

The Elongated, the Squat and the Spherical: Selective Pressures for Phytoplankton Shape

Lee Karp-Boss and Emmanuel Boss

Introduction

The size and shape of a phytoplankter are important morphological traits that impact resource acquisition (light, nutrients), vertical motion (sinking), and interactions with grazers. Consequently, selection for size and form is reflected in phytoplankton community structure (Kruk et al. 2010; Fraisse et al. 2013). The ecological significance of cell size has been the subject of numerous studies (e.g., Chisholm 1992; Karp-Boss et al. 1996; Litchman and Klausmeier 2008; Litchman et al. 2009; Finkel 2007; Maranon 2015 and many others) and will not be discussed further here. As for cell shape, it can justly be said that it has been studied a great deal but understood very little. Shape has been used to classify phytoplankton since the nineteenth century, and taxonomists have provided detailed drawings and descriptions of phytoplankton forms. What is not clear is how the shape of a phytoplankter might affect its performance and contribute to natural selection. Several hypotheses have been put forth as to the potential selective value(s) of cell shape (Smayda 1970; Lewis 1976; Sournia 1982), but relatively few studies have approached this question mechanistically, and empirical evidence from fitness experiments is difficult to obtain.

Phytoplankton exhibit striking morphological diversity (e.g., in shape, solitary vs. colonial growth, presence/absence of spines and other projections, types of cell coverings and ultrastructural features), and classification schemes of “morphological types” have been produced since the early days of oceanography (reviewed in Sournia 1982). The general shape of cells, though, appears to be restricted to a finite number of geometric forms (Lewis 1976; Hillebrand et al. 1999). As a first approximation, phytoplankton shape can be represented by a series of spheroids and cylinders with varying aspect ratios. For example, Nguyen et al. (2011) showed that the motion of a cell with spines or projections (e.g., *Thalassiosira* sp.) could be well

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predicted from theory of the motion of spheroids in a simple shear flow, providing that the cell is described by the smallest inscribing spheroid that encompasses both the cell and its spines. The aspect ratio of a spheroid (E) is defined as the ratio between the principal axis of revolution and the maximum diameter perpendicular to this axis; thus two dimensions are sufficient to describe these shapes. An analysis of the distribution of aspect ratios of more than 8000 coastal microphytoplankton cells, representing different seasons and environmental conditions, indicates that attenuated shapes such as prolate spheroids and elongated cylinders ($E > 1$) are much more prevalent than spheres ($E = 1$), oblate spheroids or disks ($E < 1$; Fig. 1). These observations beg the question: Why is a prolate or rod-like shape much more common among microphytoplankton compared to oblate and discoid shapes? Assuming that shape selection is driven by environmental pressures, what are the selective advantages associated with elongated shapes compared to other shapes with similar volume and surface area?

