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Motion of diatom chains in steady shear flow

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Abstract

Information on the motion of phytoplankton in shear flows is essential for predicting or understanding effects of turbulence on processes such as nutrient uptake, aggregate formation, and phytoplankton–herbivore interactions. Of particular interest is the motion of diatom chains because they are expected to benefit most from enhancement of nutrient flux due to turbulence and are often the most abundant components in aggregates. We studied the motion of two chain-forming diatoms, *Skeletonema costatum* and *Thalassiosira nordenskiöldii*, in steady shear flow and in the light of available theory for rigid, elongated spheroids. Both species underwent periodic rotation upon exposure to a simple shear flow, as predicted by theory. Whereas the rotational orbits of *S. costatum* resembled those predicted by theory for rigid spheroids, the rotational motion of *T. nordenskiöldii* was more like the motion of flexible fibers observed in engineering applications. Periods of rotation of *S. costatum* increased linearly with increasing axis ratio, whereas no clear relationship was observed between periods of rotation and axis ratios for *T. nordenskiöldii*. Measured periods of rotation of both species were smaller than predicted by theory for rigid spheroids of similar axis ratios. The diverse behaviors observed imply that fluxes of nutrients and collision frequencies experienced vary greatly with detailed shapes and mechanical properties of chains and their unit cells.

Despite the prevalence of turbulence in nature and the potential for turbulence-generated shear flows to enhance nutrient fluxes arriving at a cell surface, little is known about the motion (hereafter termed behavior) of phytoplankton cells in such flows. Calculation of the advective contribution to nutrient flux requires accurate description of the local flow field relative to the cell. The flow field to which a small phytoplankton is exposed in turbulent water is a laminar shear (Lázier and Mann 1989). Such a flow would, in general, cause the phytoplankton to both translate and rotate. Whether and how a cell rotates in the flow determines the extent to which streamlines in its vicinity are open or closed and hence the contribution of advection to the flux of nutrients. This motion, as well as departure from spherical shape (Pahlow et al. 1997), need to be taken into account in calculating nutrient fluxes to diatoms and other nonspherical cells.

Behavior in flow also plays a role in other important planktonic processes, such as aggregate formation and pred-

ator–prey interactions, because it determines the volume swept by the phytoplankton and hence its likelihood of encounter with other particles or with the appendages of herbivores. Of particular interest is the behavior of diatom chains because large cells and chains are the ones expected to experience substantial enhancement of nutrient flux in a shear field (Karp-Boss et al. 1996). In addition, diatom chains have a major role in the formation of aggregates in coastal waters and are often the most abundant components in such aggregates (Smetacek 1985; Alldredge and Gotschalk 1989; Riebesell 1991), making their behaviors in flow of particular interest in coagulation studies.

Despite all these reasons for interest in the behavior of phytoplankton cells in flow and despite a long history of bulk evaluations of the net effects of shear on nutrient uptake, growth, and aggregate formation (Pasciak and Gavis 1975; Thomas et al. 1995; Waite et al. 1997), we know of no published studies on the behavior of phytoplankton cells in well-defined flow fields. The behavior of particles in a shear flow, however, has long been studied in the context of rheological properties of suspensions (reviewed by Goldsmith and Mason 1967). Of potential relevance to chains is Jeffery's theory, which predicts the behavior of elongate, rigid spheroids in simple shear flow (Jeffery 1922). Jeffery's theory has been applied only recently to phytoplankton in a study that modeled the effects of turbulence on nutrient uptake by diatoms (Pahlow et al. 1997). Jeffery's theory, however, assumes a rigid particle of perfectly spheroidal

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shape, whereas the morphologies of most diatoms deviate widely from this assumption. Spines and threads that often are present are expected to affect behavior in the flow dramatically. Moreover, diatom chains display a wide range of means by which cells are connected to each other and thereby differ not only in their morphologies but also in their mechanical properties (i.e., rigidity vs. flexibility). Empirical studies with both paper pulp and textile fibers reveal strong dependence of behavior on the mechanical properties of the particle (Arlov et al. 1958; Forgacs et al. 1958). Lack of quantitative information on the mechanical properties of chains, however, makes it difficult to predict their behaviors in the flow, and thus there is abundant need for direct observation.

