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Motion of dinoflagellates in a simple shear flow

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Abstract

Turbulence can be highly significant to dinoflagellates by affecting their swimming motion. We examined the effects of simple shear flow on swimming trajectories and orientations of two species of dinoflagellates *Glenodinium foliaceum* and *Alexandrium catenella*. In the absence of either shear or a cue that can cause directional motion, swimming orientations of both species were insignificantly different from random. Although cells of *G. foliaceum* maintained their random swimming orientations upon exposure to shear, swimming orientations of both single cells and chains of *A. catenella* were affected by shear. Magnitude of the effect increased with shear rate. Changes in decorrelation times, as a result of exposure to shear, were observed for both species, providing another indication that shear affects swimming behavior. Decorrelation times for the swimming directions of both species were of the same order as the characteristic time scale of turbulence that would produce shear rates comparable to those examined in this study. Theoretical models that assess the effects of turbulence on vertical migration of dinoflagellates and predator–prey interactions commonly assume that swimming motion of dinoflagellates in the presence of shear flow can be described by simple superposition of the flow on the swimming motion in the absence of flow. Our results suggest that this assumption is not universally true.

It has long been noted that dinoflagellate blooms are associated with periods of weak turbulence (Malone 1980; Margalef and Estrada 1981). Furthermore, laboratory experiments in which dinoflagellates were grown under strong agitation suggest, in general, a negative effect of turbulence on dinoflagellate cell division and growth (reviewed by Estrada and Berdalet 1997). Turbulence could be highly significant to dinoflagellate motility by affecting cell trajectories. Many photosynthetic dinoflagellates migrate vertically in the water column (Kamykowski 1995; Levandowski and Kaneta 1987). Under turbulent conditions, dinoflagellates may be unable to maintain their swimming directions. Furthermore, flow-induced cell rotation around any axis that is not parallel to the swimming direction can impair both nutrient transfer (Karp-Boss et al. 1996) and the cell's ability to orient itself in the water column.

At the scale of a dinoflagellate, viscosity acts to dissipate the kinetic energy of turbulence, and the flow experienced by the cell is a laminar shear, intermittent in both time and space (Lazier and Mann 1989). In general, a motile cell in a shear flow both translates and rotates relative to the fluid in which it is immersed. Swimming direction in the presence of shear will be determined by the balance between gravitational and viscous torques (Kessler 1985; Pedley and Kessler 1992). Gravitational torque results from an unbalanced mass distribution relative to the cell's geometric center (Levandowski and Kaneta 1987; Kamykowski 1995). Viscous torque results from spatial variation in fluid velocity. If gravitational torque is zero and the cell is not swimming, it will rotate with an angular velocity that depends linearly on the vorticity of the flow. Elongated nonmotile cells and chains, in this case, will have a preferred orientation aligned with the streamlines and will rotate periodically with a characteristic orbit (Jeffery 1922; Karp-Boss and Jumars 1998). If the cell is swimming, orientations and angular velocities are likely to be modified (Pedley and Kessler 1992).

Theoretical simulations of the effect of turbulence on swimming trajectories of dinoflagellates commonly describe trajectories by superimposing swimming velocities of dinoflagellates on a vector model of turbulence (Yamazaki and Kamykowski 1991; Kamykowski 1995; Kamykowski et al. 1998). Swimming behaviors have been modeled as functions of light, temperature, gravity (Yamazaki and Kamykowski 1991), and metabolic state (Kamykowski and Yamazaki 1997). Dinoflagellates, however, may also alter swimming behavior in response to shear; in this case, resultant swimming trajectories could not be predicted by simple superposition of the ambient flow field and an inherent swimming motion.

Limited observations on the direct effects of turbulence on the swimming behaviors of dinoflagellates have been reported. Estrada et al. (1987) found changes in the local concentrations of *Prorocentrum micans* cells between stirred and unstirred culture vessels, suggesting that turbulence can affect swimming and migration. Turbulence parameters, however, were not defined or measured. Thomas and Gibson (1990) described qualitative changes in swimming behavior of *Gonyaulax polyedra* upon exposure to simple shear flow. Whereas cells in the control swam forward vigorously, cells

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Table 1. Statistics for tests of uniformity. For distributions that are of a von Mises population, we used the Rayleigh test. In cases for which the von Mises distribution did not provide a good fit to the data, we used two nonparametric tests: Kuiper's and Watson's tests.

	Shear rate	No. of observed steps (No. of individuals)	Test for uniformity
G. foliaceum	No shear	490 (36)	Rayleigh = 5.08
	$G = 0.5\ s^{-1}$	501 (37)	Rayleigh = 5.46
	$G = 1\ s^{-1}$	420 (44)	Rayleigh = 2.01
A. catenella single cells	No shear	749 (36)	Rayleigh = 3.13
	$G = 0.5\ s^{-1}$	509 (30)	Kuiper's $V^* = 2.35^*$
			Watson's $U^{*2} = 0.32^*$
	$G = 1\ s^{-1}$	377 (41)	Kuiper's $V^* = 3.27^*$
			Watson's $U^{*2} = 0.82^*$
A. catenella chains	No shear	635 (30)	Rayleigh = 4.6
	$G = 0.5\ s^{-1}$	532 (37)	Kuiper's $V^* = 2.23^*$
			Watson's $U^{*2} = 0.26^*$
	$G = 1\ s^{-1}$	564 (51)	Kuiper's $V^* = 2.48^*$
			Watson's $U^{*2} = 0.5^*$
Chain body orientation (ϕ_{body})	No shear	29 chains	Rayleigh = 5.42
	$G = 0.5\ s^{-1}$	33 chains	Rayleigh = 1.6
	$G = 1\ s^{-1}$	32 chains	Kuiper's $V^* = 2.8^*$

* Distribution is significantly different from uniform ($\alpha = 0.05$).

under shear lost their trailing flagellum and seemed to spin in place. Shear rate in their study, however, exceeded natural levels. Here we take an empirical approach to examine the effects of simple shear flow on swimming directions (hereafter, orientations) of two species of dinoflagellates, *Alexandrium catenella* and *Glenodinium foliaceum.* We address the case of randomly swimming cells and chains; that is, in the absence of a cue that may cause directional motion.