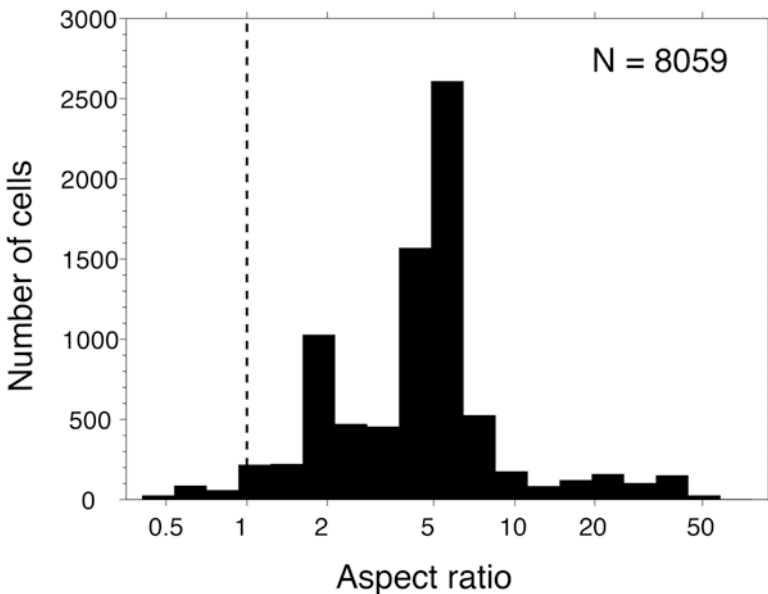


Fig. 1 Frequency distribution of aspect ratios of phytoplankton. Figure modified from Clavano et al. (2007). *Data source:* California State Department of Water Resources and the U.S. Bureau of Reclamation. A subset of the data (2002–2003) was randomly selected for the analysis, representing a variety of aquatic habitats: from fresh water in the Sacramento-San Joaquin delta to estuarine environments in the Suisun and San Pablo Bays (California, USA). Data include phytoplankton from five different classes, including Bacillariophyceae (diatoms), Chlorophyceae, Cryptophyceae, Dynophyceae, and Cyanophyceae ($N=8059$ cells). The aspect ratio is calculated as the ratio in length along the rotational and equatorial axes of a cell, based on the three-dimensional shape associated with each species as provided in Hillebrand et al. (1999). *Vertical, dashed line* highlights the position of spheres along the X-axis (Aspect ratio=1)

Effects of Shape on Diffusion

To address these questions we first look at diffusion, a fundamental physical factor in the life of a phytoplankton and a primary selective pressure that drives natural selection in organisms that live on solutes. Diffusion governs the exchange of solutes between a cell and its surrounding environment, including nutrients, dissolved gases, info-chemicals, toxins, and other metabolites. While relative flow may enhance nutrient delivery to large phytoplankton cells (Karp-Boss et al. 1996), in the vicinity of the cell diffusion is always the dominant transport mechanism. Dependence on diffusion sets a constraint on cell size and, as we argue here, has also influenced cell shape. Of all convex shapes, a sphere has the lowest surface area-to-volume ratio for a given unit of volume (from here on we denote surface area, S , and volume, V , and their ratio S/V). Hence, deviation from sphericity will confer competitive advantage, especially in the case of larger cells. Since S/V decreases with size for any given shape, one would expect transport limitation to increase with size. Observations of 57 species of unicellular algae show that size-dependent variation in surface area and volume deviates from the one expected for any series of objects that differ in size but share the same geometry ($S \propto V^{2/3}$), indicating that cell shape changes with body size (Niklas 2000). Increasing surface area, however, is costly since the cell has to invest additional material and energy in constructing and maintaining a larger envelope per unit of volume (i.e., membranes and organic or mineralized cell walls). Competitive advantage will therefore be conferred only when the enhancement of diffusive flux will exceed the costs associated with added surface area. Different combinations of shapes and sizes can converge to the same V and S/V . If maximizing S/V were the only guiding principle that influences shape, then elongated, rod-like and flat, disk-like shapes would be equally likely to be found in nature. Yet, disk-like shapes are significantly less common among phytoplankton (Fig. 1), or other osmotrophs such as bacteria (Dusenbery 1998; Young 2006). Dusenbery (1998), addressing the same question from the perspective of a bacterium, suggested that a disk-shaped cell is the optimal form with respect to increasing surface area because a disk has the largest surface area for a given minimum radius of curvature. Because bacteria are rarely shaped as disks, he concluded that increasing surface area is not a major component of fitness for bacteria (Dusenbery 1998).

The philosopher Marcus Aurelius (121–180 AD) said, “Look beneath the surface; let not the several quality of a thing nor its worth escape thee.” For phytoplankton (including photosynthetic bacteria), elaboration of surface area is important for both nutrient and light acquisition, but S/V per se is not the best predictor of whether a specific shape contributes or not to the fitness of phytoplankton. To demonstrate this point, we compare fluxes of solutes to a series of spheroids and cylinders of identical surface areas and volumes. The rate of mass transfer to a particle of a given shape, F , is given by

$$F = \phi(C_{\infty} - C_0)D, \quad (1)$$

where C_{∞} and C_0 are the ambient concentration and the concentration at the surface of the cell, respectively, D is the diffusion coefficient of the molecule of interest

(dimensions: $L^2 T^{-1}$) and ϕ is a shape factor that has dimensions of length, L (also called external conductance because the Laplace equation applies to both electrical conductivity and molecular diffusion of mass; Clift et al. 1978; Murray and Jumars 2002). Analytical solutions have been derived for a number of geometric forms including spheroids, cylinders, rectangular plates, and cubes (Clift et al. 1978). For the purpose of this study, we applied solutions for prolate and oblate spheroids and cylinders (Table 1). If the diffusion coefficient, ambient concentration and concentration at the cell surface are the same for all shapes, the flux ratio is equal to the ratio of their respective shape (conductance) factors.

