

Algal Biophysics

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Introduction

General physical principles that apply across taxa can help us to understand and predict how organisms interact with their environments (e.g. Koehl 1984, 1996; Denny 1988; Niklas 1992; Jumars 1993; Vogel 1994). In this review we discuss how algae interact with moving water, focusing on the importance of temporal changes in velocity to a variety of biological processes for both benthic macroalgae and phytoplankton. Although there are floating macrophytes and benthic microalgae, for brevity and contrast we focus here on attached macroalgae and phytoplankton.

Water motions affect a variety of critical functions of algae. Macroalgae attached to the substratum risk being dislodged or broken by ambient currents and waves, yet they also depend on moving water for transport (reviewed in Norton *et al.* 1981; Koehl 1982, 1984, 1986, 1999; Denny 1988; Vogel 1994; Hurd 2000). Moving water transports dissolved nutrients and gases to attached algae, removes waste products or sediment, and disperses gametes and spores of macrophytes as well as the epibionts living on them. Thalial designs that enhance an alga's interaction with the water flowing around it improve transport, but also increase the hydrodynamic forces that can deform it (thereby affecting light-gathering) or rip it from the substratum. In contrast, planktonic microalgae are transported by ambient water motion, which affects the large-scale patterns of their vertical and horizontal distributions. At the scale of an individual algal cell, relative water motion affects the mass transfer of nutrients and gases toward the cell and of wastes and signal compounds away from it. Small-scale ambient fluid motion also influences encounter-based processes such as phytoplankton aggregation, development of bacteria-phytoplankton associations, encounters between herbivores and algae, and gamete fertilization. Fluid shear can also deform, damage, or break microalgae or the chains that they form. Recent research is highlighting the importance of unsteady water motion from turbulence and waves to these various flow-mediated functions of both macrophytes and microalgae.

Size and attachment differentiate the flow interactions of phytoplankton and macroalgae. At the small size scales of microalgae (micrometers), the resistance of water to being sheared (viscosity) is large relative to inertial forces, and flow is laminar. In contrast, at the big size scales of seaweeds (centimeters to meters), inertial forces are large relative to viscosity, disturbances to the fluid tend to persist, and flow is messy and turbulent. Reynolds number (Re) represents the relative importance of fluid inertia to viscosity ($Re = LUIV$, where L is a linear dimension of the alga, U is the velocity of the water *relative to the alga* (with U tending to be

larger for macrophytes attached to the substratum than for microalgae carried in the water), and V is the kinematic viscosity of the water, 1.004×10^{-6} and $1.047 \times 10^{-6} \text{ m}^2/\text{s}$ for fresh water and seawater, respectively, at 20°C ; Vogel 1994). Although the Re 's of macrophytes are high, viscous effects along their surfaces play an important role in both mass and momentum transfer. Conversely, Re 's of microalgae are low, but time-varying fluid motions in the turbulent water column affect their function.

Recent developments: macroalgae

Flow habitats of macroalgae

Measurements of water motion in habitats of benthic macroalgae have shown that the flow is generally unsteady. Seaweeds living in deep water or at sites protected from waves encounter unidirectional currents, or tidal currents that flow in one direction for several hours. Although mean flow experienced by macroalgae in such currents is unidirectional, it is turbulent, so instantaneous water velocities fluctuate (e.g. Koehl 1984; 2000) and materials transported by the swirling water (e.g. nutrients, spores) are mixed and spread (reviewed in Okubo 1992; Hurd 2000). Most seaweeds attached to the substratum in shallow coastal habitats are also exposed to waves. At sites in which water depth is less than one-half of the crest-to-crest distance between waves, macrophytes on the bottom encounter back-and-forth flow with a period of seconds when a wave passes overhead, while blades just beneath the air-water interface are subjected to orbital motion. In intertidal habitats seaweeds are exposed to breaking waves and to the rapid shoreward rush and seaward backwash of broken waves. Although instantaneous water velocities, accelerations, and turbulence intensities can be extremely high at wave-swept sites (e.g. Koehl 1977a, 1982, 1984, 2000; Denny *et al.* 1985, 1998; Denny 1988; Bell & Denny 1994; Gaylord 1999), net horizontal transport of water and water-borne materials across such habitats is slow (Koehl *et al.* 1993; Koehl & Powell 1994).

The hydrodynamic microhabitat of a seaweed can be quite different from the gross flow regime characterizing a site. When water flows across the substratum, the layer of water in contact with the bottom does not slip relative to it, and a velocity gradient (the boundary layer) develops in the fluid between the substratum and the free-stream flow. The boundary layer becomes thicker with distance as water flows along a surface; hence the boundary layer can be more than a meter thick over benthic marine habitats, although the steepest velocity gradient occurs within a few centimeters of the substratum. Therefore, crustose algae, germlings, species with short thalli, and floppy macrophytes lying along the substratum experience lower mean water velocities than their taller neighbors. Flow in benthic boundary layers is turbulent (except in the very thin viscous sublayer right along the substratum), so swirling eddies mix mass and momentum between the free stream and the bottom (reviewed in Nowell & Jumars 1984). The benthic boundary layer under waves is much thinner than in unidirectional flow because it takes time for a boundary layer to build up when water begins to flow over a surface (e.g. Denny *et al.* 1985; Denny 1988). Thus, benthic algae growing in wave-swept habitats can encounter faster flow at a much smaller size than they do at sites subjected to unidirectional flow at the same peak velocity.

