

Vortical ciliary flows actively enhance mass transport in reef corals

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The exchange of nutrients and dissolved gasses between corals and their environment is a critical determinant of the growth of coral colonies and the productivity of coral reefs. To date, this exchange has been assumed to be limited by molecular diffusion through an unstirred boundary layer extending 1–2 mm from the coral surface, with corals relying solely on external flow to overcome this limitation. Here, we present direct microscopic evidence that, instead, corals can actively enhance mass transport through strong vortical flows driven by motile epidermal cilia covering their entire surface. Ciliary beating produces quasi-steady arrays of counterrotating vortices that vigorously stir a layer of water extending up to 2 mm from the coral surface. We show that, under low ambient flow velocities, these vortices, rather than molecular diffusion, control the exchange of nutrients and oxygen between the coral and its environment, enhancing mass transfer rates by up to 400%. This ability of corals to stir their boundary layer changes the way that we perceive the microenvironment of coral surfaces, revealing an active mechanism complementing the passive enhancement of transport by ambient flow. These findings extend our understanding of mass transport processes in reef corals and may shed new light on the evolutionary success of corals and coral reefs.

coral microenvironment | coral reef evolution | diffusion boundary layer | microfluidics | biological fluid mechanics

A scleractinian coral is often described as a holobiont (1), harboring a complex consortium of microorganisms, including, in particular, photosynthetic algal symbionts living within the coral's tissue. For this holobiont to thrive, the coral animal must support the metabolic requirements of its symbionts by supplying nutrients and eliminating toxic byproducts, such as excess oxygen accumulated as a byproduct of the symbionts' photosynthetic activity (2–4). The algal symbionts, in return, provide the coral with organic carbon (2, 5), and their activity underpins the calcification and skeletal growth that is at the basis of the coral reef ecosystem (6, 7). These processes and other key metabolic processes involve the continuous exchange of nutrients, inorganic carbon and dissolved oxygen between the coral and the surrounding seawater. Identifying and quantifying the processes controlling mass transport at the coral surface are, therefore, paramount to the prediction of coral sustainability and coral reef development (8), particularly in the face of changing environmental conditions (9, 10).

Corals are simple multicellular organisms, lacking the circulatory and respiratory organs (11) used by higher animals to ensure elevated rates of mass transport (12). Accordingly, corals are generally viewed as oxyconformers (7, 13), with metabolic processes involving the exchange of oxygen or other dissolved molecules being limited by molecular diffusion through an unstirred mass transport boundary layer. To enhance this exchange, corals have been assumed to depend entirely on ambient flow, which by compression of the coral's boundary layer (14), shortens the distance that molecules must traverse. Indeed, increased

ambient flow is known to positively affect essential physiological processes, including nutrient uptake (15), photosynthesis (2), respiration (16), growth (17, 18), and calcification (18, 19).

Many corals, however, frequently experience extended periods of weak ambient flow. Such conditions occur on a daily basis on reefs where flow is dominated by tidal cycles (20, 21) and in sheltered areas within lagoons or on leeward parts of the reef (18, 22, 23). Furthermore, ambient flow is significantly reduced within densely branched corals, where parts of the colony experience over 90% reduction in fluid flow compared with conditions outside the colony (18, 23, 24). At such places and times, mass transport enhancement due to ambient flow is restricted and may even jeopardize coral survival (17, 25).

Here, we show that reef-building corals are not solely dependent on ambient flow to overcome mass transport limitations. Instead, corals can actively mix a layer of water extending up to ~2 mm from the coral surface by means of vortical flows produced by the coordinated beating of the coral's epidermal cilia. This stirring action considerably enhances mass transport, particularly under conditions of weak ambient flow, and thus, seems to represent a vital adaptation to the reef environment.

Results and Discussion

Visualization of Vortical Ciliary Flows. Using video microscopy and image analysis, we provide direct visual evidence of fast vortical flows exceeding 1 mm s^{-1} next to the surface of the reef-building coral *Pocillopora damicornis* (Fig. 1). We found that a repeating pattern of counterrotating vortices, extending up to 2 mm into

Significance

The fitness of corals and their ability to form large reefs hinge on their capacity to exchange oxygen and nutrients with their environment. Lacking gills or other ventilating organs, corals have been commonly assumed to depend entirely on ambient flow to overcome the mass transport limitations associated with molecular diffusion. Here, we show that corals are not enslaved to ambient flow but instead, can actively enhance mass transport by producing intense vortical flows with their epidermal cilia. By vigorously stirring the water immediately adjacent to their surface, this active process allows corals to increase mass transport and thus, can be a fundamental survival mechanism in regions or at times of weak ambient flow.

