

Unravelling Three-Dimensional Active Transport by Ciliary Arrays on Coral Surfaces

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Cilia-driven flows in corals are crucial for exchanging nutrients, removing waste, and maintaining the ambient conditions necessary for corals' survival. While various studies have identified that ciliary activity can influence mass transport, the effect of local ciliary orientation and heterogeneity remains relatively unexplored. In this study, we combine noninvasive experimental measurements of ciliary distribution and alignment, with quantification of flow fields and spatial oxygen distributions among several species of reef-building corals, and develop a mathematical model based on singularity solutions of the Stokes equations to investigate mass transport near the coral's surface. Our findings reveal that counter-rotating vortices robustly emerge in three dimensions as a result of the ciliary arrangement on the coral surface. The rate at which ciliated tissue can exchange nutrients with the surrounding fluid depends strongly on the diffusivity of the dissolved organic matter and is enhanced through the inherent heterogeneity in ciliary orientation—for nutrients with low molecular diffusivity, ciliary heterogeneity increases mass transport by more than 50%. However, the presence of an externally imposed shear flow serves to diminish the overall rate of mass transport across all cases studied. This study highlights the critical role of ciliary orientation in modulating transport processes and exemplifies the role of ciliary transport, particularly in low-flow regimes.

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I. INTRODUCTION

Corals are sessile, calcifying marine animals that form coral reefs, providing a crucial supply of nutrients and shelter for many species, while protecting the shoreline from high tides and erosion [1,2]. Corals and the entire reef ecosystem depend on the symbiosis between the animal host and dinoflagellate microalgae [3]. When exposed to light, these symbionts produce an excess of oxygen, which accumulates at the coral surface [4]. However, oxygen exchange is not driven by external flow and diffusion alone, as assumed previously [5–7]. Experimental observations show that active stirring by cilia—threadlike elastic structures on coral surfaces—enhances mass transport processes [8]. The emitted oxygen is redistributed by cilia-generated flows, which can reduce

oxidative stress in the animal and alleviate the impacts of environmental stressors [9–12].

Cilialike structures are a defining feature of many eukaryotic organisms [13], including algae [14], ciliates [15], mammals [16], and starfish larvae [17], and are found in different arrangements, e.g., as a single structure (e.g., sperm [18,19]), in pairs (e.g., green algae [20–22]), or in larger arrays (e.g., coral [8,9] and mammal airways [23,24]). The beating of cilia is known to modulate the local flow field, which facilitates locomotion in microorganisms [25,26], establishes left-right asymmetry in developing embryos [27], transports nutrients [8], and provides defense against pathogens on multiciliated surfaces [10,28,29]. Furthermore, cilia tend not to have a homogeneous density, length, or orientation, particularly within multiciliary patches [24]. This spatial heterogeneity is suggested to play an active role in shaping fluid dynamics [30], enhancing mixing [17], and enabling efficient removal of debris from biological surfaces [24]. Its functional impact has been explored in mammalian mucociliary systems [24], but the significance of ciliary heterogeneity for mass exchange processes in environments with external flow, particularly sessile marine animals such as corals, remains poorly understood.

In this study, we develop a high-fidelity mathematical framework informed by experimental measurements of flow

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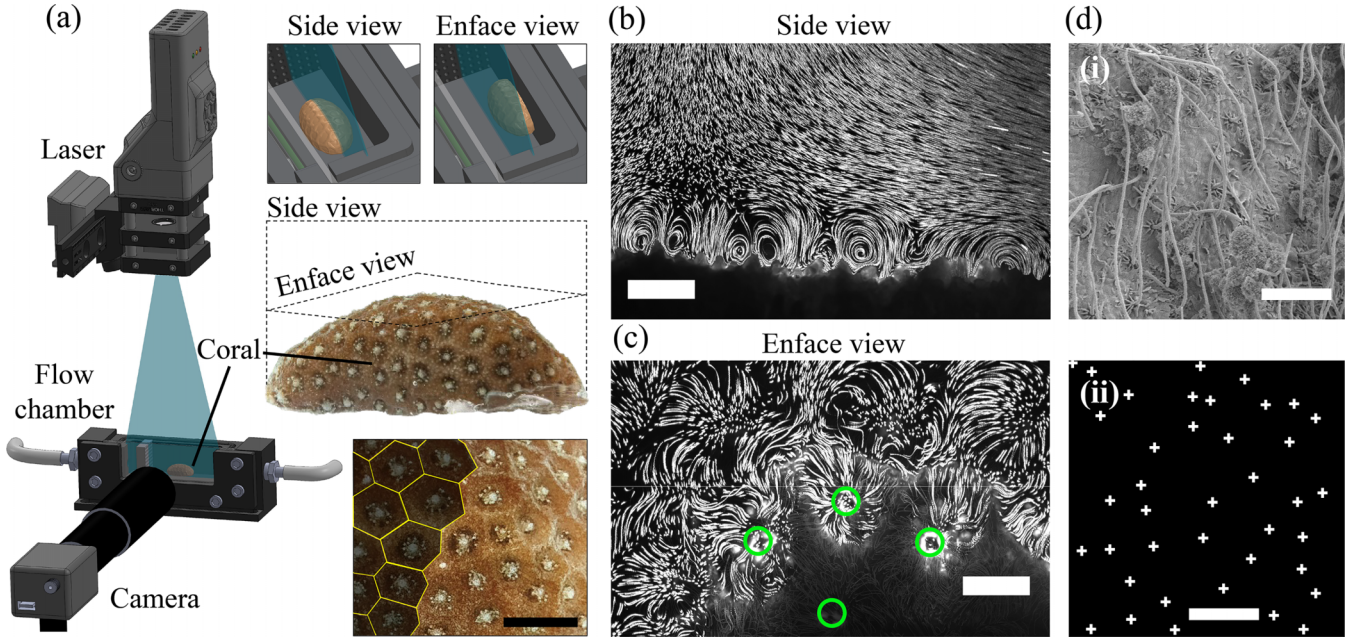


FIG. 1. Experimental measurement of ciliary flows in corals. (a) Schematic illustrating the experimental apparatus used for conducting particle image velocimetry (PIV). The coral specimen is placed in the flow-through chamber, illuminated from above by the laser, and imaged by a camera positioned laterally to the light sheet of the laser. Two orthogonal imaging planes, namely, enface (parallel to the coral surface) and side views (perpendicular to the coral surface), are shown in the inset plots (figure not to scale). The repeated hexagonal structure is clearly visible from the polyp arrangement. The black scale bar represents 2 mm. The flow field of the coral *Porites lutea* is shown in (b) side view and (c) enface view, plotted using a maximum intensity projection derived from 100 sequential frames (1 second total). The white scale bars in (b) and (c) represent 1 mm. Green circles indicate the locations of the polyp mouths. (d) Measurements of ciliary density for the tissue between polyps: (i) representative scanning electron microscopy (SEM) images of a $20 \times 20 \mu\text{m}$ area of coral tissue and (ii) binary image where the white crosses correspond to the attachment positions of individual cilia based on the SEM image. The white scale bar in (d) represents $5 \mu\text{m}$.

fields around reef-building corals to study how the local ciliary architecture affects transport processes by multiciliated surfaces. Our findings reveal that in a regime where advection of particles dominates over their diffusion, flow fields generated by beating cilia—which develop vortical structures on a spatial scale that far exceeds that of individual cilia—are highly effective at transporting particles. The presence of strong external shear flows, which are ubiquitous across marine systems but vary significantly in strength over time, weakens the vortical structures and, consequently, the relative mass transport in corals. Our results also reveal that orientational heterogeneity in cilia enhances mass transport, contrary to related predictions for mucocilia [24].

In our framework, we rely on being able to compute the flow field due to ciliary beating, which is accurate across multiple scales, from the near field around an individual filament ($\sim$ micrometer scale) through to the large-scale collective flows by thousands of cilia ($\sim$ centimeter scale and beyond). The former is typically achieved by resolving the individual ciliary motion, e.g., through slender-body theory [31], or alternative models with temporal resolution [32,33], but this becomes costly when computing flows generated by patches of cilia. However, coarse graining by replacing the velocity of multiple ciliary tips using a collective waveform, as is done in the classical models involving squirmers [15,34,35], fails to resolve the flow field on the length scale of a cilium, and hence the particle transport controlled by such flow [24]. Instead, we follow Selvan *et al.* [36] in approximating the steady-state

flows generated by individual cilia using “rotlets,” mathematical representations of point torques in low Reynolds number flow (Stokes flow). This has been shown to be accurate and efficient in resolving the steady-state mass transport due to an individual cilium [37], and here we upscale the approach to investigate collective flows and mass transport by an active coral surface covered with a vast carpet of cilia.