Although most studies of seaweed hydrodynamics have focused on individual thalli, many macroalgae in nature occur in aggregations. Both field and flume studies have shown that canopies of benthic macrophytes alter water movement. Water velocities are reduced in kelp forests (e.g. Jackson & Winant 1983; Eckman *et al.* 1989; Koehl & Alberte 1988; Jackson 1998), which can also attenuate waves (e.g. Elwany *et al.* 1995; Dubi & Tørum 1996; Mork 1996). Beds of macrophytes can alter the temporal scales of turbulence (e.g. Anderson & Charters 1982; Ackerman & Okubo 1993), and slow advection, but sometimes increase dispersion of water-borne materials (e.g. Koehl *et al.* 1993; Worcester 1995), and induce vertical flow (Nepf & Koch 1999). Effects of canopies on water movement depend on macrophyte density (e.g. Worcester 1995; Nepf *et al.* 1997); when dense macrophyte stands resist water penetration, rapid, skimming flow of redirected water just above the canopy can occur (e.g. Gambi *et al.* 1990; Worcester 1995; Koch & Gust 1999). Therefore, flow encountered by an individual macroalga within a

canopy can be very different from that experienced by an isolated individual at the same site.

Water velocities encountered by macrophytes in nature not only fluctuate rapidly, (turbulence, waves), but also change over longer time scales. Tidal currents vary on the scale of hours, and peak current velocities change over weeks (neap versus spring tides). Daily differences in wind, and seasonal patterns in the frequency and severity of storms and wave action can have profound effects on flows over benthic algae. Furthermore, velocities encountered by an individual can increase as it grows through the benthic boundary layer, or change as a canopy develops or is removed around it. Because the flow environment changes on a range of temporal scales, it is important to quantify the aspects of water movement in the habitat that are relevant to the physiological, biomechanical, or ecological processes being investigated. For example, if one is interested in photosynthesis, small-scale turbulence along blade surfaces needs to be quantified on short temporal scales matched to uptake rates of cells (reviewed in Hurd 2000), and brief light flecks within canopies of algae jostled by waves are important (Wing *et al.* 1993; Wing & Patterson 1993). In contrast, seasonal patterns of peak velocities need to be matched to ontogenetic changes in algal morphology, mechanical properties, and reproduction if one is interested in thallus breakage by hydrodynamic forces (reviewed in Koehl 1986, 1999; Johnson & Koehl 1994).

Effects of moving water on macroalgae

Effects of flow on mass exchange between macroalgae and surrounding water, and the consequences for their physiology and productivity have recently been reviewed (Hurd 2000); thus we focus here on momentum exchange. Moving water imposes hydrodynamic forces on benthic algae that can deform or break them. Recent field, laboratory, and modeling studies have revealed how sizes, shapes, and mechanical properties of seaweeds affect the forces that they experience in flowing water.

Momentum exchange in unidirectional currents

Drag (D) is the hydrodynamic force pushing an organism downstream. Drag on a macroalga at high Re is due to the pressure difference across the thallus that occurs when a wake forms behind it (form drag), and to the viscous resistance of the fluid in the boundary layer along the surface of the thallus to being sheared (skin friction drag) (e.g. Vogel 1994):

$$D = 0.5 \rho C_D U^2 S \quad (1)$$

where ρ is fluid density, C_D is the drag coefficient of the thallus (and depends on shape and surface texture), U is the water velocity relative to the alga, and S is plan area of the organism. Since velocities fluctuate in turbulent ambient currents, the magnitude of the drag on a thallus also rapidly varies. For stiff organisms, the projected area of the organism normal to the flow is often used for S (e.g. Vogel 1994; Denny 1988), whereas for very flexible macroalgae, the maximal plan area of the thallus is generally used for S (e.g. Koehl 1986; Vogel 1989; Carrington 1990; Gaylord *et al.*, 1994; Friedland & Denny 1995; Gaylord & Denny 1997). Drag in unidirectional currents rises as algae grow since both S and the U encountered increase. Morphological features that decrease the size of the wake that forms on the downstream side of a macroscopic organism reduce drag. Such features include orientation parallel to the flow direction, streamlined shape (i.e. a shape that is long and tapered on the downstream side), and porosity (i.e. gaps between branches or lobes that permit water to flow through the structure) (e.g. Koehl 1977a; Vogel 1994).

Macroalgae are flexible and are passively reoriented parallel to ambient water currents, and thus normal to incident light (Hurd *et al.* 1996). In addition, flexible organisms can be passively reconfigured into more streamlined shapes as flow velocity increases, also reducing wake size and form drag (e.g. Koehl 1977a; 1986; Vogel 1984; Koehl & Alberte 1988; Carrington 1990). An index of the drag reduction due to such reconfiguration by a flexible organism is the "figure of merit" (B), the slope of a log-log plot of speed-specific drag (D/U^2) as a function of velocity; the greater the absolute value of the negative slope, the greater the relative drag reduction experienced with an increase in velocity (Vogel 1984, 1989). B measured for a variety of rhodophytes

and phaeophytes ranges from - 0.3 to - 1.5 (reviewed in Koehl 2000). If the flexibility of a benthic alga permits it to be pushed down into the slow flow close to the substratum, drag is further reduced (Koehl 1986, 2000). Aspects of thallus shape such as blade undulation can affect C_D (e.g. Koehl & Alberte 1988; Armstrong 1989; Dudgeon & Johnson 1992; Johnson & Koehl 1994), although very flexible species of blade-like and branching seaweeds converge toward similar C_D values (in spite of their different morphologies) when subjected to high velocities that compact them into similar, streamlined bundles (Carrington 1990). Self-shading in such compact blade bundles can reduce photosynthesis (Koehl & Alberte 1988). C_D values measured for diverse species of rhodophytes, chlorophytes, and phaeophytes are low, ranging from 0.01 to 0.5 (reviewed in Koehl 2000).