Here we report the first observations on the behavior of two chain-forming species, *Skeletonema costatum* and *Thalassiosira nordenskiöldii*, in steady shear flow. These two species were chosen because they differ widely in morphologies and mechanical properties. Chains of *S. costatum* appear to be rigid and comprise relatively small, elliptical cells joined by long, marginal, siliceous processes that can exceed the length of the cells themselves (Cupp 1943). The chains are long (reaching about 800 μm in our cultures) and thin (width $<10 \mu\text{m}$). *T. nordenskiöldii*, on the other hand, forms flexible chains by means of thin, central, chitinous threads (Cupp 1943). Cells are octangular, with long, chitinous threads that project at various angles from the principal axis of the chain. Chains are typically shorter and wider than in *S. costatum*.

Theoretical considerations and predictions

We used Jeffery's (1922) theory to guide our observations of these two species. It predicts that neutrally buoyant, rigid spheroids subjected to a simple shear flow will undergo periodic rotation. An elongated spheroid of large axis ratio (the ratio in length between major and minor axes) remains, for most of the time, with its major axis almost parallel to the streamlines (in its most stable configuration), but it then "flips" periodically (Jeffery 1922; Goldsmith and Mason 1967). The period of rotation, T , depends only on the magnitude of the shear rate, G [T^{-1}] and the axis ratio of the particle, r_a (Jeffery 1922):

$$T = \frac{2\pi}{G} \left(r_a + \frac{1}{r_a} \right), \quad (1)$$

For elongated spheroids ($r_a > 1$) the period of rotation increases with increasing axis ratio (Fig. 1). The period of rotation has a minimum at $r_a = 1$; a perfect sphere rotates faster than any other rigid spheroid (Fig. 1).

Empirical studies with spheres show excellent agreement with Eq. 1 (Trevelyan and Mason 1951). Because it has been difficult to make small, regular ellipsoids of revolution to test Jeffery's theory, short glass cylinders and discs have been used as models of prolate (cigar-shaped) and oblate (discus-shaped) spheroids, respectively. Rotational orbits of rigid cylinders and discs conform well to predictions of Jeffery's theory (Trevelyan and Mason 1951; Goldsmith and Mason 1962). Measured periods of rotation, however, are

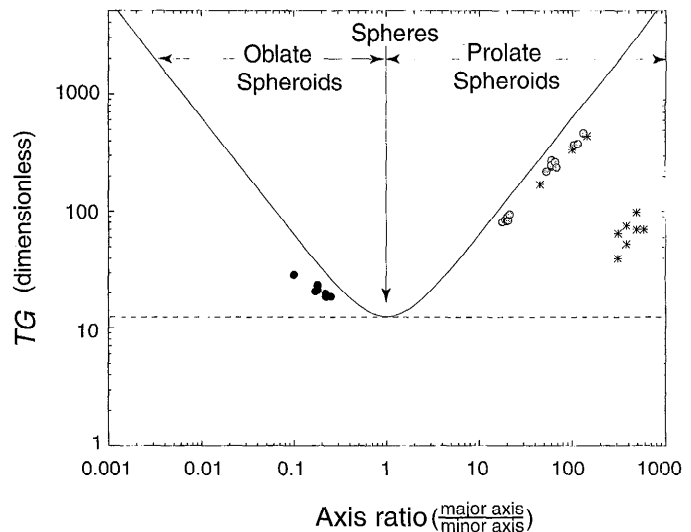


Fig. 1. The product TG (where T is the period of rotation [T] and G is the shear rate [T^{-1}]) as a function of axis ratio. Predicted values based on Jeffery's (1922) theory (Eq. 1) for oblate (discus-shaped) spheroids and prolate (cigar-shaped) spheroids are given by the solid line. Empirical studies show that TGs of particles that deviate from a perfectly spheroidal shape, such as rigid cylinders (grey circles, data from Trevelyan and Mason 1951; Mason 1954), disks (full circles, data from Goldsmith and Mason 1962) and flexible rods (stars, data from Forgacs et al. 1958) are always smaller than predicted by theory for spheroids of the same axis ratio. The lower bound on TG is given by spheres (axis ratio = 1) and is described by the dashed line, which we extended across the range of axis ratios.

shorter than predicted by Eq. 1 for spheroids of equivalent axis ratios (Fig. 1) (Trevelyan and Mason 1961; Goldsmith and Mason 1962). The abrupt ends of the cylinder versus the smooth, gradual taper of radius in a spheroid make the cylinder less stable at the position parallel to the streamlines, causing it to flip more frequently.

