Manta rays feed using ricochet separation, a novel nonclogging filtration mechanism

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Solid-liquid filtration is a ubiquitous process found in industrial and biological systems. Although implementations vary widely, almost all filtration systems are based on a small set of fundamental separation mechanisms, including sieve, cross-flow, hydrosol, and cyclonic separation. Anatomical studies showed that manta rays have a highly specialized filter-feeding apparatus that does not resemble previously described filtration systems. We examined the fluid flow around the manta filter-feeding apparatus using a combination of physical modeling and computational fluid dynamics. Our results indicate that manta rays use a unique solid-fluid separation mechanism in which direct interception of particles with wing-like structures causes particles to “ricochet” away from the filter pores. This filtration mechanism separates particles smaller than the pore size, allows high flow rates, and resists clogging.

INTRODUCTION

Several fundamental mechanisms for solid-fluid separation have been described in the biological and engineering literature, including sieve (1, 2), cross-flow (3–6), hydrosol (7), and cyclonic separation (8). Sieve filtration passes a mixture of particles and fluid through a structure with regularly sized pores, causing the particles to be retained while the fluid is drained. Although effective, sieve filters must have pore sizes smaller than the particle size, and they inevitably clog in use (2, 8, 9). Cross-flow filtration is similar to sieving, except that the incoming flow runs parallel rather than perpendicular to the filter. This configuration shears captured particles off the filter’s surface, which reduces but does not eliminate clogging (5, 6). Unlike sieve and cross-flow filters, hydrosol and cyclonic filtration do not require regularly sized pores. Hydrosol filtration captures particles using “sticky” structures within the filters, which allow these filters to capture particles smaller than their pore size, although they also invariably become clogged (10, 11). Cyclonic filtration uses a high-speed, rotating flow that flings dense solid particles to the periphery while allowing fluid to pass through the center (8, 12, 13). This separation mechanism requires the solid particles to be denser than the fluid but is resistant to clogging (12) and has been widely used within the bagless vacuum industry (12, 13).

A large diversity of aquatic animals feed by filtering plankton and other food particles out of the water. It had long been thought that many teleost fish species capture prey by sieving, passing plankton-laden water through elongate gill rakers that protrude from the gill arches into the pharynx. However, gut content analysis in several teleost fish species demonstrated that fishes routinely capture plankton into the pharynx. However, although effective, sieve filters must have pore sizes smaller than the particle size, and they inevitably clog in use (2, 8, 9). Cross-flow filtration is similar to sieving, except that the incoming flow runs parallel rather than perpendicular to the filter. This configuration shears captured particles off the filter’s surface, which reduces but does not eliminate clogging (5, 6). Unlike sieve and cross-flow filters, hydrosol and cyclonic filtration do not require regularly sized pores. Hydrosol filtration captures particles using “sticky” structures within the filters, which allow these filters to capture particles smaller than their pore size, although they also invariably become clogged (10, 11). Cyclonic filtration uses a high-speed, rotating flow that flings dense solid particles to the periphery while allowing fluid to pass through the center (8, 12, 13). This separation mechanism requires the solid particles to be denser than the fluid but is resistant to clogging (12) and has been widely used within the bagless vacuum industry (12, 13).