II. EXPERIMENTAL MEASUREMENTS

We experimentally investigate mass transport near coral surfaces by performing fluidic experiments using seven specimens of the coral *Porites lutea*, depicted schematically in Fig. 1(a). This colonial coral consists of many small polyp animals, each embedded in a calcium carbonate skeleton matrix and with its tissue covered by cilia of average length $\langle l_c \rangle \approx 10 \mu\text{m}$ and beating period $T_c = 1/15 \text{ s}$. Our observations using optical microscopy reveal that each polyp mouth is surrounded by a roughly hexagonal ciliated structure of connective tissue (coenosarc) of radius in the range $R_h \sim 5\langle l_c \rangle - 50\langle l_c \rangle$. Such hexagonal arrangements are common in closely packed hexacorallian tissues, where constructional constraints naturally favor hexagonal tiling as the most efficient space-filling geometry [38,39]. To quantify the density of cilia, we performed scanning electron microscopy (SEM) (Quanta 200, FEI, USA) on the coral surface. We randomly selected a series of $20 \times 20 \mu\text{m}$ regions between the polyp mouths, as shown in Fig. 1(d)(i), and analyzed the spatial

distribution of cilia by identifying their position of attachment to the surface [white crosses in Fig. 1(d)(ii)]. We measured a ciliary density of $\rho_n = 0.081 \pm 0.013$ cilia/ μm^2 , which corresponds to $\rho_n \approx 10$ cilia/ $\langle l_c \rangle^2$ if defined using the length of a cilium. For the purpose of modeling in this study, we assume a uniform spatial distribution of cilia across different regions of the coral surface. However, guided by our observations, we allow their orientation (i.e., beating direction) to vary spatially.

Imaging fluid flow. We visualized the flow field near the surface of the coral using a custom-built particle image velocimetry (PIV) system, shown schematically in Fig. 1(a). The experimental setup consisted of the coral specimen of approximate size $15 \times 12 \times 7$ mm³ placed in the flow chamber of size $40 \times 14 \times 17$ mm³ filled with seawater [12]. For experiments under external flow conditions, a stable flow of seawater (10 mL/min) through the chamber was controlled by a pump (MasterFlex Ismatec, Germany). This flow rate corresponds to ecologically realistic low-flow conditions commonly encountered by corals in sheltered reef environments, including the Heron Island lagoon [40], where the coral samples were collected. As shown in the insets of Fig. 1(a), the measurements were obtained through enface (i.e., scanning parallel to the surface) and side (i.e., scanning perpendicular to the surface) views. The coral surface was illuminated using a 1-mm-wide light sheet emitted from a laser diode (460 nm; LD-PS 5 W, OPTOLUTION, Germany) that was positioned above the chamber. Water inside the chamber was seeded with 5 μm neutrally buoyant fluorescent tracer particles (Applied Microspheres GmbH, Germany; excitation: 468 nm; emission: 530 nm), at a seeding density of $\approx 10^6$ particles/L and imaged using a camera (OPTOCam 2/80, OPTOLUTION, Germany) equipped with a lens (Optem FUSION 12.5:1, QIOPTIQ, Germany) and placed laterally to the light sheet on the side of the chamber. The particle motion was reconstructed from the images recorded at 100 fps using ImageJ [41]. To obtain the velocity field, the image sequences were analyzed with PIVlab [42] (MATLAB) [43] using four interrogation windows (256, 128, 64, and 32 px) with a 50% overlap each. All experimental flows have been averaged over a period of up to 2 s, which is longer than both the timescales of ciliary beating and advection of particles across the domain. However, our observations of time-dependent PIV data show that the flow does not change with time, validating the steady-state approach utilized throughout the present paper.

A side view (i.e., plane perpendicular to the coral surface) of the stony coral *Porites lutea* in Fig. 1(b) shows the counter-rotating vortices (see Supplemental Movies 1 and 2 in the Supplemental Material [44]), qualitatively similar to those observed in the reef-building coral *Pocillopora damicornis* [8]. On the other hand, the enface view in Fig. 1(c) shows the flow field in the vicinity of periodically distributed polyp mouths (i.e., marked by green circles) surrounded by hexagonal structures. In the absence of external flow, active stirring by multiple cilia creates a radial fluid outflow from each mouth tangential to the coral surface (see Supplemental Movies 3 and 4 in the Supplemental Material [44]). This hexagonal distribution of cilia, and radial alignment of the local flow away from the coral mouth, was observed across all seven specimens of *Porites lutea* used in these experiments,

and across multiple different coral species (see Fig. S1 in the Supplemental Material [44]).

Imaging oxygen field. We noninvasively measured the spatial distribution of dissolved oxygen within the fluid near the coral surface by filling the flow chamber with oxygen-depleted seawater (obtained by nitrogen flushing) and seeding it with a mixture of small fluorescent tracer particles (as described above) and oxygen-sensitive luminescent nanoparticles (SensPIV), which consist of PtTFTPP and Macrolex Yellow stained 500 nm polydimethylsiloxane (PDMS) particles. These measurements were performed only in the presence of pump-induced seawater flow. SensPIV particles were added at a 1:55 dilution of a 3.5 mg/mL stock solution (for methodological details, see [10,11,45]). The colony was then illuminated for 10 min at a photon irradiance of 150 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ using a halogen lamp (Schott KL2500LED, Schott GmbH, Germany) before it was imaged. This was achieved by shining a laser sheet produced by the same laser diode as described above, and capturing images from the side with a Grasshopper3 camera (FLIR, USA) mounted on a long-distance microscope (K2 DistaMAX, INFINITY, USA). We implemented the Lifetime-Proportional Luminescence imaging method [45] using scripts in Python [46] to capture a total of 100 image pairs at 27 fps. The image sequences were analyzed in MATLAB [43] to generate color-coded two-dimensional (2D) maps of oxygen concentration, such as those shown in Fig. 7(b). These measurements were calibrated by imaging the suspended particles in the flow chamber under light-sheet illumination at defined oxygen concentrations and temperature to extract their oxygen-dependent luminescence intensity and lifetime. The two-dimensional oxygen distributions, measured directly in the water column above coral surfaces, are compared to predictions of our model in subsequent sections.

III. MODEL OUTLINE

Flow field. We model the coral surface as a planar periodic domain of length L and width W containing hexagonal structures characterized by an outer (inner) radius of R_h ($\sqrt{3}R_h/2$) and centered around a polyp mouth, so that $L = 3R_h$ and $W = \sqrt{3}R_h$ [see Fig. 2(a)]. Unless otherwise stated, we assume $R_h = 6\langle l_c \rangle$. Given the ciliary length scale, the associated flow operates at extremely low Reynolds numbers, typically $O(10^{-6})$ – $O(10^{-4})$, and is therefore well described by the Stokes equations [36]. Following Selvan *et al.* [36], individual cilia are represented by point torques of magnitude $\Omega_c = 0.271\mu\langle l_c \rangle^3/T_c$ in a liquid of dynamic viscosity $\mu = 10^{-3}$ Pa s, and are placed at a distance $d = 0.629\langle l_c \rangle$ above the no-slip boundary. The surface is covered with a dense, spatially heterogeneous distribution of point torques, as indicated by the purple dots in Fig. 2(a), following the cilia density measurements in Sec. II. Inspired by the enface view flow shown in Fig. 1(c), we orient each point torque radially outward from the local center of the hexagonal lattice, so that the expression for the m th point torque ($m \in \mathbb{Z}_+$) is given by

$$\mathbf{\Omega}^{(m)} = \Omega_c \mathcal{R}(\theta_r^{(m)}) \hat{\mathbf{e}}_y, \quad (1)$$

