Putting corallites on a pedestal: identifying corallite morphologies that optimize mass transfer across platelike corals.

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ABSTRACT

Mass transfer in corals is dependent on sufficient flow over individual polyps, and thus is influenced by both gross coral morphology and local surface texture. This study uses plaster dissolution models and flow analysis to examine the effects of verrucose, pocked, and furrowed surface morphologies on potential mass transfer across plate corals. It also examines how flow interacts with these surfaces across platelike and cylindrical objects. Generally, dissolution per unit profile area increased with added ornamentation and surface area. However, there were diminishing returns with regards to material investment; the more surface area there was for dissolution, the less efficient dissolution was per unit surface area. Secondly, surface texture dictated flow of water, either directing flow to or away from the colony, or quelling movement completely. Surface texture also directs flow differently depending on gross morphology. Understanding flow at small scales, particularly around locations of polyps, is important for understanding mass transfer. This study is a first order attempt to address this issue, but further work is needed to quantify flow at the locations of polyps and the role of particular surface textures in engineering local flow regimes.

INTRODUCTION

Diffusion of gas or nutrients between an object and a fluid is directly reliant upon flow at the boundary surface. As a result, the size and shape of an object, as well as the speed and turbulence of the fluid, heavily influence the amount of flux. Organisms that rely on nutrients or food in the water column often must engineer themselves to deal with these variables in order to experience the right kind of flow, all the while balancing out structural integrity, and where applicable, exposure to sunlight.

Corals are one of many organisms that rely on plankton and detritus in the water column for the nutrients necessary for growth (Ferrier-Pages et al., 2003; Lesser & Weis, 1994). Coral reef environments are nutrient-poor, so diffusion of nutrients into corals from the water column is very limited. However, corals can take advantage of their prey, which concentrate those nutrients into convenient, edible packets. As a result, corals grow well when there is good enough flow for polyps to encounter their prey. To an extent, the more water that flows by and the longer particles are kept in eddies near the polyp, the more likely it is to catch its prey.

Much work has been done on gross morphology and its effect on flow, particularly with inference to its effects on mass transfer. The flow-baffling and flow limiting of coral plates or fingers, as well as the relative constancy of flow across encrusting corals, has been expounded upon by multiple authors (Helmuth et al., 1997; Sebens et al., 1997; Woesik et al, 2012). However, little work has been done with smaller-scale surface morphology, which has a more direct control over flows local to polyps.

Some amount of surface roughness can create turbulence, which facilitates mass transfer. On a community-level scale, this has been shown with total reef roughness and ammonium uptake (Thomas & Atkinson, 1997). Roughness on a smaller scale could produce local turbulence, which may bring about similar changes in local uptake, but studies aimed to parse the effects of surface texture have been inconclusive, with potential signals being overprinted by effects related to changes in flow speed and colony size (Gardella & Edmunds, 2001).

The primary aim of this study is to examine the relationship between small surface structures and gross colony morphology with respect to engineering local water flow to promote mass transfer. More specifically, it examines efficiency of mass transfer between objects with the same shape, but different surface patterns. I use plaster tile dissolution experiments as an analog to examine the effects of surface morphology on mass transfer across a platiform colony. Secondly, flow across these tiles is qualitatively compared to flow over cylinders with similar surface morphologies.

METHODS

Four types of surface morphologies were examined: furrows (lateral grooves, extending across the tile), hemispherical wells, hemispherical protrusions (verrucae), and smooth surfaces (Fig. 1). These surface textures were examined across tiles and cylinders, representing platiform and fingerlike corals. Mass transfer was simulated by the dissolution of plaster tiles with these particular surface morphologies. Due to time limitations, plaster cylinders were not created, but cylindrical models were set aside for later flow analyses. Flow was then analyzed using dye across both tiles and cylinders.

The tiles and cylinders with each of these surface textures were originally sculpted out of clay. Each tile was approximately 8.5 x 8.5 cm in profile and each cylinder was about 5.5 cm in diameter and 12.5 cm in length, including 2 cm clay plugs on either side for attachment to 2-1/4 inch PVC pipe. Three plaster copies of each clay tile were created using a mold comprised of a mixture of silicone caulk and cornstarch. Profile area and total surface area of each mold was determined by overlaying with aluminum foil and calculating the area of the tile outline (profile) and the area of the aluminum foil when set flat (total surface area).

Upon setting hard and lying untouched for 12 hours, the plaster tiles were kept in a drying oven at 75°C for another 16 hours before use. The duration time in the oven was experimentally determined using sample molds, with the ultimate drying time determined to be when the change in largest model mass, after an additional hour in the oven, was no more than one-hundredth of a gram.