We first examine the flux to spheroids and cylinders of varying aspect ratios relative to the flux to a sphere with an equal volume (a proxy for mass). We refer to the ratio between these fluxes as the “relative flux.” The range of aspect ratios in these calculations was determined from observations (i.e., Fig. 1). As expected, a spherical cell experiences the lowest flux compared to oblate or prolate spheroids, disks, and elongated cylinders, because this shape has the lowest S/V for a unit mass (Fig. 2). Next, we compare “relative fluxes” between prolate and oblate spheroids of the equal surface area and volume and elongated cylinders and disks of equal surface area and volume. Depending on the aspect ratio, the relative flux to a prolate spheroid and cylinders is up to 30% higher than that to oblate spheroids and disks of the same S/V (Fig. 3). Differences in fluxes between shapes of equal S/V arise from the fact that diffusion is not uniform over the surface area of an object of an arbitrary shape, but is affected by edges, corners, and the curvature of the object (Clift et al. 1978); prolate spheroids have, on average, higher curvature than flat disks of the same volume.

This result strongly suggests selective pressure for specific shapes rather than a convergence of different shapes that maximize S/V . For the same unit volume and investment in surface area, an elongated cell is expected to have a competitive advantage over a squat or flat one. Among elongated shapes, within the range of aspect ratios that is representative of phytoplankton and again for equal volume, cigar-like cells are predicted to experience slightly higher fluxes than cylindrical cells (Fig. 3). This theoretical prediction is not only consistent with the observation of the prevalence of rod-shaped cells compared to disk-shaped cells among phytoplankton and bacteria, but it is further supported by experimental results. Sommer (1998) conducted competition exclusion experiments with natural phytoplankton assemblages, grown under different silicate:nitrate (Si:N) ratios. Non-diatom species in these natural populations tended to be spherical, whereas diatoms were morphologically diverse. At (quasi) equilibrium, four of the six most successful diatom competitors were species with thin, elongated shapes; none of the diatom species that were excluded was very elongated (Sommer 1998).

The diffusion model presented here does not take into account cell physiology that by itself is under selective pressure. Using a physiological model, Grover (1989) examined the influence of cell shape on competition for phosphate. His model combines the Droop model for algal growth (growth as a function of internal stores of nutrients; Droop 1973) and empirical relationships between a physiological process (uptake rate) and cell volume and surface area that were derived from the freshwater literature. These allometric relationships show that while maximal uptake is proportional to surface area (Smith and Kalff 1983), the minimal nutrient

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Table 1 (A) Geometric relations for spheroids and cylinders (Beyer, 1987) and (B) diffusion shape factor (conductance), after Table 4.2 in Clift et al. (1978)

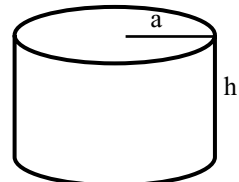
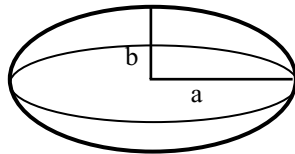
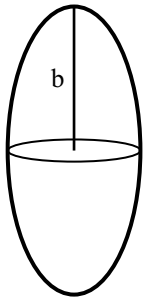
A		
Shape	Surface area	Volume
Oblate spheroid ($b/a < 1$)	$\frac{2\pi}{\sqrt{a^2 - b^2}} \left[a^2 \sqrt{a^2 - b^2} + ab^2 \ln \left(\frac{a + \sqrt{a^2 - b^2}}{b} \right) \right]$	$\frac{4\pi}{3} a^2 b$
Sphere ($a = b$)	$4\pi a^2$	$\frac{4\pi}{3} a^3$
Prolate spheroid ($b/a > 1$)	$2\pi a^2 + \frac{2\pi ab^2}{\sqrt{b^2 - a^2}} \sin^{-1} \left(\frac{\sqrt{b^2 - a^2}}{b} \right)$	$\frac{4\pi}{3} a^2 b$
Cylinder	$2\pi a(a + h)$	$4\pi a^2 h$
B		
Shape	Shape factor (conductance)	
Oblate spheroid ($b/a < 1$)	$\frac{4\pi a \sqrt{1 - E^2}}{\cos^{-1}(E)}, E \equiv \frac{b}{a} < 1$	
Sphere ($a = b$)	$4\pi a$	
Prolate spheroid ($b/a > 1$)	$\frac{4\pi a \sqrt{E^2 - 1}}{\ln(E + \sqrt{E^2 - 1})}, E \equiv \frac{b}{a} > 1$	
Cylinder	$a \left[8 + 6.95 \left(\frac{h}{2a} \right)^{0.76} \right]$	

E is the aspect ratio (b/a) for spheroids where “ b ” is the axis of revolution and “ a ” is the equatorial axis. For cylinders, “ h ” is the height and “ a ” is the radius (see illustration below)

