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Hydrodynamics of microbial filter feeding

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Microbial filter feeders are an important group of grazers, significant to the microbial loop, aquatic food webs, and biogeochemical cycling. Our understanding of microbial filter feeding is poor, and, importantly, it is unknown what force microbial filter feeders must generate to process adequate amounts of water. Also, the trade-off in the filter spacing remains unexplored, despite its simple formulation: A filter too coarse will allow suitably sized prey to pass unintercepted, whereas a filter too fine will cause strong flow resistance. We quantify the feeding flow of the filter-feeding choanoflagellate *Diaphanoeca grandis* using particle tracking, and demonstrate that the current understanding of microbial filter feeding is inconsistent with computational fluid dynamics (CFD) and analytical estimates. Both approaches underestimate observed filtration rates by more than an order of magnitude; the beating flagellum is simply unable to draw enough water through the fine filter. We find similar discrepancies for other choanoflagellate species, highlighting an apparent paradox. Our observations motivate us to suggest a radically different filtration mechanism that requires a flagellar vane (sheet), something notoriously difficult to visualize but sporadically observed in the related choanocytes (sponges). A CFD model with a flagellar vane correctly predicts the filtration rate of *D. grandis*, and using a simple model we can account for the filtration rates of other microbial filter feeders. We finally predict how optimum filter mesh size increases with cell size in microbial filter feeders, a prediction that accords very well with observations. We expect our results to be of significance for small-scale biophysics and trait-based ecological modeling.

protozoans | choanoflagellates | filter feeding | microswimmers | computational fluid dynamics

Heterotrophic microorganisms in the oceans inhabit a dilute environment and they need efficient feeding mechanisms to acquire enough food to sustain growth (1, 2). At the microscale the Reynolds number is low and viscous forces govern hydrodynamical interactions. This implies extensive, long-range flow disturbances around moving particles and microswimmers, impeding cell–cell contact and prey capture (3, 4). However, to encounter enough food, purely heterotrophic plankton that rely solely on prey capture typically need to clear a volume of water for prey corresponding to 1 million times their own body volume per day (4). Thus, heterotrophic microbes face a difficult challenge, and the prevailing viscous forces must strongly influence prey capture and shape the various feeding modes through evolution.

Many unicellular flagellates as well as colonial sponges and metazoans, e.g., tunicates, use filter feeding to catch bacteria-sized prey (1, 5–7). They establish a feeding current, from which prey particles are sieved using filter structures. Such filter feeders benefit from having filters with small mesh size that allow the organisms to capture small prey (5, 8). However, filter spacing involves a trade-off: The finer the mesh size is, the higher the availability of food but the lower the clearance rate due to a dramatic decrease in filter permeability (9). An optimum mesh size must therefore exist. While microbial filter feeding has been studied regarding the pressure drop across the filter and the observed clearance rates (5), clearance rates have never been

related to the force production of the flagellum that drives the feeding current. Can a beating flagellum even produce sufficient force to account for the observed clearance rates through such fine filters?

Choanoflagellates are the prime example of unicellular filter feeders (1, 10, 11). They are equipped with a single flagellum that is surrounded by a funnel-shaped collar filter made up of microvilli extending from the cell. Some species are sessile and attach with a stalk to solid surfaces whereas others are freely swimming and have a basket-like structure (lorica) that surrounds cell, flagellum, and filter (Fig. 1). The beating flagellum creates a feeding current that transports bacteria-sized prey to the outside of the collar filter from where the prey are transported to the cell surface and phagocytosed (10, 12–16). Far-field flows created by choanoflagellates have recently been measured and modeled for the sessile choanoflagellate *Salpingoeca rosetta* (14). However, the essential near-cell feeding flow in choanoflagellates is poorly understood and has not been resolved quantitatively in experiments (10, 11).

As a model organism of microbial filter feeders, we focus on the choanoflagellate *Diaphanoeca grandis* that swims freely and carries a lorica (Fig. 1). The lower part of the lorica has large openings, whereas the upper part is covered by a fine web with small pore sizes (13). The collar filter therefore supposedly functions as an internal filter, and prey particles should not circumvent the filter once inside the lorica.

