Nutrient acquisition is crucial for oceanic microbes, and competitive solutions to solve this challenge have evolved among a range of unicellular protists. However, solitary solutions are not the only approach found in natural populations. A diverse array of oceanic protists form temporary or even long-lasting attachments to other protists and marine aggregates. Do these planktonic consortia provide benefits to their members? Here, we use empirical and modeling approaches to evaluate whether the relationship between a large centric diatom, *Coscinodiscus wailesii*, and a ciliate epibiont, *Pseudovorticella coscinodisci*, provides nutrient flux benefits to the host diatom. We find that fluid flows generated by ciliary beating can increase nutrient flux to a diatom cell surface four to 10 times that of a still cell without ciliate epibionts. This cosmopolitan species of diatom does not form consortia in all environments but frequently joins such consortia in nutrient-depleted waters. Our results demonstrate that symbiotic consortia provide a cooperative alternative of comparable or greater magnitude to sinking for enhancement of nutrient acquisition in challenging environments.

**Global models of oxygen and carbon dioxide alterations depend upon transfer rates between small phytoplankton cells and surrounding surface waters of the world’s oceans (1–3). Although these cells are important on large scales, their individual interactions occur at microscopic dimensions that are dominated by viscosity. In this viscous environment, critical cellular processes, such as the exchange of nutrients, metabolites, and wastes, rely upon diffusion (4). While diffusion is an effective means of nutrient transport for the smallest microbes (5), it also creates a depleting region around the cell surface, referred to as the diffusion boundary layer (DBL), that limits nutrient consumption and cell growth (6, 7). The DBL for a cell at rest extends nine cell radii from the cell surface before the nutrient concentration reaches 90% of ambient levels (8), creating formidable disadvantages for nutrient acquisition by large cells requiring nutrient diffusion across large distances relative to their cell size (9). Phytoplankton have evolved mechanisms to mitigate the limitations of diffusive transfer rates by swimming or sinking (10) to generate relative motion between the cell and surrounding fluid. Diatoms—barrel-shaped, nonmotile eukaryotes—are considered to be one of the most ecologically important groups of phytoplankton (11–14) that absorb nutrients across their whole cell surface (15) but often increase sinking rates when experiencing nutrient limitation (16). Sinking thins the DBL surrounding the diatom cell and reduces the distance over which diffusion limits nutrient transport (8, 17). One potential disadvantage of this mechanism for DBL reduction is the high probability for a cell to sink out of sunlit regions, and sinking diatoms are major contributors to organic mass flux from surface to deep oceanic waters (1). A widespread but unevaluated alternative for such large cells involves teamwork with other smaller, motile cells that combine to form multicell consortia. Consortia are typically comprised of larger nonmotile host cells with smaller, surface-adhering motile cells termed epibionts. Although infrequently studied, epibionts are ubiquitous in the micrometer-scale world of planktonic organisms (18), and flagellated or ciliated epibionts often attach to larger objects (19) or marine snow (20). The selective forces favoring epibiont attachment remain in question. A range of fluid dynamic effects on prey encounter as well as biological factors such as reduced predator encounter risk or elevated prey availability surrounding host attachment sites have been proposed to explain the widespread nature of epibiont attachment (21, 22). However, the movement of motile epibiont cilia or flagella alters flows and, hence, creates an altered fluid dynamic environment surrounding the consortia. What are the consequences for the consortium host—does a larger, nonmotile cell benefit by membership in consortia? While advantages to the epibiont have been examined, the impacts on the host cells within a consortium have remained largely unconsidered. One reason for this is that physical associations between members of consortia are often temporary, and the short time scales of these relationships have hampered direct evaluation of the fluid mechanical interactions between consortium members.

Here, we describe experimental work in combination with mathematical models that quantify the effect of the epibiont’s advective currents on nutrient availability to host cells within consortia formed by a large diatom, *Coscinodiscus wailesii*, and its peritrich ciliate epibiont, *Pseudovorticella coscinodisci* (Fig. 1A). Consortia composed of *C. wailesii* and *P. coscinodisci* are common along the Atlantic coast of South America (23, 24) and have provided a valuable opportunity for measuring fluid interactions characterizing a planktonic host–epibiont association.

**Significance**

Nutrient acquisition is a challenge that often favors small individual phytoplankters because they are superior competitors at low nutrient levels. An alternative to these individual solutions is the union of different species into consortia that rely upon division of labor for competitive advantage. Although planktonic epibionts are well documented, the advantages of consortia for the larger host cells have remained unclear. Here, we demonstrate that attached ciliates dramatically increase the flux of dissolved nutrients to host phytoplankton cells, providing the necessary conditions for large diatoms to thrive in oligotrophic ecosystems. This demonstrates that unions between different species can substantially increase rates of nutrient flow to host cells and provides an alternative to sinking for protists living in low-nutrient conditions.

