Article

Migration of Gyrotactic Micro-Organisms in Water

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Abstract: Understanding the swimming characteristics of micro-organisms is significant for modelling the migration of motile cells and corresponding ecological risk assessments associated with harmful algae in oceans and estuaries. Presented in this paper is an experimental and numerical investigation of swimming characteristics of a typical gyrotactic micro-organism, Heterosigma akashiwo (H. akashiwo) in water, based on the technology of planar laser-induced fluorescence and the finite volume method. Two-dimensional swimming velocity of algal cells are obtained by analyzing cells’ trajectories in the vertical plane, and three-dimensional swimming velocity is reconstructed based on the assumption that cells’ swimming is isotropic in the horizontal plane. Four important parameters are given to reflect the swimming characteristics of gyrotactic cells in still water, including the mean swimming speed \( V_s = 146 \, \mu m/s \), the relative strength of reorientation by gravitational torque to rotational diffusion \( \lambda = 1.96 \), the time scale of reorientation \( B = 5.6 \, s \), and rotational diffusivity \( D_r = 0.046 \, rad^2/s \). A database of the ambient vorticity, mean swimming velocity and diffusivity tensor is established, by solving Fokker-Planck equation for the probability density function of cells’ swimming under the combined action of gravity, rotational diffusion, and the ambient vorticity. The mean swimming velocity and translational diffusion tensor of H. akashiwo are found to change with the horizontal and vertical vorticity. It is also shown that gyrotactic cells swim in a given direction for a weak horizontal vorticity, in contrast to cells’ tumbling and being trapped for a strong horizontal vorticity.

Keywords: gyrotactic micro-organisms; Heterosigma akashiwo; swimming velocity; vorticity

1. Introduction

Gyrotactic micro-organisms are one type of motile micro-organisms widely existing in aqueous environments, such as oceans, lakes, rivers, and reservoirs, which can swim in a particular direction in fluid flowing with a weak horizontal vorticity (or tumble unsteadily in the fluid with strong horizontal vorticity) [1]. The swimming characteristics of gyrotactic micro-organisms are essential to understand various ecological phenomena associated with bioconvection [1–4], algal patches [5,6], thin phytoplankton layers [7], harmful algal blooms [8–10], etc.

Regarding the swimming characteristics of gyrotactic micro-organisms, there have been various theoretical, numerical, and experimental studies with focus on typical species, such as Heterosigma akashiwo [11,12], Chlamydomonas nivalis (C. nivalis) [1,2,13,14], Chlamydomonas reinhardtii (C. reinhardtii) [15–17], Dunaliella salina (D. salina) [18], etc. H. akashiwo is one typical gyrotactic micro-organism in red tide, which is a serious threat for fish, shellfish, etc. if they greatly accumulate in ambient water bodies [19,20]. Previous studies showed that the swimming behavior of H. akashiwo, such as, swimming modes, swimming speed, vertical swimming velocity, and turning rate were influenced by light, halocline [21], pH [22], salinity [8,23], predators [12,23,24], and strains [25,26].
Three typical parameters to characterize the swimming behavior of gyrotactic micro-organisms are the mean swimming speed $V_s$, the rotational diffusion coefficient $D_r$, as well as the time scale $B$ for cells’ reorientation by the gravitational torque against the viscous torque caused by flow shear. Several ways have been adopted to obtain these parameters based on microscope-based tracking methods [13,27,28], laser-based tracking methods [29,30], and video-based tracking methods [12,21,31], in which a key point is to capture the trajectories of cells for statistical analysis. The microscope-based tracking method can provide a high spatial resolution for cells’ trajectories, while the laser-based and video-based tracking methods can offer a large field of view which is beneficial to track more trajectories each time. Hill and Häder [13] proposed a biased random walk model to calculate the swimming direction and rotational diffusion coefficient of micro-organisms. Leptos et al. [32] measured the swimming velocity and compared the diffusion of $C. reinhardtii$ and Brownian motion of passive particles. Croze et al. [18] measured the gyrotactic parameters of $D. salina$ in the still water. Recently, Sengupta et al. [26] investigated the time scale for reorientation of different strains of $H. akashiwo$.

Many efforts have been made to understand the swimming characteristics and distribution of gyrotactic micro-organisms in various flows, such as Poiseuille flow [33,34], horizontal shear flow [7], steady vortical flow [5,35], density stratified flow [36], free surface flow [37,38], as well as the flow past a single vertical circular cylinder [14]. The gyrotaxis of micro-organisms was first observed and analyzed by Kessler [33]. A generalized analysis and model were given by Pedley and Kessler [1,2]. Recently, some important phenomena in turbulence are found to depend on the gyrotaxis of micro-organisms [35,37–40], including the formation of a thin phytoplankton layer caused by gyrotactic trapping [7,10], the microscale patches of motile phytoplankton [5,35], accumulation at free water surface [37,38,41,42], turbulent channel flows in photobioreactors [43], etc. Results show that the swimming of gyrotactic phytoplankton species is influenced by gravitational torque and the viscous torque induced by flow shear in the fluid flowing with non-zero vorticity. However, up-to-date, the rotational diffusion coefficient, the relative strength of reorientation to rotational diffusion and the swimming characteristics of $H. akashiwo$ in a three-dimensional vorticity field have not been understood very well, especially the swimming direction and translational diffusion under the combined action of horizontal and vertical vorticity, although they are very important for the prediction of corresponding concentration distribution.