Jeffery's (1922) theory may well predict rotational orbits of rigid, smooth, rod-like particles, but it is inadequate to predict the behavior of flexible, rod-shaped particles. Flexible, elongate particles bend as they rotate, and their rotational orbits can be classified into distinct groups that correspond to the degree of flexibility of the particle (Mason 1954; Arlov et al. 1958). The period of rotation of a flexible, rod-shaped particle is typically shorter than that of a rigid, prolate spheroid of the same axis ratio (Fig. 1) (Mason 1954; Arlov et al. 1958)—a result of the lower resistance of a flexible particle to the flow (i.e., lower drag) and its deformation due to flow-induced forces (Arlov et al. 1958). Nevertheless, for all morphologies and mechanical properties so far studied empirically, Jeffery's theory appears to set the upper (rigid spheroids) and lower (spheres) bounds on the period of rotation of particles in a simple shear flow (Fig. 1) and hence remains useful. Measured periods of rotation of particles other than rigid spheres and spheroids fall between these limits (Fig. 1). If the motion of diatom chains in simple shear flow is indeed periodic, their periods of rotation should also fall within these bounds.

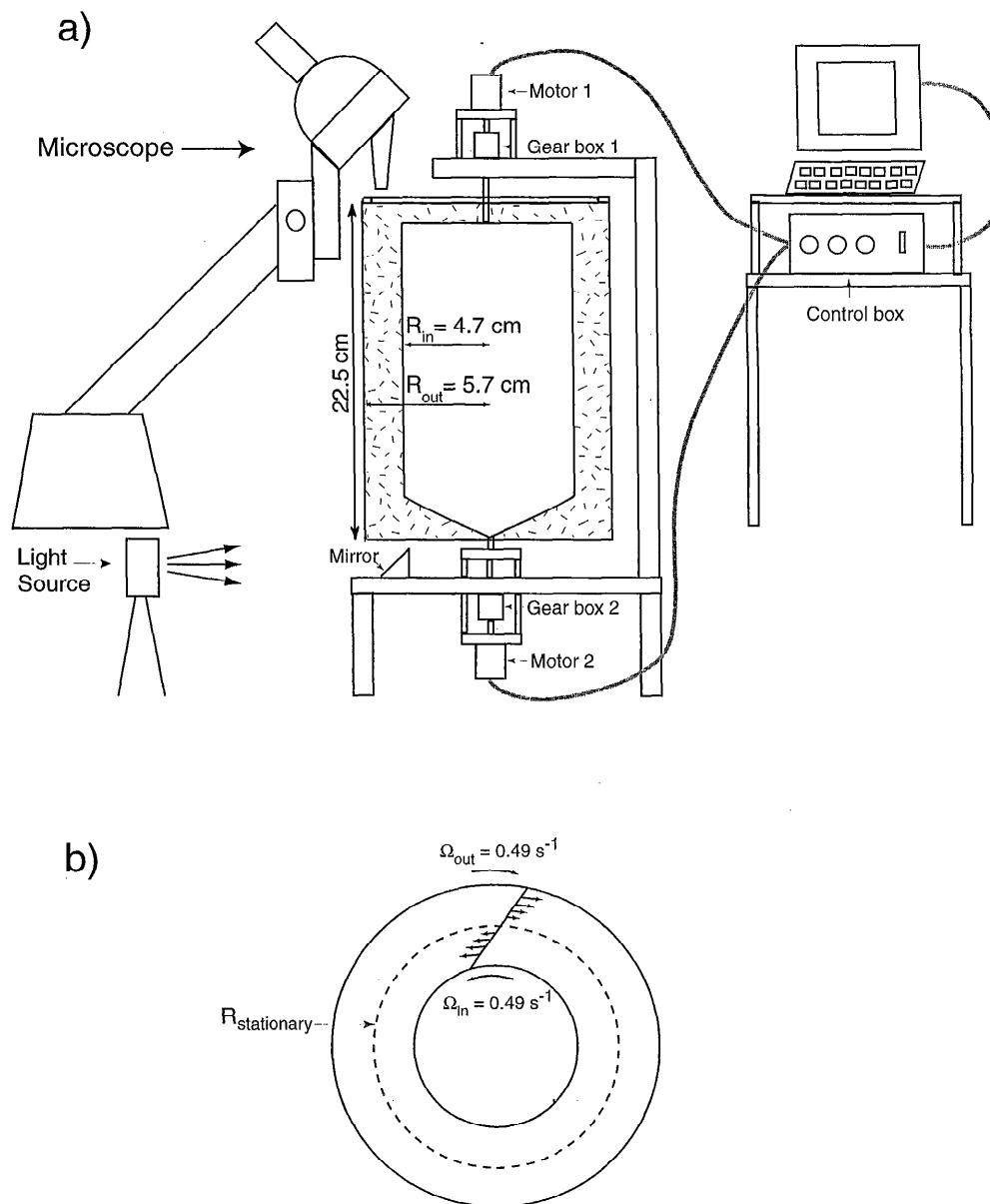


Fig. 2. (a) Experimental apparatus. It consists of two coaxial, cast-acrylic cylinders, each driven by a separate stepper motor. To ensure concentricity of the two cylinders, the removable inner cylinder is held centered by spindles at its top and bottom, a bearing at the center of the acrylic cap on top of the apparatus, and three roller bearings at the circumference of the acrylic cap. The top spindle of the inner cylinder is connected with a spring pin to a motor through a gear box. The outer cylinder is held on a hub with a spring pin to which a second gear box and motor are connected. The gap between the two cylinders contains the culture medium (approximately 800 ml). R_{in} and R_{out} are the radii of the inner and outer cylinder, respectively. (b) Top view, in the plane of shear. Arrows indicate direction of flow. Dashed line indicates the region in which there is no relative translational motion of particles ($R_{stationary}$). Ω_{in} and Ω_{out} are the angular velocities of the inner and outer cylinder, respectively. The shear rate at any given point across the gap between the two cylinders can be calculated from Eq. 3.

Methods