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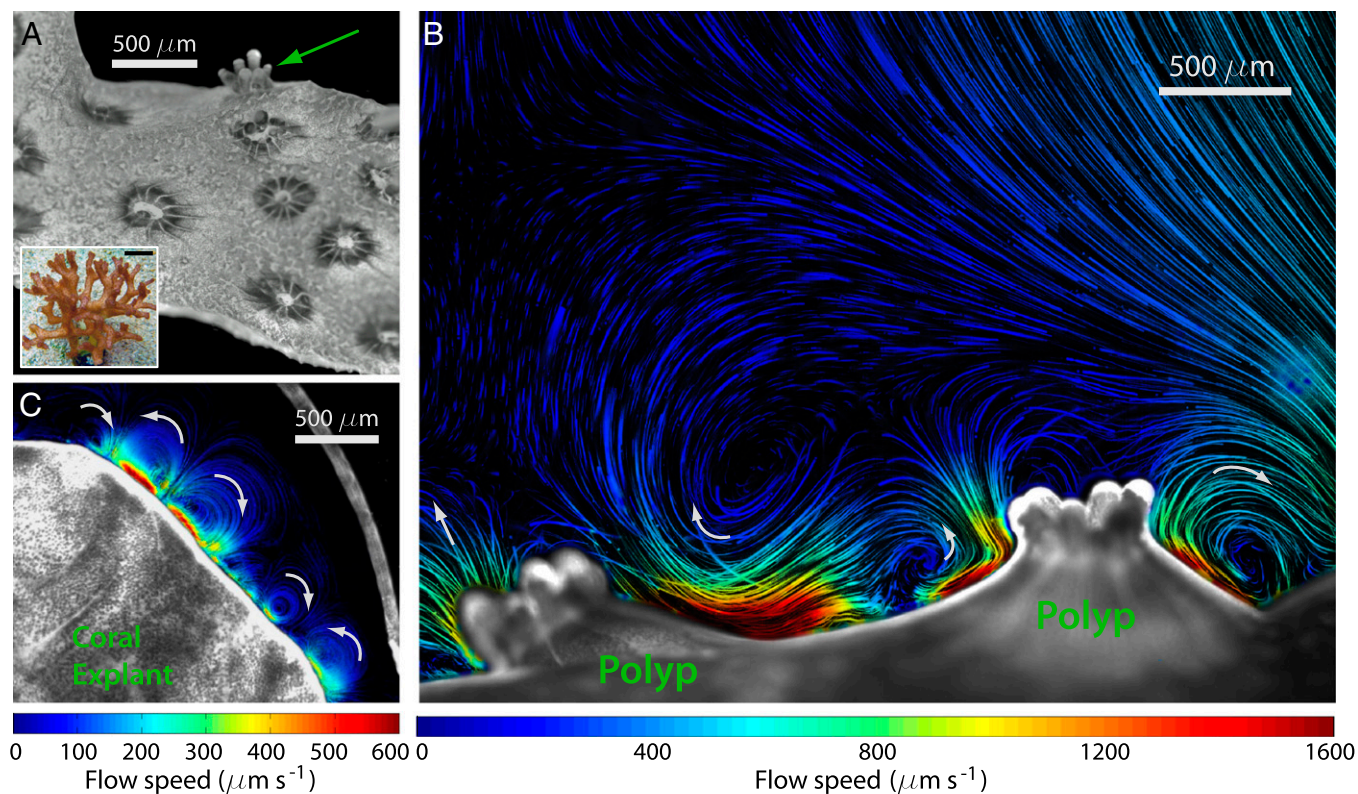


Fig. 1. Vortical flows on the surface of the scleractinian coral *P. damicornis*. (A) Deconvolution microscopy image of a single branch of a *P. damicornis* coral showing both retracted (dark rings) and extended (green arrow) polyps. (Inset) *P. damicornis* fragment. (Scale bar: 1 cm.) (B and C) Cilia-driven vortical flows between two polyps on the surface of (B) a small branch and (C) an explanted *P. damicornis* polyp. Particle trajectories from each video are color-coded based on the local flow speed, and white arrows denote local flow direction. An image of the coral has been overlaid on the trajectories in order to show the surface and polyp locations (additional information in *SI Materials and Methods*).