Using *D. grandis*, we here ask: What are the mechanisms of particle capture in choanoflagellates, and what is the optimum filter spacing? We use high-speed videography and particle tracking to quantify the feeding flow. For comparison, we use

Significance

Microbes compose the majority of life in aquatic ecosystems and are crucial to the transfer of energy to higher trophic levels and to global biogeochemical cycles. They have evolved different foraging mechanisms of which our understanding is poor. Here, we demonstrate for filter-feeding choanoflagellates—the closest relatives to multicellular life—how the observed feeding flow is inconsistent with hydrodynamic theory based on the current understanding of the morphology. Instead, we argue for the widespread presence of flagellar vanes and suggest an alternative pumping mechanism. We also demonstrate a trade-off in filter spacing that allows us to predict choanoflagellate prey sizes. These mechanistic insights are important to correctly understand and model microbial heterotrophs in marine food webs.

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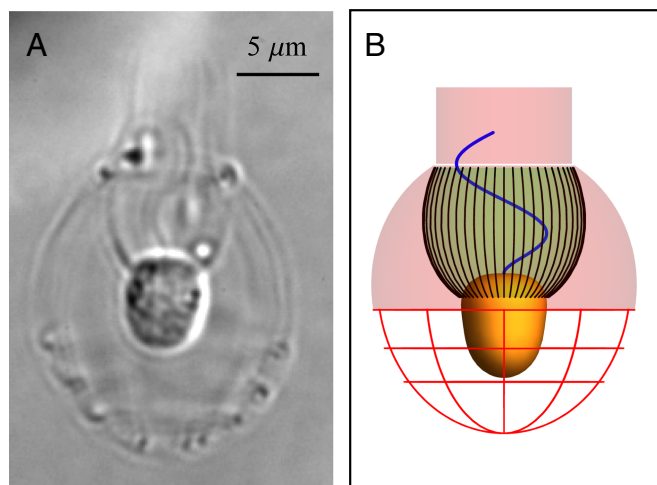


Fig. 1. Morphology of *D. grandis*. (A) Microscopic image of freely swimming choanoflagellate. (B) Model morphology with cell (orange), collar filter (green surface and black lines), flagellum (blue), and lorica (red). The ribs (costae) in the lower (posterior) part of the lorica are indicated, whereas for clarity the ribs in the finely netted, upper (anterior) part of the lorica are not shown.

computational fluid dynamic (CFD) simulations and simple estimates of the filter resistance and the force production due to the beating flagellum. Our analysis shows that modeling the beating flagellum as a simple, slender structure produces a force that is an order of magnitude too small to account for the observed clearance rate. This demonstrates the strong trade-off in small-scale filter feeding and leads us to suggest an alternative flagellar pumping mechanism.

Results

Observed Feeding Flow and Clearance Rate. We developed a generic model morphology of *D. grandis* to collate particle track observations from individual cells (*Model Morphology and Observed Flow*, Table S1, and Fig. 1). The feeding flow is driven by the beating flagellum. The flow transports particles from the region below the choanoflagellate, in through the large openings in the lower part of the lorica and up toward the collar filter on which the particles are caught (Fig. 2 and Movie S1). The detailed visualization reveals a true filtration flow that undoubtedly passes through the filter, confirming the current understanding of filter feeding in choanoflagellates (11). However, our results are for a loricate species, and it is uncertain whether, and to what extent, nonloricate species can filter the same way, since flow could pass along the filter on the outside and circumvent the filter. From the flow field, one important function of the lorica seems to be the separation of in- and exhalent flow, reducing refiltration. The clearance rate Q can be expressed as the volume flow rate through the filter

$$Q = \int_{A_F} v \, dA, \quad [1]$$

where A_F is the surface area of the filter and v is the normal component of the flow velocity. The observed velocity field shows that the water that passes the filter first passes the equator ($z = 0$) in the annular region between the cell and the finely netted part of the lorica. We determine the clearance rate as the volume flow rate upward across the annular region in the equator plane. This procedure is more precise than directly using the flow through the filter. No-slip boundary conditions would suggest reduced flow velocities near the cell and lorica. At the spatial resolution of our experiment, however, the z components of the flow veloci-