Observations and measurements were made using a Taylor-Couette apparatus in which chains were observed on the plane of the shear (Fig. 2). The apparatus, modified after

Bartok and Mason (1957), consists of two coaxial, cast-acrylic cylinders. Great care was taken to ensure concentricity of the two cylinders. The cylinders can rotate in opposite directions by means of a dual stepper motor (MD-2, Arrick Robotics) controlled by a computer. As a result, laminar

shear is created in the fluid that fills the gap between the two cylinders (Fig. 2b). Rotation of the cylinders in opposite directions enabled us to maintain the center of a chain in a stationary position ($R_{stationary}$) in the field of view of a microscope for a period long enough to observe its rotational behavior (Fig. 2b). The location in the gap in which the center of a chain will have no translational motion depends on the radii and rotation rates of the outer and inner cylinders (Trevelyan and Mason 1951):

$$R_{stationary} = \left(\frac{R_{out}^2 R_{in}^2 (\Omega_{out} + \Omega_{in})}{R_{out}^2 \Omega_{out} + R_{in}^2 \Omega_{in}} \right)^{1/2}, \quad (2)$$

where R_{out} and R_{in} are the radii of the outer and inner cylinders (with $R = 0$ defined as their joint center), and Ω_{out} and Ω_{in} are the angular velocities [T^{-1}] of the outer and inner cylinders, respectively.

The shear rate, $G[T^{-1}]$, at any position across the gap between the cylinders is calculated as (Trevelyan and Mason 1951):

$$G(R) = \frac{2(\Omega_{out} + \Omega_{in})R_{out}R_{in}}{R^2(R_{out}^2 - R_{in}^2)}, \quad (3)$$

Note that the field of motion in the Taylor-Couette apparatus does not provide the constant G assumed by Jeffery (1922), but one that increases between the outside and inside boundaries of the gap. The increase in G along a distance equal to the length of the chain is so small, however, that the error introduced is negligible (Trevelyan and Mason 1951), and the flow can be approximated as a simple shear flow.

Dimensions of the apparatus and the rotational rates of the cylinders (Fig. 2) were chosen to satisfy three conditions: (1) the gap between the cylinders is much larger than the largest chain observed, (2) the region in which a particle is observed is located well away from the tank walls, and (3) the flow is strictly laminar (Taylor 1922). We chose to do all our observations at a shear rate, $G(R_{stationary}) = 0.5 \text{ s}^{-1}$. This rate is on the same order of magnitude experienced by phytoplankton under strong, natural, mixed-layer turbulence (Lazier and Mann 1989).