Macroalgae in a current can also experience lift (L), the hydrodynamic force acting at right angles to drag:

$$L = 0.5 \rho C_L U^2 S \quad (2)$$

where C_L is the coefficient of lift. The local pressure on the organism is lower where the flow along its surface is faster; thus an alga presenting an asymmetric shape to the oncoming current can experience a net lateral or vertical pressure if the water speeds up more around one side than the other to move around a thallus (e.g. Denny 1988; Vogel 1994). Even a symmetrical structure, such as the cylindrical stipe of a kelp, can experience transient lateral lift, alternating from side to side as vortices are shed in the wake behind it (explained in Denny 1988). If such stipes are flexible, they wobble side to side as water flows past. Flexible algal blades also flutter like flags as vortices are shed and as they are subjected to ambient turbulence. Such wobbling and fluttering increases wake size, and hence drag (e.g. Koehl & Alberte 1988), but the reduction in self-shading and the transient light flecks due to such blade movement also can enhance photosynthesis (e.g. Koehl & Alberte 1988; Greene & Gerard 1990).

Momentum exchange in waves

Attached algae exposed to waves experience back-and-forth water motion. Thus hydrodynamic forces can rapidly change in magnitude and direction. A quasi-steady approach is used to calculate the instantaneous drag and lift on an organism in waves; these forces are proportional to $\{U, |U|\}$, where U_i is the instantaneous velocity relative to the organism.

In addition to drag and lift, organisms in the accelerating flow in waves also are subjected to an acceleration reaction force (A_i).

$$A_i = \rho C_M (dU/dt), V \quad (3)$$

where A_i is the instantaneous acceleration reaction, C_M is the inertia coefficient, (dU/dt) is the instantaneous water acceleration relative to the organism, and V is the volume of water displaced by the organism (e.g. Keulegan & Carpenter 1958; Koehl 1977a; Denny *et al.* 1985; Denny 1988). For an attached organism past which fluid is accelerating, acceleration reaction is the sum of the "added mass" of water whose acceleration is affected near the organism's surfaces (and "added mass" is also experienced by organisms accelerating through fluids, as described below for unattached microalgae), and of the "virtual buoyancy" due to the pressure gradient on a sessile body displacing a volume of accelerating fluid (described in e.g. Denny 1988). Body shapes that deflect the path of water accelerating around them a great deal (e.g. bluff bodies; plates normal to the flow) have higher C_M values than do those that deflect the flow less (e.g. streamlined bodies; plates parallel to the flow) (Daniel 1984). Since A_i is proportional to an organism's volume, it should increase at a greater rate than drag or lift (proportional to area) as an organism grows (Denny *et al.* 1985; Denny 1999), but in the case of many macroalgae with blades of constant thickness, volume and area increase at roughly the same rate as thalli grow. If water is trapped between the branches or blades of an algal thallus, the functional volume of the alga affecting A_i is the volume of that water in addition to the volume of the thallus (Gaylord *et al.* 1994).

The instantaneous net force on an organism in waves is the vector sum of the acceleration reaction, drag, and lift at that instant (e.g. Koehl 1977a; 1984; Denny *et al.* 1985; Denny

1988). When water is speeding up, A , acts in the same direction as drag, but when water is slowing down, A , acts in the opposite direction from drag. Since it takes time for a wake to develop behind an organism when water starts to move past it, hydrodynamic forces on an organism in the back-and-forth flow in waves depend on the time course of the development of the wake behind the organism. The greater the distance relative to the size of an organism that the water travels before it flows back in the opposite direction, the more developed the wake becomes. Thus, in oscillating flow a common way to account for wake history is to let C_D and C_M vary with a dimensionless "period parameter", $U_{max}PL$, where U_{max} is the peak velocity, P is the wave period, and L is a linear dimension of the organism (Keulegan & Carpenter 1958).

Flexible macrophytes can move back and forth passively with the oscillating water in waves. Since hydrodynamic forces depend on the velocity and acceleration of the water relative to the thallus, only those portions of a thallus that are fully extended in the direction of flow and experiencing relative water motion are subjected to hydrodynamic forces that pull on the holdfast. However, a flexible macrophyte moving with the flow can be jerked to a halt if it "reaches the end of its rope" before the water in a wave begins to flow back in the opposite direction; the thallus and holdfast sustain a brief inertial force (proportional to the mass, and hence to the V of the organism) when this occurs (Denny *et al.* 1998). The length of a flexible macrophyte relative to the distance the water in a wave moves before it flows the other way determines when in the wave cycle the organism is jerked to a halt and begins to experience flow relative to its body. Therefore, thallus length can have a profound effect on the flow and the forces experienced by wave-swept algae. As macroalgae grow, the total force they experience in waves increases (e.g. Gaylord *et al.* 1994). However, once they grow long enough relative to the displacement of water in the waves, they reach the end of their rope only after the flow has begun to decelerate (Koehl 1986) and forces are lower. Therefore, further growth may not lead to an increase in force on the holdfast, as shown by experiments with model algae (with mass distributed evenly along their lengths) in an oscillating-flow tank (Koehl, 1996) and by measurements of forces on similar real kelp on wave-swept shores (Koehl 1999). However, mathematical models of kelp with all their blades at the end of stretchy or bendable stipes show that this is not always true: the tuning of the time-dependent material properties of the stipes relative to the frequencies at which these structures must resist high inertial loads in wave-swept environments determines their likelihood of experiencing large forces (Denny *et al.* 1998).