the surrounding seawater (Fig. 1B), results in vigorous stirring at the coral–seawater interface under otherwise quiescent conditions. These vortices occurred irrespective of the distance of the coral surface from the walls of the observation vessel (Fig. S1 and Movie S1), ruling out wall-induced recirculation as their cause (26). The observed vortices are a product of opposing surface flows (Fig. S1D) combined with the natural topography of the coral surface. We observed similar vortical flows on four other species of branching corals (Fig. S2 A–D) as well as in a massive, large-polyped colony (*Favia* sp.) (Fig. S2E), suggesting these stirring flows to be a widespread feature of scleractinian corals of different lineages and colony forms.

High-speed video microscopy of the motion of tracer particles within 100 μm of the surface of coral tissue explants (27) revealed strong flows tangential to the epidermal surface (Fig. 2A). Surface-parallel flow velocities increased from zero at the coral surface to up to $\sim 1 \text{ mm s}^{-1}$ at a distance of 10–15 μm from the surface (Fig. 2C). SEM (Fig. 2B) and high-resolution video microscopy (Movie S2) of the coral epithelium showed dense forests of cilia of length $L_C = 12.6 \pm 1.8 \mu\text{m}$ beating at a frequency $f_C = 16.9 \pm 4.1 \text{ s}^{-1}$ (Fig. 2C, Inset and Movie S3). The concerted action of these cilia (Movie S2) drives flow on scales two orders of magnitude larger than the length of an individual cilium. The distance from the coral surface and the magnitude of the maximal fluid velocity correspond closely to the thickness of the ciliary envelope covering the coral (Fig. 2A and C, green dashed line) and the tip speed of the cilia ($2\pi f_C L_C \sim 1 \text{ mm s}^{-1}$; Movie S3), respectively. No vortical flows were observed when ciliary beating was arrested by the addition of 0.1 mM sodium orthovanadate to the water (*SI Materials and Methods* and Fig. 3B),

confirming the active role played by the coral animal in stirring its own boundary layer.

Energetic Cost of Ciliary Beating. The energy invested in powering the ciliary beating that drives the observed vortical flows is a negligible fraction of the coral’s metabolic budget. The energetic cost for one cilium to complete one beat cycle depends on the cilium length as well as the density and synchronization of surrounding cilia (28, 29). SEM (Fig. 2B) revealed a ciliary density of $\sim 3 \times 10^6 \text{ cilia cm}^{-2}$ corresponding to an average distance between cilia of $\sim 6 \mu\text{m}$. Because both this spacing and the length of the cilia (12.6 μm) are of the same order as those found in *Paramecium* [12- μm length (28) and $\sim 3\text{-}\mu\text{m}$ spacing (29)], we here use the cost of $2 \times 10^{-16} \text{ J}$ per stroke estimated for *Paramecium* (28) to quantify energy expenditure in *Pocillopora*. For the observed ciliary beating frequency of 16.9 s^{-1} , this calculation yields an energy expenditure of $3.7 \times 10^{-5} \text{ J cm}^{-2} \text{ h}^{-1}$, equivalent to $3.7 \times 10^{14} \text{ ATP molecules cm}^{-2} \text{ h}^{-1}$ (28). In comparison, the oxygen consumption of *P. damicornis* during respiration is $1\text{--}5 \mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$ (18), which assuming 5 mol ATP gained per 1 mol oxygen respired (28), yields an estimated $0.3\text{--}1.5 \times 10^{19} \text{ ATP molecules cm}^{-2} \text{ h}^{-1}$. Even assuming a 20% energy conversion efficiency (28), the estimated cost of ciliary beating is $<0.1\%$ of the coral’s total energy budget, and thus, we surmise that it is easily compensated for by the enhanced mass transport afforded by ciliary beating.