To examine how these animals capture plankton, we examined flow over a physical model of the filter apparatus. A three-dimensional (3D) printed model of an array of filter lobes was manufactured using morphological parameters measured in Manta birostris (Fig. 1, A and B). We positioned this model in an open-ended flow tank that was adjusted to mimic the flow conditions in the buccal cavity of M. birostris (Fig. S1A). Since experimental measurements of the flow velocities in the buccal cavity are not available, the freestream and transverse flow velocities were estimated using swimming speeds, the continuity equation, and anatomical data (see Materials and Methods). Neutrally buoyant particles larger than the pore size would be expected to be filtered with 100% efficiency. To test the performance limits of the filter, we examined neutrally buoyant particles (hydrated Artemia sp. cysts; average diameter, 275 μm) that were smaller than the pore size (>99% of the cysts smaller than pore size of 340 μm; fig. S1B) and would pass through the model if it were functioning as a sieve filter. Filtered and unfiltered water was collected and used to calculate filtration efficiency. We found that a large fraction of these particles were also
Similarly, we observed increases in the vertical velocity at positions leading edge and were then re-entrained within the freestream flow. For the wing orientation, we observed that particles often directly impacted the filter while allowing fluid to pass through? To address this question, we placed a 3D-printed physical model of a filter lobe array into a recirculating flow tank, again matching the freestream and transverse flow velocities to estimates for the buccal cavity. Flow around the filter was visualized by injecting dye upstream and imaging the dye pathlines around the filter (Fig. 1, C and D). This approach allowed us to identify the flow structures around the filter lobes, even in cases where small spaces, reflection, and occlusion would complicate quantitative analysis (for example, particle image velocimetry). We found that the flow over the filter lobes is markedly different than expected for a typical sieve filter. In the wing orientation, flow separation occurred behind the leading edge of each filter lobe, resulting in a large, captive vortex within each pore. Filters and spoiler orientations (wing, 1161 Pa s m$^{-1}$; spoiler, 1673 Pa s m$^{-1}$), consistent with previous experimental measurements (11). Since the energetic cost of filtration is proportional to the hydrodynamic resistance for a fixed flow rate, these low hydrodynamic resistance values may have an important role in limiting energetic expenditure and achieving energy balance in this group of animals.

To better understand how solid particles interacted with the filtering apparatus, we next introduced neutrally buoyant particles (hydrated Artemia sp. cysts) into the upstream flow and recorded the trajectory of these particles as they passed over the filter (Fig. 1, E and F). For the wing orientation, we observed that particles often directly impacted the leading edge and were then re-entrained within the freestream flow. Similarly, we observed increases in the vertical velocity at positions leading edge and were then re-entrained within the freestream flow. In the spoiler orientation, particles passing over the filter appeared to glide over the trailing edge of each filter lobe before being re-entrained within the flow, and there were similar increases in the vertical velocity at corresponding locations.

What physical forces cause the particles to be repelled away from the filter while allowing fluid to pass through? To address this question, we constructed a computational fluid dynamics (CFD) model of the flow over an array of filter lobes (Fig. 2A). As with the physical models, the model geometry was based on morphological measurements in M. birostris, and the freestream and transverse flow velocities mimicked those in the buccal cavity. To visualize the flow fields, we calculated the fluid streamlines that pass through a pore near the center of the array. For the wing orientation, these streamlines indicate that water glides above the lobe array, forms a thin boundary layer on the upstream surface of the lobe, is swept around a captive vortex within the pore, and is then washed into the filtrate flow. The streamlines for the spoiler orientation are surprisingly similar, except that the streamlines exhibit more pronounced curvature as they pass around the captive vortex. These flow fields closely mirror the results from our dye visualization experiments. In addition, the computed hydrodynamic resistance was very low for both the wing and spoiler orientations (wing, 1161 Pa s m$^{-1}$; spoiler, 1673 Pa s m$^{-1}$), consistent with previous experimental measurements (11). Since the energetic cost of filtration is proportional to the hydrodynamic resistance for a fixed flow rate, these low hydrodynamic resistance values may have an important role in limiting energetic expenditure and achieving energy balance in this group of animals.

To understand how these flow patterns produce solid-fluid separation, we next constructed a computational model to simulate the motion of particles carried by the flow (Fig. 2B). Spherical particles were introduced into the flow upstream of the filter array, with initial positions distributed across the fluid streamlines that passed through a filter pore near the center of the array. Since the solid particles were released along fluid streamlines, deviation of a solid particle from the corresponding streamline indicates solid-fluid separation and solid particles that do not pass through the pore represent filtration events.