The future: macroalgae

Recent developments in research on macrophyte hydrodynamics are revealing the importance of the unsteady nature of ambient flow both to the exchange of substances between thalli and the surrounding water (reviewed by Hurd 2000) and to the mechanical loads that can deform or dislodge benthic algae. One important direction for future research is linking the temporal responses of macroalgae to the temporal fluctuations in flow that they experience in nature. For example, while effects of the time-dependent mechanical properties of animal tissues to their responses to time-varying environmental loads has long been recognized (e.g. Alexander 1968; Koehl 1977b; Vincent 1990), the importance of these relationships for macroalgae is now an active area of research. Although compliant kelp stipes can act as shock absorbers, protecting holdfasts from transient, large loads in turbulent, unidirectional currents by stretching and absorbing mechanical energy (Koehl and Wainwright 1977), recent models indicate that such stretching can make things much worse for macrophytes in waves (Denny *et al.* 1998; Gaylord *et al.* 2001). Another direction for future research is assessing the size scales over which velocity fluctuations occur in nature (e.g. Gaylord 2000) relative to the sizes of algae.

Future research should also link the biophysics of algae to their ecological performance. Although biomechanical analyses enable us to quantify how defined aspects of morphology affect specific functions, we need to understand how those functions affect growth, reproduction, and survivorship of macroalgae in the changing environments in which they live. For example, the life-history strategies of some organisms with "bad" engineering designs enable them to thrive in mechanically stressful environments (e.g. Highsmith 1982; Koehl 1996, 2000).

Rather than focusing just on adult thalli, more biophysical studies should be done that follow the ontogeny of body design, hydrodynamic environment, and performance of ecologically important functions such as photosynthesis, growth, or resistance to dislodgement. Some macroalgae change their morphologies or tissue properties in response to their hydrodynamic environments (reviewed in Koehl & Alberte 1988; Hurd 2000) or damage (e.g. Lowell *et al.* 1991), but much remains to be learned about the mechanisms responsible for these changes and the ecological and evolutionary consequences of such phenotypic plasticity.

Recent developments: microalgae

Flow environments of planktonic particles and their simulation

Flows in upper mixed layers generally are turbulent. Although intuition for some aspects of turbulence is quite good because of the high Re range in which people live, intuition for the statistics of turbulence is poorer because they are decidedly non-Gaussian. The theory of turbulent flows predicts that velocities and accelerations spend comparatively little time near their mean conditions, and quite a bit of time near the two extremes. These theoretical predictions only recently have been confirmed in direct measurements of the extreme accelerations involved (LaPorta *et al.* 2001). Large vortices provide shear fields that strain and re-orient smaller vortices, stretching them axially and thereby making them thinner and faster spinning, much as a skater spins faster with arms pulled in toward the body. At sufficiently small scales, viscosity dominates and effectively dissipates energy from the smallest vortices as heat. The more energetic the turbulence, the smaller the vortices it can support. Yet even under the most energetic but still realistic conditions in upper mixed layers, diameters of the smallest vortices generally fall in the 1-10 mm range. Most phytoplankton cells, chains and other particles are still smaller and hence are contained within those vortices, where they experience a roughly linear shear whose magnitude increases with the intensity of the turbulence (Lazier & Mann 1989).

To simulate flows that cells and other particles experience, various devices have been used, but all are problematic (Sanford 1997; Peters & Redondo 1997). Turbulence generated by an oscillating grid is very regularly periodic in time and has extreme spatial gradients normal to the grid, not to mention the hazard of hitting the grid itself. As in real turbulence, cells in oscillating grid tanks experience a broad range of flow conditions, but the breadth of range itself makes it difficult to identify the conditions to which contained cells respond. To provide a narrower range of shears and simulate conditions inside the smallest vortices, Couette flows have been used, often in a gap between two concentric cylinders. Shear is produced by differential rotation of the inner and outer cylinders. Although a good deal has been and will be learned from such experiments, some realism has been traded for reproducibility. Whereas shear under constant rotation rate of the cylinders is *steady*, natural flows are *unsteady*. Directions and magnitudes of shears inside the smallest vortices in nature typically last no longer than a few seconds because they pass their energy on so effectively to viscosity and heat and are replaced by newly formed vortices rotating at different speeds and in different directions.

Significance of low- Re flows to phytoplankton ecology and physiology

Low- Re flows are important to microalgae in many aspects of their lives. Flows can accelerate mass transfer of nutrients and signal compounds toward the cell and of waste materials, signal compounds and general leakage away from the cell. Reducing the thickness of diffusional boundary layers around cells is very effective at speeding solute transport because diffusion times scale with the square of diffusion distances. The significance of fluid motion to delivery of nutrients at the cell surface generated early and continuing interest (Munk & Riley 1952). As this topic has been reviewed recently (Karp-Boss *et al.* 1996) we will go into few details here except to note that enhancement of solute delivery to the cell surface largely depends on the flow regime and the size of the cell. For flows similar to the ones produced by natural turbulence, a cell radius of $\sim 60 \mu\text{m}$ is needed before nutrient flux can be enhanced by 50% over the still-water

case (Karp-Boss *et al.* 1996). Predictions for flow effects on mass transfer to microalgae have primarily considered spherical cells, whereas microalgae display a wide range of cell morphologies and mechanical properties. Murray & Jumars (2002) reviewed an analog modeling approach whereby any arbitrary shape can be investigated for its costs and benefits in stagnant water, but that approach is not yet generalized easily to moving fluids.