Prolate spheroid

Oblate spheroid

Cylinder



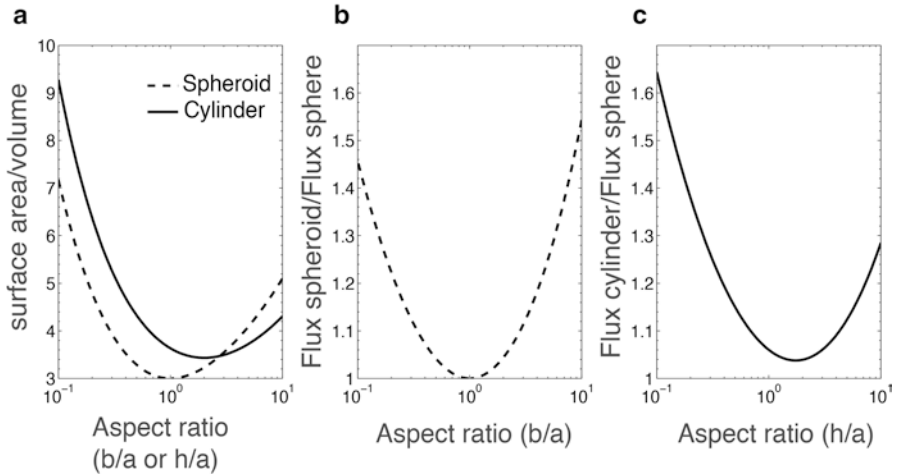


Fig. 2 (a) A comparison of S/V for spheroids of different aspect ratios. (b) “Relative flux” for spheroids as a function of aspect ratio (the flux to a spheroid relative to that of a sphere of equal volume). (c) “Relative flux” for cylinders as a function of aspect ratio (the flux to a cylinder relative to that of an equal volume sphere)

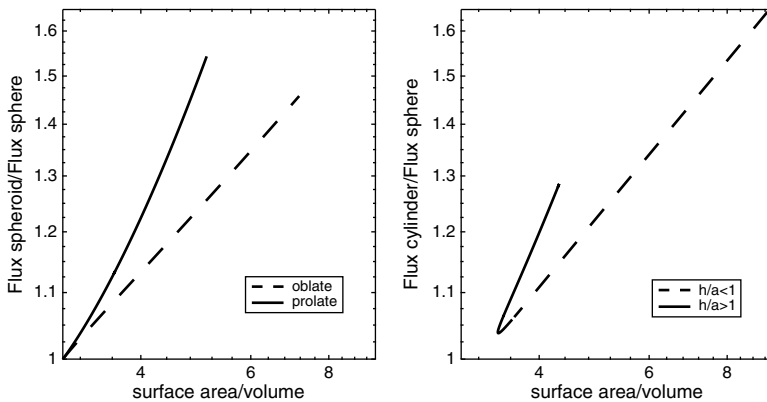


Fig. 3 (a) Relative flux to oblate and prolate spheroids as a function of S/V and (b) relative flux to elongated cylinders ($h/a > 1$) and disks ($h/a < 1$) as a function of S/V

requirement per cell is less than proportional to cell volume (Grover 1989). Consequently, prolate cells with high aspect ratio will have a competitive advantage over smaller cells because the increase in surface area (i.e., their potential to acquire nutrients) is high relative to nutrient requirements (Grover 1989). While this evidence is circumstantial, it is remarkable that all these independent approaches lead to the same conclusion that competition for nutrients favors elongated shapes. If an elongated shape indeed contributes to fitness, as suggested here, it may not be a coincidence that in the evolution of diatoms an elongated cell outline was acquired independently in pennate and centric diatoms (Alverson et al. 2006).