For the wing orientation, simulated solid particles initially follow fluid streamlines and glide over the top of the filter array. However, as the fluid approaches a filter element, streamlines pass very near to the leading edge of the filter lobe before being diverted into the filter pore. Since they have finite size, solid particles cannot follow this path and encounter the leading edge of the filter lobe by direct interception. Instead of sticking as in classic hydroos filtration, contact forces cause the particles to “ricochet” away from the filter pore and back into the
faster-moving freestream flow. This process repeats at the next filter lobe and causes the particles to be repeatedly excluded from the filtrate. These conclusions and the simulated particle trajectories are in agreement with the results of our physical modeling experiments (Fig. 1, E and F, versus Fig. 2B). Contact forces also appear to play a key role in solid-fluid separation for filters in the spoiler orientation. In this case, we found that simulated solid particles initially followed streamlines as they passed over the filter array. However, the fluid streamlines then passed very close to the trailing edge of the preceding lobe. As for the wing orientation filters, solid particles with finite size cannot follow these streamlines and contact forces cause the particles to ricochet back into the faster freestream flow. This process has parallels to direct interception hydrosol filtration in which a particle following a streamline collides with a sticky surface and is captured (1). However, here, the particle recoils elastically from the surface and moves into streamlines that pass over the filter pore, resulting in concentration of particles in the water above the filter.

We next calculated the filtration efficiency for particles with a range of sizes and densities. We found that filtration efficiency increased markedly when the particle size exceeded ~200 μm, which is notably smaller than the filter pore size of 340 μm (fig. S2B). In contrast, changes in particle density had relatively little effect on filtration efficiency, within a biologically realistic range of densities. This size selectivity agrees with our physical modeling and with estimates from wild manta rays as well (11, 18). Insensitivity of the filtration process to particle density is consistent with the ricochet solid-fluid separation mechanism, which results from contact forces that are not directly affected by the specific density of the solid particle. It is possible that the complex shapes and escape responses of zooplankton would also affect capture dynamics (21, 22). Although these effects are difficult to quantitatively model with the data available, the shear stress at the filter lobes might be expected to elicit escape responses away from the filter, which could also enhance the observed filtration effects.

Since the freestream flow velocity appeared to have a major role in establishing the flow fields that drive the solid particles to contact the filter lobes (fig. S3, A and D), we next asked how the freestream flow velocity affects filtration efficiency. The CFD model was solved for a range of freestream velocities (0.05 to 0.7 m/s), while the pressure across the filter was held constant, and the filtration efficiency was calculated for 300-μm neutrally buoyant particles (fig. S3, E and F). We found that filtration efficiency increased sharply when freestream velocity exceeded 0.300 m/s, which is about half of the estimated velocity. This dependence on the freestream flow velocity is consistent with the proposed mechanism and also suggests that the mechanism operates effectively over a large range of freestream flow velocities.

In classic direct interception filtration, capture efficiency increases with Reynolds number (Re) as a result of streamline compression (23, 24). To determine whether there is a corresponding effect in moulid filters, the CFD model was solved for a range of Re values, and the filtration efficiency was calculated for neutrally buoyant particles (fig. S3, G and H). To preserve similitude, Re was varied by changing fluid viscosity while holding freestream and transverse velocities constant. For both spoiler and wing configurations, the predicted filtration efficiency was zero for low Re, increased with Re, and reached 100% for Re greater than ~900. This threshold is just below the value estimated for freely swimming M. birostris (Re = 1075), which may suggest that Re is maintained at a value large enough to produce filtration but small enough to limit turbulence. These results also indicate that smaller particles cannot be captured by simply scaling down the filter morphology while holding fluid properties and flow velocities constant.
constant, since this is equivalent to decreasing Re and results in a decrease in filtration efficiency. However, smaller particles would be expected to be filtered if the morphology was scaled down while fluid velocities were increased to hold Re constant.