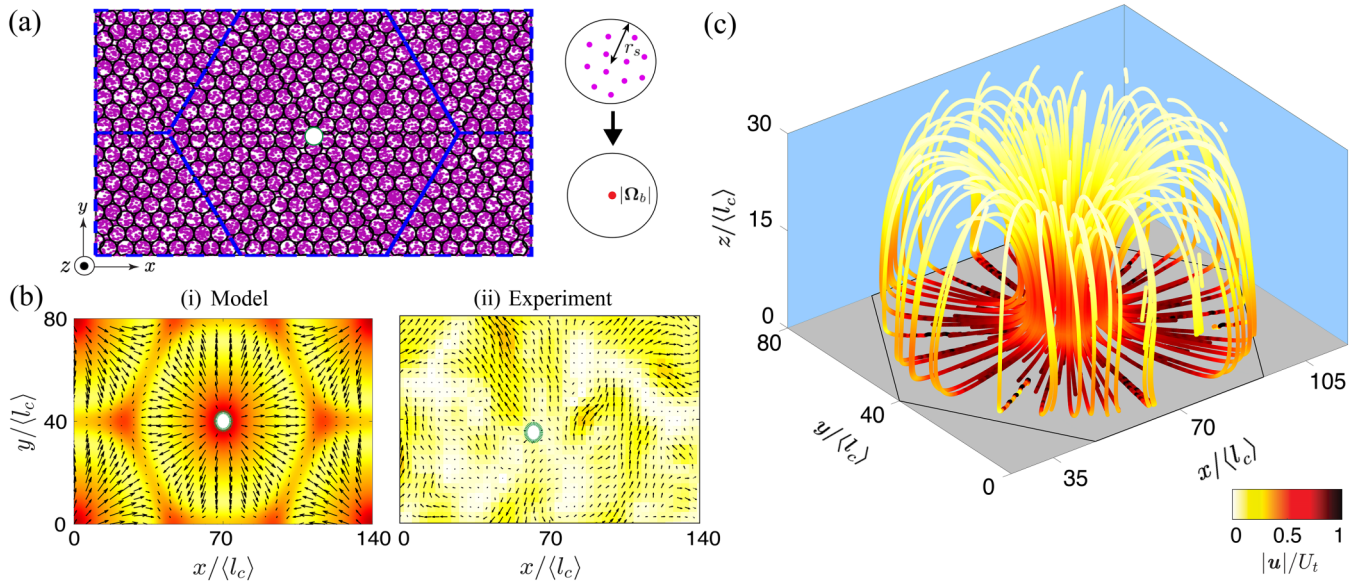


FIG. 2. Mathematical model for the surface of the coral *Porites lutea*. (a) A periodic domain centered on a polyp's mouth and surrounded by a hexagonal structure containing point torques [shown with purple dots; their distribution is dictated by the ciliary density measurements in Fig. 1(d)]. Torques within closely packed circles of radius r_s have similar orientations (radially outwards from the hexagon center) and are modeled using super rotlets of strength $|\Omega_b|$ positioned at the centers of the small circles. (b) Heat map of the velocity magnitude (normalized by the velocity of the ciliary tip $U_t = 2\pi \langle l_c \rangle / T_c$) and the flow direction visualized using quiver arrows in enface view along the plane $z = 5\langle l_c \rangle$ for the active flow of ciliary carpet (i) calculated with $R_h = 46\langle l_c \rangle$ for rotlet flow model and (ii) in the corresponding experiment, with green circles representing the polyp mouth in both. (c) Selected three-dimensional particle trajectories are shown in the domain corresponding to a single hexagon, clearly demonstrating a toroidal-like flow due to the active ciliary carpet. The trajectories are color coded based on the instantaneous velocity magnitude at each point. The blue- and gray-shaded regions denote the fluid environment and coral surface, respectively. Here and elsewhere, unless specified otherwise, calculations were performed with the default values of the other parameters (see Secs. II and III), e.g., $|\Omega_b| = 10\Omega_c$.

with

$$\mathcal{R}(\theta_r^{(m)}) = \begin{bmatrix} \cos \theta_r^{(m)} & -\sin \theta_r^{(m)} & 0 \\ \sin \theta_r^{(m)} & \cos \theta_r^{(m)} & 0 \\ 0 & 0 & 0 \end{bmatrix}. \quad (2)$$

Here, $\mathcal{R}(\theta_r^{(m)})$ is the 2D rotation matrix in the xy plane and $\theta_r^{(m)}$ is the reference angle between the $+x$ axis and the position vector connecting the m th point torque with the local hexagonal center. Hence, if the point torque and the hexagonal center are positioned at $\mathbf{x}_r^{(m)} = (x_r^{(m)}, y_r^{(m)}, d)$ and $\mathbf{x}_c = (x_c, y_c, z_c)$, respectively, then $\theta_r^{(m)} = \arctan[(y_r^{(m)} - y_c)/(x_r^{(m)} - x_c)]$.

The model is further adapted by introducing a set of small circles, each with radius r_s , that densely pack the hexagonal lattice, as illustrated in Fig. 2(a). Each of these circles encapsulates a cluster of cilia that share a nearly identical orientation relative to the center of the hexagonal lattice, so we assume that within the small circle, cilia are distributed uniformly and have the same orientations. We then proceed to represent the collective influence of multiple cilia within each small circle by a single point torque of the same orientation but greater magnitude, $|\Omega_b|$, positioned at the circle's center [Fig. 2(a)], that we refer to as a *super rotlet*. Hence, its expression is given as

$$\Omega_b^{(m)} = |\Omega_b^{(m)}| \mathcal{R}(\theta_r^{(m)}) \hat{\mathbf{e}}_y. \quad (3)$$

The radius of the small circle, r_s , and the magnitude of the super rotlet, $|\Omega_b^{(m)}|$, are selected as discussed in Sec. II of the Supplemental Material [44] for a range of ciliary densities, ρ_n . We show that choosing $r_s = d$ captures the overall transport characteristics of the multiple cilia confined within the circle. Furthermore, this results in $\rho_n \propto |\Omega_b|/\Omega_c$ (see Fig. S2(b) in the Supplemental Material [44]), so for the coral *P. lutea* (with $\rho_n \approx 10$ cilia/ l_c^2), we obtained the magnitude of the super rotlet to be $|\Omega_b| = 10\Omega_c$. As before, we assume that the latter is constant for all cilia on the surface, but the model can be adapted to account for spatial heterogeneity in ciliary density by allowing the magnitude of the super rotlets to vary spatially.

Coral surfaces are constantly influenced by oceanic waves and currents, creating an external flow in addition to the ciliary-induced fluid motion. In our experiments, we subject the samples to steady laminar pump-induced flow. We model this by imposing a linear shear flow in the fluid above the coral surface (i.e., $\mathbf{u}_b = \dot{\gamma} z \hat{\mathbf{e}}_x$). The fluid velocity at the point $\mathbf{x} = (x, y, z)$ generated by the combined effects of external shear flow and the collection of super rotlets in the domain is therefore given by

$$\mathbf{u}(\mathbf{x}) = \mathbf{u}_b + \frac{1}{8\pi\mu} \sum_{m=1}^{M_d \cup M_i} A(\mathbf{x}, \mathbf{x}_r^{(m)}) \cdot \Omega_b^{(m)}, \quad (4)$$

where $\mathbf{A}(\mathbf{x}, \mathbf{x}_r^{(m)})$ is the Green's function,

$$A_{ij}(\mathbf{x}, \mathbf{x}_r^{(m)}) = \frac{\epsilon_{ijk} r_k^{(m)}}{(r^{(m)})^3} - \frac{\epsilon_{ijk} R_k^{(m)}}{(R^{(m)})^3} + 2d\epsilon_{kij} \left(\frac{\delta_{ik}}{(R^{(m)})^3} - \frac{3R_i^{(m)} R_k^{(m)}}{(R^{(m)})^5} \right) + \frac{6\epsilon_{kij} R_i^{(m)} R_k^{(m)} R_3^{(m)}}{(R^{(m)})^5}, \quad (5)$$

and $i, j, k \in \{1, 2, 3\}$, $\mathbf{r}^{(m)} = (r_1^{(m)}, r_2^{(m)}, r_3^{(m)}) = (x - x_r^{(m)}, y - y_r^{(m)}, z - d)$, $r^{(m)} = |\mathbf{r}^{(m)}|$, $\mathbf{R}^{(m)} = (R_1^{(m)}, R_2^{(m)}, R_3^{(m)}) = (x - x_r^{(m)}, y - y_r^{(m)}, z + d)$, and $R^{(m)} = |\mathbf{R}^{(m)}|$, while ϵ_{ijk} and δ_{ij} represent the Levi-Civita symbol and the Kronecker delta, respectively. Note that Eq. (4) has been obtained by superimposing the contribution of M_d super rotlets in the domain shown in Fig. 2(a) and M_i super rotlets from the image layer introduced around this domain to ensure periodic flow conditions; as discussed in Sec. III of the Supplemental Material [44], the flow becomes periodic when the layer thickness is $R_h/2$ along both x and y axes, and further increasing the size of the image layer does not change the flow field predicted by Eq. (4). Similarly, calculations have been performed for z of up to $40\langle l_c \rangle$.