Tiles were weighed individually and set in a wooden frame to minimize dissolution around tile edges (Fig. 2). The frame was lowered into a flume, oriented perpendicular to flow during each run. Water velocity was kept at a steady 8.6 cm/s and each tile was left to dissolve for 2-hours. Afterwards, tiles were removed and placed in the oven once more for 20 hours before being weighed again. Differences in mass were set against profile area and exposed surface area.

While plaster or clay models were in the flume, dye was placed on different surface locations to examine local flow. The clay cylinders were mounted on wooden dowel and placed into the flume for flow analysis, with either end fit into PVC pipe to limit edge effects. Each shape was examined at low flow (2.5 cm/s) and higher flow (8.6 cm/s).

RESULTS

Dissolution experiment

Dissolution of each object ranged from 0.88g to 1.83g (Table 1). Set against profile area, plates with raised bumps show greater dissolution per unit profile area than any other surface (Fig. 3). Plates with wells and with furrows follow with slightly less dissolution per unit profile area, and the smooth plate shows the least dissolution per unit area. When dissolution is set against surface area, the raised bump plates show the lowest dissolution per unit surface-area (Fig. 4). Unadorned plates and furrowed plates show the highest dissolution rates relative to surface area.

Flow Observations

Flow across the flat tiles and flattened cylinders shows little turbulence. Water is directed in straight lines away from a center point 1/3 of the way down from the top of the tile (Fig. 5A). Flow around the cylinder is uniform across the length of the object, with linear flow towards the rounded sizes. Flow across furrowed tiles and cylinders is more turbulent. Water was channeled into the furrows of the tile, with vortices directing water off the edges (Fig. 5B). Dye was observed hugging the surface of the object between furrows or being ejected into the water column from the higher ridges. Around the cylinder, few vortices form except those that appear periodically at the forward edge of the object. However, funneling of water into grooves is prominent, with quick linear flow proceeding round the sides of cylinder. An increased amount of turbulence is observed on the leeward side of the object.

The wells in platiform and cylindrical models differ in their effect on flow as well. The depressions in the center of the tiles are low-energy zones, with visibly-reduced movement (Fig. 5C). Dye placed in the wells stays there until a small eddy enters the depression and wisps up dye into the water column. Closer to the sides of the tile, flow over the openings increases, and dye is less likely to stay in these wells. In cylinder form, the wells show stronger eddies on the forward edge, but show little to no obstruction of flow around the sides. Turbulence in the wake of this cylinder is similar to that of the smooth control cylinder, with low turbulence on the leeward side than in the furrowed example (Fig 6). On the other hand, the cylinders with raised bumps show strongly increased turbulence immediately downstream. In addition, strong eddies form at the forward edge, directing flow across the sides of the cylinder (Fig. 7). These eddies form in the spaces between the elevated bumps, and water is directed across the side of the cylinder with some avoidance of raised bumps. The plates with raised bumps show faster movement near the tips of the protrusions, while dye at the base of the ornamentation is slowly channeled out the sides of the block (Fig. 5D).

DISCUSSION

Adding ornamentation or surface texture appears to increase the amount of flux relative to profile area. This suggests that for corals that are spatially limited, adding surface roughness of any kind might be more advantageous than having a smooth surface. However, there may be diminishing returns, as dissolution does not scale up linearly with surface area. Tiles with greater surface area were less efficient in dissolution per cm^2, even though they appear more efficient per cm^2 of profile area. As there is a cost to growing more skeleton, there is an energy balance corals must keep. If spatially limited, a coral wants to become more spatially efficient but it may be limited in how much it can invest into building outward.

Although these experiments were done with surface structures similar to that of modern corals, they ignore the shape of the soft tissue of the polyps. Although dissolution may vary between the forms tested, what matters is where that dissolution is occurring. Absorption of nutrients depends on the kind of flow experienced by the polyp itself, and thus where the polyp is and how large it is will have an effect on efficiency of mass flux. For example, if water movement is minimal in a depression and the polyp remains in that depression, it never encounters much flow. However, if it extends above the depression to take advantage of the turbulence created, it may encounter food and nutrients far more often. Likewise, if it rests within a groove like on the furrowed plates, it may experience good flow, even if local water movement is limited. With this mindset, we can look at examples of modern corals and gain some insight from observed flow over models.