We also examined how qualitative changes in the filter morphology might affect filtration. Micro–computed tomography (μCT) was used to reconstruct the 3D morphology of the filtering apparatus of *Mobula tarapacana*, which have a similar filtering apparatus to *M. birostris* except with pore sizes approximately four times larger (Fig. 3A and fig. S4). As above, a computational model was used to predict the flow field and plankton trajectories around the filtering apparatus using free-stream and transverse velocities estimated for *M. tarapacana*. Although the pore was 1100 μm wide, filtration efficiency rapidly increased for particles larger than ~250 μm. Similar to *M. birostris*, simulated plankton particles were excluded by the filter following contact with the tips of the filter lobes. These results indicate that *M. tarapacana* and *M. birostris* feed using a similar solid-fluid separation mechanism and that this mechanism can effectively filter particles that are much smaller than the pore size (Fig. 3B). Compared to *M. birostris*, the filtering apparatus of *M. tarapacana* was predicted to operate with approximately six times smaller transverse velocity (~10 mm/s versus ~57 mm/s) and require approximately seven times smaller pressure head (wing, 11 Pa versus 56 Pa; spoiler, 11 Pa versus 100 Pa) but filter plankton particles of similar size (Fig. 3C). These differences may reflect specialization of the filtering apparatus for different foraging strategies. Since *M. tarapacana* is predicted to have a lower flow rate and pressure head, it would be expected to have reduced plankton consumption but would also be expected to have decreased drag and energetic expenditure. A detailed comparison would require more information on feeding behaviors and the plankton size distribution where the fishes are actively feeding but would be a very interesting area for future studies.

Our results suggest that the manta ray filtering apparatus operates through a unique solid-fluid separation mechanism, which we have termed ricochet separation. This solid-fluid separation mechanism may have interesting industrial applications, since it operates at high flow rates, effectively filters neutrally buoyant particles, and resists clogging. Captured particles are concentrated above the filter rather than forming a cake over the filter, which may obviate the need for secondary cleaning mechanisms that are often costly and time consuming (8, 25). In addition to the engineering applications, mobulid rays are increasingly being targeted by illegal commercial and artisanal fisheries (26–28), and an improved understanding of the physiology of filter feeding may be useful for predicting the habitat usage of mobulid rays and implementing appropriate protective measures.

**MATERIALS AND METHODS**

**Specimen collection and examination**

The morphology of the *M. birostris* filtering apparatus was measured from two specimens (one provided by the Smithsonian Museum of Natural History and one donated by R. Rubin and maintained by A. Summers). Calipers were used to measure the dimensions of the filter lobes (fig. S2B). The morphology of *M. tarapacana* was measured by performing a μCT scan of a specimen provided by the Scripps Institution of Oceanography. *M. tarapacana* rakers were scanned using high-resolution μCT imaging (Bruker SkyScan 1272) scanned at 60 kV, with a resolution of 38.9 μm at the University of Washington Friday Harbor Laboratories. μCT scans were then reconstructed from 8-bit tagged image file format stacks as 3D images using Amira software (version 6.4). The μCT model was then used to measure the dimensions of the filter lobes (fig. S4).

**Construction of physical models**

Mobulid filters are composed of repeating filter lobes connected by a central cartilaginous raphe [see Paig-Tran et al. (18) for full description]. Computer models of the filtering apparatus of *M. birostris* were constructed from the measured morphology (Autodesk software 123D Design), and then, physical models were 3D printed. For the filtration
efficiency experiments, multiple rows of filter lobes were positioned together so that they could be inserted into the bottom surface of the flow tank (fig. S1A). Models were printed at 1× scale [32-μm layer thickness, 10 filter rows in lateral direction, and 13 filter lobes in streamwise direction; ProJet 3510SD (3D Systems)]. For the dye visualization experiments, models consisted of a single row of filter lobes at 4× scale [100-μm layer thickness, one filter row in lateral direction, and 13 filter lobes in streamwise direction; ProJet 460 (3D Systems)]. For particle tracking experiments, models were also a single row of filter lobes but were printed at 1× scale [50-μm layer thickness, one filter row in the lateral direction, and 13 filter lobes in streamwise direction; Form 2 printer (Formlabs)].

