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Coral physiology: Going with the ciliary flow

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Corals have long been known to generate local fluid flows using ciliary beating, but the importance of these ciliary flows is just being discovered. Two new papers shed light on how ciliary-flow physics plays a key role in shaping coral physiology.

Coral reefs are experiencing dramatic declines across their spatial range. Despite this, there are bright spots of hope where corals have escaped severe stress[1], with dynamic biological and physical processes operating at multiple scales conferring this resilience. Researchers have already linked oceanographic circulation to climate refugia[2], identified acclimatization and adaptation strategies that provide resistance to thermal stress[3], and recognized the role of novel symbioses in alleviating the most harmful effects of global change[4]. However, the extent to which corals can modulate their physiology and resilience to climate change through control of their local microenvironment has remained underexplored. Two new papers in *Current Biology* by Bouderlique, Petersen, Faure *et al.*[5] in a recent issue and Pacherres, Ahmerkamp *et al.*[6] in this issue explore the biophysical mechanisms employed by corals to actively generate microscale flows, revealing how coral polyps work together as part of an integrated colony and fend off oxidative stress. These two papers breathe new life into our understanding of coral ciliary flows and lead to new questions and research directions for defining species' sensitivities to global change.

Corals are sessile colonial invertebrates that lack neuromuscular organs. Consequently, their physiology is constrained by the fluid (sea water) surrounding the colony[7]. However, corals are thickly ciliated and can generate their own fluid flows to interact with their environment. Early studies suggested that these currents served solely as feeding and cleansing mechanisms[8,9]. Yet, a recent discovery of vortical ciliary flows enhancing mass-transport rates[10] has renewed the coral biology community's interest in epidermal cilia and has also attracted the attention of biophysicists.

Cilia are hair-like structures that protrude from many types of cells and are the fundamental organelles that convert chemical energy into mechanical work, giving rise to an oscillatory beating motion[11]. Beating cilia generate fluid flows that enable the swimming and feeding of many marine organisms such as ciliates and plankton[12], and ciliary flows also help several benthic marine invertebrates like sponges to filter feed[11]. The ubiquitous occurrence and remarkable diversity of ciliary flows in organisms have attracted the attention of many fluid physicists who are interested in understanding these flows using quantitative experiments, mathematical modeling, and simulations[13,14].

Despite our nearly century-long observations of ciliary organelles and their flows, we are only just beginning to understand the role of coral cilia and the flows they generate in determining their physiology (Figure 1). A recent study has demonstrated that the harmonic beating of cilia stirs the water next to the coral and can increase the mass transport of nutrients and ions by up to 400%[10]. These ciliary flows persist under ambient currents and create distinct gradients to increase the diffusion of solutes across the diffusive boundary layer[15]. New papers published in *Current Biology* now delve further into the biophysics behind this generation of ciliary flows[5,6].

In the first paper, published in a recent issue of *Current Biology*, Bouderlique, Petersen, Faure *et al.*[5] investigated the mechanisms underlying the colonial nature of corals. Multiple modeling and observational experiments across 14 coral species describe coordinated, mucus-enriched flows that bring particles to the polyps. The authors found that these horizontal surface currents had reproducible, species-specific patterns, whereby mucus concentrations controlled the speed of the currents (Figure 1D), and postulated that these currents aligned with the individual feeding strategies of the different species. Bouderlique, Petersen, Faure *et al.*[5] employed fluorescent confocal microscopy experiments and analytical tools from fluid dynamics, as well as convection modeling, to quantify flow patterns in their experimental data. The microscopic observations of the coral's internal gastrovascular tubing system revealed oppositely ciliated surfaces that give rise to circular currents connecting clusters of polyps. Mathematical models of the flow incorporating Newton's laws of motion identified discrete surface zones where neighboring polyps could compete for resources, and particles had long residence times in the polyps that captured them. The authors refer to this feeding strategy as a "selfish sharing" model, in which singular polyps retain their trapped particles before ultimately sharing with the colony through the gastrovascular canals. In a separate computational fluid-dynamics model, Bouderlique, Petersen, Faure *et al.*[5] demonstrated that ciliary currents created low-pressure zones that increased the downward circulation of water to the polyps. Together, these observations highlight previously unappreciated flows that corals generate both on the surface and within the colony to integrate individual polyps into a colonial organism.