ties in the annular region do not depend on the distance from the longitudinal axis (Fig. S14). To determine the clearance rate we therefore use the average value $v_z = 7.3 \pm 4.4 \mu\text{m}\cdot\text{s}^{-1}$ (mean \pm SD) times the area of the annular region. We find $Q = (1.22 \pm 0.72) \cdot 10^3 \mu\text{m}^3\cdot\text{s}^{-1}$, or 1.20 million cell volumes per day, where the cell volume $V_C = 88 \mu\text{m}^3$. The corresponding flagellar beat frequency is $f = 7.3 \pm 2.6 \text{ Hz}$ (Fig. S1B).

Computational Fluid Dynamics and Theoretical Clearance. To explore the feeding flow theoretically we numerically solve the Navier–Stokes equation and the equation of continuity for the incompressible Newtonian flow due to the beating flagellum with the known morphology (*CFD Simulations* and Figs. S2–S5). The collar filter consists of ~ 50 evenly distributed microvilli (13), with a fairly uniform filter spacing and permeability along most of their length (Fig. 1). The finely netted upper part of the lorica has pore sizes in the range $0.05\text{--}0.5 \mu\text{m}$ (13), and for simplicity we treat it as an impermeable, rigid surface and neglect the ribs in the lower part of the lorica. *D. grandis* carries a standard eukaryotic flagellum with diameter $b = 0.3 \mu\text{m}$ (23), and high-speed videography showed that the flagellum beats, like most other eukaryotic flagella, in a single plane (Movie S2). For computational simplicity we model the flagellum as a thin sheet of width b that is oriented perpendicular to the plane of beating and moving with a simple traveling wave motion in the positive z direction. Based on our validation of the CFD simulations, we estimate that this approach underestimates the flagellar forces by $\sim 20\%$ (Tables S2 and S3). The time-averaged CFD flow is an order of magnitude weaker than the flow observed experimentally for *D. grandis* (Fig. 2). The model leads to the time-averaged flagellum force in the z -direction $F_{0.3} = 1.1 \text{ pN}$, the time-averaged power $P_{0.3} = 0.31 \text{ fW}$, and the clearance rate $Q_{0.3} = 95 \mu\text{m}^3\cdot\text{s}^{-1}$, which is ~ 13 times lower than the clearance rate based on the observed flow field.

To generalize our CFD results and roughly estimate the clearance rates of other species of choanoflagellates, we model filter resistance and flagellum force. We describe the filter locally as a row of parallel and equidistantly spaced solid cylinders, and we model the flow far from the filter as uniform and perpendicular to the filter plane. For such simple filters we can express the flow speed through the filter

$$v = \kappa \frac{a}{\mu} \Delta p, \quad [2]$$

where Δp is the pressure drop across the filter, κ the dimensionless permeability of the filter, and μ the dynamic viscosity. The dimensionless permeability κ is a function only of the dimensionless filter spacing l/a . We model κ by combining previous theoretical work on closely and distantly spaced filter structures, respectively (24, 25). The dimensionless permeability κ increases strongly with l/a and contributes to the filter spacing trade-off as discussed above (Fig. S6). For the model morphology we find the average dimensionless permeability $\langle \kappa \rangle = 0.41$. With a flagellum of length L and diameter b we can estimate the flagellum force

$$F_T = C_F \mu L U = 4 C_F \mu L A f, \quad [3]$$

where C_F is the drag coefficient, $\mu = 1.0 \cdot 10^{-3} \text{ Pa}\cdot\text{s}$ the viscosity, and A the amplitude of the flagellar beat. The average speed of the flagellum is estimated as $U = 4 A f$. For simplicity we take C_F to be the drag coefficient of a slender spheroid that is moving sideways, $C_F = 4\pi / (\ln(2L/b) + 1/2)$ (26). The estimate neglects the presence of filter and lorica structures surrounding the flagellum and assumes that all (primarily transversal) drag on the flagellum is converted into longitudinal flow. The corresponding power estimate is $P_T = F_T U = 16 C_F \mu L A^2 f^2$. To estimate the theoretical clearance rate we assume that the pressure drop is $\Delta p = F/A_F$ and we obtain