Mass transport. We study mass transport using the Langevin framework [24,37], whereby molecules emitted from the coral's surface are modeled as an ensemble of Brownian particles with radii a_b , carried by the flow given by Eq. (4). Hence, their dynamics are governed by

$$\frac{d\mathbf{x}}{dt} = \mathbf{u}(\mathbf{x}) + \sqrt{2D_0} \cdot \boldsymbol{\eta}(t), \quad (6)$$

where $\mathbf{u}(\mathbf{x})$ is the flow velocity experienced by the particle positioned at $\mathbf{x} = (x, y, z)$, a superposition of flows generated by the super rotlets and the external shear. White noise $\boldsymbol{\eta}(t)$ satisfies the standard properties of a delta-correlated process with zero mean: $\langle \boldsymbol{\eta}(t) \rangle = \mathbf{0}$ and $\langle \boldsymbol{\eta}(t) \boldsymbol{\eta}(\bar{t}) \rangle = \delta(t - \bar{t}) \mathbf{I}$, where δ and $\mathbf{I}$ are the Dirac delta function and identity matrix, respectively. Further, the diffusivity D_0 is related to the particle radius a_b through the Stokes-Einstein relation: $D_0 = k_B T / 6\pi\mu a_b$, where $k_B = 1.38 \times 10^{-23}$ J/K and $T = 298$ K denote the Boltzmann constant and temperature, respectively. As established in Selvan *et al.* [37], walls have negligible effects on Brownian particles under the assumed Langevin setup. In marine environments, the cilia-driven flows facilitate the transport of a broad spectrum of particles, from micron-sized microorganisms and debris down to amino acids, dissolved organic molecules, and gases. This encompasses diffusivities in the range $D_0 \approx 0.1\text{--}1400 \mu\text{m}^2/\text{s}$ [8,37], and constitutes the parameter range studied here.

Assuming a particle traverses the positions $\{\mathbf{x}(t_0), \mathbf{x}(t_1), \mathbf{x}(t_2), \dots\}$, its position at the end of the n th subinterval $[t_{n-1}, t_n]$ ($n \in \mathbb{N}$) can be obtained from Eq. (6) as follows:

$$\mathbf{x}(t_n) = \mathbf{x}(t_{n-1}) + \int_{t_{n-1}}^{t_n} \mathbf{u}(\mathbf{x}) dt + \sqrt{2D_0} \cdot \mathcal{N}(0, \sqrt{\Delta t}), \quad (7)$$

where the vector $\mathcal{N}(0, \sqrt{\Delta t})$ is the normal distribution of mean 0 and standard deviation $\sqrt{\Delta t}$ that generates the Brownian motion. Here, we use $\Delta t = 0.01$ s, which is approximately equal to $\min\{\tau_a, \tau_d\}/100$, where τ_a and τ_d are advective and diffusive timescales, respectively (see further discussion

in [37]). Equation (7) is solved for a system of N_p particles emitted from a source on the coral surface. A constant concentration boundary condition ($C = C_0$ at $z = 0$) is enforced by maintaining the volumetric concentration of particles, $C_0 = N_p/LWh_s$, within a shallow source of height, $h_s = 0.25d$, at the coral surface. For individual cilia, this has been shown to accurately represent a surface concentration boundary condition [37]. Additionally, we assume periodic boundary conditions in the directions parallel to the walls. That is, for the rectangular domain defined by $0 \leq x \leq L$ and $0 \leq y \leq W$, a particle exiting the domain from one end, say $x = 0$, will reenter the domain from the opposite end, say $x = L$. We also impose the reflecting boundary condition on the rigid wall ($z = 0$) with the upper boundary of the computational domain left open. For computational efficiency, particles are not traced if their z coordinate exceeds $9\langle l_c \rangle$ in most simulations, the exception being the case where a direct comparison is made with the experiments.

To quantify the particle emission from the source (coral tissue), we evaluate the current (i.e., a net emission rate), defined as $I = N_e/T_e$, where N_e is the number of particles emitted from the source within a time interval T_e . This quantity describes the net flux from the coral surface and depends on the ciliary density, ciliary orientations, strength of external flow, and the diffusivity of the particles. We choose $T_e = 50$ s, so that $T_e \gg \min\{\tau_a, \tau_d\}$.

IV. RESULTS

A. Mass transport due to active ciliary flows

The fluid flows driven by the ciliary carpet influence the distribution of particles emanating from the coral surface, and therefore the rate of mass transport between the tissue and the water column. The predicted flow field near the coral surface generated by the ciliary carpet is shown in Figs. 2(b)(i) and 3(a) in enface and side views, respectively. Note that these results have been obtained for $R_h = 46\langle l_c \rangle$, enabling direct comparison with our experimental measurements. In the xy plane [with $z = 5\langle l_c \rangle$, Fig. 2(b)(i)], local ciliary arrangements lead to a surface flow directed radially outward from the polyp mouth which, in this plane, attains its maximum value away from the hexagonal boundaries. Similar flow structures were observed in the corresponding PIV experiments [Fig. 2(b)(ii)], which measured the flow field in the single hexagon from Figs. 1(b) and 1(c) (see Supplemental Movies 3 and 4 in the Supplemental Material [44]). Note, however, that the observed flow field was slightly perturbed by heterogeneities in the ciliary carpet, as discussed below. In the xz plane [with $y = x/\sqrt{3}$, Fig. 3(a)], large counter-rotating vortices emerge on the length scale of the hexagon. These steady vortical structures are generated by patches of cilia between the polyps' mouths (or on either side of a polyp's mouth) with opposite orientations and are the persistent feature of the flow in all side (cross-sectional) views. In three dimensions, these manifest as a toroidal-like flow [see example trajectories in Fig. 2(c)].

Experimental measurements of the active flow near the coral surface, recorded using particle image velocimetry (PIV), are shown in Fig. 3(b). These reveal the same features as in the model, with the velocity reaching maximum magni-

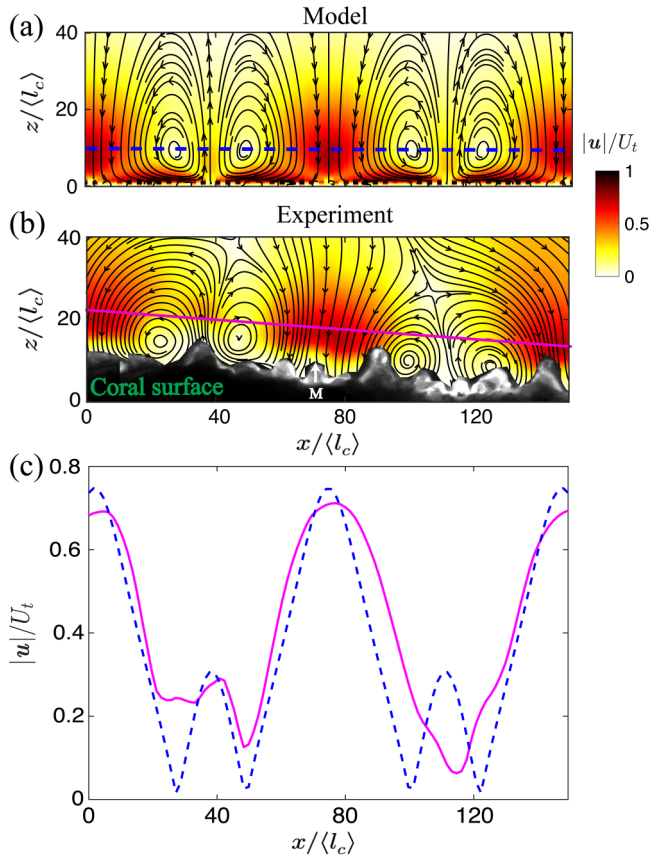


FIG. 3. Comparison between experimental and model flow fields. Heat map of the normalized velocity magnitude and streamlines in a side view ($y = x/\sqrt{3}$; i.e., along the diagonal of the periodic domain) of the active flow generated by a ciliary carpet in (a) the rotlet flow model with $R_h = 46\langle l_c \rangle$ and (b) the corresponding experiment with the coral *Porites lutea*. Here, “M” in (b) indicates the polyp mouth. (c) Scaled velocity magnitude $|u|/U_t$ as a function of $x/\langle l_c \rangle$ calculated along the dashed (blue) and solid (magenta) lines in (a) and (b), respectively. The lines are selected to pass through the local maxima of the velocity magnitude, at approximately $z = 10\langle l_c \rangle$ above the coral surface.

tude near the polyp’s mouth (i.e., hexagonal center) between two vortical structures, where the fluid is driven towards the coral surface. Figure 3(c) directly compares the normalized velocity magnitudes in the xz plane at the distance of $z \approx 10\langle l_c \rangle$ above the coral surface, as obtained from experimental measurement and using the mathematical model. The results reveal strong agreement between the two, with similar levels of agreement obtained at other positions above the coral surface. Across full spatial profiles, we find an average absolute difference between the model predictions and experimental measurements of less than 12% across scaled velocity components (i.e., u_x/U_t and u_z/U_t) and their magnitude $|u|/U_t$ (see Sec. IV of the Supplemental Material [44] for more details). Similar levels of agreement are observed for all other flow-field measurements presented throughout the manuscript.