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Results

Epibiont-Generated Flows. The ciliate *P. coscinodisci*, when attached to *C. wailesii*, generated flows that entrained fluid toward the diatom along the direction normal to its surface and then around the diatom body (Fig. 1B and C and SI Appendix, Movies S1–S3). Particle image velocimetry (PIV) transects demonstrated that the microcurrent speeds were maximal near the center of the ciliary crown and decreased away from the crown, at times forming small viscous eddies on either side of the ciliary crown (Fig. 1B and C), that became exaggerated when near the fluorodish wall (SI Appendix, Movie S1). Eddies characterize feeding currents near infinitely-long flat walls and could limit the benefits of advective nutrient transport by recirculating fluid past the ciliate feeding apparatus after nutrients have been removed (25, 26). We observed a recirculation component within the consortium flow (Fig. 1B), but the limited diatom cell surface allowed substantial flow past the epibiont and along the diatom cell body (Fig. 2A and SI Appendix, Movies S1 and S5). Surface geometry is an important determinant of viscous eddy recirculation for attached ciliates (25, 27), and the finite diatom body minimized recirculation of advected fluid within viscous eddies for *Coscinodiscus–Pseudovorticella* consortia. Additionally, ciliate feeding currents generated forces and torques capable of altering the consortia’s motion as well as orientation in the fluid (SI Appendix, Movie S5). Such whole-consortia movements can disrupt eddy formation compared to infinite, static surfaces. Such disruptions caused by whole-consortia rotations may introduce fresh fluid—and nutrients—to the consortia (28, 29).

Due to compression of fluid streamlines near the ciliated crown (30), the portion of the microcurrent entering the ciliary feeding region, and therefore eligible for clearing prey particles (31), was about half of the total microcurrent flow (46%, SD = 3.1%, n = 8 ciliates). Much of the microcurrent flow (54%) did not enter the ciliary crown region but passed to either side of the ciliate, potentially transporting fresh nutrient-laden fluid to the diatom surface. Indeed, the fluid entering the crown exited as an excurrent flow that was distinct, relative to the fluids that did not pass through the ciliary crown (SI Appendix, Movies S2–S4). Flow velocities entering the ciliary crown reached values of $U \geq 500 \mu m \cdot s^{-1}$, with average maximum $= 496, SD = 59 \mu m \cdot s^{-1}$, and mean across ciliary crown $= 362, SD = 44 \mu m \cdot s^{-1}$, for $n = 8$ ciliate–host replicates (Fig. 1C). These flows are of similar velocities to those measured for peritrich

![Fig. 1. Diatom–ciliate association: (A) diatom C. wailesii and its epibiont P. coscinodisci. Scale bars represent 100 microns in length. (B) Flow around a single ciliate directed toward the diatom cell surface. (C) Velocity field for the same diatom–ciliate pair with a blue line indicating the transect line used for measurement of flow field velocities. The magenta segment represents the microcurrent component that directly intercepts the ciliary crown.](https://doi.org/10.1073/pnas.2018193118)

![Fig. 2. Diatom–ciliate model: (A) Streamlines of particle paths generated by the flow field of a three-member cluster of the ciliate P. coscinodisci attached to the diatom C. wailesii. (B) Streamlines produced by the diatom–ciliate model consisting of a sphere of radius $R$ and a regularized Stokeslet of dimensionless strength $F = 10$ and regularization parameter $r = 0.4R$ located at a distance $h = 0.5R$ from the sphere’s south pole and pointing toward the sphere’s center. (C) Velocity field for the same diatom–ciliate model. Scale bars represent 100 microns in length.](https://doi.org/10.1073/pnas.2018193118)
ciliates within the frequently studied genus *Vorticella* ([31, 32]) as well as euphasiids attached heterotrophic flagellates ([300 to 400 μm] [19]). By approximating the cell volume of a *P. coscinodiscus* ciliate (average height 44.2 μm ± 6.2 μm, base 40.5 μm ± 4.9 μm, volume 15,246.6 μm³ ± 6,786.4 μm³; *n* = 58 individuals, *SI Appendix*, Fig. S5 and Table S7), we estimate the average volume transported to the ciliated crown feeding surfaces, and therefore eligible for clearing prey particles, of an individual, attached *P. coscinodiscus* ciliate to be ∼1.8 × 10⁵ body volumes h⁻¹. Total flow, including fluid not passing through the ciliary crown, was ∼3.8 × 10³ body volumes h⁻¹. Both values fall well within volume-specific clearance rate estimates for other protists that range between 10⁶ and 10⁷ body volumes h⁻¹ of prey particles (*SI Appendix*, Table S6), indicating that the microcurrent traits that we measured for the *Coscinodiscus–Pseudovorticella* consortia are representative of other protists living in a variety of aquatic environments.