be questioned, most obviously perhaps through the notion that various types of flagellar hairs often line eukaryotic flagella and could increase the force output of the flagellum (23). However, the force estimate is only weakly influenced by the flagellum diameter (Eq. 3), as long as we neglect interaction between flagellum and filter, and simple flagellar hairs would have little influence on the clearance rate. It is thus difficult to see how the flagellum would be able to deliver the force required to account for the experimentally observed clearance rate, unless some major aspect of its morphology or function has been overlooked.

Pumping Mechanism Conjecture. A few choanoflagellate species have been shown to have a so-called flagellar vane composed of a sheet-like structure along the length of the flagellum (17, 20, 27). Although a flagellar vane has been observed in a few choanoflagellate species, the structure remains elusive. Leadbeater (27) went so far as to call it a “mystery” because the structure is notoriously difficult to visualize using electron microscopy. While a vane cannot account for the clearance rate due to increased flagellum drag as long as interactions between flagellum and filter are neglected, this structure could still offer a satisfactory solution to the apparent paradox: With a vane, the distance between flagellum and the inside of the collar would be reduced, reducing transversal flow past the beating flagellum inside the collar. Instead, more fluid would be forced upward, and the resulting low pressure would have to be equalized by a flux through the filter. With a flagellar vane nearly as wide as the collar, or even physically attached to the inside of the collar, the pumping mechanism would be radically different. The highly similar choanocytes of aquatic sponges have been shown to have flagellar vanes that indeed are attached to the filter or span its width (20, 28, 29). The flagellum together with its vane would function as a waving wall forming two adjacent peristaltic pumps (30), one on each side of the vane, that draw in water through the filter and expel it out of the chimney of the lorica. To explore such a pumping mechanism we replace the flagellum in the CFD model with a $b = 5\text{-}\mu\text{m}$ -wide sheet that spans almost the entire width of the filter (Movies S3–S5). The time-averaged CFD flow agrees well with the flow observed for *D. grandis* (Fig. 3). The model leads to the time-averaged flagellum force in the z -direction $F_5 = 12.1\text{ pN}$, the time-averaged power $P_5 = 2.20\text{ fW}$, and the clearance

rate $Q_5 = 898\text{ }\mu\text{m}^3\cdot\text{s}^{-1}$, slightly lower than the experimentally observed clearance rate.

To explore the vane-based pumping mechanism conjecture for other choanoflagellates we make a rough estimate of the clearance rate as the volume flow rate given by the simple model

$$Q_V = AW\lambda f, \quad [5]$$

where W is the diameter of the chimney of the lorica and λ the flagellar wavelength. We assume that the flagellum is moving in the central beat plane with amplitude A and that the flagellar vane is attached to filter and chimney. The average peak-to-peak amplitude of the flagellar vane must therefore be A , and we assume that a water volume $AW\lambda$ is forced through the filter and out of the chimney per flagellar beat period. For *D. grandis* we find the estimate $Q_V = (1.41 \pm 0.50) \cdot 10^3\text{ }\mu\text{m}^3\cdot\text{s}^{-1}$ in good agreement with the clearance rate based on the observed flow field (Table 1).