Flows are also fundamental to encounter-based processes because they influence relative velocities between particles. Affected are phytoplankton aggregation, encounter between algae and their herbivores and between gametes for sexual reproduction. The theoretical framework and observations of flow effects on encounter-based processes have also been reviewed recently (Shimeta & Jumars 1991; Kjørboe 1997), so we do not repeat them here.

Several publications have shown negative effects of turbulence on growth of dinoflagellates and other algae (reviewed by Estrada & Berdalet 1997; Hondzo & Lyn 1999). Cell destruction, interference with cell behavior and physical disturbance to the mechanisms responsible for chromosome separation in dinoflagellates have been postulated to explain growth inhibition by turbulence (Estrada & Berdalet 1997; Hondzo & Lyn 1999). It is important to note that shear rates in these experiments often exceeded natural rates in the upper mixed layer. Timing of the exposure of dinoflagellates to shear flow relative to the light-dark cycle and the growth phase of the culture may affect growth responses to the flow (Juhl *et al.* 2000). Observations of increase in cellular volume and nucleic acid content, while cell division is inhibited, suggests that nutrient uptake, biosynthesis and cell division are affected to different degrees by turbulence (Berdalet 1992). At natural shear rates with cyanobacteria, Moisander *et al.* (2002) found reduced nitrogenase activity and carbon fixation in some taxa, as well as reduced filament length. These results are consistent with the association of some cyanobacteria with calm waters, but the large filaments and aggregates studied by Moisander *et al.* (2002) sometimes occupied a substantial fraction of the Couette gap, and in these cases the results should be viewed with caution because forces experienced by the algae may have been increased by temporary adhesion to one or both cylinder walls.

Most theoretical studies that have examined effects of small-scale turbulence on nutrient delivery or encounter-based processes have assumed a spherical, rigid cell in a steady shear field. Laboratory experiments provided bulk measurements of rates (*i.e.* uptake, growth, encounter) but very little information of how individual particles interact with the flow. Flows have been simulated primarily as steady, one-dimensional, linear shear flows, largely in Couette tanks, whereas natural shear flows produced by turbulence are unsteady. Quantification of more realistic flow fields around microalgal cells and better understanding of the interactions of unsteady flows with cell morphologies are now crucial for further progress.

Unsteady motion at low Re: How significant is it?

The flow that a microalga or other particle experiences is the relative flow past it — just as is the case with a macroalga. The complication of adding a solid particle and asking how its motion and flow around it differ from that of the ambient fluid is subtle but overwhelmingly important. The particle may rotate, deform and (or) translate, just as may fluid parcels (Kjørboe & Visser 1999). If the cell is spherical and neutrally buoyant, a constant shear rate, G [T^{-1}] will make it rotate with a period, T , of $4\pi/G$. A shear rate in a given direction is simply the difference in velocity [$L T^{-1}$] divided by the difference in distance [L], both in that direction. Jeffery (1922) predicted that for spheroids, the period of rotation becomes dependent not only on the shear rate, but also on an axis ratio, r_a (major to minor axis or vice versa), of the particle:

$$T = \frac{2\pi}{G} \left(r_a + \frac{1}{r_a} \right) \quad (4)$$

More interestingly, the rotation rate becomes unsteady, with the spheroid spending the most time in the most stable configuration with its axis parallel to the flow direction (perpendicular to the dominant shear). Although small spheroids suitable for Couette experiments are hard to find, results with rigid, right circular cylinders generally support these predictions but show slightly

shorter periods, presumably because their blunt ends add to flow instabilities (Trevelyan & Mason 1951; Mason 1954). Rigid, curved rods in turn rotate faster than straight ones because they have no stable, flow-parallel posture (Mason 1954). Uneven distribution of mass along a cell or chain also reduces stability (Bretherton 1962), as does an offset of the center of mass (e.g. Jonsson *et al.* 1991) for all but the case where the gravity vector and shear happen to be orthogonal. Flexible fibers, on the other hand, rotate faster than their nominal axis ratio would suggest because their effective axis ratio is reduced as they are bent by the flow, and very limp fibers tend to "ball up" into their most stable configuration and rotate with nearly the period of the inscribing sphere (Arlov *et al.* 1958; Forgacs and Mason 1959).

Through numerical modeling, Pahlow *et al.* (1997) extended predictions for shear effects on nutrient delivery by considering rotation of spheroidal cells under steady shear. They found that the net effect of shear thinning on flux of nutrients toward the cell increased with axis ratio in individual cells, but net gain depended upon spacing between cells in chains. What enhances the calculated flux is not steady rotation, but the unsteady flipping. Steady rotation closes streamlines and so tends to reduce diffusive fluxes relative to cells experiencing the same amount of shear without rotation (Karp-Boss *et al.* 1996).

Translation adds another degree of complexity to relative motion. It can be caused by either a difference in density (positive or negative) between the particle and the surrounding fluid or by self-propulsion through some swimming mechanism. Again for brevity and simplicity but with relevance to some real phytoplankton, we treat explicitly only the case of a particle that is rigid and spherical and is accelerated by buoyancy alone through an otherwise stagnant water column. We use the term buoyancy, as do most fluid mechanicians, to include both positively and negatively buoyant particles. The two cases for which we show solutions (Fig. 1) are cases where particle density (ρ_s) exceeds the fluid density (ρ), so the particle will settle downward. Non-spherical particle geometry, propulsion by forces other than buoyancy, or pre-existing laminar or turbulent flow fields through which the particle must pass would complicate terms in the equations that we present or would add further terms. Rather than attempt to treat a more general case, we will emphasize which terms require modification.