This work is to investigate the swimming characteristics of $H. akashiwo$ in still fluid and the three-dimensional vorticity field. The specific objects are: (1) to measure the fluorescence spectrum of $H. akashiwo$, (2) to obtain the swimming speed and direction, (3) to analyze the relative strength of reorientation to rotational diffusion, (4) to obtain the typical values of $B$ and $D_r$, and (5) to calculate the mean swimming velocity and translational diffusion tensor in three-dimensional vorticity field.

2. Materials and Methods

2.1. Experimental Setup

The experimental setup in the present work was based on the design of an experimental setup by Vladimirov et al. [30], and some modifications were made according to the swimming speed of $H. akashiwo$. The experimental system mainly consisted of a test tube, an acrylic box, an imaging system, an injection system, and a planar laser with wavelength of 447 nm (MDL-F-447NM-3.5 W-1601, Changchun New Industries Optoelectronics Technology, Changchun, China), as shown in Figure 1. The test tube (15 mm × 15 mm × 190 mm) was modified based on that used by Vladimirov et al. [30], which was located in an acrylic box (200 mm × 200 mm × 300 mm) full of water to maintain a thermostatic environment. Two thin rubber tubes that threaded through the sides of acrylic box were respectively connected with the inlet and outlet of the test tube. The 1.5 mm-thick laser sheet was used to illuminate cells in the centerplane of the test tube, which was controlled by a synchronizer to ensure that the cells were only illuminated during the exposure time. The imaging acquisition system consisted of a 16-bit CMOS (Complementary Mental Oxide Semiconductor) camera (PCO.edge 5.5,
Intelligent Laser Applications of Germany, Aachen, Germany) with a resolution of $2048 \times 2048$ pixels, a lens (EF-S 60 mm f/2.8 USM, Canon, Tokyo, Japan), a 550 nm high-pass filter (Beijing JJAM Technology Limited corporation, Beijing, China), and an imaging analysis software (CamWare, Intelligent Laser Applications of Germany, Aachen, Germany). The injection system included a syringe pump (Pump 11 elite, Harvard Apparatus, Holliston, MA, USA) and injection syringes (Himilton, Reno, NV, USA) with various capacities, which was connected with the rubber tube to provide fluid for the test tube.

The swimming speed of *H. akashiwo* measured in the present paper was larger than that measured by Hill and Häder [13], and the test tube in the present work was extended in the length and width compared with that of Vladimirov et al. [30] to suit the faster cells. The measurement area (14.23 mm $\times$ 14.23 mm) was located 140 mm away from the bottom of the test tube. The design of the test tube considered the swimming speed of the motile cells and the injection time to weaken the influence of the injection on the fluid in the test tube.

The trajectories of *H. akashiwo* could be recorded by camera due to its fluorescent characteristics under the illumination of a laser with an appropriate wavelength. One preliminary work in the present paper was to measure the fluorescence spectrum of *H. akashiwo* using a fluorescence spectrophotometer (F-7000 FL, HITACHI, Tokyo, Japan). The cells were stimulated by the laser with various wavelengths, and the optimum wavelength that made the fluorescent intensity of cells reach its maximum was selected from 430–470 nm, as shown in Figure 2. The horizontal and vertical axes respectively represent the wavelength and the logarithm of the normalized light intensity. The left five peaks were from the excitation light, and the peaks that almost coincide in the right were from the emission light by the algae. The enlarged peaks in the inset show that under the illumination of 450 nm laser, the emission of *H. akashiwo* has the maximum peak, and the peak of fluorescence spectrum locates at 685 nm. Thus, a laser with a wavelength 447 nm and 550 nm high-pass filter were selected in the present work, and all the experiments in present paper were performed in a dark environment to eliminate interference from other lights.
where \( t = 0 \) min. The number of motile cells in the measured zone at \( t = 20 \) min is adequate to get reasonable statistics, and therefore, the first set of images (30 successive frames) were recorded at \( t = 20 \) min, with a 50 ms exposure time. Then images were taken every 5 min for an hour with the camera and laser keeping the same setting. The above operation was one test, and three tests were performed over the whole experiment.