We now quantify the mass transport (between the coral tissue and the water above) induced by this active flow and investigate how this is influenced by the properties of particles in the fluid. To begin with, we calculate the average

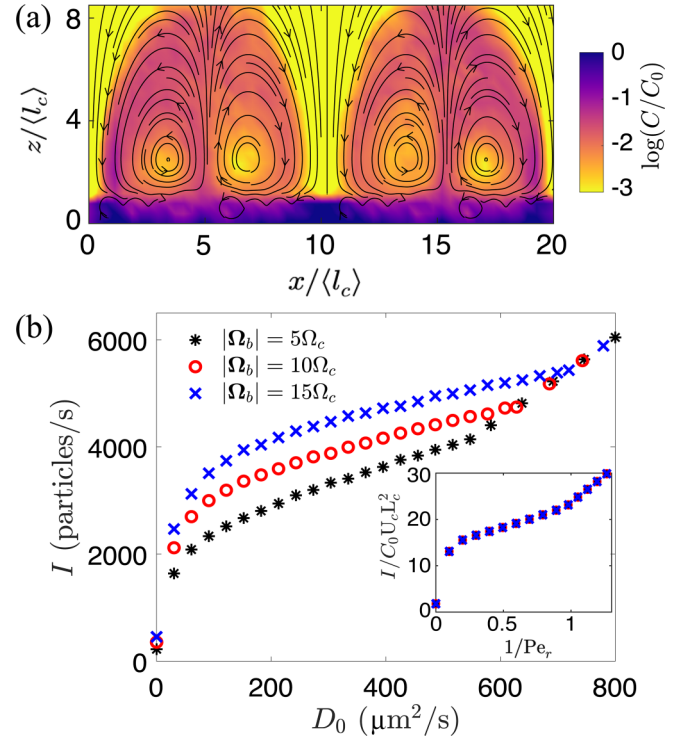


FIG. 4. Mass transport by model ciliary flows. (a) Side view (cross section at $y = x/\sqrt{3}$) of the normalized average concentration of particles with diffusivity $D_0 = 6.5 \mu\text{m}^2/\text{s}$ emitted from the source (coral tissue) of concentration $C_0 = 0.01 \mu\text{m}^{-3}$. The super rotlet magnitude is $|\Omega_b| = 10\Omega_c$ and the flow is illustrated using streamlines. (b) Particle current I (particles/second) as a function of diffusivity D_0 for various ciliary strengths (super rotlet magnitudes) $|\Omega_b|$, with fixed boundary concentration $C_0 = 0.02 \mu\text{m}^{-3}$. The inset shows the scaled current as a function of the inverse rotlet Péclet number, $1/\text{Pe}_r = D_0/U_c L_c$.

concentration profile for particles of relatively low diffusivity, $D_0 = 6.5 \mu\text{m}^2/\text{s}$. The detailed procedure for evaluating the 2D average concentration profile in a side view, $C(x, z)$, is provided in Sec. V of the Supplemental Material [44]. The color map in Fig. 4(a) shows a logarithm of the relative average concentration in the xz plane ($y = x/\sqrt{3}$), which is determined by the flow field illustrated by black streamlines. A high concentration of particles is observed inside the vortices due to the advective flow induced by oppositely oriented ciliary patches. All vertical cross sections of the domain exhibit the same behavior, with the average concentration being largest in the regions within the vortices.

Figure 4(b) illustrates how particle current I varies as a function of particle diffusivity D_0 for different values of the super rotlet magnitude $|\Omega_b|$, which serves as a proxy for the ciliary density. At high diffusivities, in which diffusion due to Brownian motion dominates over advection by the flow, the current varies linearly with D_0 . However, in the advection-dominated regime, the current varies nonlinearly with D_0 (advection significantly enhances the emission rate), with I increasing further when the magnitude of the super rotlet is increased. Similar observations were made in the case of a single cilium [37].

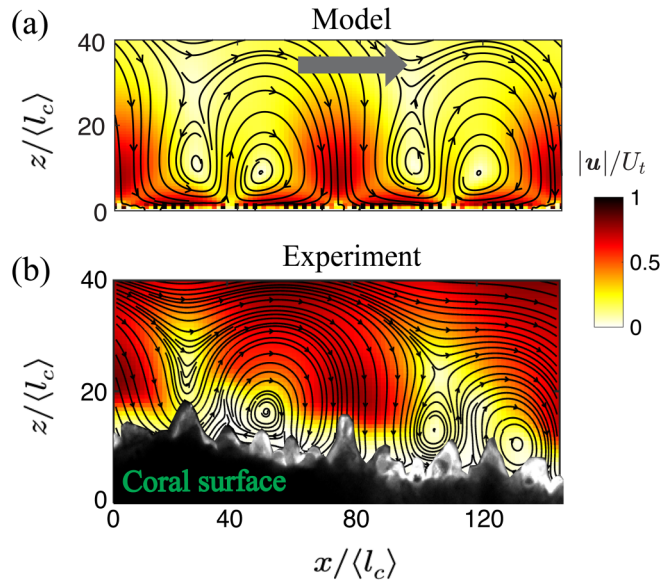


FIG. 5. Comparison between experimental and model flow fields in the presence of external flow. The normalized flow speed (heat map) and streamlines through a side view cross section ($y = x/\sqrt{3}$) are shown for the active flow generated by a ciliary carpet in the presence of external shear flow ($\dot{\gamma} = 0.5 \text{ s}^{-1}$) in the (a) rotlet flow model with $R_h = 43\langle l_c \rangle$ and (b) corresponding experiment with the coral *Porites lutea*. The gray block arrow indicates the direction of external shear flow.

The data in Fig. 4(b) can be collapsed by using the appropriate scales for characteristic length and velocity. The advection of particles into large vortical structures, such as those shown in Fig. 4(a), is mainly driven by the flow at a vertical distance, $L_c = 2d$, above the coral surface, where L_c is approximately equal to the length of cilia. Choosing L_c as the characteristic length scale, and the spatially averaged velocity magnitude at this height as the characteristic velocity U_c scale (note that U_c is also sensitive to the magnitude of the super rotlet and the radius of the hexagon), we obtain the rotlet Péclet number $Pe_r = U_c L_c / D_0$. Plotting the scaled current, $I / C_0 U_c L_c^2$, as a function of $1/Pe_r$ collapses the data into a single profile [see the inset in Fig. 4(b)]. At $1/Pe_r = 1$, the system transitions from an advection-dominated to a diffusion-dominated regime, highlighting that the mass transport driven by the ciliary distribution is controlled by the rotlet Péclet number Pe_r .

B. Effect of external shear flow on mass transport

In this section, we investigate how external shear flows above the ciliary layer influence both the hydrodynamic flow patterns and the resulting mass transport. The model predictions for the flow induced by the cilia in these circumstances are shown in side view in Fig. 5(a). To compare our findings with experimental results in Fig. 5(b), calculations have been performed with $R_h = 43\langle l_c \rangle$ and $\dot{\gamma} = 0.5 \text{ s}^{-1}$ (corresponding to an experimental flow rate of 10 mL/min). This velocity falls within the lower range of flows documented in sheltered reef environments such as the reef flat on Heron Island [9,10]. In this regime, the ciliary flow is still quite strong at $z = 1.25\langle l_c \rangle$, so the enface view (i.e., xy plane)

of this flow broadly resembles Fig. 2(b). However, in the xz plane shown in Fig. 5(a), the imposed shear changes the flow structures compared to, e.g., Fig. 3(a). Although a pair of counter-rotating vortices still exists, one of the vortical structures is much weaker. If the external flow direction is opposite to the ciliary-driven outward flow from the polyp's mouth, a strong vortex is formed. By contrast, if the external flow aligns with the ciliary-driven outward flow, a weak vortex is formed. The corresponding PIV measurements [Fig. 5(b)] have the same features, with slight differences arising from surface heterogeneities and the fact that the external flow is not precisely parallel to the coral surface.