As we discussed for macrophytes, a useful way of integrating the effects of relative flow past a phytoplankter is to evaluate the forces exerted on it. In steady motion, as in the case of a cell settling in stagnant fluid, only two forces act, drag and buoyancy. As noted earlier, drag on a body is due to viscous stresses (*i.e.* skin friction) and the dynamic pressure distribution on its surface. At low Re ($Re \ll 1$), two-thirds of the fluid drag arises from skin friction and one-third from symmetrical dynamic pressure differences between fore and aft (high under and low above in the case of settling; Leal 1992). Integrating these shear stresses and dynamic pressure forces over the surface of the sphere yields the total drag on the body, $F_{drag} = -6\mu r_0 U$, where μ is the dynamic viscosity of the fluid, r_0 is the radius of the cell and U is the relative velocity between the cell and the fluid (Leal 1992; Vogel 1994). The other force acting on the settling body, buoyancy, is the net sum of the body force of gravity on the sphere's volume, $(4/3)\pi r_0^3 \rho_s g$, and of the hydrostatic pressure integrated over the surface of the sphere, $(4/3)\pi r_0^3 \rho g$ (Leal 1992, p. 144). Since the flow is steady, drag and buoyancy balance, leading to the familiar form known as Stokes' solution for the terminal velocity of a settling, rigid sphere:

$$U = \frac{2r_0^2 g(\rho_s - \rho)}{9\mu} \quad (5)$$

In unsteady motion, however, two other forces operate, and the relative velocity of the sphere, U , is a function of time. Accounting for the forces acting on a rigid sphere in unsteady, uniform flow, we have applied a theoretically (Leal 1992) and empirically (Clift *et al.* 1978) supported version of the Oseen correction, f , to the first term because Stokes' solution strictly is for velocities approaching zero:

$$F = -6\pi\mu r_0 U f + \frac{4}{3}\pi r_0^3 (\rho_s - \rho)g - \frac{2}{3}\pi r_0^3 \rho \frac{dU}{dt} - 6r_0^2 \sqrt{\pi\rho\mu} \int_0^t \frac{dU}{\sqrt{t-\tau}} d\tau \quad (6)$$

where the correction factor, f , is:

$$f = 1 + \frac{3}{8} Re + \frac{9}{40} Re^2 \ln Re + O(Re^2) \quad (7)$$

and the last term of the correction is read as "of order Re^2 ." As Re rises, the fraction of the drag on the sphere that is due to skin friction gradually declines. Empirically, this correction factor works reasonably well without that last term so long as $Re < 1$ (Clift *et al.* 1978). The first term on the right is already familiar, with the provisos that in the unsteady case the relevant U is the instantaneous relative velocity and the term's name is changed slightly to "quasi-steady drag." This quasi-steady drag term would change with both object shape and orientation to the flow, and these changes are often accommodated through the convenience of Re -dependent drag coefficients. The second term on the right of Eq. 6 is the familiar buoyancy force and remains independent of velocity and time. Shape changes are easily accommodated in the terms ahead of the parentheses so long as they adequately represent the volume of the object. The third term is the so-called "added mass" or "acceleration reaction," that accounts for kinetic energy imparted to nearby fluid. For a sphere, the correct accounting of imparted kinetic energy is achieved as if a volume of liquid equal to one-half of that of the sphere were accelerated to the same extent as the sphere, but with the sign reversed, as the fluid is resisting the acceleration. In the biologically more familiar coefficient formulation applied to unsteady motion (Daniel 1984), the added-mass coefficient is 0.5 for a spherical body. This coefficient, in turn, is closely related to the inertia coefficient of our Eq. 3 (but C_M in Eq. 3 incorporates virtual buoyancy on an attached organism as well as added mass, *cf.* Denny 1988, pp. 156-157); we would need to incorporate virtual buoyancy if the settling cell were embedded in a flow field that changed the dynamic pressure distribution around it (Hao and Prosperetti 2000), as would be the case for a cell settling through a turbulent flow field (Maxey and Riley 1983).

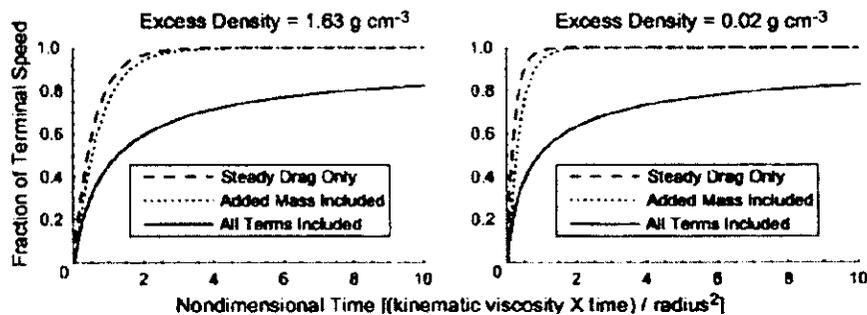


Figure 1. Importance of the history-integral term under constant acceleration by gravity of a solid sphere from rest, following Clift *et al.* (1978; Eq. 2, p. 289) and calculated for spheres of two different excess densities. Note that in the absence of a history-integral term, a steady velocity is achieved quickly, and even more quickly with less excess density. The history-integral term affects velocity longer and is less sensitive to excess density or the final velocity over the full range of potential phytoplankton densities. With 50 μm for a diatom radius only 82% of steady velocity is achieved after 0.025 s (nondimensional time = 10). For a 0.5-mm *Noctiluca*, that time would increase to 2.5 s. For a bacterium (radius = 0.5 μm), by contrast, the time is 2.5×10^{-4} s, allowing the memory integral and other time-dependent terms to be ignored. Dynamic viscosity is taken to be 1.1 N s m^{-2} and fluid density to be 1030 kg m^{-3} , but results for fresh water would be quite similar.

