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Research papers

Trapping of gyrotactic organisms in an unstable shear layer

Martín S. Hoecker-Martínez*, William D. Smyth

College of Oceanic and Atmospheric Sciences, Oregon State University, 104 COAS Administration Building, Corvallis, OR 97331-5503, United States

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Abstract

To explore new mechanisms for planktonic thin layer formation, particle and continuum models of gyrotactically swimming phytoplankton are embedded in simulations of a dynamically unstable stratified shear layer. Two trapping mechanisms are observed in the developing Kelvin–Helmholtz (K–H) billow train. Within the K–H billows, a particle can remain preferentially in downwelling regions, cancelling its upward swimming motion. In the braids that separate the billows, intense shear defeats the gyrotactic stabilization mechanism and causes cells to tumble. Particle and continuum models are compared statistically to reveal both consistencies and weaknesses in each. A scaling based on Reynolds number and swimming speed is used to predict the maximum concentration generated by an instability event. Although K–H billows are short lived in comparison with planktonic thin layers observed in the coastal oceans, the resulting trapping causes rapid aggregation. We conclude that trapping in a growing K–H instability could contribute to the development of the observed cell concentrations.

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1. Introduction

Shear flows can disorient motile phytoplankton, in some conditions causing them to aggregate (Durham et al., 2009). Dense biological layers of thickness $\sim 1$ m have been observed in fjords (Dekshenieks et al., 2001) as in more open coastal areas (Cheriton et al., 2007; Churnside and Donaghy, 2009; Benoit-Bird et al., 2009; Steinbuck et al., 2009; Sullivan et al., 2010a). Spatial and temporal distribution patterns of phytoplankton determine which grazing behaviors will be successful at higher trophic levels. They also affect the planning and interpretation of biological sampling efforts, which include implicit assumptions about the distribution. Distributions are controlled by the surrounding flow and by swimming behavior: speed and orientation. One mechanism of orientation is gyrotaxis, wherein a gravitational torque acts as a restoring force and flow vorticity acts to twist the organisms away from a vertical orientation (Kessler, 1986; Durham et al., 2009, 2011). Development of stratified shear flow is often understood through the evolution of unstable Kelvin–Helmholtz (K–H) modes (Miles, 1961; Hazel, 1972; Corcos and Sherman, 1984; Klaassen and Peltier, 1985, 1991; Caulfield and Peltier, 1994, 2000; Smyth and Moum, 2001; Smyth et al., 2011). In this study we focus on the interaction of a motile gyrotactically orienting organism with a growing Kelvin–Helmholtz billow train.

The ability of micro-organisms to propel themselves through the fluid can create complex patterns and interactions between the underlying flow field and the concentration. For phytoplankton, the magnitude of the swimming velocity $V_{s}$ is much smaller than the flow velocity, so that the relative motility $V_{r} = V_{s}/U$ is much less than one, where $U$ is a characteristic fluid velocity. The low relative motility does not preclude vertical migration in the water column, as oceanic flows are dominated by horizontal motions. Non-zero $V_{r}$ distinguishes the types of aggregation possible (Childress et al., 1975; Kessler, 1986; Pedley et al., 1988; Torney and Neufeld, 2007) from the analogous trapping of sinking inert particles (Stommel, 1949; Fung, 2000). For a uniform concentration and swimming orientation in non-divergent flow, there can be no accumulation or rarefaction. Only if orientation is allowed to vary can aggregations emerge from a state with uniform concentration and orientation.

The aggregation of small organisms into coherent structures has been observed at many scales. In the coastal ocean large layer structures have been observed. There is not yet a consensus definition of biological thin layers, though there are commonalities among the differing definitions. In an overview of the Layer Organization in the Coastal Ocean (L.O.C.O.) project Sullivan et al. (2010b) summarize the diverse definitions into three qualitative rules:

(1) The layer structure must persist over time and space;
(2) the layer vertical thickness must be below some maximum,
and there must be an objective, clearly defined method for calculating the vertical thickness; and (3) the layer maxima must meet a minimum signal strength (e.g., 2 or 3 times greater than background values).

Here, we investigate the possibility that Kelvin–Helmholtz instability could lead to a layer which satisfies these criteria.

Under controlled conditions at laboratory scales the aggregation mechanisms of particular species have been studied (e.g., Kessler, 1986; Durham et al., 2009). Initial studies focused on cases with no background flow (Kessler, 1986; Childress et al., 1975; Pedley et al., 1986). More recently, Durham et al. (2009) showed how an imposed shear can cause the aggregation of the model gyrotactic organism Chlamydomonas nivalis into laminar structures in a laminar. These experiments suggest a possible mechanism for the formation of concentrated layers of motile species as they traverse a flow field.