2.2. Image Processing and Analysis Methods

A sample of individual cells was recorded in each frame with a spatial resolution 6.95 µm/pixel, as shown in Figure 3a. The trajectories of cells shown in Figure 3b were obtained by overlaying 30 successive images. Each trajectory, containing several walks, is defined as a track, as shown in Figure 3c. In the present work, 13,684 tracks in 3 tests were collected, and 6292 tracks that contain at least 10 walks were selected to calculate the swimming velocity and direction.

Consider a Cartesian coordinate system with \( x \)-axis parallel to the laser sheet, \( y \)-axis perpendicular to the plane of laser sheet, and \( z \)-axis upward along the axis of the test tube. The swimming velocity of cell \((V_x, V_z)\) is calculated by

\[
V_x = \frac{x_k - x_{k-1}}{\Delta t}
\]

\[
V_z = \frac{z_k - z_{k-1}}{\Delta t}
\]

where \((x_k, z_k)\) and \((x_{k-1}, z_{k-1})\) are the pixel positions of algal cells on the \(k\)-th frame and \(k-1\)-th frame, \(K\) (6.95 µm/pixel) is the conversion coefficient between pixel and physical coordinates, and \(\Delta t\) (0.5 s) is

![Figure 2. Emission spectra of Heterosigma akashiwo under various spectrums of lasers.](image-url)
the time interval between two continuous images. We assume that the swimming velocity of cells in the x-y plane is isotropic \((V_x = V_y)\), and the resultant speed \((V)\) is defined as

\[
V = \sqrt{V_x^2 + V_y^2 + V_z^2} = \sqrt{2V_x^2 + V_y^2 + V_z^2}
\]

where \(V_r\) is the total swimming velocity in the x-y plane, and the r-axis is determined by \((V_x, V_y, 0)\). The swimming direction of motile cells in r-z plane and x-z plane are defined as \(\theta (0\sim180^\circ)\) and \(\alpha (-180^\circ\sim180^\circ)\), respectively, as shown in Figure 4.

\[
\theta = \arctan \frac{V_r}{V_z} \quad (V_z > 0)
\]

\[
\theta = \frac{\pi}{2} \quad (V_z = 0)
\]

\[
\theta = \pi + \arctan \frac{V_r}{V_z} \quad (V_z < 0)
\]

\[
\alpha = \arctan \frac{V_x}{V_z} \quad (V_z \neq 0)
\]

\[
\alpha = \frac{\pi}{2} \quad (V_x > 0, \ V_z = 0)
\]

\[
\alpha = -\frac{\pi}{2} \quad (V_x < 0, \ V_z = 0)
\]

Figure 3. Images of motile cells: (a) algal cells (represented by dark spots) in one frame, (b) trajectories of cells in 30 frames, (c) one track/trajectory with dozens of walks, and three swimming patterns: (d1) helical trajectories, (d2) straight trajectories, and (d3) trajectories combined helical and straight ones.

\(V, V_x, \) and \(V_z\) calculated by Equations (1)–(3) are divided into square bins of width \(\Delta v = 10 \mu m/s\) to obtain probability density function (PDF) of swimming velocity,

\[
f_i = \frac{n_i}{k \cdot N_0 \cdot \Delta \nu}
\]

\[
f_{ij} = \frac{n_{ij}}{k \cdot N_0 \cdot \Delta \nu^2}
\]
where \( k \) (the value is 10) is the number of walks in one track, \( N_0 \) is the number of tracks in Table 1, \( n_i \) is the number of walks in the \( i \)-th bin for velocity ranging from \([i \times \Delta v, (i + 1) \times \Delta v]\), and \( n_{ij} \) is the number of walks that \( V_x \) and \( V_z \) located in the \( i \)-th and \( j \)-th bins. Discrete values of \( f_i \) and \( f_p \) constitute the one-dimensional \( f(V_x), f(V_z), f(V) \) and two-dimensional probability density function \( f(V_x, V_z) \). \( f(V, \theta) \) are obtained by use of the same computational method as above.

### Figure 4. Definition of swimming direction.

Table 1. The number of tracks at different time for three tests.

| Sets | 20 min | 25 min | 30 min | 35 min | 40 min | 45 min | 50 min | 55 min |
|------|--------|--------|--------|--------|--------|--------|--------|--------|
| 1    | \( N_{11} \) | \( N_{12} \) | \( N_{13} \) | \( N_{14} \) | \( N_{15} \) | \( N_{16} \) | \( N_{17} \) | \( N_{18} \) |
| 2    | \( N_{21} \) | \( N_{22} \) | \( N_{23} \) | \( N_{24} \) | \( N_{25} \) | \( N_{26} \) | \( N_{27} \) | \( N_{28} \) |
| 3    | \( N_{31} \) | \( N_{32} \) | \( N_{33} \) | \( N_{34} \) | \( N_{35} \) | \( N_{36} \) | \( N_{37} \) | \( N_{38} \) |
| Sum  | \( N_1 \) | \( N_2 \) | \( N_3 \) | \( N_4 \) | \( N_5 \) | \( N_6 \) | \( N_7 \) | \( N_8 \) |