Next, we explore the mass transport induced by such flow by using particles with relatively high rotlet Péclet number, $Pe_r = 80$, which corresponds to food particles such as plankton of size 5–20 μm [47]. Figure 6(a) shows the effect of external flow strength $\dot{\gamma}$ on their average concentration profile. Once again, the particles are largely confined within the vortical structures of the flow. Increasing the shear rate suppresses the ciliary vortices, resulting in the average particle distribution being closer to the coral surface.

The effect of external flow on particle transport can be further quantified by analyzing the particle current I over a range of scaled hexagonal radii $R_h/\langle l_c \rangle$, for particles with $D_0 = 10 \mu\text{m}^2/\text{s}$ [Fig. 6(b)]. The overall trend suggests that the particle current increases with hexagon size, consistent with a greater number of cilia contributing to the transport. Although changing radius R_h alters the rotlet Péclet number Pe_r for the particular geometry, the underlying physics, i.e., the mechanism by which the particles are transported, remains the same. Increasing the external shear rate $\dot{\gamma}$ has the opposite effect—it decreases the particle current by reducing the size of ciliary vortices [Fig. 6(a)].

In Fig. 6(c), we investigate how the particle current I varies with particle diffusivity D_0 , while keeping $R_h = 6\langle l_c \rangle$. This reveals a similar trend as depicted in Fig. 4(b): the current scales linearly with diffusivity for sufficiently large values of D_0 , while a nonlinear relationship between the two is observed for smaller values of D_0 . In the advection-dominated regime (small D_0), the particle emission rate decreases with increasing shear rate, in line with our previous observations in Figs. 6(a) and 6(b). We note that while the largest studied shear rate $\dot{\gamma} = 5 \text{ s}^{-1}$ is usually a rare occurrence near the reef flat, it allows us to test the robustness of ciliary-driven transport at moderate flow conditions. The data in Fig. 6(c) can be rescaled as in Fig. 4(b) by adjusting the velocity scale to account for the shear flow. Hence, using the same characteristic length $L_c = 2d$ as in Sec. IV A, and redefining U_c by adding the shear flow contribution $\dot{\gamma}L_c$, the data are collapsed into a single relationship between the scaled current, $I / C_0 U_c L_c^2$, and a new Péclet number, $Pe = Pe_r + Pe_{\dot{\gamma}} = Pe_r + \dot{\gamma}L_c^2/D_0$; see the inset in Fig. 6(c). Once again, $Pe = 1$ demarcates the boundary between diffusion-dominated and advection-dominated mass transport.

Predictions of our model are also compared with the SenSIV measurements discussed in Sec. II, which are used to quantify transport of dissolved oxygen with diffusivity of the order of $10^3 \mu\text{m}^2/\text{s}$ above the coral surface with $R_h = 46\langle l_c \rangle$. In our experiments, oxygen is transported with the characteristic velocity of 600 $\mu\text{m}/\text{s}$, which corresponds to

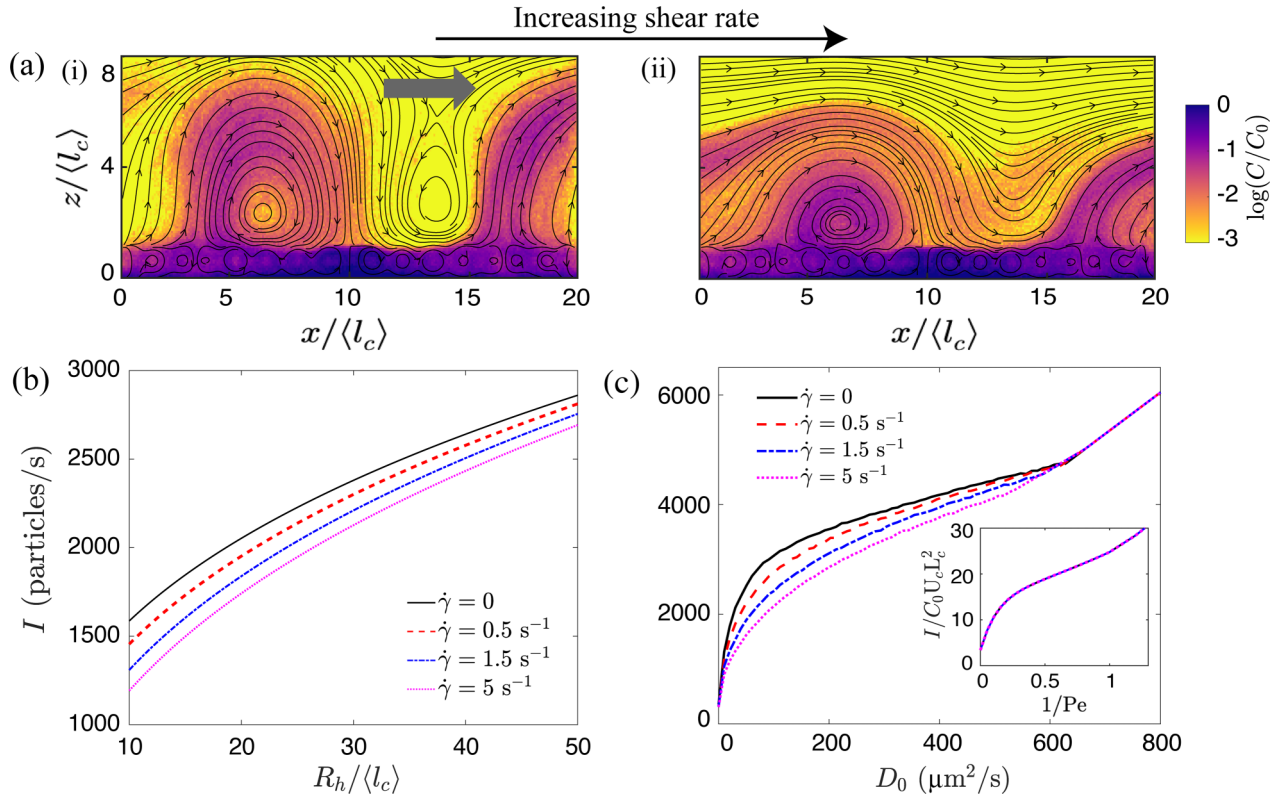


FIG. 6. Mass transport in ciliary arrays is affected by external flow and particle diffusivity. (a) Side view ($y = x/\sqrt{3}$) of the normalized average concentration of particles with $\text{Pe}_r = 80$ (i.e., $D_0 = 6.5 \mu\text{m}^2/\text{s}$) emitted from the source (coral tissue) of concentration $C_0 = 0.01 \mu\text{m}^{-3}$ into a flow that is a superposition of the ciliary flow and the shear flow characterized by (i) $\dot{\gamma} = 0.1 \text{ s}^{-1}$ and (ii) $\dot{\gamma} = 0.5 \text{ s}^{-1}$, and illustrated using streamlines. The gray block arrow denotes the direction of external shear flow. Particle current I as a function of (b) scaled hexagonal radius $R_h/\langle l_c \rangle$ for fixed $D_0 = 10 \mu\text{m}^2/\text{s}$ and (c) diffusivity D_0 for fixed $R_h = 6\langle l_c \rangle$, for various values of the shear rate $\dot{\gamma}$ with $C_0 = 0.02 \mu\text{m}^{-3}$. The inset in (c) shows the scaled current as a function of the inverse Péclet number, $1/\text{Pe}$.

the spatially averaged velocity magnitude measured at a distance $\langle l_c \rangle$ above the surface. Hence, this mass transport is described by the rotlet Péclet number $\text{Pe}_r \approx 8$ and is firmly in the advection-dominated regime. We therefore study the particle transport model assuming $\text{Pe}_r = 8$ and matching other experimental conditions, e.g., the shear rate that corresponds to the flow rate of 10 mL/min [Fig. 7(a)]. As expected, in this regime, mass transport is dominated by advection, so particles largely follow the flow. More specifically, the external flow acts to redistribute the particles that have diffused from the ciliary vortex, thereby carrying particles away from the surface. Further, the concentration of particles transported by the ciliary vortex exceeds the concentration at the source.