**Filtration efficiency**

The filtration efficiency was determined by placing 1× scale physical models into a customized flume, introducing particles upstream of the filter and measuring the particle concentration in the filtrate and unfiltered water (fig. S1A). The working section of the flume was cylindrical (diameter, 48 mm), and the physical model was the bottom half of the working section. The freestream flow velocity was adjusted so that the Reynolds number in the flume was similar to the flow in the buccal cavity of a freely swimming animal

\[
Re = \frac{\rho u D}{\eta}
\]

where \(Re\) is the Reynolds number, \(\rho\) is the fluid density, \(u\) is the freestream fluid velocity, \(D\) is the distance between the lobes, and \(\eta\) is the fluid dynamic viscosity. The Reynolds number was estimated as \(Re = 1075\), taking the freestream velocity within the buccal cavity for a freely swimming animal as 550 mm/s (80% of swimming speed of 680 mm/s) (18). The flow rate through the filter was controlled using a valve downstream of the filter array and was adjusted so that the ratio of freestream to transverse velocity matched estimates for a freely swimming animal. This ratio was approximated from the continuity equation

\[
\frac{u_t}{u_i} = \frac{A_x}{A_m}
\]

where \(u_t\) is the freestream velocity, \(u_i\) is the transverse velocity, and \(A_x/A_m\) is the ratio of the filter cross-sectional area to the mouth area. The ratio \(A_x/A_m\) was estimated as 10:1 from available photographs of feeding animals and preserved gill arches (Fig. 1, A and B). Hydrated Artemia sp. cysts were used as particles (size distribution in fig. S1B; density, 1.02 to 1.08 g/ml) and were introduced into the flow via a Venturi injector. This method of injection ensured that particles were uniformly distributed throughout the upstream flow and were undamaged. Water exited the experimental system by passing either through the filter array or through the unfiltered outlet. In either case, the flow was passed through a fine mesh filter (100 μm) to collect the particles and then into a reservoir to record the total water volume. The particle concentration was calculated as the mass of the particles divided by the water volume. The filtration efficiency was then calculated as

\[
E = 1 - \frac{\sigma_f}{\sigma_u}
\]

where \(E\) is the filtration efficiency, \(\sigma_f\) is the particle concentration in the filtrate, and \(\sigma_u\) is the particle concentration in the unfiltered water. Trials lasted for 2 min each (n = 3). The size distribution of the injected particles was measured by imaging the hydrated Artemia sp. cysts (ZEISS Stemi 508, Carl Zeiss Microscopy) and then analyzing the images using a custom-written MATLAB script (n = 4321 particles).

**Dye injection flow visualization**

Physical models at 4× scale were suspended in the center of the working section of a recirculating flume (Research Water Tunnel Model 1520, Rolling Hills Research Corporation). Blue dye (ESCO Foods, Deep Blue Shade) was released upstream of the filter models and imaged passing over the model [resolution, 4000 × 3000 pixels; 60 frames per second (fps); Panasonic Lumix DMC-FZ300]. The freestream flow velocity was adjusted so that the Reynolds number in the flume (\(Re = 745\)) approximately matched the filtration efficiency experiments. The physical model was angled relative to the freestream (~20° angle of attack) until the ratio of freestream to transverse velocity also matched the filtration efficiency experiments (10:1). This ratio was measured by recording the angle at which the dye stream approached the filter array [\(\theta = \arctan(u_t/u_i) = 6^\circ\)].