#### 2.3. Fokker-Planck Model

We assume that the swimming speed of cells, \( V_s \) (equate to \( V \) in Section 2.2) is constant independent of the swimming direction \( p \). The mean swimming velocity \( V \) can be computed as [2]

\[
V = \langle V_s p \rangle = \langle V_s \rangle \langle p \rangle \tag{12}
\]

where \( f(p) \) is probability density function of swimming direction of \( H. \textit{akashiwo} \). The cell’s translational diffusivity tensor \( D \) is given by [2]

\[
D = V_s^2 \tau [\langle pp \rangle - \langle p \rangle \langle p \rangle] \tag{14}
\]

where \( \tau \) is the correlation time. In this work, the translational diffusion coefficient is computed based on the Equation (14). Here, the correlation time, for simplicity, is assumed to be constant following the work [2]. However, the constant correlation time is not a good approximation for all flow conditions, especially for the flow with a high shear rate. A better approximation is given by ‘generalised Taylor dispersion theory’ [43–47]. Hwang and Pedley [3] gave detailed comments on the Equation (14) and the generalised Taylor dispersion theory.

The probability density function of swimming direction, \( f(p) \), satisfies the Fokker-Planck (FK) equation:

\[
\frac{\partial f}{\partial t} + \nabla \cdot (pf) = D \nabla^2 f \tag{15}
\]
where $\nabla$ is the gradient operator in $p$-space, $\dot{p}$ is the gyro tactic reorientation rate, and $D_r$ is the rotational diffusivity. For spherical cells (e.g., *H. akashiwo*), $\dot{p}$ is given, for the weak fluid acceleration, by

$$\dot{p} = \frac{1}{2B} [k - (k \cdot p)p] + \frac{1}{2} \omega \wedge p$$

(16)

where $k$ is the unit vector in the vertically direction, $B$ is the reorientation time of gyro tactic *H. akashiwo*, and $\omega$ is the vorticity of ambient flow.

Equation (15) is solved based on the finite volume method [14]. The initial uniform distribution of probability density ($1/4\pi$) is specified, and the periodical boundary condition $f(\theta, 0, t) = f(\theta, 2\pi, t)$, is specified. In the present paper, the vorticity is inputted as a parameter of Equation (15). Equation (15), with the same initial and boundary conditions, is solved for a set of vorticities ($w_x, w_y, w_z$), to obtain the relationship of the mean swimming velocity and the translational diffusivity tensor.

### 3. Results

#### 3.1. Swimming Velocity and Direction Distribution

The one-dimensional distribution of probability density function of swimming velocity in all tests is shown in Figure 5a with the average value of $V_x, V_y, V_z$ locating at 143.57, 0.37, 104.54 $\mu$m/s. The $f(V_x)$ is approximately subjected to Gaussian distribution $f(V_x) = 1/\sqrt{2\pi}\sigma e^{-V_x^2/(2\sigma^2)}$, where $\sigma = 62.82$. The PDFs for $V_x, V_y$ and $V_z$ at different time are shown in Figure 5b–d, which change little over time (20–50 min).

![Figure 5](image_url)

**Figure 5.** Distribution of probability density of swimming velocity: (a) $f(V), f(V_x)$, and $f(V_z)$ in all tests, (b) $f(V_x)$ at different time, (c) $f(V_z)$ at different time, and (d) $f(V)$ at different time.

The distributions of $f(V_x, V_z)$ in the $x$-$z$ plane at 20–55 min are shown in Figure 6, in which the areas with high probability density are similar to the shape of mushrooms. The value of $V_x$ is mainly within $[-80, 80]$ $\mu$m/s with the symmetric axis around $V_x = 0$ $\mu$m/s, while $V_z$ is basically above 80 $\mu$m/s. It is obvious that the spatial distribution is less clustered at $t = 55$ min with the accumulated area surrounded by red, dashed line extending in the $z$-direction and narrowing in the $x$-direction, as shown in Figure 6a,h.
The mean swimming velocities, standard deviations ($\sigma$), and deviation coefficient ($C_s$) are computed with Equations (17)–(19),

$$\bar{U} = \frac{1}{kN_j} \sum_{j=1}^{kN_j} U_j \quad i = 1, 2, \ldots, 8$$

(17)

$$\sigma = \sqrt{\frac{\sum_{j=1}^{kN_j} (U_j - \bar{U})^2}{(kN_j)}}$$

(18)

$$C_s = \frac{\sum_{j=1}^{kN_j} (U_j - \bar{U})^3}{(kN_j\sigma^3)}$$

(19)