The flow geometry we examine is that of a shear layer including the influence of stratification. This system is an idealized representation of the shear at the base of the surface mixed layer (e.g., Woods, 1968; Spigel et al., 1986; Dale et al., 2008). In strong shear there is a dynamic Kelvin–Helmholtz instability, which causes the shear layer to coalesce into a series of Kelvin–Helmholtz billows connected by thin regions of intense shear. Fine scale observations of displacements consistent with Kelvin–Helmholtz billows have been observed in the seasonal thermocline (Woods, 1968) tidal flows (Geyer and Smith, 1987; Seim and Gregg, 1994), internal solitary waves (Moum et al., 2003), and in the deep ocean (van Haren and Gostiaux, 2010). Little is known of the horizontal scales of these events. Moum et al. (2011) observed K–H billow trains with ~10 billows in the along stream direction and Thorpe (2002) has observed a knotted in the cross stream direction which occurs at ~4 times the down stream spacing before more complex flow patterns emerge. Additional regions where the Richardson number is at or below 1/4, and where K–H billows can therefore grow (Miles, 1961; Howard, 1961), have been observed associated with biological layers (Dekshenieks et al., 2001) and elsewhere in the coastal ocean (e.g., Suanda, 2009). Turbulence statistics in mixing patches observed in the thermocline compare favorably with those drawn from direct numerical simulations (DNS) of Kelvin–Helmholtz billows (Smyth et al., 2001).

The coupling of shear flows and plankton population dynamics to form laminar structures have most often been modeled assuming only advective and diffusive forcings (Franks, 1995; Stacey et al., 2007; Birch et al., 2008). These mechanisms rely on shear to steer a plankton aggregation into a planar shape. Durham et al. (2009) model gyrotactic stability as a critical point in a continuum model where the transition to gyrotactic instability is discontinuous and the orientation is replaced with a null vector if the ratio of viscous to gravitational torques exceeded the stability criterion in the steady shear flow. Others (Pedley and Kessler, 1990; Lewis, 2003; Thorn and Bearon, 2010) use a probability distribution of orientation. Hopkins and Fauci (2002) use the full torque balance including inertial terms and solve the second order differential equation for orientation in their particle model. The torque balance without the inertial term is used by the particle model of Durham et al. (2009).

In the present study we use a two dimensional direct numerical simulation of stratified flow to examine the distribution of simple gyrotactic organisms in the presence of an unstable shear layer. The two-dimensional model is restricted to the early stages of the K–H instability, shortly after the appearance of overturns a Rayleigh–Bernard convective instability in the billows causes the flow to become fully three-dimensional (Klaassen and Peltier, 1985, 1991; Smyth and Moum, 2001). Organisms are modeled both as individual particles and as a continuous concentration field to study the trapping and aggregation of gyrotactic organisms in the developing shear instability.

The detailed description of the relevant dynamics for small gyrotactic particles in stratified shear flow are elaborated in Section 2 and we describe the numerical methods to simulate these phenomenon. Results are given in Section 3 and our interpretation is given in Section 4. Appendices give further information on numerical methods and physical assumptions made in the design of the models.

2. Methods

Here we describe our model for the flow physics as well as individual and continuum models for the biology.

2.1. Flow model

The fluid is modeled using the Boussinesq approximation. For notational simplicity buoyancy $b = -g/\rho_0 (\rho - \rho_0)$ and reduced pressure $p = P/\rho_0$ are used instead of density $\rho$ and pressure $P$. The constants $\rho_0$ and $g$ represent mean density and gravitational acceleration respectively. This reduces the Boussinesq equations to

\[
\frac{\partial u_i}{\partial t} = -u_j \nabla u_i - \nabla p + b \delta_{ij} + v \nabla^2 u_i
\]  
\[
\frac{\partial b}{\partial t} = -u_j \nabla b + k \nabla^2 b
\]  
\[
\nabla^2 p = -((\nabla u_i)\nabla^2 u_i) + \frac{\partial b}{\partial \xi_3}
\]

where Eq. (3) follows from Eq. (1) and the continuity condition $\nabla u_i = 0$. The simulation domain is horizontally periodic and free slip in the vertical. Details of the numerical methods and code validation are given in Appendix A.

The initial state of the fluid is a two layer shear flow with no vertical velocity. At the boundary there is no horizontal stress, no vertical flow, and the buoyancy is held fixed. The initial profiles of velocity and density are given by

\[
u = \Delta U \tanh z/h
\]  
\[
\Delta b = \Delta b \tanh z/h + b_{\text{noise}}
\]

where $\Delta U$ and $\Delta b$ are half of the velocity and buoyancy difference across the layer (Hazel, 1972; Klaassen and Peltier, 1991; Smyth and Peltier, 1993). This choice of scaling gives a simple form for the initial Reynolds number $Re = \Delta U h / v$ and Richardson number $Re = \Delta b / \Delta U^2$ which govern the stability of the flow (Miles, 1961; Howard, 1961; Tennekes and Lumley, 1972).