To observe the chains, a dissecting microscope equipped with a television microscope coupler (model 2500, Optic) and a video camera were mounted on a stable holder normal to the shear plane. Illumination of the field was from a light source focused via a green magnifying glass to a mirror positioned at an angle to the bottom of the gap between the two cylinders. By using a green magnifying glass, which absorbs in the red, we reduced the potential for thermal convection in the tank. To avoid wall effects from the top and bottom end caps of the apparatus, we focused on chains 5–7 cm deep in the gap.

S. costatum (CCMP783, Provasoli-Guillard culture collection) and *T. nordenskiöldii* (isolated from the Washington coast in October 1996) were grown in a sterile-filtered, modified Institute of Marine Research medium (Perry et al. 1981) at 20°C in a 15:9 light:dark cycle. For each species, an exponentially growing culture was placed gently in the gap between the two cylinders; all visible bubbles were removed, and the stepper motors were turned on. Once steady, laminar

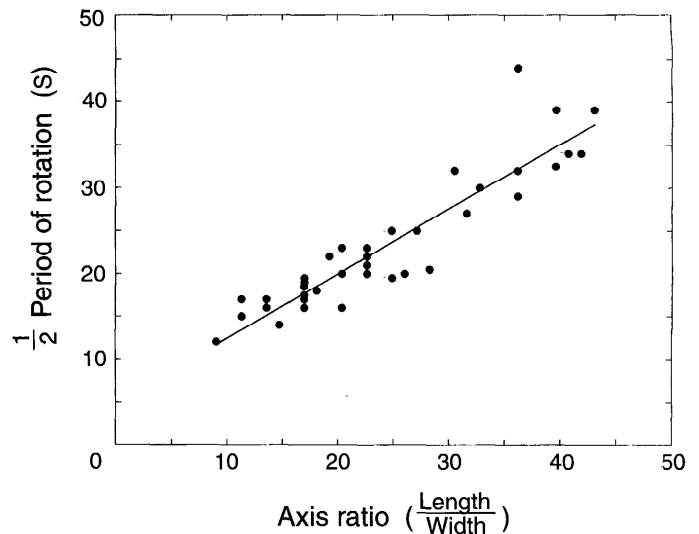


Fig. 3. Period of half rotation of *S. costatum* as a function of axis ratio of the chain. Each point represents an individual chain. The observed chains ranged in length between 62.5 and 297 μm . We used an average cell width ($6.9 \pm 1.3 \mu\text{m}$, where the latter is the standard deviation [SD]) for the calculations of the axis ratios.

shear flow was established, the behavior of individual chains was recorded, with sizes and periods of rotation measured.

The period of rotation of individual chains was obtained from video replay by stopping the tape at successive half rotations (at the orientation in which the chain is aligned perpendicular to the flow streamlines) and recording the time. Time was measured to the nearest 0.5 s. The length of each chain was obtained from manual measurements of its size on the monitor screen. Lengths were measured to the nearest 8 μm . Widths of the chains could not be measured directly from the screen because they were on the same order as the precision of such measurements (especially for *S. costatum*). Therefore, in each experiment we took subsamples of the culture and measured widths using an inverted microscope (Axiovert 35, Zeiss) equipped with a digitizer (SummaSketch II, Summagraphics). The average width of the chain (not including the spines in the case of *T. nordenskiöldii*) was used for the calculations of axis ratios. For several of the observed chains (especially the long ones), only one-half of the full rotation cycle could be measured before they disappeared from the field of view. To be consistent, we present our results in terms of a half-period of rotation.