The fourth term on the right in Eq. 6 has been called the Bassett or history term, although Boussinesq (1885a,b) first derived it, but we will call it and terms like it "memory-integral" terms (Yang and Leal 1991) to give better intuition for their origin. Moreover, a rigid sphere appears to be the only object for which the unsteady forces on the sphere from evolving flow fields around it can be embodied in a single memory-integral term (Yang and Leal 1991). We avoid "wake history" for this low- Re term (Michaelides 1997), even though we used it for macroalgae above, because in the common vernacular and to those versed in high Re this name implies only the flow region downstream of the object. Although unsteadiness reduces the upstream-downstream symmetry of flows at low Re , forces may be transmitted to the object from any direction as the flow field evolves during acceleration or deceleration. The memory-integral term, where τ indicates a prior time (much as in the Lotka-Volterra equations with time lags), explicitly accounts for the fact that it takes some time for near and far streamlines to adjust when an object changes speed or direction. Because effects on streamlines propagate so far from objects at low Re (Visser 2001), these adjustments cannot be instantaneous for bodies much larger than bacteria. Memory integrals have not been widely used in the biological fluid dynamics literature, going unmentioned in Daniel (1984) and Vogel (1994), partly because both of these classic treatments deal with unsteadiness primarily at high Re rather than at low. Even within engineering fluid mechanics, their application has been inconsistent (Michaelides 1997). Lastly, if self-propulsion is involved, near- and far-field flows will change (Visser 2001), affecting terms one, two and four, and another (positive) term will be needed for the thrust force.

But how important are the unsteady terms in this simplest case that we can find, that of a sphere accelerating under gravity from rest? First, is this case relevant? Such accelerations occur all the time: The cell may just have been released, for example, from the last decaying vortex in a bout of turbulence and start to drift buoyantly upward or to sink, depending on its relative density. For particles in the range of specific gravities found among phytoplankton, the memory integral dominates the unsteady terms when the problem is nondimensionalized (Fig. 1). To determine absolute importance of unsteady terms requires insertion of the physical dimensions of the particle. The unsteady terms have little practical significance for particles of the size of bacteria, which is fortunate, since tracking of particles of a few micrometers in diameter or smaller thus is a reliable way to measure flow and has become a staple of laser-Doppler velocimetry (LDV) and particle-imaging velocimetry (PIV). But unsteady terms, and history integrals in particular, certainly can strongly influence particles in the size range of 0.1 - 10 mm, where many larger phytoplankton cells and chain-formers lie.

Acceleration from rest is a simple case, and spherical shape is a further simplification. A natural question is whether current theory is up to the task of dealing with realistic shapes and more complex patterns and sources of acceleration. Work at low Re benefits from the linear nature of the terms, making multiple effects generally additive and linear as well. Swimming and sinking are fundamentally different because in sinking all the fluid forces retard the motion, whereas in swimming the fluid is involved both in thrust (*i.e.* the rate of addition of momentum to a moving fluid) and drag (*i.e.* the rate of removal of momentum from a moving fluid). At low Re , however, the solution for streamlines in swimming while sinking can be found simply by adding solutions for the two separately (*e.g.* Visser 2001; Jiang *et al.* 2002). A useful simplification is to model flows around particles as though they were produced by forces acting at a point, or at a small number of points, yielding so-called singularity and multipole solutions (*e.g.* Chwang & Wu 1975; Kim & Karilla 1991; Visser 2001). Shape effects can be modelled in this way as well (Kim & Karilla 1991). Theory to treat spheres in arbitrary, turbulent flows has been available for some time (Maxey & Riley 1983), but theory to extend singularity and multipole solutions to unsteady flows has come available only very recently (Chan & Chwang 2000; Shu & Chwang 2001). It has not yet been applied to specific phytoplankton shapes and flow regimes.

Phytoplankton in flows: observations

There are remarkably few observations of individual phytoplankters in characterized flows. A large part of the problem is certainly technological; until very recently, it has not been

feasible to visualize flows around individual real (as opposed to scaled-up, model) phytoplankton cells or chains in field or model flows, so most studies of flow interaction with phytoplankton have measured integrated (over time), average (over individuals) responses to bulk flows.

Observations of rotation in steady, linear shear at realistic rates are limited to a few chain-forming diatoms and dinoflagellates. Two non-motile diatom chain formers, *Skeletonema costatum* and *Thalassiosira nordenskiöldii*, rotate with periods intermediate between those predicted for spheroids of equivalent axis ratios and spheres. *T. nordenskiöldii* is the more flexible and so deforms and tumbles at the greater rate for a given axis ratio (Karp-Boss & Jumars 1998). Single-celled *Glennodinium foliaceum* and both single cells and chains of *Alexandrium catenella* have been examined. Abilities of both morphs of *A. catenella* to orient were significantly affected by shear (Karp-Boss *et al.* 2000).