**Benefits of Epibiont-Generated Flows to the Diatom Host.** We predicted that the presence of microcurrents would accelerate solute transport to and from the diatom host. These consortia were isolated from surface oligotrophic waters in which nutrient availability would be expected to constrain diatom growth ([33]). Small molecules, such as oxygen and dissolved silica with diffusivities that are in the order of D = 10⁻⁹ m² s⁻¹, when transported by the observed flows, traverse a distance R (the cell radius) = 100 μm at a speed U = 100 μm s⁻¹ in approximately R/U = 1 s. In contrast, solutes transported by diffusion alone take a considerably longer time, R²/D = 10 s, to traverse the same distance. The ratio of diffusive to advective timescales is measured by the Pécellet number (Pe = UR/D). When Pe << 1, mass transport is controlled by molecular diffusion. For the range of speeds that we observed, we obtain Pe = 10 to 50, implying that advection dominated even the slowest epibiont flows that we recorded (*SI Appendix*, Tables S1 and S2). This dimensional analysis suggests that the flows generated by the ciliate epibiont substantially enhance the transport of solutes to and from the diatom surface.

**Quantifying Nutrient Availability to the Diatom.** To quantify the benefits of the epibiont-induced flows to the diatom, we developed a mathematical model that allows comparison of the corresponding nutrient flux to i) diffusive flux and ii) flux to a sinking diatom. The model (*SI Appendix*) approximated the diatom by a sphere of radius R and subsumed traits of the ciliate flow into a single averaged parameter—the force F that the ciliate exerts on the fluid. Dimensional analysis shows that this force scales as F = η U Rₘₐₓ, where η = 10⁻³ kg m⁻¹ s⁻¹ is the viscosity of seawater. For an individual ciliate, Rₘₐₓ = 20 μm and U = 100 to 500 μm s⁻¹, F = 2 to 10 nN (*SI Appendix*, Table S1).

The fluid velocity u created by the ciliate vanishes at the surface of the diatom and decays to zero far from the diatom surface. Because inertia is unimportant at this scale, u must satisfy the Stokes equation V/P = η Δu, where P is pressure; it must also be incompressible V • u = 0. We solved these equations analytically to obtain the velocity field u generated by a regularized Stokeslet force, emulating the effect of the epibiont ciliated crown, located at a distance h/R from the diatom surface and pointing toward the center of the diatom ([34]). Although not an exact replica of empirically measured flows, the three-dimensional flow field of the regularized Stokeslet captures the main features of the flow observed experimentally: 1) flow directed toward the spherical diatom along the direction normal to its surface, 2) compression of fluid streamlines near the regularized Stokeslet, 3) highest flow speeds around the regularized Stokeslet, and 4) zero flows at the diatom surface (Fig. 2 and *SI Appendix*, Fig. S3).

To determine the effect of these advective currents on nutrient availability to the diatom, we numerically solved the advection-diffusion equation ∂u/∂t + u • V = D • C for the steady-state concentration of nutrients around the diatom surface. Here, u • V C = D • C for the steady-state concentration of nutrients around the diatom surface. Here, u • V C = D • C and DAC are, respectively, the advective and diffusive rates of change of the nutrient concentration field C (*SI Appendix*). We normalized the concentration field by its far-field value at large distances away from the diatom. At the diatom surface, the concentration is zero and reflects the assumption that nutrient absorption at the cell surface greatly exceeds transport rates of molecular diffusion ([4, 7, 8]). By Fick’s law, a gradient in concentration yields a flux. The diatom nutrient uptake rate is the integral of the inward flux \( j = \oint D_n \cdot V C \, ds \) over the surface area of the diatom, where \( V C \) is the concentration gradient and \( n \) is the unit normal to the diatom surface. In the absence of advective flows, the nutrient concentration is governed by molecular diffusion only ([Fig. S4]). The diffusive nutrient uptake rate \( I_d \) scales linearly with the diatom radius R, imposing serious limitations on diatom size ([8, 35]). In contrast, for a diatom sinking at Pe = 100 (Fig. 3B and *SI Appendix*, Figs. S1 and S2), the diffusive boundary layer gets thinner around most of the diatom, with only a plume or “tail” of nutrient depletion, characteristic of decaying marine snow ([36]), extending behind the sinking diatom. This constriction of the depletion zone enhances nutrient uptake to the sinking diatom by over threefold. When a diatom is in consortium with ciliated epibionts, the epibiont-induced flows change the concentration field around the diatom model (Figs. 2B and C and 3C and *SI Appendix*, Fig. S3). We first considered the flow field induced by a pair of epibionts symmetrically attached at opposite poles of the diatom to ensure that forces and moments on the diatom are balanced, accounting only for the effect of ciliate-driven flows (*SI Appendix*, Table S3). The nutrient depletion zone is thinnest near the epibiont attachment locations on both sides of the diatom (Fig. 3C), and nutrient uptake is improved at a level that is comparable, even slightly higher than that of the sinking diatom.