The initial density profile (5) includes a random noise field whose amplitude is chosen so that no overturns (Thorpe, 1977) are created by the perturbation. This is accomplished by defining

\[
b_{\text{noise}} = r \times \Delta b
\]

which is the product of a uniform random variable $r \in (-0.5, 0.5)$ and a first order estimate of the difference in buoyancy $b$ between adjacent levels. The uniform random variable $r$ ensures that potential energy is placed into all available horizontal wave numbers equally.
2.2. Biological modeling

The organisms in this study are assumed to be neutrally buoyant and smaller than the Kolmogorov scale. This allows for a simplification of the governing equations. Particles smaller than flow features act as though they have no inertia and follow the flow trajectories (Crowe et al., 1996). Similarly the moment of inertia may be neglected for particles much smaller than the smallest vortices in the fluid, and we may assume the vorticity is uniform in the vicinity of the particle. This line of reasoning follows Kessler (1986) where the two principal torques are (1) the viscous torque $\tau_\nu$ of the fluid motion, opposing the relative rotation of the particle, and (2) the gravitational torque $\tau_g$ which acts to restore the orientation of the particle (Fig. 1). The action of $\tau_g$ is called gyrotactic reorientation. The equation of motion for the angular motion of the particle has the form

$$\dot{\Omega} = \frac{4\pi \rho r^3 (S - 2\Omega)}{c_r} + \frac{4\pi}{3} r^3 \rho (l \times \hat{g})$$

(7)

where $\dot{\Omega}$ is the angular acceleration, $\hat{g} = \nabla \times \vec{u}$ is the vorticity, and $\Omega$ is the angular velocity of the particle (Kessler, 1986; Hopkins and FAuci, 2002). If we assume a small particle we may ignore the inertial term, and find an equation for the angular velocity directly (Kessler, 1986; Pedley and Kessler, 1987, 1990, 1992; Jones et al., 1994; Lewis, 2003; Durham et al., 2009)

$$\dot{\Omega} = \frac{1}{2} \frac{S - \Omega}{B} \times \hat{k}$$

(8)

where $B = 3\nu/\lVert \vec{g} \rVert$ is identified as the gyrotactic reorientation time. The balance of gravitational and viscous torques can be used to define another non-dimensional number the gyrotactic stability $BS = B \Omega_1$. A body is gyrotactically unstable when the product $BS > 1$.

To model particle orientation, we use Eq. (8). We further simplify our equations by treating gyro tactic organisms as spherical objects whose moment of inertia may be ignored following Kessler (1986). The details of the spherical assumption and its validity in unstable sheared flow is shown in Appendix B. Modeling the dynamics of small organisms can be done as an ensemble of individuals or in terms of concentrations. As the number of individuals in a model increases, the collective statistics will converge to the concentration model if the two models are consistent. Individual models can yield information about trajectories and trapping mechanisms while the concentration model is more suited to showing distribution patterns. Because of these disparate strengths and weaknesses both types of models are developed for gyro tactic organisms in a shear flow.

2.2.1. Particle model

The particle tracking model uses bilinear interpolation (Press et al., 1992) of the velocity $\vec{u}$ and vorticity $\vec{S}$ to propagate the position $\vec{x}$ and orientation $\vec{p}$ of each organism. The position is advected by fluid flow and by the organism’s motility, while the orientation is dictated by the balance of viscous and gravitational torques in Eq. (8). These give rise to

$$\frac{d\vec{x}}{dt} = \vec{u} + \nabla \cdot \vec{p}$$

(9)

$$\frac{d\vec{p}}{dt} = \left( \frac{1}{2} \frac{S - \vec{g}}{6v} \vec{p} \times \hat{x}_3 \right) \times \vec{p}$$

(10)

where the term in parentheses is the rate of rotation of the particle (Durham et al., 2009). Since $\vec{p}$ represents an orientation and Eq. (10) preserves magnitude, $\lVert \vec{p} \rVert = 1$.

2.2.2. Continuum model

The concentration of the organisms is governed by advection by the fluid, their own motility and diffusion. This is expressed through a flux conservation equation

$$\frac{\partial c}{\partial t} + V_x(\partial c/\partial x + V_y p_c) = \nabla \cdot (D \nabla c)$$

(11)

The left hand side of Eq. (11) is the sum of local aggregation, fluid advection, and biological advection rates. This sum is equal to the divergence of a diffusive flux on the right hand side of Eq. (11). The particle model has no analog for this diffusive flux; it is added to maintain numerical stability in regions of steep concentration gradients.