Observations of phytoplankton orientation in unsteady shears have been made in two contexts, both relating to siphon flows, *i.e.* flows into the apertures of instruments that sample phytoplankton and flows into herbivore feeding structures. Just as in Couette flow and for the same reason, cells tend to align with their long axes parallel to the intake streams of instruments (*e.g.* Kachel *et al.* 1990) and copepods (Visser & Jonsson 2000); the shear is predominantly perpendicular to the flow axis, and elongate cells tend toward their most stable configurations.

Fluid motion itself can induce morphological changes in microalgal cells. Recently, Zirbel *et al.* (2000) showed that long-spined cells of the dinoflagellate species *Cratocorys horrida* transformed into short-spined cells after being agitated. The observed morphological change was completely reversible with a few cell divisions. Upon return to still water, long-spined cells became dominant again.

The future: microalgae

Complex interactions between unsteady flows and the morphologies of microalgal cells raise interesting questions concerning ecological trade-offs, adaptations, and evolution of planktonic algae. Microalgae not only appear in many shapes, but also display a range of mechanical properties. In chain-forming diatoms some chains are connected with multiple interlocking spines and behave as rigid particles, whereas others are connected with thin, chitinous threads and are flexible. Variations in rigidity and elasticity further add to the complexity of the interaction of micro-algae with unsteady flows. An intriguing conjecture is that elasticity, returning the cell to its unstrained shape, would displace the cell from its chemical halo and help, analogous to squid ink, to confuse herbivores about its true spatial location at the same time that it thinned diffusional boundary layers for nutrient uptake. Kinetic energy of the flow is stored as elastic potential energy, producing motion of the cell relative to the water after the movement-initiating flow has dissipated. A large class of cyclic motions relying on body elasticity should be qualitatively different from anything possible for rigid or limp objects. It is possible that common biological structures thereby have the potential to become self-organizing engines (Smith 1998, 1999) that extract useful work from turbulent shear flows, much as enzyme and muscle molecules extract useful work from random Brownian motions at much smaller scales (Oster 2002). Moreover, if elasticity plays a role in motion of organisms that do not swim, it also likely plays a role in organisms that do. Propulsion mechanics of appendages are likely to be tuned to useful frequencies related to their material properties (elasticity) and the local turbulence climate.

It is also possible that the mechanical strength of phytoplankton and especially chains of phytoplankton will be exceeded, and they will fail in a mechanical sense. It is not clear, however, whether breakage into shorter chains or individual cells enhances or detracts from fitness. The net effect likely depends on subsequent conditions. Flexibility can reduce the risk of breakage by flow, but too much flexibility would reduce the effective size of the particle.

Relative motion of fluid and phytoplankton also complicates the issue of bacterial chemotaxis toward a diffusing source of nutrients (Luchsinger *et al.* 1999). Moreover, the rotation of even rigid cells entails velocities that are substantial with respect to bacterial swimming velocities, so both well-established rotation of cells and putative translation of flexible cells may affect stability and integrity of bacteria-phytoplankton associations. Translations and

rotations also have implications for the orientation of swimming organisms like dinoflagellates (Karp-Boss *et al.* 2000) and for encounter of gametes. For motile phytoplankton, turbulence above a threshold intensity is likely to preclude oriented swimming, and some formulations for this threshold have been suggested (Karp-Boss *et al.* 1996).

Phytoplankton cells often secrete filaments of exopolymers (*e.g.* Aldredge *et al.* 1993). These strands can have effects on phytoplankton motion, analogous with effects of tails on kites at higher Re . At high Re , biopolymers are associated with damping of turbulence (Vogel 1994), but polymers are wonderfully diverse. Groisman and Steinberg (2000, 2001) find that elastic polymers at very low concentrations can greatly enhance mixing by lowering the critical Re for transition to turbulence. Thus they may be of benefit in thinning of diffusional boundary layers at relative flow velocities where such thinning in water would not otherwise be expected.

Motions at this scale are critical to many important interactions of phytoplankton. We have discussed the general idea of thinned boundary layers for nutrient uptake, but a look forward at more subtle questions gives some indication of where questions about solute exchange might lead. Where on cells are active absorptive sites concentrated? How does this concentration correspond to sites where boundary layers are thinned in unsteady motions produced by decaying turbulence? Are these sites where very local nanotopography and charge concentrations further influence fluid motions (Hale and Mitchell 2002)? Given the local velocity fields around bending and twisting phytoplankton in unsteady shear flows, is it feasible for bacteria to reach and stay in elevated concentrations of solutes near a phytoplankton? How do relative and absolute motions of phytoplankton, the fluid and its solutes influence detection and encounter by herbivores? What combinations of shapes and mechanical properties are most effective at avoiding detection and encounter? Because elongate particles sweep out much larger volumes than do spheres of equivalent volume, they are known to be much more effective in encounter. Coagulation of phytoplankton with each other has been discussed as a bloom-terminating (Jackson 2001) and sometimes adaptive (Smetacek 1985) phenomenon. The phytoplankton-phytoplankton encounter problem seems to be an important one for sexual reproduction. What shapes and mechanical properties facilitate and inhibit encounter and staying together after encounter?

We have identified several areas of research that are likely to benefit from studies on the interactions between unsteady flows and the morphologies and mechanical properties of microalgae. With PIV reaching the resolution at which flows about individual phytoplankton cells can be visualized (*e.g.* Santiago *et al.* 1998), we expect to see a rapidly expanding body of observations concerning flow effects on phytoplankton. Theory and measurement technology are maturing simultaneously to illuminate how flows, mechanical properties and behaviors interact.

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