One example candidate would be *Agaricia tenufolia*, which has a structure similar to the furrowed test plates. The polyps are small, set into the furrows, and do not reach out of the grooves with tentacles extended (K. Sebens, *pers comm*). In this situation, the polyps could take advantage of the water funneled by these ridges. Even if flow is low, the funneling effect should increase flow across the colony. *A. tenufolia* is noted for its ability to carry out photosynthesis at maximum capacity, even in low flow (Sebens *et al*, 2003). This funneling mechanism could act as an aid to obtaining nutrients at low flow. In addition, these furrows directs old water away from the colony, and may help ensure already-filtered water is not passed over neighboring polyps, operating just as monticules do for particular bryozoans. This morphology appears to be widespread in vertical, platelike corals, including other *Agaricia* spp., *Pavona varians* and *Montipora* *capricornis*, which may reflect a functional efficiency that is suitable to such a gross morphology.

Raised bumps, as seen in corals such as *Acropora palmata*, would lift the polyps above the boundary surface and expose them to more turbulent flow than they would experience otherwise. So long as the branching isn't dense enough to create a new stable flow boundary, flow across those polyps should be elevated. The dissolution model suggests this higher flow across the tips of bumps is also true for situations in which the angle of attack is perpendicular to water flow. The model also suggests that such a morphology is spatially efficient, allowing for more uptake over a smaller space. This is primarily due to the drastically-increased surface area. When dissolution is normalized for surface area, the morphology seems grossly inefficient. However, if the areas that are dissolving most are the points where polyps would be, perhaps that inefficiency is negligible to the coral, particularly if the cost of maintaining soft tissue and mucus over the increased surface area isn't exceptionally high. Further study would be needed in order to examining this kind of energy balance in such morphologies.

Corals with polyps set inside welled chambers would have a great deal of trouble getting sufficient flow if facing an oncoming current, particularly if flow is already very low. However, those welled chambers may allow for comfortable feeding in high-flow environments. As the polyps would not be as exposed, they may not be battered by oncoming currents as much as polyps set on pedestals. They may rather take advantage of eddies that would be stirred up within the chamber due to the high flow over the opening. This is purely speculative without measurements of flow in the wells or observation of such corals in high-energy environments, but the potential for such flow exists in these structures and should be examined.

Although this study is a good first step into examining the intersection of surface texture and mass transfer, there is much more that can be done to better visualize and quantify their relationship. First and foremost, additional study is needed in order to pinpoint regions of high flow and turbulence across the diverse types of surfaces presented by corals. Furthermore, a greater understanding of the dynamics between surface texture and gross morphology is needed in order to confidently apply the results of this study to modern corals. Measuring or modeling mass transfer in corals requires an understanding of flow dynamics from the micro to regional scale, taking into account not only different coral forms, but also both unidirectional and oscillatory flow. Surface texture is just one of many elements that must be considered, but at the most local of scales, it likely has a strong influence in determining where colonies will be able to live and grow.

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FIGURES AND TABLES

Figure 1: Plaster molds of tiles and clay cylinders. From left to right: flat(unadorned), furrowed, raised bumps, inset wells.

Figure 2: Frame for plaster tiles. Each time was inset within the frame, with the surface of the tile at the same height as the surrounding frame. In this setup, bumps rise above the frame plane while wells and furrows are set below the plane. Nonstick clay was used to fill gaps between plaster and wood

Table 1: Dissolution figured from each plaster model. Figures represent 2 hours of dissolution in the flume.

Smooth surface							
Run/Batch	Starting Mass (g)	Final Mass (g)	Difference	Dissolution / Aprofile	Dissolution / $A_{surface}$	Profile area (cm^2)	Surface area (cm^2)
1	110.89	110.01	0.88	0.013420772	0.01293547	65.57	68.03
2	133.77	132.52	1.25	0.019063596	0.018374247	65.57	68.03
3	132.31	131.31	1	0.015250877	0.014699397	65.57	68.03
Average	125.6566667	124.6133333	1.04333333	0.015911748	0.015336371	65.57	68.03
SD	12.80912695	12.66132036	0.18876794	0.002878877	0.002774775		

Furrowed surface							
Run/Batch	Starting Mass (g)	Final Mass (g)	Difference	Dissolution / Aprofile	Dissolution / $A_{surface}$	Profile area (cm^2)	Surface area (cm^2)
1	139.69	138.67	1.02	0.015967439	0.013089173	63.88	77.927
2	137.06	135.84	1.22	0.019098309	0.015655678	63.88	77.927
3	123.93	122.65	1.28	0.02003757	0.016425629	63.88	77.927
Average	133.56	132.3866667	1.17333333	0.018367773	0.015056827	63.88	77.927
SD	8.44286089	8.550101364	0.13613719	0.002131139	0.001746984		

Inset wells							
Run/Batch	Starting Mass (g)	Final Mass (g)	Difference	Dissolution / Aprofile	Dissolution / $A_{surface}$	Profile area (cm^2)	Surface area (cm^2)
1	112.12	110.91	1.21	0.018105641	0.013074014	66.83	92.55
2	129.5	128.1	1.4	0.020948676	0.015126958	66.83	92.55
3	141.12	139.98	1.14	0.017058207	0.012317666	66.83	92.55
Average	127.58	126.33	1.25	0.018704175	0.013506213	66.83	92.55
SD	14.59502655	14.61560467	0.13453624	0.002013111	0.00145366		