In the second paper, published in this issue of *Current Biology*, Pacherres, Ahmerkamp *et al.*[6] explored how ciliary currents redistribute oxygen across the polyp to reduce oxidative stress. The team first mapped out chlorophyll-*a* concentrations across the polyps of *Porites lutea* using scanning hyperspectral imaging to serve as a proxy for the densities of symbiotic algae. Next, they simultaneously imaged oxygen fluxes and ciliary flows using a pioneering oxygen-sensitive nanoparticle-based technique[16]. When overlaid, the composite images demonstrate how vortical ciliary flows transport oxygen away from the symbiont-rich areas into the ambient seawater and recirculate the lower oxygen concentrations back to the site of oxygen production for further transport (Figure 1C). This 'conveyor belt' of oxygen increases the diffusive flux compared to molecular diffusion alone, thereby preventing oxidative stress in symbiont-rich coral tissue. Pacherres, Ahmerkamp *et al.*[6] then applied their observations to a two-dimensional transport-reaction model and found that ciliary vortices reduced oxygen concentrations at the coral surface by 53% compared to models without ciliary flows. Importantly, the authors discovered that the precise location of the vortices relative to the site of oxygen production enhances oxygen ventilation. For example, if the vortex's position is opposite the experimentally observed locations, the area exposed to harmful oxygen concentrations is doubled during periods of oxidative stress.

In the face of widespread coral bleaching due to global warming[17], the resilience mechanisms by which corals can cope with oxidative stress may dictate individual sensitivities to rising seawater temperatures. The newly discovered homeostatic control mechanism reported by Pacherres, Ahmerkamp *et al.*[6] and the species-specific ciliary flows identified by Bouderlique, Petersen, Faure *et al.*[5] may help to confer differential bleaching patterns across coral species. However, the contribution of ciliary flows to bleaching resilience relative to already-established mechanisms, such as high ambient flows[18] and novel symbioses[4], remains to be explored. Additionally, the role of ciliary flows in providing resilience to ocean acidification also requires investigation since microscale pH heterogeneities in the diffusive boundary layer may also provide some resilience[19].

Our understanding of ciliary flows has evolved from a simple particle-transport model to a complex resource-sharing and distribution model. These ciliary currents integrate individual polyps into coral colonies and maintain homeostasis during periods of excess oxygen production. The new studies by Bouderlique, Petersen, Faure *et al.*[5] and Pacherres, Ahmerkamp *et al.*[6] demonstrate the utility and advantages of bringing together interdisciplinary teams to answer fundamental biological questions. Indeed, these researchers discovered hidden physiological roles of appendages that have been observed for over a century. The case for researching coral ciliary flows has never been stronger; the complete suite of physiological mechanisms and the resilience that these flows provide are waiting to be unraveled. These exciting coral ciliary-flow studies will also inspire and advance research in