where $k$ (the value is 10) is the number of walks in one track, $U$ is the variable to represent $V$, $V_x$, or $V_z$, and $N_i$ is the number of tracks in the last line in Table 1. Figure 7a presents the mean swimming velocities at three tests, and the dashed lines in Figure 7a represent the mean swimming velocity for all the tests. The values of $V$ and $V_z$ decrease with time to some extent, while the value of $V_x$ fluctuates around $V_x = 0$ $\mu$m/s. The variation of standard deviations of $V_x$ and $V$ are weak compared with that of $V_z$, as shown in Figure 7b. The deviation coefficients do not change greatly with time, as shown in Figure 7c, which indicates that the distribution patterns remain stable. The results illustrate that the swimming characteristics of cells in the $x$-$y$ plane is time-independent, the differences of PDFs for $V_z$ increase slightly with time due to the smaller $V_z$ of the cells coming later, and the swimming ability changes a little in tests.

The PDF of swimming direction in $r$-$z$ plane is shown in Figure 8a. The $f(\theta)$ increases with the decreasing $\theta$ to reach the maximum value at $\theta = 0^\circ$, i.e., the vertical direction ($z$-axis). Figure 8b presents more intuitively the variation of $f(\theta)$ with $\theta$ after injection, which changes little over time. The $f(\theta)$ rises obviously when $0^\circ < \theta < 90^\circ$, while keeps stable around 0.001 in the case that $\theta > 90^\circ$. The results show that the $H. akashiwo$ tends to swim upwards, and this conclusion is also verified by the trajectories of 100 cells within 5 s at $t = 20$ min and 55 min, as shown in Figure 9. The origin of each trajectory in Figure 9 has been moved to the same point to compare. Both the gravitaxis and randomness can be observed in Figure 9. It is noted that a number of downward trajectories have been observed at $t = 55$ min, and corresponding reasons are not clear.
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Figure 7. Statistical parameter of the swimming velocity $V$, $V_x$, and $V_z$ and at different time: (a) mean velocity, (b) standard deviations ($\sigma$), and (c) deviation coefficient ($C_s$).

Figure 8. Distribution of $f(\theta)$, (a) spatial distribution of $f(\theta)$, and (b) $f(\theta)$ at different time.

Figure 9. Swimming trajectories (100 tracks) of H. akashiwo cells in x-z plane: (a) $t = 20$ min, and (b) $t = 55$ min.
3.2. Relative Strength of Reorientation by Gravitational Torque to Rotational Diffusion

According to the theoretical analysis of gyrotactic micro-organisms given by Pedley and Kessler [2], \( f(V, \theta) \) and \( \ln[f(V, \theta)] \) are subjected to

\[
f = \mu_1 e^{\lambda \cos \theta} \\
\ln f = \lambda \cos \theta + \ln \mu_0
\]

where \( \lambda \) represents the relative relationship between the random diffusion and the preferred migration, and \( \mu_0 = \lambda/(4\pi \sinh \lambda) \).

The \( f(V, \theta) \) of motile cells shows that the cells with \( V = 80–180 \ \mu m/s \) and \( \theta = 0^\circ–60^\circ \) occupy the majority in all tests, as shown in Figure 10. The peaks of \( f(V, \theta) \) drop to smaller values in the \( V \)-axis, and the small peak appearing in Figure 10d represents the slower cells that coming later. The distribution of \( \ln[f(V, \theta)] \) at different swimming velocity and swimming direction is shown in Figure 11a, and according to Equation (21) the slopes in \( \cos \theta - \ln[f(V, \theta)] \) plane are the values of \( \lambda \). The linear relationships between \( \ln[f(V, \theta)] \) and \( \cos \theta \) at \( V = 80–180 \ \mu m/s \) are shown in Figure 11b. It is shown that \( \lambda = 1.44–2.60 \), and that the average value of \( \lambda = 1.96 \). We also found that the linear relation is more obvious for the case of \( \cos \theta > 0 \), in which \( \lambda = 2.53–3.98 \) with the average value, 3.44, as shown in Figure 12. In addition, \( \lambda \) can be calculated from another equation presented by Pedley and Kessler [2]:

\[
\frac{\langle V_z \rangle}{\langle V \rangle} = \coth \lambda - \frac{1}{\lambda} \\
\langle V \rangle = \int \int V f(V) d^2V
\]

where \( <> \) represents the ensemble average. The value of \( \lambda \) is 3.64 based on Equation (22).