In fact, Q_V provides a solid prediction of the observed clearance rate Q in six of the seven species for which the naked flagellum clearance rate estimate Q_T cannot account for Q (Table 1). Thus, two species seem to use a simple flagellum to drive the feeding current, whereas six choanoflagellate species and the choanocyte rely on a flagellar vane. A narrow vane has been observed in *Monosiga brevicollis*, but a vane this small would have only limited influence on the clearance rate (Fig. S5), and the apparent discrepancy is certainly within estimate uncertainties. Only for *Codosiga botrytis* does neither of the two models adequately predict Q . This species has a long and rapidly beating flagellum that extends far beyond the collar and also the finest of the choanoflagellate filters. Combined, this suggests that this species may not perform actual filter feeding, but instead relies on cross-flow filtration in which the flow passes along and not through the filter. The suggested pumping mechanism would also provide a means to avoid unwanted filter circumvention in loricate as well as nonloricate species. If the vane spans most of the collar width, a flagellum wavelength “traps” a package of water that has to be expelled with the flagellar beat. Furthermore, typical flagellar beat frequencies of eukaryotic organisms are in the range 30–70 Hz (1, 18), and the low beat frequencies found in *D. grandis* and a number of other choanoflagellate species stand out (Table 1). We speculate that the low beat frequencies are the result of extensive flagellar vanes and their high force requirements. While the dynein motor proteins themselves would easily

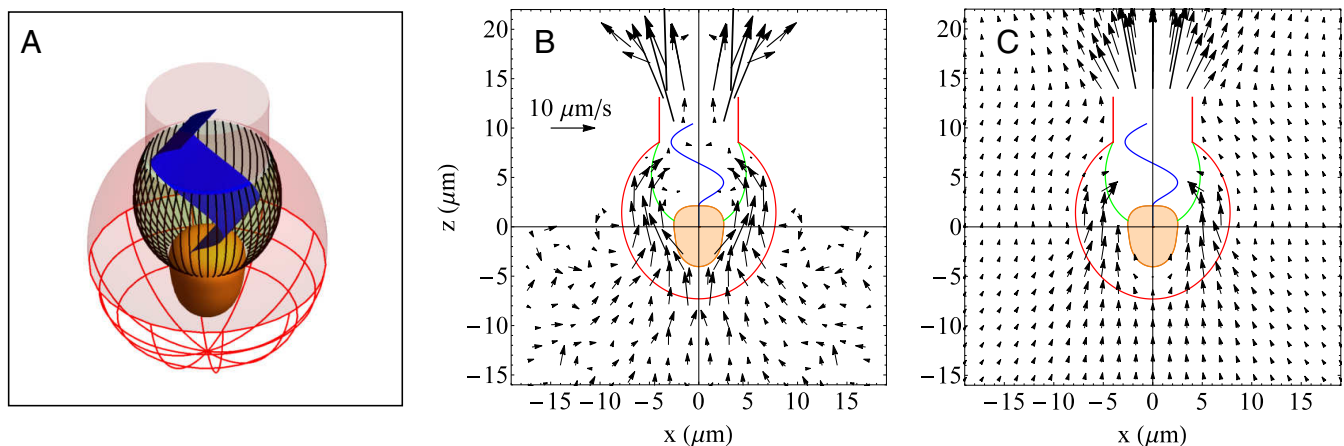


Fig. 3. Model morphology with a flagellar vane, observed average velocity field for *D. grandis*, and velocity field from CFD model including a $5\text{-}\mu\text{m}$ -wide flagellar vane. (A) The model morphology shows the cell (orange), the collar filter (green), the flagellum with a $5\text{-}\mu\text{m}$ -wide flagellar vane (blue), and the lorica (red). (B) Observed average velocity field. The velocity field is identical to the velocity field in Fig. 2B, and it is shown repeatedly to facilitate comparison with the CFD result. (C) The CFD velocity field in the xz plane is time averaged over the flagellar beat cycle, and the velocity vectors inside filter and chimney are omitted for clarity. The CFD model with a flagellar vane predicts a feeding flow in through the permeable lower part of the lorica and a clearance rate in good agreement with the experimental observations for *D. grandis*.

and the velocity field in the xz plane was constructed using a square grid with $2\text{-}\mu\text{m} \times 2\text{-}\mu\text{m}$ spatial resolution. The velocity field was assumed to have rotational symmetry about the longitudinal axis of the cell, and the observed velocity field in the xz plane was therefore correspondingly assumed to have left–right reflection symmetry with respect to the longitudinal axis. Within each grid window the manually detected particle positions were selected and for each particle track the average particle position and velocity were determined. Position and velocity associated with a given grid

window were subsequently determined as the equally weighted average over all particle tracks within the window.

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