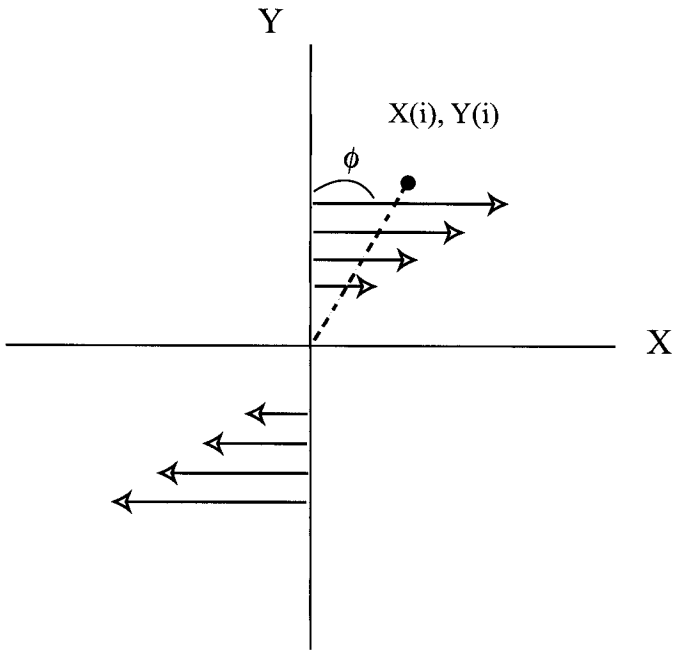

Fig. 1. Coordinate system of the flow. Arrows mark the direction of the flow. The position of the cell along its swimming path ($X(i)$, $Y(i)$) relative to the axis perpendicular to the flow is given by the angle ϕ.

Methods

Organisms and culture growth conditions—Stock cultures of *Alexandrium catenella* (isolated from East Sound, Orcas Island, Washington, in 1996) and *Glenodinium foliaceum* (previously called *Peridinium foliaceum*; University of Texas culture collection, LB 1688) were grown in sterile-filtered, modified IMR (Perry et al. 1981) at 20°C in a 15 : 9 light : dark cycle. *G. foliaceum* is a single-celled dinoflagellate found in brackish water (described and illustrated in Dodge 1982). *G. foliaceum* cells were on average (±1 SD) 22.9 ± 5 μm long and 18.5 ± 5 μm wide ($n = 52$). *A. cetenella* is cosmopolitan, often forming chains (described and illustrated in Tomas 1997). Under our culture conditions, *A. catenella* cultures contained a mixture of single cells and chains ranging up to 10 cells long. In this study, trajectories of both single cells and four-celled chains were examined. Single cells of *A. catenella* were on average 25.2 ± 3.2 μm long and 26 ± 3.1 μm wide ($n = 50$). Chains were 98.6 ± 7.7 μm long and 25.6 ± 3.3 μm wide ($n = 46$) . All cultures were maintained under exponential growth prior to experiments.

Experimental procedure and video analysis—Observations and measurements were done in the Taylor–Couette apparatus described in Karp-Boss and Jumars (1998, fig. 2). For each species, a culture was placed gently in the gap (1 cm wide) between two rotating cylinders, and all visible bubbles were removed. After 20 min of acclimation to the tank, swimming trajectories of single cells and chains on the hor-