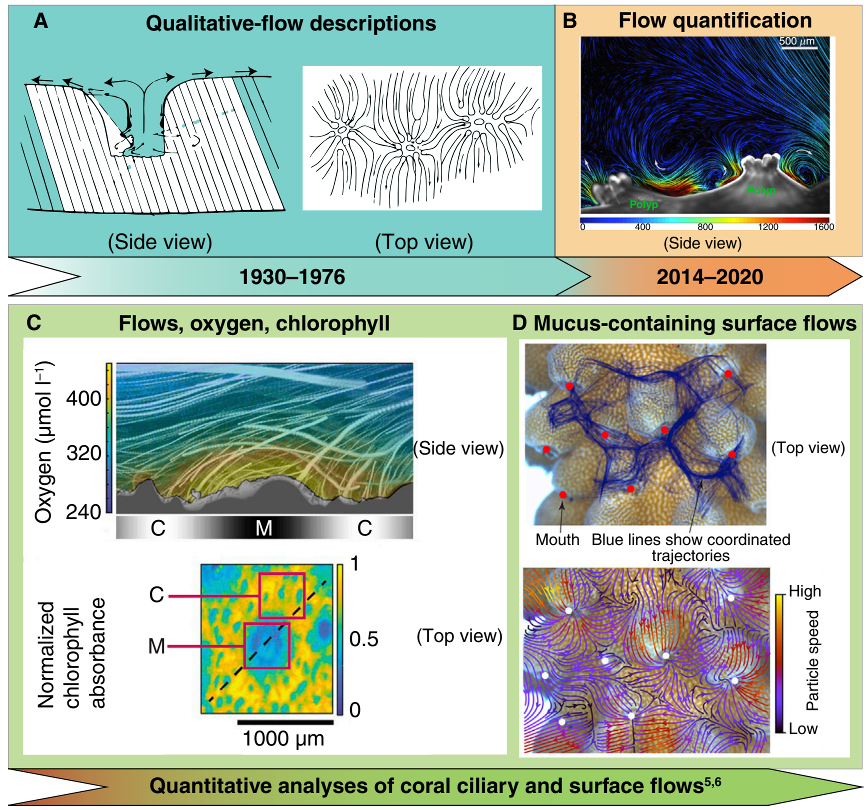

Figure 1. Timeline of coral ciliary-flow research.
A historical perspective highlighting milestones leading to our modern understanding of coral ciliary flows. (A) Landmark studies provided important yet qualitative flow descriptions. Sketches indicate flow direction on coral surfaces seen from the side view of *Fungia danai*[8] and a top view of *Agaricia lamarcki*[9]. Image credits: left panel, image from[8] (CC BY-NC-SA 4.0); right panel, image reprinted with permission from Wiley[9]. (B) First demonstration of quantitative ciliary flows. The side view shows particle trajectories revealing vortical ciliary flows on polyp surfaces of *Pocillopora damicornis*[10]. Color bar indicates flow speeds in $\mu m\ s^{-1}$ and white arrows indicate flow direction. Image from[10]. (C) Combined quantitative measurements of ciliary flows, oxygen and Symbiodiniaceae chlorophyll concentrations reveal that ciliary vortices ventilate oxygen from areas of production to prevent oxidative stress in *Porites lutea*[6]. Upper panel: Particle trajectories seen from the side view, oxygen concentration indicated by color coding, where the coenosarc (C) and mouth opening (M) are annotated. Lower panel: Top view of the coral surface showing chlorophyll concentrations. (D) Quantitative measurement of mucus-containing surface flows reveals that each of the polyps has a defined particle capture area on the colony (top view) of *Acropora muricata*[5]. Upper panel: Superposed trajectories of charcoal particles (blue lines); red dots represent polyp mouths. Lower panel: Further analysis of data in upper panel. Vectors represent averaged particle trajectories, and color coding indicates speed.

biophysics[11,13,14] and spark the development of next-generation bioinspired engineering technologies[20].

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Plant physiology: Anatomy of a plant action potential

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The Venus flytrap possesses modified leaves that can snap shut fast enough to catch a fly. A new study identifies the major components of the toolkit that allows the flytrap to fire action potentials, illustrating how different ion channels and transporters are recruited to give rise to this unique plant behavioural response.

Plants are not normally known for their fast responses to external stimuli. They have no muscles and no nerves — commonly associated with fast behavioural responses in animals. However, the Venus flytrap represents one of very few examples of fast behavioural responses in a plant. Insects are attracted to open traps on the end of flytrap leaves and their movement activates touch-sensitive trigger hair cells on the surface of the open trap. Once a fly is sensed, the trap can close very rapidly — within 0.5 seconds[1]. This is fast enough to trap the hapless insect within. Once caught, further struggles of the insect lead to complete closure of the trap, which develops into a sealed digestive organ through the secretion of digestive enzymes and absorption of nutrients into the plant[2,3]. It has been long known that rapid depolarization of the membrane potential (V_m) initiates action potentials (APs) in cells lining the trap lobe, preceding the fast closure of the trap. APs, which last for approximately 1 second, arise in the touch-sensitive hair cells that act as micro-mechanical transducers and travel along the inner surface of the trap lobes at around 0.1 meters per second[4,5]. It is also known that the flytrap can count the number of times a hair cell is stimulated by a moving insect[6]. It takes two or more