Results

Both species underwent periodic rotation upon exposure to simple shear flow. Details of the motion, however, varied both between and within species. The behavior of *S. costatum* resembled that of rigid rods. Rotational orbits, as observed on the shear plane, were similar to those predicted by Jeffery's (1922) theory. No noticeable deformation of the chains due to flow was observed for the shear rate of 0.5 s^{-1} . Strong positive correlation was found between the axis ratio and the measured period of rotation (Fig. 3), as mea-

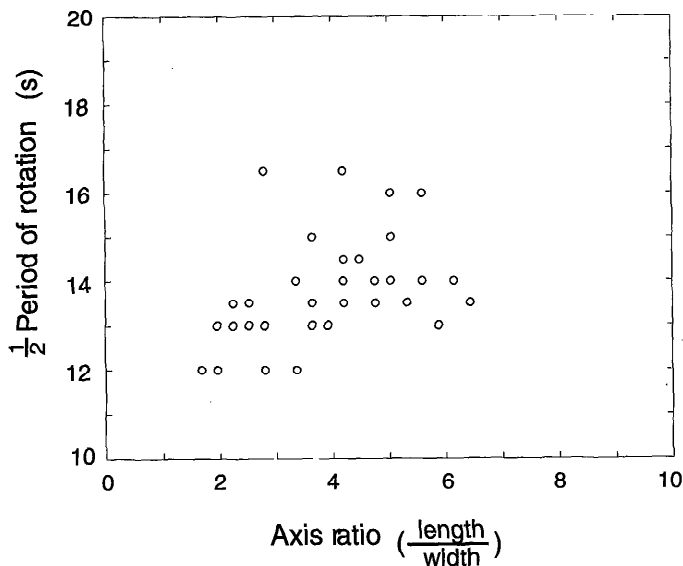


Fig. 4. Period of half rotation of *T. nordenskiöldii* as a function of axis ratio. Each point represents an individual chain. The observed chains ranged in length between 47 and 180 μm . We used an average cell width ($27.9 \pm 3.8 \mu\text{m}$, where the latter is the SD) for the calculations of axis ratios.

sured by Spearman's ρ ($\rho = 0.93$, $n = 41$; $\alpha = 0.01$, Systat, version 5.2.1). The relationship is linear, with least-squares $R^2 = 0.85$. Measured periods of rotation of *S. costatum*, however, were 0.1–0.25 times those predicted by theory for prolate spheroids of corresponding axis ratios.

T. nordenskiöldii behaved differently from *S. costatum*. Rotational orbits of short chains resembled those predicted by Jeffery's theory. As chain length increased, however, deformation at both ends of the chain was observed, and chains flexed as they rotated. Although nonparametric tests show significant positive correlation between the period of rotation and the axis ratio for all axis ratios observed (Spearman's $\rho = 0.61$, $n = 45$, $\alpha = 0.01$), linear regressions showed only a weak linear relationship (least-squares $R^2 = 0.21$, Fig. 4). Measured periods of rotation of *T. nordenskiöldii* were 0.3–0.8 times those predicted by theory for spheroids.

Discussion

Periods of rotation measured for both species fell within the bounds predicted by Jeffery's theory (Fig. 5). Nevertheless, although chains of both species are elongated, their periods of rotation fell well below predictions for prolate spheroids or those observed for rigid, rod-shaped particles of the same axis ratios (Fig. 5). Thus, applications of Jeffery's theory to describe the behavior of chains are likely to overestimate the period of rotation.

Several factors could account for the faster rotation observed with *S. costatum* compared to that predicted by Jeffery's theory. Deviation of chain morphology from perfectly spheroidal shape is the most obvious. As has been shown for cylinders, even a slight deviation from spheroidal shape is likely to cause the particle to rotate faster than predicted

