{CM}(t)$ .

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(a) 0

 $z^+$ 

40

80

120

160

0.2

 $\Psi_{|}$ 

 $\Psi_{I}$ 

 $\Psi_{\mathsf{H}}$ 

1.

С

Ri<sub>τ</sub>=500

5.

 $\langle \partial_z u \rangle_{max}$ 

40

80

120

160

5. 0.2





(one order of magnitude at least) than the time scale of selfpropelling advection. Therefore, the concentration profiles in the turbulence-dominated region are always smoothed out by turbulent advection mechanisms.

(b)

0

40

80

120

160

5.

0.2

 $Ri_{\tau}=0$ 

1.

С

 $\left< \partial_z u \right>_{max}$ 

 $\Psi_{I}$ 

 $\Psi_{\mathsf{H}}$ 

1.

С

Ri<sub>τ</sub>=165

To examine further stratification effects on swimmer dynamics, we next present orientation statistics. In particular, Fig. 6 shows the probability density function (pdf) of the streamwise and wall-normal orientation vector components,  $p_x$ and  $p_z$ , respectively, for the intermediate value of the stability number  $(\Psi_I)$  at varying Richardson numbers. Only swimmers well inside the thermocline  $(6 < z^+ < 30 \text{ for } Ri_\tau = 165 \text{ and}$  $10 < z^+ < 50$  for  $Ri_{\tau} = 500$ ) during the last stage of the simulation ( $\Delta t^+ \simeq 130$ ) are considered to emphasize shear effects on directional swimming. It is apparent that, in the absence of stratification (solid lines in Fig. 6), motile organisms are well aligned in the vertical direction and tend to swim upwards, as suggested by the symmetry of the pdf of  $\langle p_x \rangle$  in Fig. 6(a) and by the sharp peak close to unity that the pdf of  $\langle p_z \rangle$  exhibits in Fig. 6(b). An increase of stratification corresponds to a negatively skewed distribution for  $\langle p_x \rangle$  and a much flatter distribution for  $\langle p_z \rangle$ . A marginal effect is observed for  $\langle p_y \rangle$  (not shown), its pdf being always symmetric with respect to  $\langle p_v \rangle = 0$ : The absence of preferential alignment in the transverse direction demonstrates that there is no coupling between the three orientations. Altogether, these results confirm that swimmers tend to lose their stability in the direction of gravity once they enter the thermocline but also show that preferential alignment with the streamwise flow direction is attained.

To correlate swimmer orientation with vertical migration and surfacing, in Fig. 7 we show the behavior of  $\langle p_x \rangle$  and  $\langle p_z \rangle$  along the wall-normal direction, for all simulated cases. We focus our attention on the upper portion of the flow domain, where the swimmers interact with the thermocline. In the  $Ri_{\tau} = 0$  case (panels (a) and (d) in Fig. 7),  $\langle p_x \rangle$  is always small while  $\langle p_z \rangle$  increases with  $\Psi$ : It is clear that, even without thermal stratification, turbulence can disrupt directional swimming for low gyrotaxis. A similar finding has been reported for floaters.<sup>24,25</sup> As stratification increases, gravitaxis might become predominant, also allowing for swimmers to reach an equilibrium orientation in the direction opposite to gravity. In the  $Ri_{\tau}$  = 165 case (panels (b) and (e) in Fig. 7), weak (respectively, strong) vertical swimming is again observed for low (respectively, high) gyrotaxis: For the  $\Psi_L$  case, this indicates that local turbulent fluctuations are still strong enough to destabilize the directional motion of the swimmers, since  $\Psi_L \cdot \tau^+_{K,max} \mathcal{O} \sim (10^{-1})$  and stratification-induced shear seems to bring minor quantitative changes to the statistics; for the  $\Psi_H$  case, this result indicates that cell motility is mainly determined by gravitaxis, since  $\Psi_H \cdot \tau^+_{K,max} \mathcal{O} \sim (10)$  (swimmers reorient quickly in the vertical direction). In this limit, we always find  $\langle p_z \rangle \simeq 1$ . A less trivial behavior is observed for the intermediate case,  $\Psi_I$ : Compared to a neutrally buoyant flow, significantly higher values of  $\langle p_x \rangle$  (higher also than those attained for  $\Psi = \Psi_H$  and  $\Psi = \Psi_L$ ) associated with lower values of  $\langle p_z \rangle$ are now observed inside the thermocline. This non-monotonic behavior of  $\langle p_x \rangle$  with  $\Psi$  is likely due to a mean-shear effect that becomes more evident when  $\Psi_I \cdot \tau^+_{K,max} \mathcal{O} \sim (1)$ . In this situation, the re-orientation time of the swimmers is of the same order of the characteristic time scale of the turbulent eddies at the free surface: When these two competing actions balance, a



FIG. 6. Pdf of swimmer orientation components for  $\Psi_I$  at different Richardson numbers: (a)  $p_x$ , (b)  $p_z$ . Only swimmers inside the thermocline are considered.