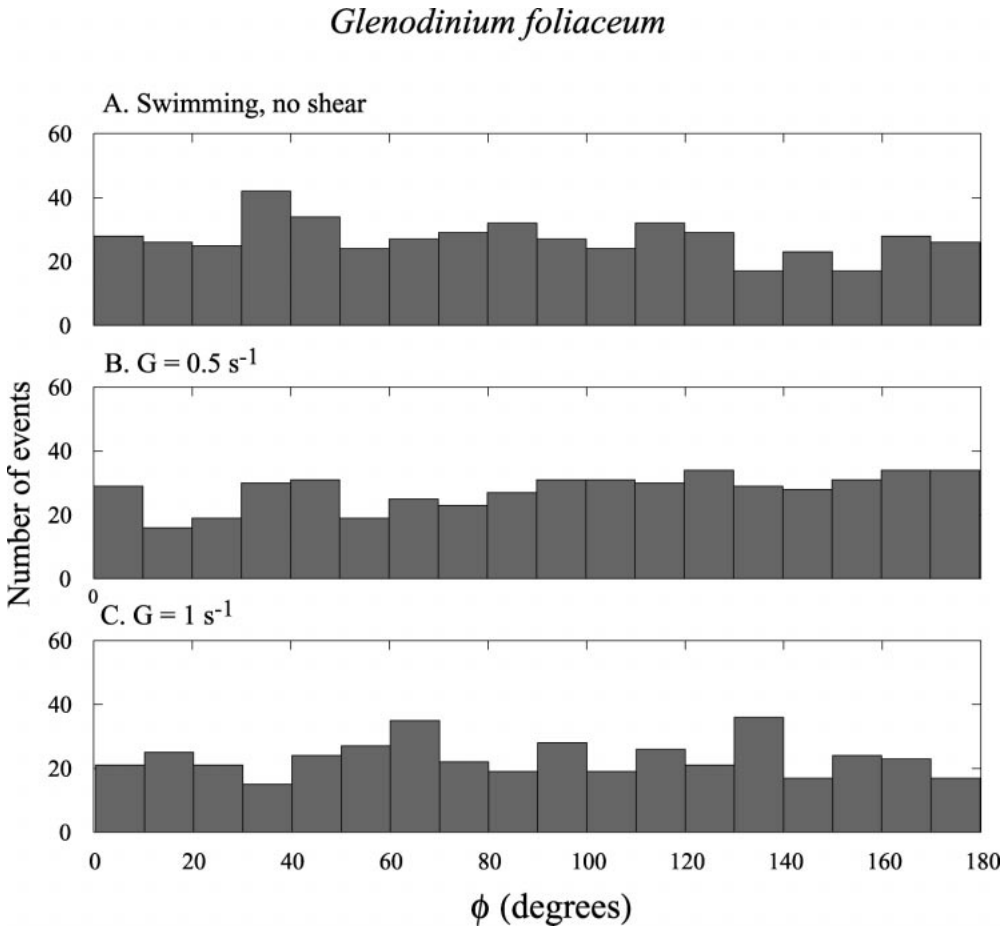

Fig. 2. Distribution of swimming orientation angle (ϕ), after subtracting the mean flow, for single cells of *G. foliaceum* at three shear rates. When $\phi = 90°$, the cell is swimming in the direction of the flow. For all shear rates, the distribution of ϕ is insignificantly different from uniform (Table 1). (A) $G = 0\ s^{-1}$; (B) $G = 0.5\ s^{-1}$; (C) $G = 1\ s^{-1}$.

izontal plane were recorded for 15 min. Each culture was then exposed to two shear rates, $G = 0.5\ s^{-1}$, followed by $G = 1\ s^{-1}$. Recording began after a laminar shear was established in the tank and lasted for 15 min.

To avoid wall effects, we focused on cells at the center of the gap and 5–7 cm deep in the tank. The microscope light was directed to a mirror at the bottom of the tank; thus, no effect of light on swimming orientation was expected on the horizontal plane (i.e., the plane of the shear). To limit cell–cell interactions, concentrations of cells in all treatments were $<800\ ml^{-1}$. By the end of the experiment, cells or chains were examined microscopically for potential damage and discarded. The experiment was then repeated with a new aliquot from the same seed culture.

Shear rates were calculated from the dimensions and rotation rates of the cylinders (Trevelyan and Mason 1951). For natural turbulence, the magnitude of the shear is proportional to ϵ, the kinetic energy dissipation rate of turbulence (Tennekes and Lumley 1972). Typical values of ϵ measured in the surface mixed layer are 10^{-4}–$10^{-2}\ cm^2\ s^{-3}$, with high values reaching order $10^{-1}\ cm^2\ s^{-3}$ (Oakey and Elliot 1982; MacKenzie and Legget 1993; Gargett 1997). Shear rates in the surface mixed layer, estimated from measurements of ϵ, are in the range 0.01–2 s^{-1}. Shear rates used in this study thus represent strong turbulence.

Video images of swimming trajectories were analyzed manually by measuring the position of the center of a cell or a chain every 0.33 s, using a VCR with frame-by-frame analysis capability (Panasonic, AG 6300). Image analysis of swimming trajectories of chains also included measurements of the positions of the ends of each chain every 0.33 s. Positions were measured to the nearest 10 μm. To determine the position of each observed step relative to the coordinate system of the flow field, prewashed polystyrene particles (30–50 μm, Particle Information Services, Inc.) were added to each culture at concentrations sufficiently low to avoid particle–cell interactions, and their trajectories were recorded and measured as described above. Error in the measurements of particle orientation did not exceed $\pm 3°$. All measured positions were transformed from the coordinate system of the screen to the coordinate system of the flow field, in which the *x*-axis is defined as the direction of the flow and the *y*-axis is the axis perpendicular to the flow streamlines in the plane of view (Fig. 1).

Data analysis—Swimming orientations were measured by calculating the angle (hereafter, ϕ) between a given position