To distinguish between the effects of a mean shear on the motile species and the dynamically unstable flow condition modeled later it is useful to begin by considering steady shear flow (4) with gyrotactically stable orientation ($BS < 1$) and no diffusion, viscosity or streamwise variability. This reduces Eq. (11) to an one dimensional conservation equation

$$\frac{\partial c}{\partial t} = -V_x \frac{\partial c}{\partial x}$$

(12)

If we further assume the organisms cross the shear layer slowly compared to the shear timescale, equivalently $V_x = 1$, then $\vec{p}$ may be assumed to be the equilibrium value of Eq. (10)

$$\vec{p} = X_{BS_{\text{max}}} \text{sech}^2 \frac{x}{h} + \frac{z_{\text{max}}}{h} \sqrt{(BS_{\text{max}})^2 - \left( \text{sech}^2 \frac{x}{h} \right)^2}$$

(13)

where $B$ is the reorientation time and $S_{\text{max}} = U/h$ is the maximum shear. Seeking a steady state solution of Eq. (12) assuming a background concentration $c_0$ yields

$$c = c_0 \sqrt{1 - (BS_{\text{max}}^2 \text{sech}^2 \frac{x}{h})^2}$$

(14)

The vertical profiles of concentration and swimming orientation are illustrated in Fig. 2.

The solution (13) and (14) relies on steady flow and gyrotactic stability $BS_{\text{max}} < 1$. Though these assumptions are not valid for the time varying flow considered later, the solution is informative. It shows the nature of the transition from stable to unstable orientation and highlights $BS_{\text{max}}$ as a critical non-dimensional quantity. Diffusive and advective effects will shift the orientation away from the equilibrium value with the local vorticity. The transition will likely occur at $BS_{\text{max}} > 1$ when these effects are included but this simple model suggests a smooth increase in the peak concentration with increasing shear in the stable regime.

We now relax the assumptions of steady flow and gyrotactic stability. To allow tumbling organisms and dynamic flow we model the mean swimming orientation over a grid box $p_i$ and
assume the swimming speed may be taken to be constant \( V_s \) and the concentration flux \( V_s c_{pi} \) obeys the continuous analog of Eq. (10)

\[
\frac{\partial}{\partial t} (V_s c_{pi}) + \nabla_j (u_j V_s c_{pi} + V_s^2 p_j p_i) = V_s \alpha_{ijk} \Omega_k p_i + D \nabla^2 (V_s c_{pi})
\]  

where \( \Omega \) is the rate of rotation given by Eq. (8) and the diffusivity \( D \) is assumed constant. By tracking both concentration and orientation we can follow the system through the transition to gyrotactic instability where \( BS > 1 \). Eqs. (11) and (15) can be solved for the Eulerian time evolution for the concentration and orientation fields

\[
\frac{\partial c}{\partial t} = -(u_j + V_s p_j) \nabla_j c - V_s c \nabla_j p_i + D \nabla^2 c
\]

(16)

\[
\frac{\partial p_i}{\partial t} = \epsilon_{ijk} \Omega_k p_j - (u_j + V_s p_j) \nabla_j c + D \nabla^2 p_i + \frac{2D}{c} (\nabla_j c/\nabla_j p_i)
\]

(17)

Together Eqs. (16) and (17) form a continuum model of gyrotactic organisms. These equations are highly non-linear, in particular the final term in Eq. (17) is proportional to \( 1/c \). We are seeking to model large variations in the concentration and cannot a priori dismiss these interactions. Despite the complex nature of the diffusive terms there is a Laplacian term for both the concentration and orientation that suggests the use of Fourier decomposition for an exact solution similar to Eqs. (A.6) and (A.7). If \( p_i \) is to serve as a unit vector representing orientation we must preserve its unit length. Eq. (17) does not conserve magnitude exactly. The unitary nature of the orientation is preserved in a separate normalizing step

\[
p_i = \frac{p_i^*}{\sqrt{p_i^* p_i^*}}
\]

(18)

where \( p_i^* \) is the result of stepping (17) forward in time.

The boundary conditions of the flow suggest boundary conditions for the concentration and orientation. Far from the shear layer the orientation is vertical \( p_i = \delta_{ij} \) and the concentration is a background value \( c_0 \). The background value is arbitrary and we may normalize by \( c_0 \). These far field conditions argue for constant boundary conditions in the vertical and corresponds to an expansion into a sine series in the vertical with the boundary values of \( c \) and \( p_i \) subtracted. The variables which enter into the Fourier transform are a reduced concentration \( \zeta = (c/c_0) - 1 \) and orientation \( p_i = p_{i} - \delta_{ij} \).

\[
e^{-i \zeta c} \frac{\partial}{\partial t} \langle e^{i \zeta c} \mathcal{F}(c') \rangle = -\mathcal{F}(u_j + V_s (p_j + \delta_{j3})) \nabla_j c' + \mathcal{F}(V_s c) \nabla_j p_i' 
\]

(19)

\[
e^{-i \zeta c} \frac{\partial}{\partial t} \langle e^{i \zeta c} \mathcal{F}(p_i') \rangle = -\mathcal{F}(u_j + V_s (p_j + \delta_{j3})) \nabla_j c' + \mathcal{F}(2D \nabla_j c / \zeta) + \mathcal{F}(\epsilon_{ijk} \Omega_k (p_i + \delta_{i3}))
\]

(20)

We assume at vertical boundaries the organisms maintain their initial concentration and orientation. A uniform initial state is used for concentration and orientation with the assumption that a near steady state will develop in the biology before the flow instability has grown significantly.