![Figure 10.](image-url) f(V, \theta) at (a) 25 min, (b) 35 min, (c) 45 min, (d) 55 min.
3.3. Time Scale of Reorientation by Gravitational Torque

The swimming direction of *H. akashiwo* is reoriented due to the torque caused by the displacement of the center of mass relative to the geometric center [1]. This intrinsic feature, resulted from bottom heaviness, can be described by the time scale of reorientation, $B$, which is determined by [48],

$$B = \frac{\mu a_{\perp}}{2\rho gh}$$

where $\mu$ is the dynamic fluid viscosity, $\rho$ is the density of cells, $g$ is the gravitational acceleration, $a_{\perp}$ is a dimensionless constant, and $h$ is the displacement of the center of mass relative to the geometric center. Kessler [34] proposed the range of $h$ is 0–0.1 $a$ and estimated $h = 0.1 \mu m$, $B = 3.4$ s for *C. nivalis*, where $a$ is the average radius of cells.

It is not easy to estimate $B$ according to Equation (24) is not so convenient to be used for other kinds of algal cells. Hill and Häder [13] built a biased random walk model to estimate the parameters of algal cells, and proposed $B = 2.7$ s for *C. nivalis* based on the swimming trajectories obtained by microscope-based tracking methods. For the experimental results in the present paper, the swimming directions of cells are subjected to

$$E[\alpha(T) - \alpha(0)] \sim T\mu_0[\alpha(0)],$$

where $\alpha(0)$ is the initial swimming angle at $T = 0$ s, which corresponds to $t = 20$ min in all tests, and $\alpha(0) = 0$ represents that the cells swim vertically upward. In one shot, 30 successive frames are
recorded by a frequency of 2 fps, thus the maximum $T$ is 15 s for each set of images. The expectations of turning amplitudes, $E[a(t)−α(0)]$, are proportional to time, and the corresponding slopes, $μ_0[α(0)]$, represent turning speed of cells with different $α(0)$, as shown in Figure 13, in which the $−85°$ and $−75°$ respectively represent the population of cells with $α(0)$ at $[−90°, −80°]$ and $[−80°, −70°]$ when $T = 0$ s. For the population characterized by $α(0) = −85°$, the cells constantly rotate to adjust the swimming direction until the rotation angle nearly reaching $85°$, and at that moment the turning amplitude does not increase with time any more, which means that the swimming directions have been upward and the cells have reached equilibrium. The turning amplitudes are almost constant for the cells $α(0) = ±5°$, because the initial positions of algal cells are close to vertical direction. The initial instant $T = 0$ is any moment for the algal cells, thus Figure 13 shows that at any time the cells constantly adjust their swimming direction to reach the equilibrium state.

![Figure 13. Variation of average turning amplitude with time at different angles $α(0)$.](image1)

The slopes in Figure 13, $μ_0[α(0)]$, are proportional to $[α(0)]$, as shown in Figure 14. The curve in Figure 14 shows that the more algal cells deviate from their equilibrium position, the greater the turning speed. The function $μ_0(α)$ represents the turning speed of motile cells from the initial position to the position of $α = 0$, which is subjected to Equation (26),

$$μ_0(α) = −d_0α = −0.18α \text{ as } t \to 0$$  \hspace{1cm} (26)

where $d_0$, a positive constant, is the drift coefficient. Thus we estimate $B = d_0^{-1} = 5.6$ s for $H. akashiwo$ in present paper.

![Figure 14. Turning speed of cells at different initial swimming angles.](image2)
3.4. Rotational Diffusion Coefficient

The variance of the turning amplitude, \( \text{Var}[\alpha(t) - \alpha(0)] \), is proportional to time,
\[
\text{Var}[\alpha(T) - \alpha(0)] \sim T \sigma_\alpha^2[\alpha(0)],
\]
where \( \sigma_\alpha^2[\alpha(0)] \) is the variance of turning speed, and the relationship is shown in Figure 15. The slopes for various initial angles, ranging from 0.023–0.156, are depicted in Figure 16. Thus, the rotational diffusion coefficient, \( D_r \), which equals to \( \sigma_\alpha^2/2 \), varies in the scope of 0.012–0.078.

![Figure 15. Variance of the turning amplitude at different time for various angles \( \alpha(0) \).](image)

![Figure 16. \( D_r \) at different initial swimming angles.](image)

The rotational diffusivity can also be calculated by the equation given by Pedley and Kessler [1]
\[
\lambda = \frac{1}{2BD_r}
\]

According to Equation (28), \( D_r = 1/(2B\lambda) = 0.034–0.062 \text{ rad}^2/\text{s} \) with a mean value 0.046 rad\(^2\)/s for all cells, and \( D_r = 0.022–0.035 \text{ rad}^2/\text{s} \) with a mean value 0.026 rad\(^2\)/s for the cells only walking vertically upwards, and \( D_r = 0.025 \text{ rad}^2/\text{s} \) if \( \lambda \) is calculated by Equation (22). The values of \( D_r \) calculated by Equation (28) are consistent with that calculated according to Figure 16.