C. Role of heterogeneity in ciliary orientation

Our experimental measurements, e.g., in Fig. 1, suggest that there is some heterogeneity in ciliary orientations of *Porites lutea*, which affects the flow near the coral surface and the associated mass transport. We study this further by employing normal distributions about the super rotlet orientations used so far in our model. For this purpose, Eq. (3) is modified as follows:

$$\mathbf{\Omega}_b^{(m)} = |\mathbf{\Omega}_b^{(m)}| \mathcal{R}(\theta^{(m)}) \hat{\mathbf{e}}_y, \quad (8)$$

where $\theta^{(m)} = \theta_r^{(m)} + \mathcal{N}(0, \sigma)$ is the angle obtained by perturbing the reference angle $\theta_r^{(m)}$ defined in Sec. III. Here, $\mathcal{N}(0, \sigma)$ is the normal distribution with mean zero and standard deviation σ . Each super rotlet possesses its own random perturbation. We restrict the standard deviation of the orientational perturbation to $\sigma = 30^\circ$. This constraint ensures that no cilia are oriented toward the mouth and thus prevents inward-directed flow. The results presented in this section and Sec. VI of the Supplemental Material [44] are based on a single realization of the rotlet configuration. This realization is reproducible using the MATLAB random number generator, where we employed seed *rng(I)* to generate the perturbed orientation angles $\theta^{(m)}$. Further, the reported results remain unchanged for other choices of random seed.

We focus on the case of advection-dominated transport, first studying the average concentration of particles with $\text{Pe}_r = 80$ in the enface view (for definition, see Sec. V in the Supplemental Material [44]). A reference case with no orientational heterogeneity in the ciliary carpet ($\sigma = 0^\circ$) is shown in Fig. 8(a)(i); the features of the corresponding active flow have been discussed in Fig. 2(b) and are illustrated with streamlines in Fig. 8(a)(i). The flow results in particle accumulation primarily around the hexagonal vertices (depicted by white dashed circles), which correspond to stagnation regions of the flow near outgoing regions. By contrast, the

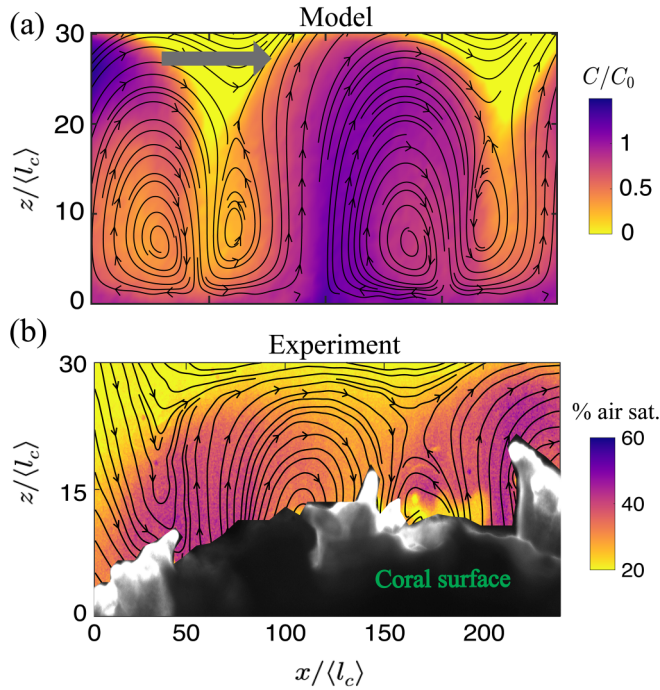


FIG. 7. Particle transport for model and experiments in the presence of external flow. (a) Side view ($y = x/\sqrt{3}$) of the normalized average concentration of particles with $Pe_r = 8$ emitted from the source (coral tissue) of concentration $C_0 = 0.01 \mu\text{m}^{-3}$. The external shear flow, denoted by the gray block arrow, is given by $\dot{\gamma} = 0.5 \text{ s}^{-1}$ and the ciliary array has geometry specified by $R_h = 46\langle l_c \rangle$. (b) Heat map of the oxygen saturation extracted from SensPIV experiments above the surface of the coral *Porites lutea* at comparable values of parameters from (a). The flows in (a) and (b) are illustrated using streamlines. In each case, the outgoing region of the flow contains the highest concentration of dissolved oxygen.

inclusion of a small degree of orientational heterogeneity in cilia ($\sigma = 20^\circ$) perturbs the hexagonal symmetry of the flow, while still preserving the directed nature of the flow away from the polyp's mouth in the horizontal plane, as indicated by the streamlines in Fig. 8(a)(ii). The resulting average concentration profile in the presence of heterogeneity [Fig. 8(a)(ii)] shows a considerable accumulation of particles along the hexagonal edges, marked by white dashed lines, specifically in the cross section of the domain parallel to and near the coral surface ($z = 1.2\langle l_c \rangle$). The particles are pushed upwards away from the coral surface by large vortices that are shown with streamlines in a side view ($y = x/\sqrt{3}$) in Fig. 8(b). The noise in the ciliary orientations changes the nature of these vortical structures, as can be seen by comparing streamlines in Fig. 8(b) to streamlines in Fig. 4(a) computed for the case of $\sigma = 0^\circ$. However, as the hexagonal radius R_h increases (see Sec. VI in the Supplemental Material [44]), the distortion of the flow field decreases in both the side and enface views (Fig. S6(b) in the Supplemental Material [44]). This reduction arises from the effective averaging of the intrinsic orientational heterogeneity of the cilia over larger hexagonal domains. Nevertheless, irrespective of the hexagonal radius, particle accumulation consistently occurs along the hexagonal edges, driven by the flow distortion

evident in the enface view (Fig. S6(b)(ii) in the Supplemental Material [44]).

Our results reveal that in the advection-dominated regime ($1/Pe_r \ll 1$), increasing the orientational heterogeneity of the cilia enhances the net emission rate of particles from the coral surface [Fig. 8(c)]. To quantify this enhancement, we plot $I/I_{\sigma=0^\circ}$ as a function of $1/Pe_r$ in the inset. The net emission rate of particles increases by more than 50% in active flows generated by ciliary carpets with orientational heterogeneity, compared to cases with $\sigma = 0^\circ$ (with maximum observed for $\sigma = 30^\circ$ in the limit of large Pe_r). This is in stark contrast with observations made for mucociliary patches in airways [24], where the inherent heterogeneity in the ciliary orientation decreases the net emission rate. Therefore, our findings suggest that the influence of such orientational disorder on mass transport is system specific and presumably shaped by the surrounding biological and physical environment.

V. DISCUSSION

Our experimental observations using scanning electron microscopy and particle image velocimetry reveal that coral surfaces are populated with numerous polyp mouths located at the centers of hexagonal units. The ciliated tissue surrounding these mouths actively drives fluid radially away from them, parallel to the coral surface, creating localized flows in each hexagonal domain. Equipped with this observation, we developed a theoretical framework based on point torques (rotlets) arranged in periodic hexagonal arrays. Each hexagonal unit contains uniformly distributed point torques directed radially outward from the center, mimicking the flow generated by the corals. While most works on ciliary transport phenomena have utilized either highly idealized velocity boundary conditions through squirmer models [10,48] or computationally intensive simulations resolving ciliary beating [26], we develop an accurate and efficient mathematical framework for resolving ciliary flows across multiple length scales. Without compromising the numerical accuracy of the model, we were able to introduce a coarse-graining step by replacing small patches of multiple cilia (that occupy a circular region of the order of the ciliary length) with a single cilium of proportionally larger magnitude, termed a “super rotlet.” This effective representation was then coupled with a Langevin particle transport model to study mass transport near the coral surface.

When situated within an otherwise quiescent fluid, the rotlet model produces steady torroidal-like three-dimensional flows, cross sections of which display counter-rotating vortices near the coral surface. These arise as a consequence of oppositely oriented ciliary patches on either side of a polyp's mouth, in qualitative agreement with experimental flow fields. Particles in the surrounding fluid become trapped and undergo recirculation within these vortices, leading to enhanced redistribution away from the surface. As the super rotlet strength increases—representing higher ciliary densities—we observe a significant enhancement in the net particle emission rate driven by ciliary advection.