2.3. Simulation parameters

Simulations were made at various points in the multi-dimensional phase space (Table 1 and Fig. 3). The Reynolds number was

![Fig. 2. Steady state profiles of normalized concentration and orientation. The gyrotactic stability parameter is \( BS_{max} = 0.865 \) and the background concentration is \( c_0 = 1 \).](image)
chosen for computational tractability. A Prandtl number of 1 was used instead of the oceanic value $\sim 7$ for all runs to allow for faster computation. For the K–H instability to create overturns the Richardson number must be below 1/4. Low Reynolds numbers further depress the threshold as the increased viscosity damps the growing instability. To mimic oceanic flows, Richardson numbers are chosen to be as close to the stability limit 1/4 as numerically feasible.

The diffusivity for the biological quantities was taken to be the same as the thermal diffusivity of each run. To keep the dimensionality of parameter space manageable gyrotactic reorientation time is chosen to be $B = h_0/\Delta U_0$ so that $BS \leq 1$ everywhere in the initial flow. The parameters of each run are summarized in Table 1 and Fig. 3. For the organisms to be considered plankton $V_b \ll 1$. The range of relative motility is further constrained from above by resolution requirements $V_b < h_0/Re \Delta x$ and from below by the requirement that the biology reach a steady state before billow formation $V_b > 1/200$. The domain size is chosen to match the wavelength of fastest growing mode in a Kelvin–Helmholtz instability found by Hazel (1972) $L_x/h = 13.95$ with the weak Richardson number dependence ignored following Smyth (2003). Simulations are halted after overturns occur as the flow can no longer be modeled two dimensional flow.

3. Results

Our main focus will be on case k (Table 1) for both biological models as it is closest to an oceanic parameter regime. Concentration and individual organism tracks are used to show the interaction of the flow and the gyrotactic organisms.

3.1. Particle tracking results

The evolved state of an initially uniform random seeding of particles in the domain reflects the shape of the shear instability (Fig. 4). The enhanced shear in the braids can exceed the limit of gyrotactic stability, causing organisms to tumble. This is most clearly evident in the dotted curve in Fig. 5, which shows the evolution of a sample particle’s orientation. After $t\Delta U/h > 220$, the particle rotates rapidly. The inverted organisms appear first in the braid region. The individual particle track in Fig. 5 and the inverted organisms (dark red and blue) in Fig. 4 illustrate the necessary conditions for entrapment as the organism travels through the growing instability. In Kelvin–Helmholtz billow trains, high vorticity fluid is moved from the braids to the billows. A particle which enters the braid region begins to rotate, and thereafter more closely follows the trajectory of a fluid parcel. The particle in Fig. 5 is essentially a tracer after scaled time 220, when it travels along the braid instead of across it (solid curve in Fig. 5b). By this mechanism, organisms are steered away from the braids and into the rotating billows.

Within the billow, vorticity is lower than in the braids and he particle may maintain a stable orientation as exemplified by the gray dotted curve in Fig. 6b. A stable orientation in the billow may not be sufficient for the particle to cross the shear layer, however. The vertical velocities in the circulating billow can exceed the swimming velocity $V_s$ in which case the trapping mechanism of Stommel (1949) can come into play (Fig. 6). The cell follows a quasi-elliptical trajectory that is offset horizontally from the center of the billow, such that it spends an increased fraction of its cycle in regions of downward flow. This asymmetry cancels the upward swimming motion, with the result that the cell remains trapped in the billow.

3.2. Continuum model results

As the instability grows, local concentration maxima are generated around the edge of the recirculating billow region and the strained braid region. The concentration field has much smaller scales than the underlying fluid flow since the biological advection admits divergent motion, unlike the physical flow field. Fig. 7a shows a snapshot of the concentration after the instability has caused unstable stratification in the billows. At this time the maximum value of concentration is 2.7$c_0$.

The concentration maximum in the braid region is a direct analogue of the quasi steady state (14) in the initial shear layer. When the concentration of shear in the braid causes gyrotactic instability $BS > 1$, the mean orientation field oscillates, causing small scale convergences and divergences in the biological flux. During the initial growth of the Kelvin–Helmholtz instability, the vorticity field has a clearly defined maximum in the braid regions, and the resulting rotation appears in Fig. 7b as expanding rings of rapidly changing orientation.