Effect of Vortical Ciliary Flows on Mass Transport. Enhanced transport is a fundamental characteristic of all vortical flows (30–32). The stirring action of such flows increases the effective diffusivity of dissolved species in bulk fluids (31) and the flux of solutes

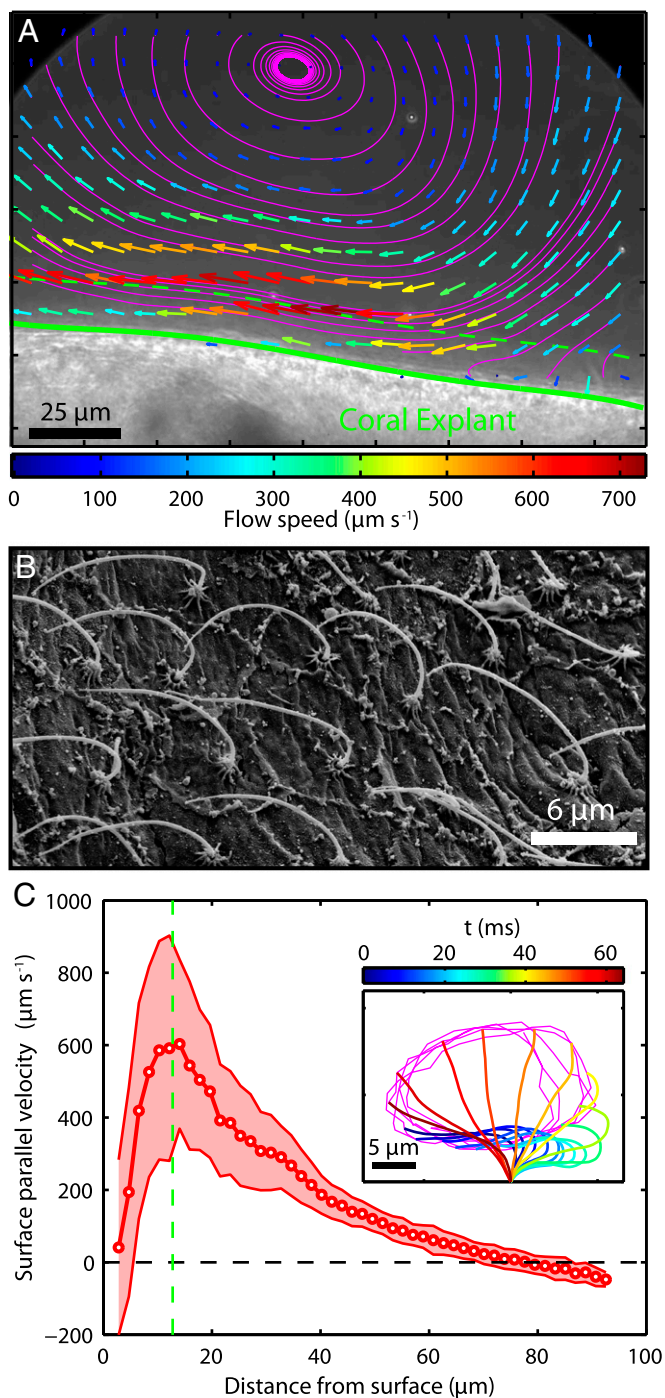


Fig. 2. Vortical flows originate from the beating of coral cilia. (A) Detailed view of the flow field associated with one vortex obtained by high-resolution particle tracking velocimetry immediately above the coral surface (solid green line). The dashed green line indicates the ciliary envelope ($\sim 15 \mu\text{m}$ from the coral surface). Arrows are color-coded by flow speed. (B) Scanning electron micrograph of the epidermal surface at the base of a polyp on a *P. damicornis* branch showing each epidermal cell having a single cilium. The average ciliary density is $\sim 3 \times 10^6$ cilia cm^{-2} . (C) The surface-parallel velocity profile corresponding to A shows that the flow speed rises sharply from zero at the coral surface to a maximum at the edge of the ciliary layer (dashed green line) before decaying in the far field. The shaded region denotes the velocity \pm standard deviation. (Inset) Measured beating pattern of one cilium over one full cycle (beat frequency ~ 17 Hz) color-coded by time. The magenta curve is the cilium's tip trajectory over five beat cycles. The smaller size of the vortex in Fig. 2 compared with Fig. 1 is because of the shallow preparation used in Fig. 2 for high-resolution imaging.