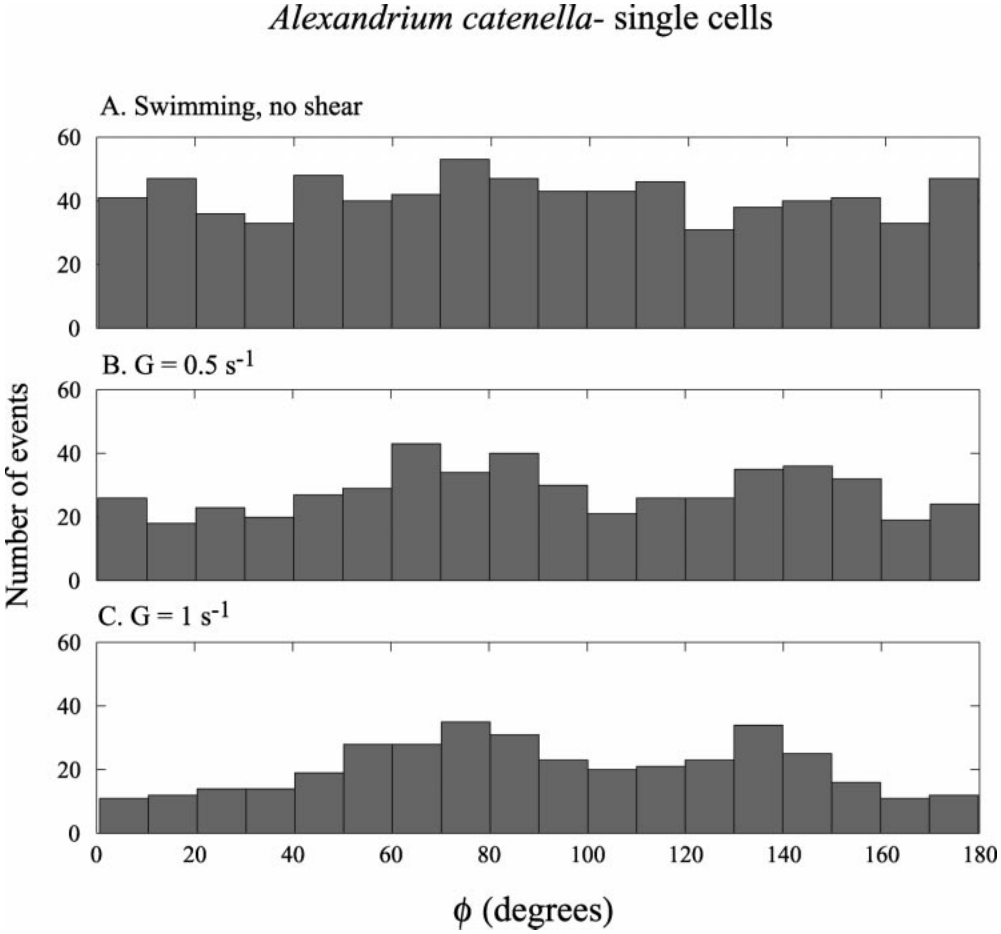

Fig. 3. Distribution of swimming orientation angle (ϕ), after subtracting the mean flow, for single cells of *A. catenella* at three shear rates. When $\phi = 90°$, the cell is swimming in the direction of the flow. (A) $G = 0\ s^{-1}$; the distribution of ϕ is insignificantly different from uniform (Table 1). (B) $G = 0.5\ s^{-1}$; the distribution of ϕ differs significantly from uniform (Table 1). (C) $G = 1\ s^{-1}$; the distribution of ϕ differs significantly from uniform (Table 1).

along the swimming trajectory and the axis perpendicular to the flow streamlines (Fig. 1). To resolve whether the observed swimming trajectories resulted from a simple superposition of the shear field on the swimming motion of cells and chains (as seen by an observer at rest) or, conversely, are due to a change in swimming behavior, we needed to remove the advective component due to the flow. To avoid effects on swimming behavior, tracer particles were added to each culture at very low concentrations. Whereas particle concentrations were sufficient to determine the coordinate system of the flow field, they were unfortunately too low for accurate measurement of local flow velocities. Nevertheless, for swimming cells with no preferential swimming in the x-direction, swimming trajectories can be used to compute the mean flow. Mean observed velocity ($U_{observed}$) is a sum of the mean flow velocity ($\bar{U}_{flow}$) and the mean swimming velocity ($\bar{U}_{swim}$).

$$\bar{U}_{observed} = \bar{U}_{flow} + \bar{U}_{swim}$$

If cells have the same preference for the $-x$-direction as for the $+x$-direction, mean swimming velocity along the x-axis ($\bar{U}_{swim}$) equals zero, and the mean observed velocity (over a large set of data) becomes $U_{observed} = U_{flow}$.

For each examined species and shear rate, the parameters of the mean flow are obtained by computing the linear regression

$$\bar{U}_{observed} = G(Y_{n-(1/2)} + Y'),$$

where G is the shear rate, $Y_{n-(1/2)}$ is the y-coordinate midway between time step n and $n - 1$ and Y' is the y-coordinate at which translational velocity equals zero. Values of G obtained by the linear regression agreed, within 20%, with the shear rates calculated based on the dimensions and rotation rates of the apparatus. Mean flow was then subtracted from each measured swimming velocity to obtain orientations of cells and chains relative to the flow (i.e., removing the advective component).

The orientation of chains in the flow may not necessarily be in the same direction at which they swim; therefore, we also measured chain body orientations relative to the flow. Chain orientation (ϕ_{body}) was measured by calculating the

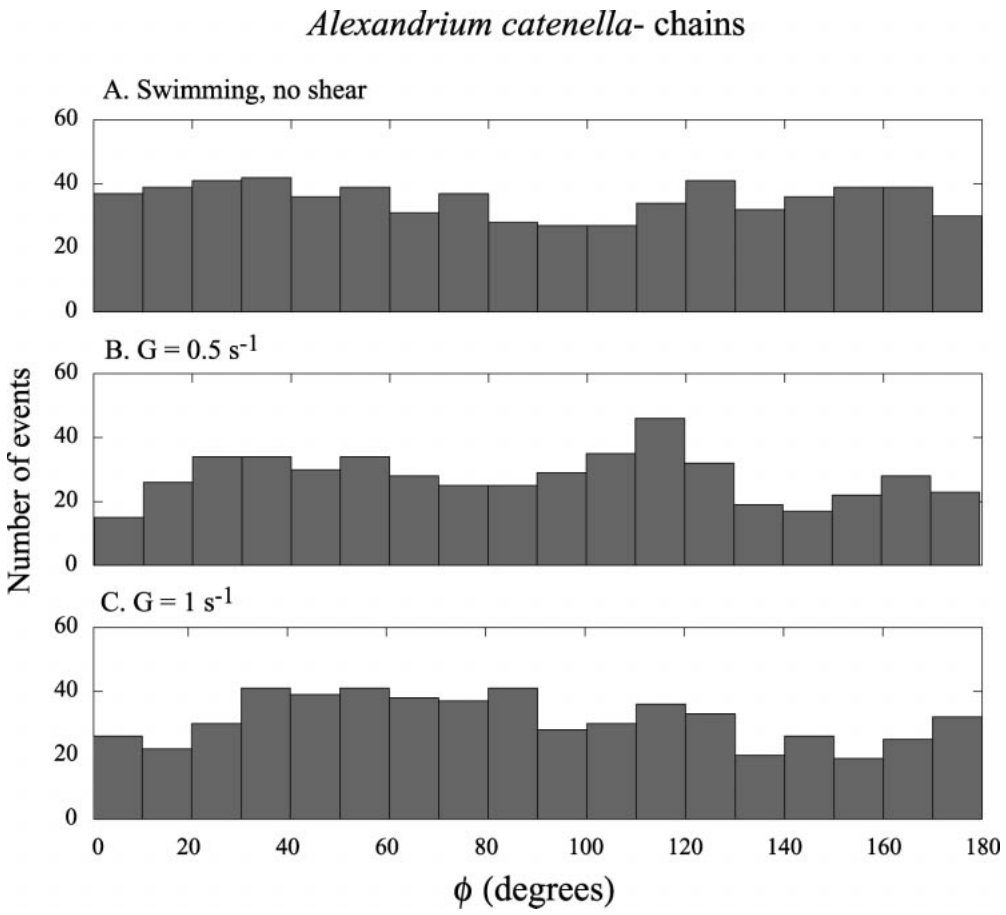

Fig. 4. Distribution of swimming orientation angle (ϕ), after subtracting the mean flow, for chains of *A. catenella* at three shear rates. (A) $G = 0$ s^{-1}; the distribution of ϕ is insignificantly different from uniform (Table 1). (B) $G = 0.5$ s^{-1}; the distribution of ϕ differs significantly from uniform (Table 1). (C) $G = 1$ s^{-1}; the distribution of ϕ differs significantly from uniform (Table 1).