In contrast, the maximum concentration in the billow is not dependent on the value of $BS$ exceeding a threshold. Trapping inside the billows depends on the circulation velocity exceeding $V_s$. Vorticity in the billows is sufficiently uniform that the orientation of organisms trapped inside remains close to the equilibrium value given by Eq. (8). This situation is analogous to the trapping mechanism described by Stommel (1949).
3.3. Pathways to trapping

The organism distribution adjusts first to the initial flow, and then to the developing instability. The orientation in the shear layer rapidly adjusts, causing a convergence of biological flux below the center of the shear layer and a divergence above. The initial uniform distribution of organisms first equilibrates to the mean flow (4), which for gyrotactically stable condition \((BS\leq 1)\) resembles Fig. 2 with a transient rarefaction that is advected upward with velocity \(V_s\). The area of increasing concentration remains at a constant depth while the area of rarefaction moves upward and is broader (Fig. 8). As the area of decreased
concentration moves away from the shear layer the vertical profile of concentration becomes similar to the steady state solution (14). Fig. 8 shows a fit to the approximation. The area of rarefaction above the shear layer is due to the initial concentration and orientation differing from the equilibrium distributions of the initial flow. In real flows the shear would be developed over time instead of being imposed instantly, this spin-up would diminish the rarefaction as the flux imbalance at the top and bottom of the shear layer would be smaller during the acceleration phase.

Subsequently trapping can occur via either of two distinct mechanisms. As the billows overturn there is an increase in the vorticity in the braid region (Corcos and Sherman, 1976; Smyth, 2003). When the vorticity at the braid is sufficient to cause gyrotactic instability \( BS > 1 \), the organisms tumble and are advected toward the billows by the strained velocity field. Once the billows overturn they form vortices which trap organisms by virtue of their vertical velocity as described in Section 3.2.

### 3.4. Model comparison

Figs. 4 and 7 show the concentration and orientation computed at the same time via two different biological models (see Sections 2.2.1 and 2.2.2). Qualitatively, the results of the two models agree quite strongly. Both exhibit an initial equilibration to the laminar shear layer similar to the steady state approximation. As the instability grows there is a further concentration of organisms. The geometry of the Kelvin–Helmholtz billow train is highlighted in both the particle and continuum models with the thinnest regions coinciding with the braids and a region of vortex trapping slightly offset from the billows.

For a quantitative comparison of the two biological models, a vertical concentration profile is constructed using binned averages (Fig. 9). The particle counts are discrete events and Poisson statistics (Bevington and Robinson, 1969) are used to estimate the uncertainty of the amount in each bin. In contrast, the continuum model is averaged to the same resolution with...
uncertainty given by standard deviation of the mean. Both show a 30% increase in the horizontally averaged concentration at the center of the shear layer (Fig. 9). The two low-concentration bands, as well as the higher mean concentration at the center of the shear layer are easily seen in the average, and support the interaction of gyrotaxis with a growing Kelvin–Helmholtz instability as a plausible mechanism of concentrated layer formation.

The continuum model includes an artificial diffusion term that is not present in the particle model. The regions of (statistically) significant discrepancies coincide with the regions where there are large gradients in the mean concentration $\overline{C}/\overline{z}$ and result from this diffusive term.

3.5. Dependence of aggregation rate on initial conditions

The figure of merit we chose to follow the evolution of the biological concentration is the maximum concentration $c_{\text{max}}$ over $x$ and $z$ at a given time. The aggregation rate $dc_{\text{max}}/dt$, where time has been scaled by the shear $\tau = \Delta U_0/h_0$, has a local maximum near the first overturn of the growing Kelvin–Helmholtz billow. The aggregation of the gyrotactic organisms is driven by a convergence in the biological flux field.

$$dc_{\text{max}} = -\overline{V_c} V_b p_1$$

This convergence occurs in the smallest biological features where up-gradient flux due to motility is countered by diffusive fluxes. The resultant convergence may be scaled as

$$dc_{\text{max}} = V_b^2 Re$$

By translating the graphs of aggregation rate by the time of maximum aggregation and scaling by $V_b^2 Re$, the various curves can be made to collapse (Fig. 10). This composite curve shows that the total change in concentration over the Kelvin–Helmholtz event is a factor of order $10 \times V_b^2 Re$. For oceanic values $V_b \sim 10^{-3}$ and $Re \sim 10^6$ the predicted layers show concentration increasing by a factor of 10. This concentration factor easily satisfies criterion 3 of Sullivan et al. (2010b).