from immersed surfaces (32). The presence of vortical flows over the entire coral surface is, thus, predicted to accelerate solute transport to or from the coral colony. Small molecules, such as oxygen, Ca^{2+} , or amino acids, with diffusivities that are in the order of $D \sim 10^{-9} \text{ m}^2 \text{ s}^{-1}$ are rapidly advected by the observed flows, traversing a vortex with diameter $L \sim 1 \text{ mm}$ and speed $U \sim 1 \text{ mm s}^{-1}$ in approximately $L/U \sim 1 \text{ s}$. In contrast, solutes transported by diffusion alone take a considerably longer time, $L^2/D \sim 1,000 \text{ s}$, to traverse the same distance. The ratio of diffusive to advective timescales is measured by the Peclet number ($Pe = UL/D$). When $Pe \ll 1$, mass transport is controlled by molecular diffusion. For the range of vortex sizes and speeds that we observed, we obtain $Pe = 500\text{--}6,000$ for the transport of small molecules, signifying an overwhelming dominance of advection over diffusion for even the slowest and smallest vortical flows that we recorded. These results suggest that the vortical flows generated by coral cilia substantially enhance the transport of solutes to and from the coral surface.

We tested the prediction that vortical flows affect mass transport for the case of oxygen by measuring the oxygen distribution near the coral surface. Oxygen transport can be critical both during the day, when oxygen accumulation reduces photosynthetic efficiency and generates damaging oxygen radicals (2, 4), and during the night, when respiration by the coral holobiont can result in the formation of anoxic conditions (14, 33). We combined video microscopy with microelectrode measurements to determine how oxygen concentration varied in relation to the cilia-driven flow field. In the presence of vortical ciliary flows, the oxygen concentration often exhibited a local maximum at a distance of $500\text{--}1,500 \mu\text{m}$ from the coral surface (Fig. 3A and Fig. S3A). This feature is in stark contrast with the monotonic decay predicted for purely diffusive transport through a stagnant boundary layer (34). Indeed, when ciliary beating was arrested by addition of sodium orthovanadate (final concentration = 0.1 mM) (35), a monotonic decay of oxygen concentration with distance from the coral surface was observed, and no vortical flows were present (Fig. 3B and Fig. S3B). These results show that oxygen transport at the coral surface is dominated by the vortical ciliary flows and not molecular diffusion, confirming predictions based on the large Peclet number values.

To visualize the effect of the vortical flow on mass transport, we mapped the 2D distribution of oxygen concentration through a vortex. The oxygen concentration map was generated from a matrix of single-point oxygen measurements taken within an individual vortex over an area of $2,500 \times 1,000 \mu\text{m}^2$ at $100\text{-}\mu\text{m}$ resolution. Overlaying the oxygen distribution onto the streamlines of the vortical flow, measured nearly simultaneously, shows that the side of the vortex where flow is toward the coral carries seawater with ambient oxygen concentration to the coral surface (Fig. 3C). In contrast, the outgoing flow on the opposite side of the vortex transports highly oxygenated water away from the coral (Fig. 3C). The location and topology of the vortex remained remarkably stable over the 90 min required to map out the 2D oxygen distribution (Fig. 3D), with the exception of small shifts caused by deformations of the adjacent coral polyps, confirming that vortices are a robust feature of the coral surface.

Quantification of Mass Transport Enhancement Caused by Vortical Ciliary Flows. To quantify the consequences of the vortical ciliary flows on mass transport, we developed a mathematical model that allowed us to compare the mass flux from a coral surface in the presence and absence of ciliary flows. We applied this model to different colony morphologies representing several prototypical coral forms and quantified results as a function of the magnitude of the ambient flow velocity under the assumption of a laminar unidirectional ambient flow (SI Materials and Methods).

The model results indicate that vortical ciliary flows can considerably enhance mass transport, particularly during periods of