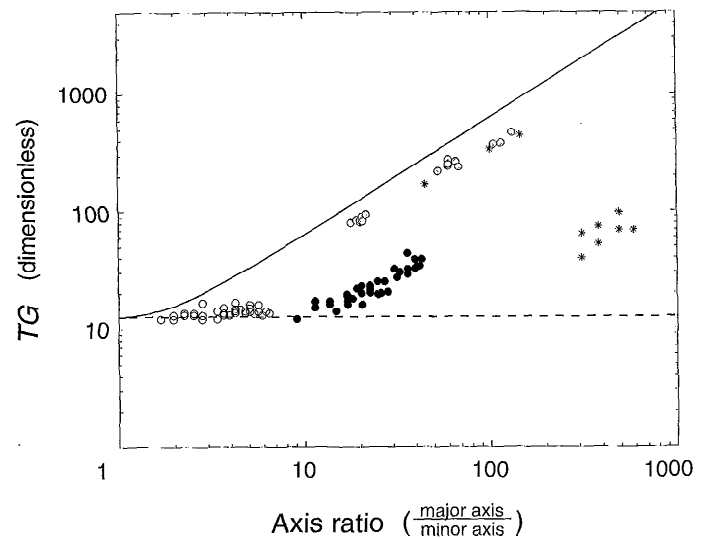


Fig. 5. Comparison of the product TG for diatoms (closed circles—*S. costatum*, open circles—*T. nordenskiöldii*), cylinders (grey circles, data from Trevelyan and Mason 1951; Mason 1954), flexible fibers (stars, data from Forgacs et al. 1958), and that predicted for prolate spheroids by Jeffery's (1922) theory (solid line), as a function of axis ratio. The dashed line represents the value for spheres (axis ratio = 1) that we extended across the full range of axis ratios as an absolute lower limit in the absence of self propulsion. Because for some individual chains we were able to measure over only one-half rotation, we multiplied the period of half rotation by two to obtain TG .

for a spheroid of the same axis ratio (Trevelyan and Mason 1951). In addition, *S. costatum* in our cultures usually formed slightly curved chains. Such curvature was present in cells grown in stagnant media and did not result from buckling by flow. Permanent curvature of a rod-shaped particle is known to decrease its period of rotation, because curvature reduces the stability of a chain in the position parallel to streamlines (Mason 1954). The stability of a chain in the flow is reduced further if mass is not distributed evenly along the chain (Bretherton 1962). Our measurements show that individual cells within a chain are not all equal in size. In addition, variations in cell-wall thickness within cells in a chain were observed in chains of *Thalassiosira* spp. (Orellana pers. comm.) and may also occur in chains of *S. costatum*.

As for *S. costatum*, the discrepancy between measured periods of rotation of *T. nordenskiöldii* and theoretical predictions could result from imperfectly spheroidal shape and unequal density distribution along the chain. In addition, it has been observed that flexible particles typically rotate faster than rigid ones of the same axis ratio (Mason 1954; Arlov et al. 1958; Forgacs et al. 1958). The flexibility of *T. nordenskiöldii* chains provides less resistance to the flow, and their deformations due to the shear forces make the effective axis ratios of chains smaller than that inferred from static dimensions. Also, because we did not include the long spines in the calculations of axis ratios, we may have overestimated the effective ones. By providing small-scale perturbations to the forces that shear exerts on cells, we expect these features

to reduce greatly the time that a cell spends in flow-parallel orientation.

Observed differences in the behaviors between *S. costatum* and *T. nordenskiöldii* are not surprising in light of differences in morphologies and the means by which cells are attached to each other. It is likely that other species that form rigid, rod-shaped chains would behave similarly to *S. costatum*, and in this case rotational orbits of the chains can be predicted. Rotational orbits of flexible chains, on the other hand, would depend on both degree of flexibility and length of the chain and therefore are more difficult to predict.

Applications to the aquatic environment—Both Jeffery's theory and our observations treat behavior of particles in steady, simple shear (two-dimensional flow). In oceans, rivers, and lakes, however, turbulence-induced shear flow is three dimensional and strongly intermittent in both space and time. The axis of the rotation of the flow thus varies in space and time. How long do direction and magnitude of shear in the flow experienced by phytoplankton remain constant, and how does this period of constancy compare with the periods of rotation observed? Steadiness of the shear can be estimated from the timescale of the smallest velocity fluctuation of flow in the ocean (Tennekes and Lumley 1972; Gargett 1997):

$$\tau \approx 2\pi \left(\frac{\nu}{\epsilon} \right)^{1/2}, \quad (4)$$

where ν is the kinematic viscosity (approximately $0.01 \text{ cm}^2\text{s}^{-1}$), and ϵ is the turbulent kinetic energy dissipation rate [L^2T^{-3}]. In our experiments the shear rate G was 0.5 s^{-1} , which corresponds to $\epsilon \approx 2.5 \times 10^{-3} \text{ cm}^2\text{s}^{-3}$ (for the conversion see Karp-Boss et al. 1996). Thus for this shear rate the timescale of the smallest turbulent fluctuations is on the order of 13 s, and flow can be considered steady over shorter periods. Measured periods of rotation are on the same order of magnitude (Figs. 3 and 4) for both species. Therefore, even in the field, chains may be able to complete a single rotation before the direction of the shear changes. For rigid chains, the likelihood that a chain will complete a rotation decreases with increasing axis ratio. Although the rotational motion of a chain in the ocean—at least over more than one period—is likely to differ from that in steady shear (Bretherton 1962), morphology and mechanical properties of chains are expected to play roles similar to those observed in our experiments. Our observations on chains in a steady, simple shear flow thus provide an initial framework for predicting motions of phytoplankton in turbulent water.