To account for more ciliates on larger diatoms, we next considered the average flow field generated by N pairs of ciliates uniformly distributed along the diatom surface (*SI Appendix*, Table S4 and Fig. S4). Ciliates typically attach randomly on either or both sides of the diatom, often causing motion of the whole consortium. Mounting experimental and numerical evidence suggests that motion relative to the fluid is beneficial for both epibiont and diatom ([21, 26, 37]). However, statistics of attachment sites and ciliates-induced motions are currently lacking. We thus focused only on stationary configurations, because they provide a lower estimate of the benefits due to ciliate attachment. Specifically, to allow enough spacing between the ciliates, we considered the number of attached ciliates N to be equal to the surface area of the spherical diatom divided by four times the area enclosed by the circular crown of the ciliate. We followed a standard algorithm for distributing the ciliates uniformly on the diatom surface using an equal area partition of the spherical surface (*SI Appendix*, Fig. S4). For example, a diatom of radius R = 100 μm can readily support eight pairs of ciliates. Assuming identical ciliates, we computed the ciliate-generated flow field in three dimensions, and we averaged the three-dimensional flow around the axis of symmetry of the ciliate distribution. We used the averaged flow field to numerically calculate an axisymmetric concentration field around the diatom (Fig. 3D). The effects of axisymmetry and underlying uniform distribution of Stokeslets are reflected in the overall concentration field (*SI Appendix*, Fig. S4).

**Sherwood Number.** To place epibiont flows within a perspective that includes the more studied phenomenon of phytoplankton cell sinking, we assessed the benefits of epibiont-induced flows with reference to sinking for nutrient flow to the diatom. The cases illustrated in Fig. 3A–D represent a diatom of radius R = 100 μm (4) in pure diffusive transport, (B) sinking, (C) in consortium with a single pair of epibionts, and (D) in consortia with eight pairs of uniformly distributed epibionts (highlighted in Fig. 3E). For this, we calculated the Sherwood number Sh = I/I_d for a range of
diatom radius \( R \). \( Sh \) is defined as the ratio of the total nutrient flux \( I \) (advective plus diffusive) normalized by the diffusive flux \( I_d; \) \( Sh = 1 \) for pure diffusion and \( Sh > 1 \) when advective currents enhance nutrient availability. For example, \( Sh = 5 \) indicates that the diatom nutrient uptake is fivefold that due to diffusion only. In Fig. 3E, we plotted \( Sh \) as a function \( R \) for 1) consortia with a single pair of epibionts and 2) consortia with increasing number \( N \) of epibiont pairs as \( R \) increases (SI Appendix, Tables S3 and S4); red circles of Fig. 3E are based on numerical computations and the solid red lines are obtained by a spline fit. For diatoms with uniform distributions of \( N \) pairs of ciliates; the values of \( Sh \) represent conservative upper estimates of the benefit of epibiont-induced flows to diatom nutrient uptake. A diatom of the same radius but smaller number of epibionts would lead to \( Sh \) values that lie within the region highlighted in red in Fig. 3E, between \( Sh = 1 \) and the computed estimate. By way of comparison, we calculated a theoretical upper bound on \( Sh \) for sinking diatoms (thin blue line, Fig. 3E). This upper bound was obtained by noting that the velocity of a sinking diatom is \( U_{sink} = 2gR^2\Delta\rho/9\eta \), where the acceleration due to gravity is \( g = 9.8 \text{ m s}^{-2} \) and the difference in density \( \Delta\rho \) between the diatom and the ambient fluid is set to the maximum reported value, \( \Delta\rho = 100 \text{ kg m}^{-3} \). At smaller density differences, \( Sh \) lies below the thin blue curve within the region highlighted in blue. The overlap between the red and blue regions indicates that, for a wide range of diatom sizes, similar enhancement in nutrient uptake can be achieved by either sinking or diatom–epibiont consortia.