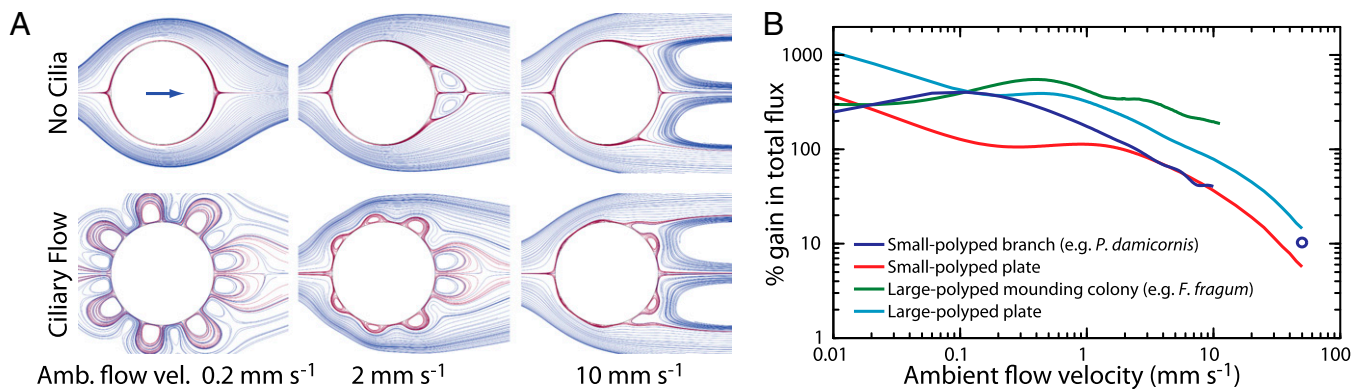


Fig. 5. Vortical ciliary flows considerably enhance mass transport under low-to-moderate ambient flows. (A) A mathematical model shows that ciliary vortical flows on a cylindrical coral branch considerably impact (Lower) the flow topology compared with (Upper) the no-cilia case for low-to-moderate ambient flow velocities. The branch diameter is 5 mm. The arrow marks the direction of the ambient flow. Streamlines are shown in blue, except for those passing within 50 μm of the branch, which are in red. (B) The predicted gain in oxygen flux due to vortical ciliary flows expressed as percent relative gain over the no-cilia case for several coral morphologies (Fig. S4) as a function of the magnitude of the ambient flow velocity. Cilia contribution is highest at flow velocities below 1 cm s^{-1} , where vortical ciliary flows enhance mass transport by tens to hundreds of percent for all coral morphologies tested. Mass transport enhancement is lower at higher ambient flow velocities, where reduced thickness of the flow boundary layer results in increased oxygen flux because of ambient flow alone. Nevertheless, a 10% gain is still predicted for the cylindrical branch model at a flow velocity of 5 cm s^{-1} (blue circle). Each curve in B is based on ~ 250 individual simulations at different ambient flow velocities.

experimentally (Figs. 1 and 3 and Figs. S1 and S2). The modeled oxygen distribution within these vortices (Fig. 4) successfully captured the main features revealed by the microelectrode measurements (Fig. 3 A and C and Fig. S3). The steady-state oxygen flux from the simulated branch was enhanced by $>40\%$ relative to the no-cilia case for ambient flow velocities below 10 mm s^{-1} and $>100\%$ for ambient flow velocities below 2 mm s^{-1} (Fig. 5B). Even for relatively high ambient flows (5 cm s^{-1}) (blue circle in Fig. 5B), when flow over the branch transitions to an unsteady vortex-shedding regime, ciliary action enhanced mass flux by $\sim 10\%$.

Vortical ciliary flows enhanced mass transport for all coral morphologies and all ambient flow velocities tested. We designed three additional models representing a range of colony geometries. These included a large-polyped, mounding (Fig. S4 E and F), and encrusting colony morphologies (Fig. S4 G and H), such as those formed by many *Favia* corals, as well as a small-polyped plating morphology (Fig. S4 C and D), such as that formed by some *Montipora* corals. For the large-polyped model, the direction of ciliary flows relative to each polyp was based on prior descriptions by Lewis and Price (37). The resulting flow-field simulations predict a pattern of opposing vortices of greater diameter than those of *P. damicornis* (Fig. S4 F and H), a prediction confirmed by microscopic observation of the surface of a *Favia* colony (Fig. S2E). *Favia*-like models returned the strongest mass transport enhancement, with the mounding colony model predicting gains of 400% and 200% for ambient flow velocities of 1 mm s^{-1} and 1 cm s^{-1} , respectively (Fig. 5B). This strong gain is likely caused by ciliary flows overcoming the mass transfer limitation associated with the surface cavities hosting the polyps (38), by connecting fluid within the cavities with the ambient flow (Fig. S4 F and H). Similar enhancements obtained for the plating and encrusting morphologies ($>100\%$ for ambient flow velocities of $<2 \text{ mm s}^{-1}$) (Fig. 5B) imply that vortical ciliary flows have a strong positive effect on mass transport, regardless of the geometrical details of colony morphology.