**Particle trajectory analysis**

Physical models at 1× scale were suspended in a flume, similar to dye injection experiments. Particles (hydrated Artemia sp. cysts) were released upstream and imaged passing over the filter (resolution, 1280 × 1024 pixels; 240 fps; Edgetronic camera, Sanstreak Corp). To accurately follow these small particles, it was necessary to decrease the flow velocity (180 mm/s), so the Reynolds number was decreased to \(Re = 309\). Dye injection experiments were used to confirm that the flow patterns around the filter were qualitatively similar to that at higher flow velocities. In addition, CFD simulations were performed mirroring this freestream velocity (180 mm/s) and freestream to transverse velocity ratio (wing, 8.5:1 at 12 Pa; spoiler, 8.3:1 at 18 Pa), and predicted particle trajectories and filtration efficiencies were similar to those at higher freestream velocities (for 300-μm neutrally buoyant particles: wing, 17%; spoiler, 54%). The trajectories of particles that interacted with the physical model were recorded using ImageJ software. The trajectories were shifted to a common origin using the first filter lobe that the particle interacted with as a reference point. Vertical velocity as a function of position was then calculated by fitting the positional data to a smoothing spline and taking the derivative (MATLAB, MathWorks Inc).

**CFD modeling**

The CFD model was constructed to mimic the geometry and flow conditions of the filtering apparatus of M. biostris (fig. S2A). This model was designed to reproduce the flow fields around individual filter lobes while avoiding the need to reproduce the complex geometry of the entire buccal cavity. Since individual filter lobes are nearly prismatic in shape, the model was constructed as a 2D cross section through the filter. Flow enters from the left side of the geometry through an inlet with a prescribed uniform velocity boundary condition (570 mm/s, \(Re = 990\) similar to physical model) and then passes over a solid structure containing a filter lobe array (no-slip boundary condition on all surfaces). A negative uniform pressure boundary condition is prescribed on the outlet behind the filter lobe array, which draws a fraction of the freestream flow through the filter pores. The magnitude of the negative pressure was varied until the ratio of the
freestream velocity to transverse velocity was approximately 10:1 (wing, 12:1 at 56 Pa; spoiler, 9.3:1 at 100 Pa) similar to that estimated for *M. birostris* and that used for the physical modeling experiments. The remaining freestream flow exits the system through an outlet surface above the filter lobe array, with a prescribed zero-pressure boundary condition. The modeled filter array consisted of 15 filter lobes, and to avoid edge effects, all analyses were performed on the fifth filter lobe in the array.

This model was solved using a commercial CFD software suite (Adina 9.3.1). The geometry was meshed with three-node triangular elements, and mesh size functions were used to refine the mesh in regions with steep velocity gradients (fig. S2C). Mesh independence was verified by decreasing the mesh size and confirming that neither the flow patterns around the filter nor the flow rate through the filter was altered. The Reynolds number for this system is intermediate, so the viscosity was altered, while the geometry, freestream velocity and transverse velocity were held constant by iteratively adjusting the downstream pressure using the secant method (fig. S3, G and H).

Simulations for *M. tarapacana* were performed similarly (fig. S4). In this species, the mouth area during feeding appears to be smaller than the cross-sectional area of the buccal cavity, and continuity requires a corresponding decrease in the flow velocity. To capture this effect, the freestream flow velocity was approximated as 0.3 m/s (Re = 1115) or 45% of the estimated swimming speed of 0.680 m/s (18). The transverse velocity was estimated as 10 mm/s from the continuity equation (Eq. 1), with $A_m = 0.0057 m^2$, $u_c = 0.612 m/s$ (90% of the swimming speed of 680 mm/s), and $A_x = 0.334 m^2$ (18). Using these estimates, the magnitude of the negative pressure was varied until the ratio of the freestream velocity to transverse velocity was approximately 30:1 (wing, 36:1 at 11 Pa; spoiler, 29:1 at 11 Pa).