Other Selective Pressures

Nutrient acquisition reflects only one of the selective pressures experienced by phytoplankton. Other selective pressures may favor other shapes or be neutral with respect to shape, resulting in the coexistence of different shapes in nature. Light absorption, for example, depends on the cross-sectional area of a particle perpendicular to the path of light. Of all convex shapes a sphere has the smallest cross-sectional area-to-volume ratio, therefore deviation from a spherical shape may again enhance fitness. Clavano et al. (2007) used a suite of numerical methods to study light absorption by randomly oriented spheroids of varying aspect ratios and compared them to spheres of equal volumes. Refractive index was chosen to be representative of phytoplankton and the derived approximate solutions cover optical regimes that span the range of cell sizes exhibited by phytoplankton. These numerical results suggest that for small particle diameters ($<1 \mu\text{m}$), absorption is similar for a spheroid and an equal volume sphere while for large phytoplankton-like particles (diameter $>50 \mu\text{m}$) absorption by a spheroid is always larger than that of a sphere of the same volume, but is similar for oblate and prolate spheroids with the same S and V (Fig. 8c of Clavano et al. 2007). For intermediate size particles ($1\text{--}50 \mu\text{m}$), the bias in absorption between a spheroid and an equal volume sphere increases monotonically with size, without an apparent advantage to one form (prolate or oblate) over the other (Fig. 8c of Clavano et al. 2007). Thus, for picophytoplankton absorption might be neutral with respect to shape selection whereas for microphytoplankton, deviation from sphericity enhance fitness relative to an equal volume sphere, but prolate and disk-like cells, of the same S and V , will have similar fitness.

Another possibly important evolutionary pressure operating on phytoplankton shape is grazing. Experiments showing morphological changes in response to grazers strongly suggest that morphology is a significant, selectable trait with respect to grazing, but thus far these studies have focused on colony or spine formation (Long et al. 2007; Selander et al. 2011; Bergkvist et al. 2012; Van Donk 1997). For solitary cells, the adaptive value of shape remains speculative with no theoretical or empirical arguments for the potential fitness of one shape over another. Encounter rates and the handling efficiency of a predator depend on the orientation of the prey item in the flow field and when intercepting the capture area of a predator. Spherical particles allow the greatest curvature of the foregut and can be swallowed without the need to re-orient the particles. Copepods can successfully re-orient elongated cells by means of their feeding currents but the efficiency of re-orientation is predicted to decrease in the presence of turbulence (Visser and Jonsson 2000). Turbulence may therefore select for rod-like shapes by reducing grazing pressures on these forms. More observations, theoretical and empirical models are needed to elucidate how grazing pressures may affect selection for shape.

Environmental forces act simultaneously, and their interactions result in a complex combination of responses, making predictions of the selective value of shape

difficult. Using a quantitative, mechanistic analysis, we can begin to highlight a few general trends about cell shape. Most notably, competition for nutrients selects for elongated shapes, while competition for light appears to be neutral with respect to shape for small cells and equally selective for prolate and oblate spheroids for larger cells. Here we touched on only three selective factors, but left out other important ones such as interaction with ambient flows, namely turbulence, gravity (the need to remain suspended), motility, and physiological benefits associated with polar differentiation of cells. More studies, including those that address evolutionary lineages of morphology, are needed to evaluate the relative contributions of these diverse selective forces to shape selection in phytoplankton.

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Lee Karp-Boss and Emmanuel Boss

We met as undergrads at the Hebrew University (Jerusalem, Israel), in Dr. Boaz Luz's "Introduction to Oceanography" class. At the end of the semester, we went diving in the Red Sea, and the rest is history. After completing our M.Sc. degrees in 1991 (Lee studied flow effects on corals while Emmanuel worked on flow instabilities), we left Israel and moved to pursue our Ph.D.s at the University of Washington. Lee became interested in biophysical interactions in the plankton and Emmanuel continued to work on problems in geophysical fluid dynamics. Serendipitously, our mentors were dual-career couples in Oceanography. Emmanuel was a student of Luanne Thompson (married to Greg Johnson) and Lee was a student of Pete Jumars (married to Mary Jane Perry who became a mentor for both of us). The Ocean Optics summer class at Friday Harbor was a turning point for Emmanuel who saw a future full of light, changed course and went to postdoc with Mary Jane Perry in the field of bio-optics. Our collaborations with Perry/Jumars continue to this day. We moved to Oregon in 1998 for postdoc positions at OSU and in 2002 we took faculty positions at the University of Maine. Over the years, we have collaborated on several papers that address phytoplankton-turbulence interactions, science education, optical properties of phytoplankton, and on field campaigns (Tara Oceans and currently NAAMES). Our most fulfilling collaboration is raising our three sons, Yuval, Tom, and Itai. The first two were born while in graduate school, both during Ocean Optics summer classes (Yuval when Emmanuel was a student in the class and Tom when Emmanuel was a TA), and took their first ferry rides to the Friday Harbor lab at age 2 days. Our kids enjoyed spending countless hours with our office mates and colleagues, "participated" in many Ocean Optics summer classes, endured Ocean Sciences meetings, and got their sea legs during a research cruise in the Red Sea and a sleepover on the R/V Tara in the middle of Paris. Not surprisingly, none is considering a career in science.

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