These results show that, under low-to-moderate ambient flows, the beating of epidermal cilia acts synergistically with ambient flow to substantially enhance mass transport for a broad range of coral morphologies. This active enhancement may account for frequent reports that the measured mass transport in scleractinian corals exceeds that predicted based on ambient

flow alone, particularly at low-ambient flow velocities (15, 34, 39). Passive enhancement of mass transport in benthic organisms strongly depends on the magnitude (18, 34) and direction (40) of the ambient flow, both of which are often variable in space and time on coral reefs (18, 40). This variability is shown, for example, by a 3-y time series recorded on a coral reef in Eilat, Israel, which included flow velocities below 2 cm s^{-1} for over 25% of the time (20) and no measurable flow for nearly 10% of the time. Extended periods of near-zero ambient flow have been recorded on a daily basis and reported in other studies and for other reefs (21, 40). During these times, the considerable mass transport enhancement afforded by ciliary flows can play a vital role for reef corals and may represent a fundamental coral survival mechanism.

Evolutionary Advantage of Coral Epidermal Cilia. Although no comprehensive census is available, a literature survey indicates that motile epidermal cilia are restricted to a small cluster of cnidarians within the Hexacorallia (Fig. S5 and Table S1). In addition to hard corals (order Scleractinia) (37), including the reef-building corals studied here, this cluster comprises the orders Antipatharia (black corals) (41) and Corallimorpharia (mushroom anemones) (42). A recent analysis suggests that these lineages diverged during the early Paleozoic era (400–550 Mya) (43). The subsequent retention of this trait suggests that motile cilia and, by extension, ciliary flows have played an important role in cnidarian evolutionary history. The enhanced fitness afforded by ciliary flows may be of particular importance to juvenile coral colonies, whose small size often results in locally reduced ambient flows because of their position within the benthic boundary layer (44, 45). For large colonies, the passive enhancement of mass transport as a consequence of ambient flow becomes limiting with increasing colony size (25) and—in branching colonies—increasing branch density (18). This limitation may result in a negative feedback between colony size and calcification rate that constrains the size and branch density of coral colonies. We suggest that the alleviation of these constraints by ciliary flows enables coral colonies to settle and thrive under otherwise limiting ambient flow conditions and to bridge periods of weak ambient flows. This effect may have contributed to the ability of corals to build the massive aragonitic skeletons that form the basis of coral reefs.

Taken together, the findings presented here add a new layer to our understanding of mass transport in reef-building corals.

Although scleractinian corals frequently rely on ambient flows for mass transport, they are not entirely at the mercy of these flows but instead, can actively enhance mass transport using their epidermal cilia. This active, dynamic nature of the coral surface may further affect the interactions between corals and the microorganisms found on and around them, including pathogenic bacteria. Quantifying the effect of ciliary flows on mass transport and other processes is, therefore, crucial to our understanding of coral physiology and coral health, and to our ability to predict the fate of coral reefs under changing environmental conditions.

Materials and Methods

Flow-Field Imaging. A small polydimethylsiloxane (PDMS) chamber (2 cm long \times 1 cm wide \times 1 cm high) was bonded to a glass microscope slide and filled with filter-sterilized artificial seawater (FASW) (Fig. 1). A small branch of *P. damicornis* (<10-mm length and \sim 5-mm diameter) was placed in the chamber, and powdered coral food (Coral Frenzy; Coral Wonders LLC), suspended in FASW and passed through a 5- μ m filter, was added to serve as tracer particles. The chamber was covered by a glass coverslip to eliminate vibrations and minimize convective currents from the water surface. The flow field was visualized at low magnification (4 \times , 0.13 N.A. objective) by dark-field microscopy and captured using an Andor Neo camera (6.5 μ m/pixel), yielding an imaging resolution of 1.625 μ m/pixel. Subsequent flow field analysis described in *SI Materials and Methods*.

Simultaneous Flow-Field Imaging and Oxygen Measurements. Imaging was performed in a PDMS chamber as described above but with the top coverslip covering only one-half of the chamber holding the coral branch to allow access for the microelectrode (Fig. 3). Illumination was set to 500 μ mol $m^{-2} s^{-1}$ for all experiments using the microscope's light source. The flow field was first imaged as described above. Based on the resulting image, the microelectrode tip was brought in contact with the coral surface at a chosen location within the flow field using a micromanipulator. The branch was then moved 2,500 μ m away from the tip using the motorized microscope stage. Dissolved oxygen was measured at this position for 2 s at a sampling rate of 1,000 Hz. A dissolved oxygen profile was then measured by moving the coral toward the microelectrode in 25 steps of 100 μ m. At each step, dissolved oxygen was measured as above after a 5-s hiatus to let any disturbance from the stage motion subside (additional information in *SI Materials and Methods*).

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