Ecological implications—Variety in behaviors of chains in flow implies that the fluxes of nutrients experienced will also vary among chains. More rigid chains experience larger shears compared to flexible chains, due to their higher resistances to the flow, and hence they experience relatively enhanced advective fluxes. In addition, deformation of flexible chains by the flow reduces their effective size and hence the volume sampled by the chains. Substantial reduction in the flux is likely if a chain becomes so flexible or so long

so that it coils about itself upon shear and rotation, and remains coiled.

Some degree of flexibility in chains, however, may be essential for surviving shear intact. Because deformation confers a lower shear rate and hence lower mechanical load, flexible chains are less susceptible to breakage by the flow than are rigid chains of similar size. This constraint is especially important in long chains in which cells are held far apart from each other by fine structures in a configuration that prevents their diffusional shells from overlapping, such as members of the genera *Thalassiosira*. We have examined chain behavior only in steady flows. In time-varying flows, as from turbulence, elasticity of the chain as it rebounds from a flow-deformed shape may well help it to shed or to expand out of nutrient-depleted water. Notably, whereas rigid rods at low Reynolds number would return to their original position upon reversal of the flow (Anczurowski et al. 1967), the motion of flexible particles relative to the fluid is irreversible (Taylor, 1966, *In Low Reynolds number flows* [an educational film]. Educational Services). These possibilities of additional mechanical aids in nutrient exchange merit further modeling and experimentation.

Morphologies and mechanical properties of chains and hence their behaviors in flow are also expected to play important roles in the formation of aggregates. Rates of aggregate formation depend on rates at which single cells or chains collide. Effective collision requires only interpenetration of rotational orbits (Mason 1954). The volume swept by a rigid chain would be larger than that swept by a sphere of equivalent cellular volume (Goldsmith and Mason 1967), and hence collision of rigid chains or elongated cells is expected to be more frequent. Thus, coagulation models for spheres should underestimate coagulation rates of chains. Flexibility and elasticity are also likely to play roles in coagulation, further motivating studies of these physical characteristics of chains. Just as these features affect encounter with other chains, they can also affect encounter with sensory and feeding currents and capture appendages of the herbivore which may have evolved in concert with chain morphology and behavior (Jonsson, pers. comm.).

Encounter is only the first step in aggregate formation or herbivory. Whether cells or chains remain together after they encounter instead of separating again depends on parameters such as their stickiness. Riebesell (1991) suggested that silica spines and gelatinous threads not only increase effective body size and hence enhance encounter but may also enhance probability of entanglement, which he termed "morphological stickiness." Mechanical properties of a phytoplankton, mainly its stiffness (i.e., rigidity or flexibility), are likely to play major roles in its morphological stickiness. Observations on the coagulation of rigid versus flexible, rod-shaped particles further demonstrate the potential role of chain stiffness in aggregate formation. Whereas rigid, rod-shaped particles tend to remain together for only a short time after encounter, flexible fibers, once they collide, entangle and continue to rotate together (Mason 1954). Based on limited numbers of observations, entanglement of fibers appears to be facilitated by an increase in flexibility (Mason 1954). These observations suggest that flexible chains would have

greater morphological stickiness and thus be likely to remain together once they encounter.

Margalef (1978) viewed the variety in life forms of phytoplankton as adaptative strategies to varied nutrient and flow environments and suggested that phytoplankton succession is controlled by the physical environment. Evaluating behaviors of cells in a simple shear flow illuminates some of the potential connections between individual fitness and fluid dynamics. Behaviors of diatom chains in flow clearly depend on their morphologies and mechanical properties, and predictions based on assumptions of simple shape and rigidity show poor accuracy, even in a simple flow field. By studying the behaviors of two chain-forming species in a simple shear flow, we have taken a first step toward understanding the behavior of real phytoplankton in natural flows but have raised more questions than we can yet answer. Systematic studies of simplified mimics and real chains of widely varying morphologies and mechanical properties in a diversity of steady and unsteady flows are needed to dissect the multiple adaptative strategies of real cells in a real ocean.

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