When external shear flow is introduced, the hexagonal symmetry of counter-rotating vortices is broken, with stronger vortices forming where the local ciliary-driven flow partially or fully opposes the external flow direction. However,

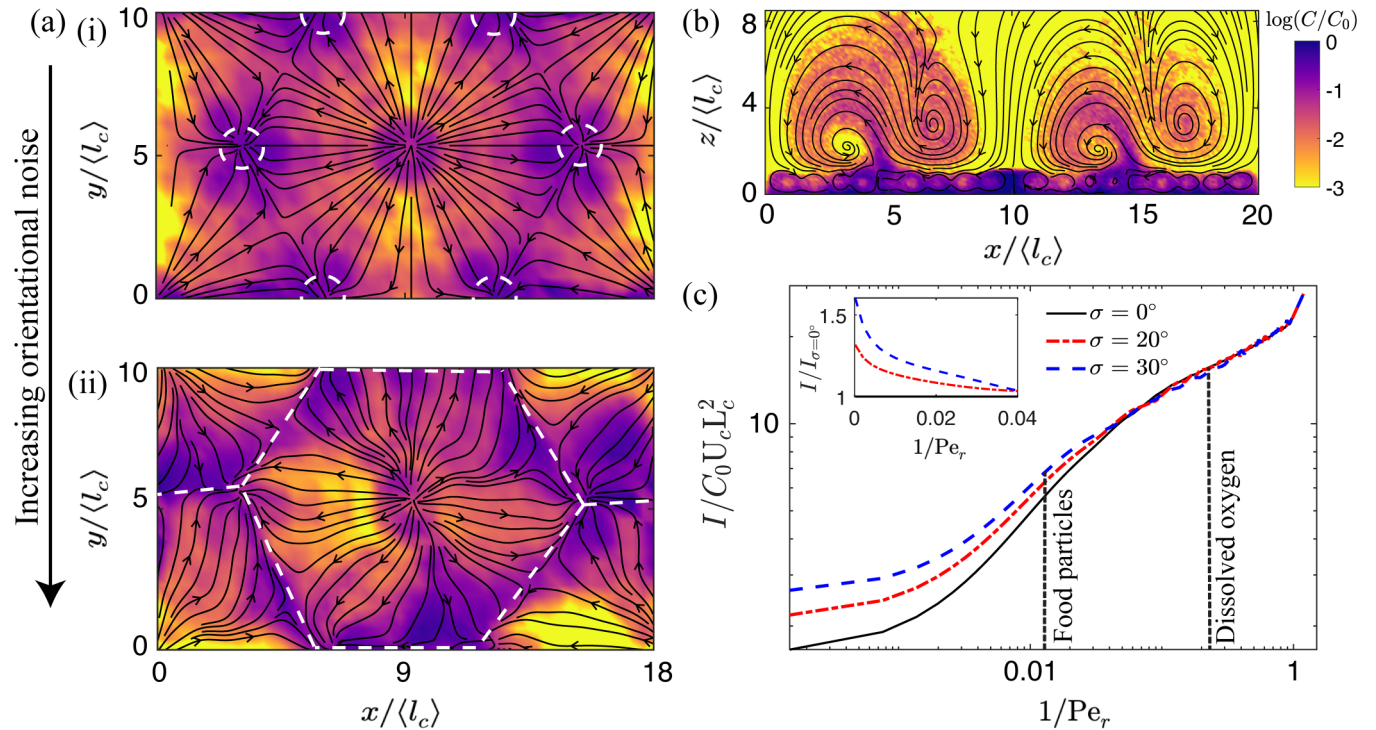


FIG. 8. Heterogeneity in ciliary alignment promotes mass transport. (a) Enface view ($z = 1.2\langle l_c \rangle$) of the normalized average concentration of particles with $Pe_r = 80$ emitted from the source of concentration $C_0 = 0.01 \mu\text{m}^{-3}$ in an active flow generated by cilia, whose orientations are defined in Eq. (8) by different noise parameters: (i) $\sigma = 0^\circ$ and (ii) $\sigma = 20^\circ$. The regions of particle accumulation are marked with the dashed circles and lines in (i) and (ii), respectively. (b) The corresponding normalized average concentration profile in side view ($y = x/\sqrt{3}$) evaluated for $\sigma = 20^\circ$. Black lines with arrows in (a) and (b) indicate streamlines of the flow in the corresponding cross sections of the domain. (c) Scaled particle current $I/C_0 U_c L_c^2$ as a function of the inverse rotlet Péclet number $1/Pe_r$, plotted on a log-log scale for various values of the noise parameter σ , with typical values of $1/Pe_r$ for a few types of particles, indicated with vertical dashed lines for reference. The inset plot shows the particle current in the heterogeneous case ($\sigma > 0$) compared with the case of zero heterogeneity, i.e., $I/I_{\sigma=0^\circ}$, where $I_{\sigma=0^\circ}$ is the particle current when $\sigma = 0^\circ$.

increasing the external shear leads to shrinking of all vortices, ultimately reducing the net particle emission rate due to the reduced ciliary influence.

Introducing orientational heterogeneity into the ciliary array also breaks the in-plane symmetry of the flow and enhances particle transport. Specifically, increasing the orientational noise in cilia results in a net particle emission rate that is up to 50% higher than in the perfectly aligned case. Notably, this behavior contrasts with observations in airway cilia, where orientational heterogeneity diminishes transport efficiency [24], and highlights that the effect of orientational heterogeneity on mass transport varies across biological environments.

The hexagonal array of coral cilia, measured from experiments and implemented in the mathematical model, results in vortical flow fields, which are observed across all cross sections of the flow and are robust for different incoming flow angles. For the purposes of plotting, we have focused on cross sections which pass through the point of the polyp mouth. However, we find that the flow within any cross section perpendicular to the xy plane exhibits qualitatively similar features. This is consistent with the fact that vortical flows are ubiquitously observed across different orientations of coral fragments in our experiments for several species (see Sec. I of the Supplemental Material [44]), and those of others [8–11].

Moreover, given the symmetry of the hexagonal domain, the topological features of the flow are relatively insensitive to changes in the incoming angle of the shear flow. This could aid the coral in maintaining nutrient exchange with its environment across a range of different flow regimes. While the structural features of the flow exhibited by the corals are determined by the spatial configuration of cilia on the surface, the resultant fluid flows are reminiscent of bioconvection patterns among swimming microorganisms [49,50] and observed modes of Rayleigh-Bénard convection [51], both of which exhibit hexagonal domains and are known to enhance transport in dynamic fluids.

Our analysis is based on several simplifying assumptions in the modeling framework. We have modeled a planar substrate, neglecting mild curvature of the coral surface present in *Porites lutea* and other coral fragments studied here (see Sec. I of the Supplemental Material [44]). While the agreement in our observed and modeled flow fields is very strong, there may be more structurally complex coral species (e.g., highly branched) for which curvature of the tissue surface could be important. In our model, we have also omitted the time-dependent beating of the cilia. However, the steady flow has been shown to accurately resolve mass transport, even at the scale of an individual cilium [37]. While our model has assumed periodic boundary conditions in the xy domain,

finite-size effects could become relevant for smaller coral specimens in strong external flows with low oxygenated incoming flow. We have also assumed that the concentration boundary condition across the coral tissue is uniform. However, there could be small spatial variation in the local oxygen production arising from heterogeneities in photosynthetic activity (e.g., through uneven illumination) or nonuniform distribution of zooxanthellae symbionts [52,53]. Notwithstanding this, our approach resolves key transport processes in the flow, revealing quantitative trade-offs between ciliary activity and external shear flow. We also note that the use of a hexagonal tiling is an intentional local approximation grounded in our observations of tightly packed polyp arrangements, a pattern common in many hexacorallian corals. However, it is not intended to represent all coral morphologies, and the geometry used in the model may be inappropriate for species with irregular, widely spaced, or phaceloid coral-lite organization.

The modeling framework presented here captures the key physical processes governing the generation of three-dimensional flow fields by heterogeneous ciliated tissues and their associated mass transport in environments with ambient flow. Given the strong agreement between theory and experiment, and the efficiency with which solutions can be calculated using the rotlet model, we anticipate that this will serve as a useful foundation for future studies involving active particles in the water column [54]. For example, the pathogenic bacterium *Vibrio coralliilyticus* has been shown to exhibit strong chemotactic responses towards exudates from reef-building corals [55] in microfluidic devices. The present model can, for example, be readily adapted to investigate the influence of ciliary flows on protection from pathogens [28],

both in corals and other ciliary systems. Furthermore, incorporating a functional dependence on the ciliary beating in terms of physiological variables such as temperature, oxygen concentration, and pH can be used to elucidate the interplay between organismal behavior and mass transport.

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The authors report no conflict of interest.

DATA AVAILABILITY

The data that support the findings of this article are openly available [58].

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