angle between the principal axis of the chain and the axis perpendicular to the direction of the flow.

Statistical analysis of swimming orientations—Swimming motion in the absence of shear and a cue (light or chemical) is expected to be random; hence, the distribution of ϕ is not expected to be significantly different from uniform. If shear does not affect swimming motion (i.e., what is observed is a simple superposition of the flow field and the swimming motion), swimming is expected to remain random after removing the mean flow. Any deviation of the distribution of ϕ from uniform would indicate an effect of shear on swimming.

Distributions of ϕ in the absence and presence of shear were tested for uniformity using statistics for directional data. Statistical theories and statistical inference for circular variables (i.e., angles) and linear variables differ. For circular data, the von Mises distribution (also called the circular normal distribution) plays a similar role in statistical inference to that of the normal distribution used for linear variables (Batschelet 1965; Mardia 1972). The von Mises density function is given by

$$f(\phi, \mu_0, k) = \frac{1}{2\pi I_0(k)} \exp[k \cos(\phi - \mu_0)],$$

where μ_0 is the circular mean direction, k is a concentration parameter, and I_0 is the zeroth-order Bessel function (Mardia 1972).

The shear in the gap between the cylinders is constant. The resultant forces acting on a cell or a chain at the angles ϕ and $\phi + 180°$ are therefore the same (Fig. 1). Our results show the same symmetry (i.e., the same pattern that is displayed 180° apart). Therefore, for statistical analysis, observations on ϕ and on $\phi + 180°$ were combined and the reported range of angles was reduced to 0–180°. Data were then treated as unimodal. For each of the measured ϕ distributions, the data were divided into 18 bins of 10° each. and a von Mises distribution was fitted to the data according to Mardia (1972, section 5.4.1). To test for uniformity, the Rayleigh test was used for data sets that could be described by a von Mises distribution (Mardia 1972). For data sets that did not fit a von Mises distribution, two nonparametric tests, Kuiper's and Watson's U^2, were used (Mardia 1972). The standard level of $\alpha = 0.05$ was used for hypothesis testing.

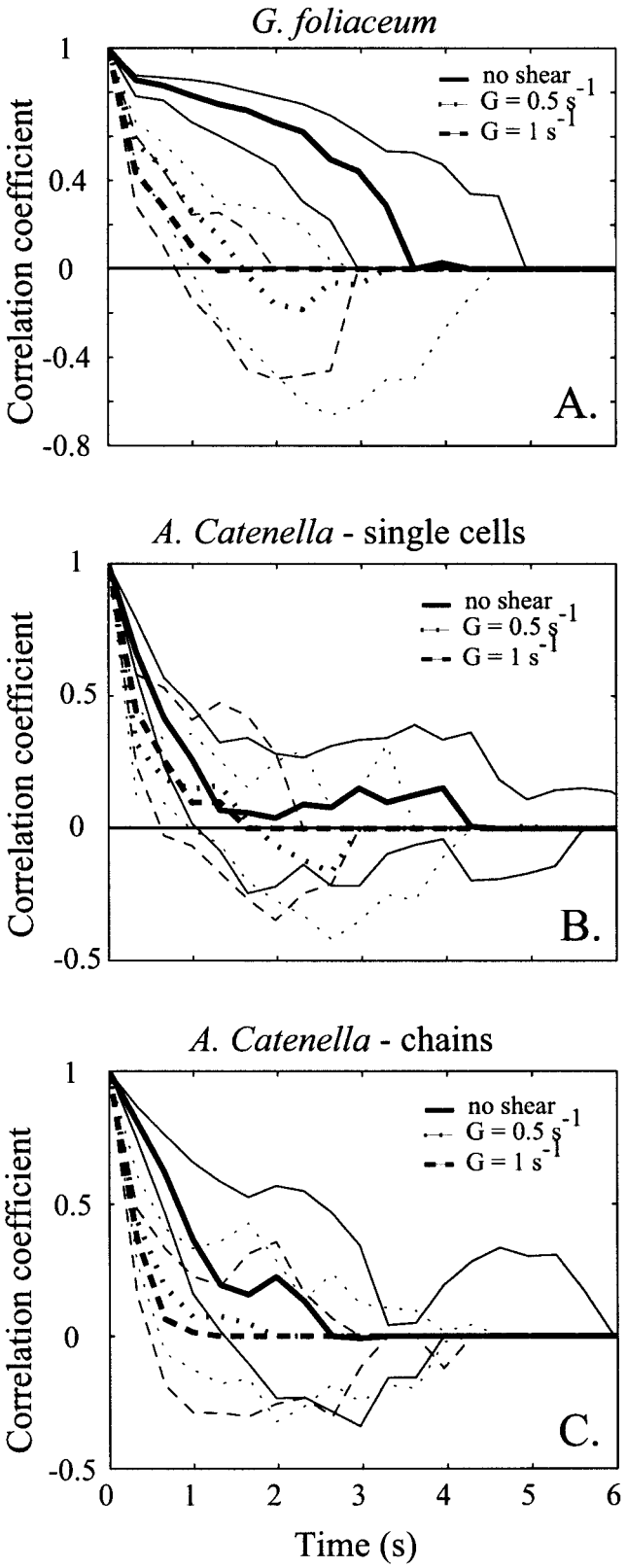

Fig. 5. The median (thick line) and the 25th and 75th percentiles (thin lines) of autocorrelation functions in the absence of shear (black, solid lines) and at shear rates $G = 0.5\ s^{-1}$ (dotted lines) and $G = 1\ s^{-1}$ (dashed lines). (A) *G. foliaceum,* (B) *A. catenella* single cells, and (C) *A. catenella* chains. When the correlation coefficient reaches zero and remains close to zero, steps separated by that interval along the trajectory are uncorrelated.