FIG. 7. Mean orientation of the swimmers,  $\langle p_i \rangle$ , along the wall-normal direction at varying gyrotaxis ( $\Psi_L$ : solid line,  $\Psi_I$ : dashed line,  $\Psi_H$ : dotted line). The free surface is located at  $z^+ = 0$ . Panels refer to different stratification regimes: (a) and (d)  $Ri_{\tau} = 0$ ; (b) and (e)  $Ri_{\tau} = 165$ ; (c) and (f)  $Ri_{\tau} = 500$ . The horizontal line in panels (b), (c), (e), and (f) indicates the location of maximum shear in the upper portion of the domain, surrounded by the higher-than-mean shear regions already shown in Fig. 3.

mean-shear effect can be observed. Note that once swimmers are able to trespass the thermocline and reach the surface, they tend to align in the horizontal flow direction because wall-normal turbulent fluctuations decay to zero and swimmers are brought about only by the residual streamwise and spanwise fluid velocities.<sup>25</sup>

The main conclusion that can be drawn from the concentration and orientation statistics examined in this section is that stratification has a strong damping effect on the surfacing of motile micro-organisms, which exhibit a narrower vertical spreading within the flow. Only organisms with highenough gyrotaxis (namely, strong-enough bottom-heaviness) can maintain their ability to swim upwards.

## **IV. CONCLUSIONS**

In this study, we used direct numerical simulation and Lagrangian tracking to investigate the role of stable stratification on the vertical migration of gyrotactic swimmers in a free-surface turbulent channel flow. An extensive campaign of simulations was performed for different stratification levels and different re-orientation times of the swimmers, representative of common motile phytoplankton species and corresponding to different quickness in responding to external fluctuations. In the present physical configuration, the flow is driven by a constant pressure gradient and the stable stratification is obtained by imposing a constant heat flux at the free surface and an adiabatic condition at the bottom

wall. Simulations were run at a Prandtl number Pr = 5, shear Richardson numbers  $Ri_{\tau} = 0$ , 165, and 500, and stability numbers  $\Psi = 0.0113, 0.113, and 1.3$ . In such a flow configuration, internal gravity waves are generated near the free surface, whereas active turbulent bursting phenomena occur near the bottom wall. Flow field modifications due to thermal stratification are found to influence the ability of swimmers to reach the surface. In particular, we find that stratification modifies the vertical spread of the swimmers and their orientation with respect to the direction of gravity. For all gyrotactic re-orientation times considered in this study (spanning two orders of magnitude of the stability number), we observe a reduction of the cell rising speed and temporary confinement under the thermocline: If re-orientation is fast, cells make it through the thermocline within the simulated time span; if re-orientation is slow, confinement lasts much longer because cells align in the streamwise direction and lose their ability to swim upwards. As a result, sub-surface layers depleted of cells form across the region of maximum hydrodynamic shear created by stratification. We believe that these findings provide useful indications to parameterize the influence of stable thermal stratification on the migration of motile algae (phytoplankton cells, in particular) and to develop models for predicting their dispersion inside large water bodies.

A future development of this study is the inclusion of cell morphology and shape effects. In this study, we have considered spherical swimmers (e.g., the *Chlamydomonas*-like algae). Yet, many motile organisms are characterized by a non-spherical shape and changes in morphology can dramatically affect the function of these organisms in fluid flows: For example, elongation changes flow-induced cell rotation, thus affecting nutrient uptake.<sup>12</sup> Non-spherical particles are known to respond not only to the turbulent vorticity but also to turbulent strain: As a result, the orientation of non-spherical swimmers becomes correlated with the velocity gradient tensor, and the resulting alignment depends strongly on the shape.<sup>13,42</sup> Zhan et al.<sup>42</sup> have shown that, even in the absence of both stratification and gyrotaxis, elongated micro-swimmers in homogeneous isotropic turbulence exhibit some level of clustering whereas spherical swimmers remain uniformly distributed. An opposite behavior is observed for gyrotactic micro-swimmers: elongated ones remain more uniformly distributed, whereas spherical ones show significant clustering. This finding was explained considering the shape-dependent sensitivity to the local shear: Elongated swimmers react more slowly to the combined action of vorticity and gravity and therefore need longer time to accumulate. Clearly, the coupling with stratification is expected to further modify swimmer dynamics, with possible effects on their capability to form sub-surface clusters and/or thin layers near the thermocline.

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