4. Discussion

In this series of simulations we have shown that a pre-turbulent Kelvin–Helmholtz instability enhances the ability of a shear layer to retain gyrotactic organisms. A continuum model is introduced which can smoothly evolve the orientation through gyrotactic instability with the addition of a diffusivity to ensure numerical stability. Comparison with a diffusionless particle model shows that the evolution of the concentration in the continuum model is not significantly altered by diffusivity (Fig. 9).

As the Kelvin–Helmholtz instability develops, the models reveal two distinct trapping mechanisms that act in different regions of the shear layer.

1. Shear in the braids causes the organisms to become gyrotactically unstable (Durham et al., 2009), thus creating thin layers of highly elevated concentration.

2. Large vertical velocities within the billows detain the upward progress of organisms via the suspension mechanism of Stommel (1949).

A scaling relationship (22) is derived such that the aggregation rate, scaled by the maximum shear, is proportional to the Reynolds number $Re$ and the square of the relative motility $V_b$. The net increase in concentration is estimated as $10 Re V_b^2$. This is motivated by an approximation of Eq. (21) as $V_b \overline{h_0} V_c$ where the gradient $\overline{V_c}$ is set by the balance between diffusive $\Delta U_0 V_b p_c$ and advective $\nabla \overline{V_c}$ fluxes. The concentration $c$ is assumed to be of order 1.

This model assumes that the organisms are smaller than the Kolmogorov scale $\eta$. Near the surface of the ocean, observed dissipation rates $\epsilon \lesssim 10^{-4}$ W/kg (e.g., Soloviev and Lukas, 2003) imply $\eta \lesssim 1$ mm. The findings are more generally applicable as a result of the weak influence of an organism’s ellipticity on its orientation in a growing Kelvin–Helmholtz instability (Appendix B).

We close by summarizing some quantitative aspects of our results in the context of the Sullivan et al. (2010b) criteria for thin layer identification cited in Introduction to this paper.

1. The phase of the K–H life cycle in which braids grow, and hence concentration in braids increases rapidly, extends over a time $\sim 10h_0/\Delta U$. For example, if $h = 0.1$ m and $\Delta U = 0.01$ m/s, the braid growth phase lasts for only a few minutes. Trapping within the billows persists over a similarly short time. These are, of course, examples of brief intervals in a much longer mixing event throughout which thin layers might be created, reinforced, or dispersed.

2. Vertical layer thickness starts off at $h_0$. The shear layer ultimately thickens, and equilibrates at a thickness $0.32 h_0/R_b$ when the turbulence extinction criterion $R_i = 0.32$ is reached (Thorpe, 1973;
Smyth et al., 2001). If $Ri$ starts off at 0.16, for example, and the initial layer thickness is 0.1 m, the thickness will double to 0.2 m. In the braids, however, this thickness decreases to $h_0/\sqrt{RePr}$, or about 1 mm.

3. The maximum local concentration increase at the time of fastest aggregation is a factor of 2.7 (Fig. 7). Horizontally averaged concentration increases by a factor of 1.5 at the time of most rapid aggregation (Fig. 9), and increases to 2 in the second half of the aggregation phase $(0 < t < 10b/DU)$ in Fig. 10). Therefore locally and in the horizontal mean the criterion suggested by Sullivan et al. (2010b) is marginally satisfied. When extrapolated to oceanic parameter regimes the concentration increase is $O(10)$.

The aggregation events modeled here are only brief episodes in a considerably longer process that will be amenable to direct simulation in the near future. The net effect of many episodes of billow and braid growth cannot be simply extrapolated from these simulations as the decay of the K–H instability is inherently three-dimensional. To compare these results with observed aggregations, the spin-up of the shear layer and the anisotropic mixing during the decay of the instability must be addressed. In particular, the turbulent mixing following the initial K–H instability could cause sufficient vertical dispersion that the aggregation criterion of Sullivan et al. (2010b) are not met.

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Appendix A. Numerical implementation

To simplify the imposing boundary conditions a linear function is removed from the buoyancy field

$$b = b - N^2 z$$

(A.1)

with $N^2$ determined by the condition that $b = 0$ at the upper and lower boundaries. For realistic ocean conditions this large scale stratification is stable and adds a quadratic term to the hydrostatic pressure field. If we define a perturbation pressure

$$p^i = p + \frac{1}{2} N^2 z^2$$

(A.2)

then we recover the original differential equation with the additional term representing the large scale stratification

$$\frac{\partial u_i}{\partial t} = - u_j \nabla u_i - \nabla p^i + b \delta_{3i} + \nu \nabla^2 u_i$$

(A.3)

$$\frac{\partial b}{\partial t} = - u_j \nabla b - N^2 u_3 + \kappa \nabla^2 b$$

(A.4)

$$\nabla^2 p = (\nabla u_j) \delta_{3j} + \frac{\partial b}{\partial x_3}$$

(A.5)