Changes in the mean decorrelation time (i.e., the duration, and hence the distance, cells and chains swim before changing direction) provide another indication of shear effects on swimming behavior. To determine the mean decorrelation time, an autocorrelation function ($C(t)$) was calculated for each trajectory ($-1 \leq C(\tau) \leq 1$ and $C(0) = 1$).

$$C(\tau) = 1/n \sum \cos \phi(t)\cos \phi(t + \tau) + \sin \phi(t)\sin \phi(t + \tau)$$

The time variable τ is defined as $n\Delta t$, where Δt is the time between one step and the next and n is an integer number of intervening frames. The summation is over all measured directions along a trajectory. When the autocorrelation coefficient reaches zero, steps along a trajectory are no longer correlated in direction.

Results

Swimming trajectories and orientations—In the absence of shear, neither species showed any preferred swimming direction. For both species, mean displacement (± 1 SD) along the *x*-axis was approximately zero (for *A. catenella* single cells, $1.3 \pm 2.6\ \mu m$; for *A catenella* chains, $2.9 \pm 2.1\ \mu m$; and for *G. foliaceum,* $1.5 \pm 4.5\ \mu m$). Distributions of ϕ were not significantly different from uniform (Figs. 2A, 3A, 4A; test statistics are given in Table 1), indicating no significant departure from random in swimming orientation by either species. Measured swimming speeds, on the horizontal plane, were $175 \pm 8\ \mu m\ s^{-1}$ for single cells of *A. catenella,* $185 \pm 7\ \mu m\ s^{-1}$ for chains of *A. catenella,* and $197 \pm 17\ \mu m\ s^{-1}$ for *G. foliaceum.*

The extent to which shear affected swimming orientations varied between the two species. Distributions of ϕ for *G. foliaceum* were not significantly different from uniform at either shear rates $G = 0.5\ s^{-1}$ or $G = 1\ s^{-1}$ (Fig. 2B,C; Table 1). Single cells of *A. catenella,* however, showed ϕ distributions at both $G = 0.5\ s^{-1}$ and $G = 1\ s^{-1}$ that were bimodal rather than uniform (Fig. 3B,C). Statistical tests reject the null hypothesis of uniformity (Table 1), indicating that swimming orientation was affected by shear. The effect increased with increasing shear (Fig. 3B,C). The distributions of ϕ for chains of *A. catenella* at $G = 0.5\ s^{-1}$ and $G = 1\ s^{-1}$ were also significantly different from uniform (Fig. 4B,C; Table 1), indicating an effect of shear on swimming orientation of chains. For neither shear rate was any apparent mechanical damage to cells and chains observed.

Decorrelation time—A general trend of a decrease in decorrelation time with increasing shear was observed in both species (Fig. 5). The decrease in decorrelation time implies that cells and chains changed their swimming direction more frequently in the presence of flow. Decorrelation time for *G. foliaceum,* as indicated by the first zero crossing of the correlogram (i.e., $C[\tau] = 0$), declined from 3.7 s in the absence of shear to 1.3 s at $G = 1\ s^{-1}$ (Fig. 5A). A similar trend was