### Solid particle trajectory simulations

The movement of solid particles through the flow field was simulated using equations of motion that included pressure gradient, added mass, drag, Saffman lift, and contact forces

$$\sum F = m_s \frac{dv}{dt} = F_p + F_a + F_d + F_{sa} + F_c$$

where $m_s$ is the mass of the particle, and $v$ is the particle velocity. The pressure gradient and added mass are

$$F_p = m_t \frac{Du}{Dt}$$

$$F_a = -\frac{1}{2} m_t \left( \frac{dv}{dt} - \frac{Du}{Dt} \right)$$

where $m_t$ is the mass of fluid displaced by the particle, and $u$ is the fluid velocity (29, 30). The drag was taken as

$$F_d = \frac{1}{2} C_d \rho_l A_p |u_s| |u|$$

$$C_d = \frac{24}{Re} \left( 1 + \frac{Re^{2/3}}{6} \right)$$

where $u_s$ is the relative fluid velocity ($u_s = u - v$), $\rho_l$ is the fluid density, $A_p$ is the projected area of the particle, Re is the Reynolds number ($Re = 2\rho_l |u_s|/\eta$), $a$ is the particle radius, and $\eta$ is the dynamic viscosity of the fluid (31). The shear-induced Saffman lift force was calculated using the following approximation

$$F_{Sa} = C_{1Sa} u_s \times \omega$$

$$C_{1Sa} = 6.46 a^2 \gamma \sqrt{\frac{\rho_l \eta}{|\omega|}}$$

$$\gamma = \begin{cases} 
(1 - 0.3314 \alpha^{1/2}) \exp \left( -\frac{Re}{10} \right) + 0.3314 \alpha^{1/2} & Re < 40 \\
0.0524(\alpha Re)^{1/2} & \text{else}
\end{cases}$$

$$\alpha = \frac{a|\omega|}{|u_s|}$$

where $\omega$ is the vorticity (32, 33). The contact force was calculated using a damped linear model that excludes tensile forces

$$F_c = \begin{cases} 
(k_s d - k_d v \cdot n)n & d > 0 \text{ and } k_s d - k_d v \cdot n > 0 \\
0 & \text{else}
\end{cases}$$

$$k_d = 2\epsilon \sqrt{k_m m_p}$$

where $k_s$ is the spring constant, $k_d$ is the damping constant, $n$ is the normal vector for the surface, $d$ is the intersection distance between the particle and the surface, and $\epsilon$ is the damping ratio (34). A sensitivity analysis suggested that $k_s$ and $\epsilon$ had little effect within a wide range of values, so $k_s$ was set to a large value to mimic infinitely stiff solids, and $\epsilon$ was set to 0.9. The Basset history term and Faxén’s correction for velocity curvature were both neglected.

The equations of motion were solved using a custom-written program, which was implemented in C for efficiency. This program solved the ordinary differential equation describing the particle trajectory using an explicit Runge-Kutta-Fehlberg method (0.025-ms time steps; GNU Scientific Library version 1.15). The fluid flow at each particle position was calculated by linear interpolation of the CFD solution using the same triangular mesh and evaluating the velocity and velocity gradient (libMesh 1.2.1).

Similar to our CFD analysis, to avoid edge effects, our simulations of particle trajectories were focused on a single filter pore (fifth lobe in array). We first calculated the flow streamlines that passed through

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this filter pore by uniformly seeding the downstream edge of the filter pore with “virtual” fluid particles and then tracing the trajectories of these fluid particles backward in time to their upstream origin (solving $dr/dt = -u$). Solid particles $(n = 30$ for each condition) were then introduced into the flow uniformly distributed across this range of upstream positions and with an initial velocity equal to the fluid velocity, and the motion of the particles over the filter array was simulated using Eq. 4. Since solid particles were introduced into the flow along streamlines that are known to pass through the pore, deviation between the solid and fluid trajectory represents solid-fluid separation and failure of the solid particle to pass through the filter pore represents a filtration event. Conservatively, we considered particles to be filtered only if they also passed over the filter pore immediately downstream of the selected pore. The filtration efficiency was then calculated as the percentage of the solid particles that were filtered.

**SUPPLEMENTARY MATERIALS**

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/9/eaat9533/DC1

**Supplementary Materials and Methods**

Fig. S1. Details of experiments used to measure particle filtration.

Fig. S2. Geometry of the *M. birostris* filtering apparatus.

Fig. S3. Computational modeling predicts particle filtration.

Fig. S4. Geometry of the filtering apparatus.

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