In these reduced variables we can impose boundary conditions which correspond to a free shear layer in a nearly two layer fluid using a Fourier decomposition (Winters et al., 2004). A transform in wavenumber space reduces Eqs. (A.3) and (A.5) to

$$e^{-ikz} \frac{\partial}{\partial t} (e^{ikz} F(u_i)) = -ik_j F(u_i) - ik_3 F(p^i) + F(b) \delta_{3i}$$

(A.6)

$$e^{-ikz} \frac{\partial}{\partial t} (e^{ikz} F(b)) = -ik_j F(u_i) - ik_3 F(b')$$

(A.7)

$$F(p') = -k_j F(u_i) - ik_3 F(b')$$

(A.8)

where integrating factors of $e^{ikz}$ and $e^{ikz}$ have been used for the diffusive terms in velocity $u_i$ and buoyancy $b'$ respectively and products in advective terms are calculated in real space and transformed into Fourier space. The FTFW routines of Frigo and Johnson (2005) are used to perform the numerical Fourier transform.

The time stepping algorithm used is an explicit predictor corrector and is accurate to second order (Burden and Faires, 2004). All variables are advanced in Fourier space. Operating in Fourier space allows for exact solution of the advective terms by the use of integrating factors (see Eqs. (A.6) and (A.7)). Advective terms are calculated in real space and then transformed back into Fourier space. Pressure is not used as a prognostic variable since it arises from the time derivative of incompressibility $(\partial / \partial t) \nabla \cdot u_i = 0$ and numerical rounding errors may allow for the flow to accure significant divergence over time. Instead pressure is solved implicitly by projection. The new velocity field $u^*$ is obtained from the possibly divergent field $u^k$ by solving

$$F(u_i) = F(u_i^*) + k_j F(u_i^*)$$

(A.9)

at each fractional time step for every non-zero wavenumber $k$. This removes any divergence introduced into the flow at that time step.

The underlying fluid model is validated comparing growth rates from Hazel (1972) at high Reynolds number, $Re = 1500$, to approximate inviscid flow and high Richardson number, $Ri = 0.17$. After the initial buoyancy anomaly rings down in Fig. A1, the layer thickness has grown from 10 $DU/h$ to 40 $DU/h$. The layer thickness has grown by $\pi DU/2Re Pr$ and the growth rate decreases by $\approx 4\%$. The growing Kelvin–Helmholtz instability is similar to the simulations of Corcos and Sherman (1976) and Patnaik et al. (1976), which supports their claims that the evolution of the flow is insensitive to the initial perturbation or the exact form of the shear layer. Their initial velocity profile was an error function with initial perturbations tuned to the fastest growing mode.

The random perturbation introduced at $t = 0$ can cause spurious mixing if it is too large. To test whether the stratification is strongly influenced by the perturbation, an integral length scale

![Fig. A1. Growth rates of buoyancy anomalies as a function of normalized time $t/\Delta h$ from run k.](image-url)
if the co-ordinate system \( x_i \) is oriented along the principal axes of the strain rate tensor so that \( \varepsilon_{x_0 x_1} = (\lambda^2 x_1, 0, 0, x_2) \) where the angle between \( x_1 \) and the \( z \)-axis is \( \phi \) and the angle between the orientation and \( x_2 \) is \( \theta \). Since the flow is two dimensional and incompressible the eigenvalues are equal in magnitude and opposite in sign a rotated version of the term in simple gyrotaxis can be recovered.

\[
\Omega = \Omega_s (\sin(\theta-\phi))/\sqrt{2} + v_0 (2a_b \partial_0 \partial_2 u_0 + 2a_b \partial_2 v_0 \sin(2\theta))
\]  

(B.4)

Assuming that the fluid vorticity is essentially a shear \( \varepsilon_{x_2 u_0} \) \( = \delta \) and using the gyrotaotic restoration rate \( B = 3v_s/\mu \) from Kessler (1986)

\[
\Omega = \frac{1}{2} \left( \frac{1}{B_2} \sin(\theta-\phi) + 1 + 2a_b \frac{\varepsilon_\partial \sin(2\theta)}{3} \right)
\]  

(B.5)

The first two terms are simply a recasting of Eq. (8). In the third term \( \sin(2\theta) \) and the shear term \( \varepsilon_0 \) are bounded by \( \pm 1 \). To estimate the relative importance of the ellipticity term, an estimate must be made for the ratio \( 2/\lambda \). The simulations of Staquet (1995) and Smyth (2003) all achieved ratios of strain to shear \( \lambda/5 \) below 1/40. This is much smaller than the instability criterion for gyrotaxis of spherical particles \( 1/5 \lambda \). We conclude that for nearly stable organisms in a Kelvin–Helmholtz instability, the influence of ellipticity may be ignored.

References