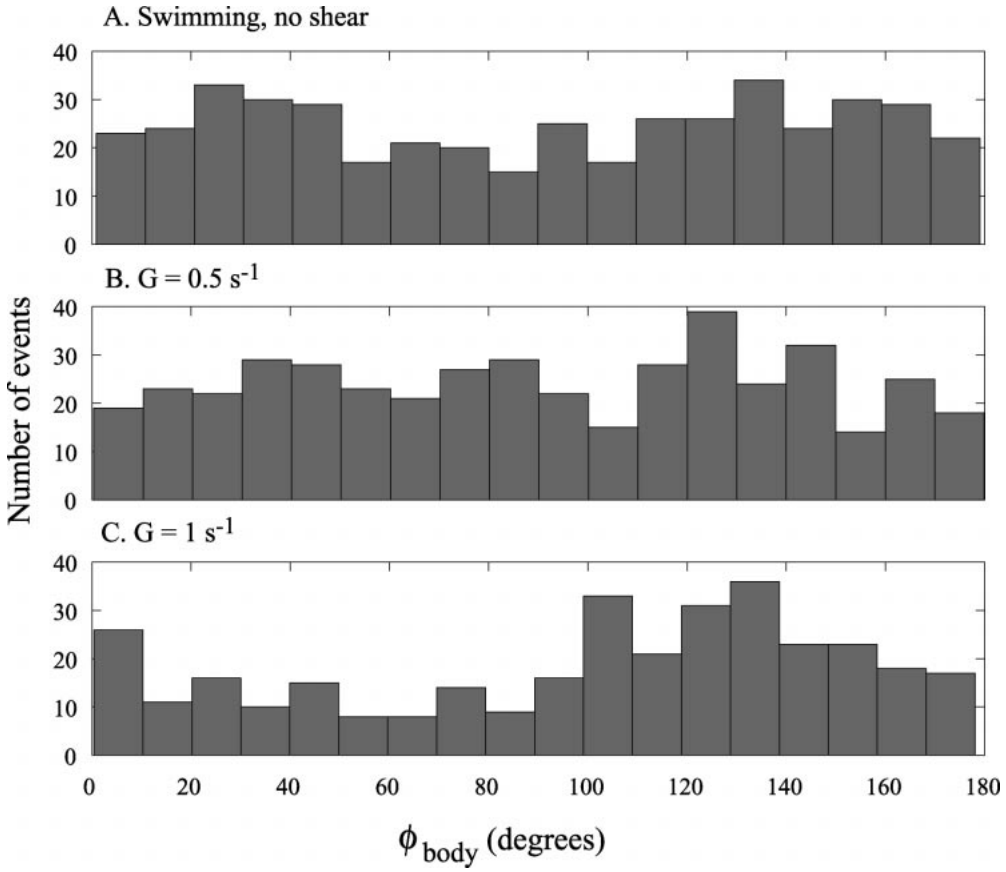

Fig. 6. Distribution of body orientations (ϕ_{body}) of chains in the flow. (A) $G = 0$ s^{-1}; the distribution of ϕ_{body} is insignificantly different from uniform (Table 1). (B) $G = 0.5$ s^{-1}; the distribution of ϕ_{body} is insignificantly different from uniform (Table 1). (C) $G = 1$ s^{-1}; the distribution of ϕ_{body} differs significantly from uniform (Table 1).

observed for *A. catenella*, where the decorrelation time for single cells decreased from 4.3 s in the absence of shear, to 1.6 s at $G = 1$ s^{-1} (Fig. 5B). For chains, decorrelation time decreased from 2.7 s in the absence of shear to 1.3 s at $G = 1$ s^{-1} (Fig. 5C). The variability around the median for *A. catenella* (particularly for single cells), however, was quite large.

Body orientations of chains of A. catenella—In the absence of shear, the distribution of the orientation of chains, ϕ_{body}, was not significantly different from uniform (Fig. 6A, Table 1). Jeffery's (1922) theory predicts that in the presence of shear, nonmotile, elongated spheroids and rod-like particles will have a preferred orientation in the flow, resulting in ϕ_{body} clustered near 90° (Fig. 7). At a shear level of $G = 0.5$ s^{-1}, the distribution of ϕ_{body} remained insignificantly different from uniform (Fig. 6B, Table 1), indicating that the random orientation of chains in the flow was not strongly affected by the shear. At a shear level of $G = 1$ s^{-1}, however, the distribution of ϕ_{body} became significantly different from uniform (Fig. 6C; Table 1), clustering around 135°.

Discussion

Dinoflagellates in oceans and lakes encounter shear flows when exposed to turbulence or when subjected to shear layers induced by currents. Swimming orientations and trajectories in the presence of shear flows will depend on whether motion of the cells is dominated by environmental fluid motion or by the inherent motion of the cells. An important question for modeling the effects of turbulence on dinoflagellates is whether swimming motion of dinoflagellates in the presence of shear flow can be described accurately by simple superposition of the flow on swimming motion in the absence of flow. The assumption of simple superposition has often been used in models to asses the effects of turbulence on vertical migration of dinoflagellates (Yamazaki and Kamykowski 1991; Kamykowski 1995) and on predator–prey interactions (Rothschild and Osborn 1988). The observed departure of swimming orientations of *A. catenella* from a uniform distribution and the observed trend of the decrease in decorrelation time with increasing shear rate observed for both species suggest that dinoflagellates respond to shear by altering their swimming behavior. Hence, the assumption of simple superposition may not be valid in all cases.

Surprisingly, swimming orientations of single cells of *A. catenella* appear to be more sensitive to shear than those of chains (Figs. 4B,C, 5B,C). In the presence of shear, there is a force acting to bring the axes of elongated shapes to a position parallel to the direction of the flow (Jeffery 1922; Fig. 7). Therefore, one would expect stronger effects of shear

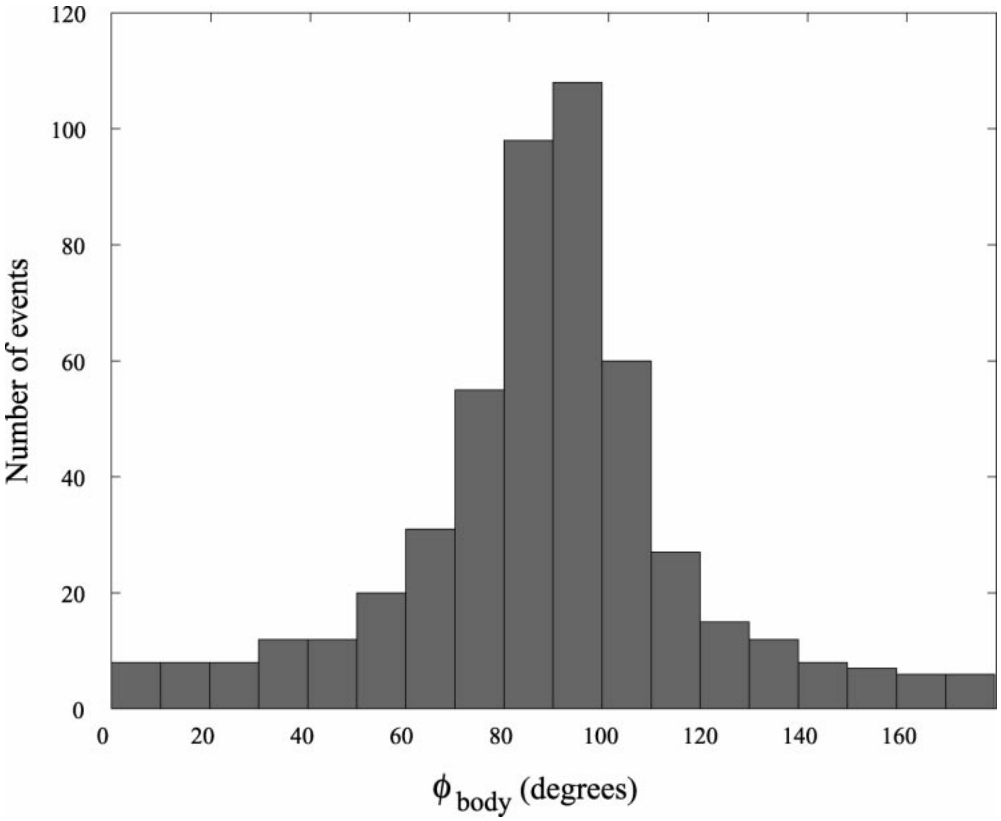

Fig. 7. Predicted distribution of body orientation (ϕ_{body}) for nonmotile chains based on Jeffery's theory (Jeffery 1922).