3.5. Swimming Characteristics of H. akashiwo in Vorticity Field

The swimming velocity \( V \) and translational diffusivity tensor \( D \) of \( H. \ akashiwo \) were found to change with the horizontal vorticity. For the case of \( w_x = 0 \) and \( w_z = 0 \), the longitudinal swimming
velocity $V_s$ increased firstly to a maximum and decreased to zero with the increase of $w_y$, the vertical swimming velocity $V_z$ decreased with the increasing $w_y$, and the lateral velocity $V_y$ kept constant, as shown in Figure 17a. When $|Bw_y| > 0.9$, $V_s$ is greater than $V_z$. For the weak horizontal vorticity, algal cells can swim with an angle against the vertical direction. However, for the strong vorticity, the cells cannot swim upwards in a fixed angle, as shown in Figure 17a, because the maximum gravitational torque due to the difference of cells’ buoyance center and mass center cannot balance the viscous torque caused by the flow shear [7]. Figure 17b presents the variation of translational diffusivity with lateral vorticity. It is shown that the diagonal components of translational diffusivity are much greater than the off-diagonal components. For the weak horizontal vorticity, the translational diffusion are found to be anisotropic. With the increase of horizontal vorticity, the anisotropic translational diffusion tends rapidly to the isotropic translational diffusion with the diagonal components equal to 1/3.

For the case of $w_x = 0$ and $w_z = 0$, the horizontal swimming velocity and the off-diagonal components of $D$ are equal to zero, and $V_z/V_s, D_{xz}/(V_s^2\tau), D_{yy}/(V_s^2\tau), D_{zz}/(V_s^2\tau)$, are equal to 0.71, 0.21, 0.21, and 0.08, respectively, which means that the single vertical vorticity cannot change the swimming direction and translational diffusion.

In the weak horizontal vorticity, $w_z$ slightly weakens the horizontal swimming velocity and components of $D$, while the strong horizontal vorticity enhances the gyrotaxis, as shown in Figures 18 and 19.

![Figure 17. Variation of swimming velocity (a) and translational diffusivity tensor (b) with $w_y$.](image1)

![Figure 18. Swimming velocity, (a) $V_x/V_s$, (b) $V_y/V_s$, and (c) $V_z/V_s$ with $w_x, w_y$, and $w_z$.](image2)
The average values of $V$ and the average values of $V$ were based on the assumption that the swimming velocity in different frames; 1935 cells, walking through all the frames, were selected from all tests. The effect of laser on the swimming direction of motile cells is studied by analyzing the swimming velocity of cells in the presence of a predator resulted in an increase of 22% and a decrease of 58% of swimming speed below and above halocline, respectively. Bearon et al. [11] noted that the gross swimming speeds of $H. akashiwo$ of different strains of $H. akashiwo$ frequently blooms, and the swimming velocity (measured at the 2nd–4th hour in the light phase) is relatively high compared with its strains, as shown in Table 2. Harvey and Menden-Deuer [12] found that the swimming speed of $H. akashiwo$ increased by 38% in the presence of a predator, while Strom et al. [23] found that the presence of a predator resulted in an increase of 22% and a decrease of 58% of swimming speed below and above halocline, respectively. Bearon et al. [11] noted that the gross swimming speeds of $H. akashiwo$ in light phase are 49–66 $\mu$m/s and 88–119 $\mu$m/s for strain CCMP452 (Provasoli Guillard Center for Culture of Marine Phytoplankton, Maine, USA) and CCAP934-1 (Culture Collection of Algae and Protozoa, North Sea, Norway), respectively. Havey et al. [25] also found similar variations of swimming velocity and turning rate due to strains. Recently, Sengupta et al. [26] revealed that different strains of $H. akashiwo$ cells have different responses to turbulence cues. The algal cells in present work are originated from Zhoushan, China, where $H. akashiwo$ frequently blooms, and the swimming velocity (measured at the 2nd–4th hour in the light phase) is relatively high compared with previous results. Parameters of various cells from previous studies and present work are listed in Table 2.

The effect of laser on the swimming direction of cells is studied by analyzing the swimming velocity in different frames; 1935 cells, walking through all the frames, were selected from all tests. The average values of $V_z$ are 100.81, 105.15, and 104.24 $\mu$m/s for 1–10, 10–20, 20–30 frames, respectively, and the average values of $V$ are 128.97, 132.55, 134.11 $\mu$m/s for 1–10, 10–20, 20–30 frames, respectively. $V_z$ and $V$ have a small fluctuation about 6 $\mu$m/s within 30 frames, much less than the mean swimming speed, which means that the effect of laser on the swimming direction of motile cells are negligible.
The swimming velocity of *H. akashiwo* probably depends on various factors, such as species, temperature, illumination, culture media, etc. With regard to the difference from previous works, some probable reasons we think come from the tiny difference of algal species, temperature of culture media, and the diel light cycle. The cells in the work [26] are cultivated at 21 °C or 18 °C under the diel light cycle (14 h light: 10 h dark), while the cells are the present experiment are cultivated at 25 °C under the diel light cycle (12 h light: 12 h dark). Furthermore, the cells (GY-H24, *H. akashiwo*, from Zhoushan, China, provided by Shanghai Guangyu Biological Technology Co., Ltd., Shanghai, China) used in the present work differ from those in the works [11,23–26]. The range of swimming velocity of *H. akashiwo* ranges from 20 to 156 µm/s [11,12,23–26], and the present velocity is closed to these results in References [12,24,26]. Besides, the present reorientation time of *H. akashiwo* is close to the results found in Reference [26].