To complete this analysis, we compiled a set of experimental measurements of diatom (\( C. wailesii \)) sinking velocities from the literature (16, 17, 38, 39), and we calculated the corresponding \( Pe \) and \( Sh \) numbers (SI Appendix, Table S5). Results are shown in gray symbols in Fig. 3E. For each diatom radius, we report two values of \( Sh \) corresponding to the minimum and maximum measured sinking velocities. The results lie well in the overlap region of \( Sh \) values and demonstrate that combining with even a low number of epibionts allows nutrient enhancement that is of similar magnitude to that observed for sinking diatoms.

**Discussion**

Associations of the large nonmotile host and its smaller, motile epibiont can contribute to beneficial fluid dynamic outcomes for both members of the *Coscinodiscus–Pseudovorticella* consortia. Hydrodynamic effects on protists that use microcurrents to feed while attached to larger particles have been previously considered (19–22, 40, 41), so we concentrated here on alterations of nutrient availability to the larger diatom host cell. For a large diatom such as *C. wailesii*, microcurrent advection is a substantially more rapid mechanism of dissolved mass transport than diffusion (Fig. 3).

Advection by epibiont ciliary flows substantially thins diffusive boundary layers (Fig. 3C and SI Appendix, Fig. S3), allowing greater access to dissolved nutrients in waters surrounding the consortium.
The increased nutrient access due to epibiont-based advection is of a similar or greater magnitude than that due to diatom sinking without epibionts (Fig. 3E). Sinking allows a large diatom such as *C. wailesii* to create advective flows past itself (*SI Appendix, Fig. S1*) and thereby thin its diffusive boundary layer (*SI Appendix, Fig. S2*), resulting in higher nutrient flux rates than nonsinking cells (8, 17). Comparison of Sh values indicate that the relative advantages of either strategy—sinking or association with epibionts—depends on the diatom size and number of associated epibionts (Fig. 3 and *SI Appendix, Fig. S2*). The parameter values we used to derive these assessments (*SI Appendix, Tables S1 and S2*) are conservative, and we expect that the epibiont-induced impacts on nutrient uptake to the diatom are robust estimates. Under natural conditions, it appears that strategies of either sinking or consortia formation coexist and some phytoplankton species, such as *C. wailesii* (17, 24), employ either strategy in different circumstances.

Our model underscores the need for greater understanding of consortia formation and maintenance in nature. By placing epibionts in an axisymmetric arrangement on the host surface, the model balances forces generated by the epibionts around the host surface and eliminates clumps or random groups of epibionts, which could create both elevated flows (42) and unbalanced forces that result in translation or rotation of the whole consortium (e.g., *SI Appendix, Movie S4*). Such epibiont-generated motions would likely create transient flows that increase mass transfer rates (17, 21, 37) to a consortium. Hence, we expect our projections using balanced forces and established diffusive boundary layers to be conservative estimates of epibiont-generated nutrient benefits for diatoms in these consortia.

The hydrodynamic benefits of consortia formation between large cells and microcurrent-generating epibionts appear to be valuable, particularly in nutrient-poor environments where nutrient diffusion rates influence phytoplankton community composition. This suggests a question—if consortia formation is mutually beneficial, why are they not more commonplace in nature? It is possible that the full extent of such marine relationships may be underappreciated (43-46) because associations are often ephemeral and difficult to sample with conventional approaches. For example, members of the *Coscinodiscus-Pseudovorticella* consortium separated within 30 min of collection and require a rapid research protocol. More broadly, a mutual benefit may not be enough to maintain a consistent symbiotic relationship. Evolution of mutually beneficial relationships between epibionts and their hosts face a variety of obstacles (47-50) that limit consortia evolution or lessen mutual benefits for the collaborators and their offspring (51). Potential loss of active photosynthetic area for diatom surfaces occupied by epibionts or removal of ciliates from productive regions on a sinking diatom both represent potential liabilities to members of *Coscinodiscus-Pseudovorticella* consortia. In response to a variety of conditions, protistan consortia have evolved a diverse spectrum of solutions (52-54) involving facultative partners, such as *Coscinodiscus-Pseudovorticella*, as well as obligate relationships, such as the diatom-ciliate consortia of *Chaetoceros coultertactus–Vorticella oceanaica*. Both of the latter consortia are found in the same geographic region and often occur simultaneously (24). Although member identities and the nature of these relationships vary, hydrodynamic benefits such as those experienced by *Coscinodiscus-Pseudovorticella* consortia and other multicellular groups (35, 55) create a physical benefit that can serve as a foundation for the evolution of more complex relationships.

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