on swimming orientations of chains. At a shear rate of $G = 0.5\ s^{-1}$, the orientation of chains was insignificantly different from random (Fig. 6B; Table 1), suggesting that swimming may be sufficient to overcome the forces induced by the flow. At $G = 1\ s^{-1}$, chains displayed a preferred body orientation clustered about 135°, indicating an effect of shear. We do not have sufficient information to explain why the orientation of chains is clustered about 135°, but the explanation is likely to involve differences in drag forces on the body and flagella.

Swimming behavior comprises two components: orientation and swimming speed. Swimming motion of chains may be less affected by shear, compared to single cells, if they swim faster. Fraga et al. (1987) predicted that since the drag force acting on cells in a long chain is less than on those same cells if they were unattached, chains should swim faster than single cells. They observed that swimming speeds of chains of *Gymnodinium catenatum* and *Alexandrium affine* were indeed faster than those of single cells (Fraga et al. 1987). In our study, measured swimming speeds in the direction perpendicular to the flow (the *y*-direction; Fig. 1) suggested that swimming speeds of chains were, on the average, slightly higher than those of single cells (average swimming speed in the absence of shear [±1 SD]: 134 ± 3.4 $\mu m\ s^{-1}$ and 111 ± 2.8 $\mu m\ s^{-1}$ for chains and single cells, respectively). Whereas the average swimming speed of chains in the direction perpendicular to the flow increased as a result of exposure to shear (172 ± 4.6 $\mu m\ s^{-1}$ for shear rate $G = 1\ s^{-1}$), average swimming velocity of single cells decreased slightly (105 ± 2.7 $\mu m\ s^{-1}$ for shear rate $G = 1\ s^{-1}$).

Little is known about the evolutionary and ecological significance of chain formation. The question becomes even more fascinating when chains of motile cells are considered. Swimming behavior among individuals in chains of *A. catenella* appears to be highly coordinated in both the presence and absence of shear. The underlying mechanism that enables cells in chains to maintain coordinated swimming behavior under various hydrodynamic conditions is a subject for future studies.

Although simple shear flow does not mimic the natural hydrodynamic environment, partially because turbulence is intermittent in both time and space, it provides a well-defined environment to assess the effects of shear on the motility of dinoflagellates and can provide insight into the interplay between self propulsion of a dinoflagellate and a flow with a velocity gradient. If the time scale of reorientation of cells inherent in their swimming behavior is shorter than the time scale of the smallest fluctuations in the turbulent flow, it can be argued that it may be possible for them to reorient effectively. The time scale of the smallest fluctuations in a turbulent flow is given by the Kolmogorov microscale of time ($\tau = 2\pi(\nu/\epsilon)^{1/2}$), where ν is the kinematic viscosity (approximately 0.01 $cm^2\ s^{-1}$) and ϵ is the turbulent kinetic energy dissipation rate ($cm^2\ s^{-3}$) (Tennekes and Lumley 1972)). Assuming $G \approx (\epsilon/\nu)^{1/2}$ (Karp-Boss et al. 1996), we estimated

the time scale of the smallest velocity fluctuations of the flow in the ocean to be on the order of 12.5 s for turbulence that would produce a shear rate $G = 0.5\ s^{-1}$ and 6 s for turbulence that would produce a shear rate $G = 1\ s^{-1}$. Under the experimental conditions, decorrelation times for both *A. catenella* and *G. foliaceum* are smaller than the characteristic time scale of turbulence that gives a shear rate comparable to $G = 0.5\ s^{-1}$ and of the same order as the characteristic time scale of turbulence that gives a shear rate comparable to $G = 1\ s^{-1}$. This result suggests that under natural turbulence (for which G is generally smaller than $1\ s^{-1}$) cells will be able to reorient themselves.

Shear rates used in this study ($G = 0.5\ s^{-1}$ and $G = 1\ s^{-1}$) reflect very strong turbulence. Although such conditions have been observed in the field, they probably represent an upper limit. Under turbulent conditions, cells, on average, experience lower shears than those we produced (MacKenzie and Legget 1993). Despite the differences between the shear environment in the Taylor–Couette tank and that experienced by dinoflagellates in nature, our results suggest that in nature, strong turbulence will be required to overwhelm swimming efforts of *A. catenella* and *G. foliaceum.* Under natural conditions of weak and moderate turbulence, with shear rates typically smaller than those imposed in this study, both species are expected to be able to maintain their swimming orientations. If this generalization holds for other dinoflagellates, direct interference of natural turbulence with swimming orientation is unlikely alone to account for their reduced prevalence under such conditions. On larger scales, when strong vertical mixing occurs in the water column, dinoflagellates may still be able to maintain a preferred orientation, although they may not be able to maintain their vertical position against advection.

More observations and measurements, with more realistic shear flows, are required to determine the effects of natural shear flows on swimming motions of dinoflagellates. Improved instrumentation to examine all three vectors of swimming motion, as well as the rotational motion of the cells, would fortify future studies. Our study took an initial step toward understanding the effects of shear flows on swimming behavior of dinoflagellates. The combination of a shear flow with a cue (e.g., light) in future experiments would add further to the understanding of the role of turbulence in the migratory behavior of dinoflagellates.

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