| Algae                     | V (µm s⁻¹) | B (s) | Dr (rad² s⁻¹) | Paper |
|---------------------------|------------|------|---------------|-------|
| *C. nivalis*              | 63         | 3.4  | 0.067         | [1,2] |
| *C. nivalis*              | 55         | 2.7  | 0.084         | [13]  |
| *C. nivalis*              | 38         | 6    | 0.036         | [30]  |
| *D. salina*               | 62.7 ± 0.4 | 10.5 ± 1.3 | 0.23 ± 0.06 | [18]  |
| *H. akashiwo*             | -          | 2    | -             | [7]   |
| *H. akashiwo* (CCMP3107) | -          | 4.9 ± 1.5 | -             | [26]  |
| *H. akashiwo* (CCMP452)   | 74.5 ± 42.4 | 19.3 ± 13.5 | -             | [26]  |
| *H. akashiwo* (CCMP452, a) | 73.8 ± 46.2 | −23.1 ± 10.2 | -             | [26]  |
| *H. akashiwo* (CCAP934-1) | 49–66      | -    | -             | [11]  |
| *H. akashiwo* (CCMP3107)  | 88–119     | -    | -             | [11]  |
| *H. akashiwo* (CCMP452)   | 20–145     | -    | -             | [12]  |
| *H. akashiwo* (CCMP452)   | 25–58      | -    | -             | [23]  |
| *H. akashiwo* (CCMP3107)  | 85–135     | -    | -             | [24]  |
| *H. akashiwo* (7 strains) | 33–115     | -    | -             | [25]  |
| *H. akashiwo* (GY-H24)    | 117–156    | 5.6  | 0.046         | Present work |

*a* The population of algae that swim upwards (negative gravitaxis). *b* The population of algae that swim downwards (positive gravitaxis).

The vertical migration of gyrotactic cells depends on the gyrotactic parameters of algal cells, hydrodynamic characteristics, and other external conditions, such as light, nutrients, temperature, etc. Mashayekhpour et al. [41] proposed that the high-gyrotaxis swimmers may reach the free water surface to form a high-concentration area, but the thermal stratification in lakes and oceans may disrupt cells’ motility and hinder corresponding accumulation [37]. Strong horizontal vorticity can make cells tumble [7], resulting in some interesting ecological phenomena, for example thin phytoplankton layer. In this study, it was shown that the vertical vorticity can weaken the effect of the strong horizontal vorticity on the vertical swimming velocity, as shown in Figure 19, which means that the gyrotactic swimmers can swim more easily towards the free surface in the flow with the strong vertical vorticity than in the flow with the weak vertical vorticity. The circulation with the strong vertical vorticity exists in the realistic flows due to topography and external factors, such as wind. However, further investigations needs to be performed to understand the effect of the combined actions of horizontal and vertical vorticity on the distribution of microorganisms in a specific flow.
5. Conclusions

The swimming characteristics of *H. akashiwo* in still water and a three-dimensional vorticity field were investigated based on the laser-based tracking method and the finite volume method. The results showed that the peak of fluorescence spectrum of *H. akashiwo* locates at 685 nm under the illumination of 450 nm laser. The swimming ability of *H. akashiwo* cells is independent of time for a given period about 50 min, and most motile cells swim vertically upwards due to the negative gravitaxis, though several cells walk down due to randomness. For all motile cells, the dimensionless parameter $\lambda$, which represents the relative strength of reorientation by gravitational torque to rotational diffusion, is in the range of 1.44–2.60, while for the cells only walking upward, corresponding range is 2.53–3.98. The reorientation time and rotational diffusivity are 5.6 s and 0.046 rad$^2$/s, respectively. The swimming velocity and translational diffusion tensor of *H. akashiwo* change with the horizontal and vertical vorticity. Algal cells are able to keep the swimming direction in the weak horizontal vorticity, while they cannot swim towards a given direction in the strong horizontal vorticity. In the presence of horizontal vorticity, the effect of vertical vorticity enhances with the increase of $w_x$ and $w_y$, though a single vertical vorticity would not change the swimming direction and diffusion characteristics.

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