Raised bumps							
Run/Batch	Starting Mass (g)	Final Mass (g)	Difference	Dissolution / Aprofile	Dissolution / $A_{surface}$	Profile area (cm^2)	Surface area (cm^2)
1	154.68	152.99	1.69	0.021669445	0.014037711	77.99	120.39
2	147.92	146.09	1.83	0.023464547	0.015200598	77.99	120.39
3	150.45	149.03	1.42	0.018207462	0.011795	77.99	120.39
Average	151.0166667	149.37	1.64666667	0.021113818	0.013677769	77.99	120.39
SD	3.41544043	3.462542419	0.20840665	0.002672223	0.001731096		

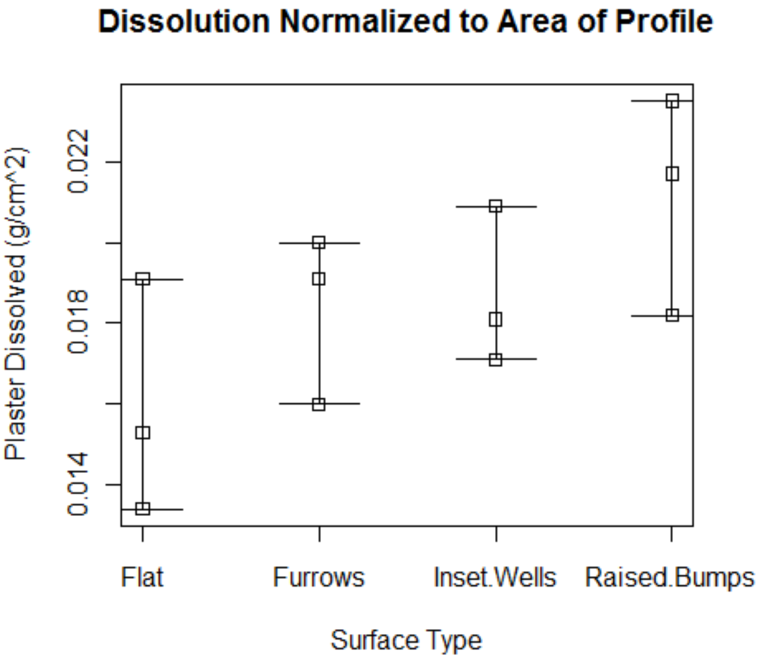


Figure 3: Dissolution of plaster tiles normalized to profile area. Note the verrucose surface shows the greatest apparent spatial efficiency per cm^2 of tile.

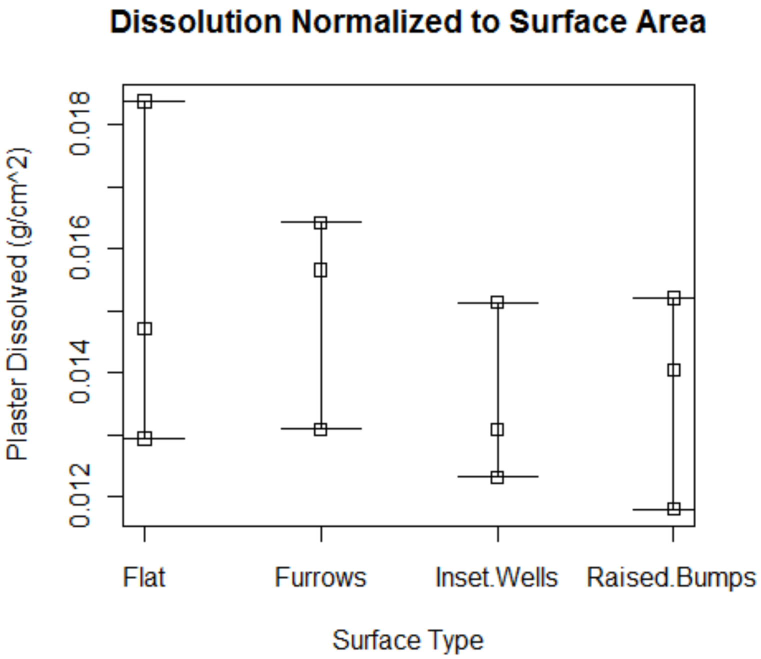


Figure 4: Plaster dissolution of tiles normalized to surface area. X-axis lists textures with increasing surface area, from left to right. Note that with increasing surface area comes greater inefficiency of dissolution per unit area.

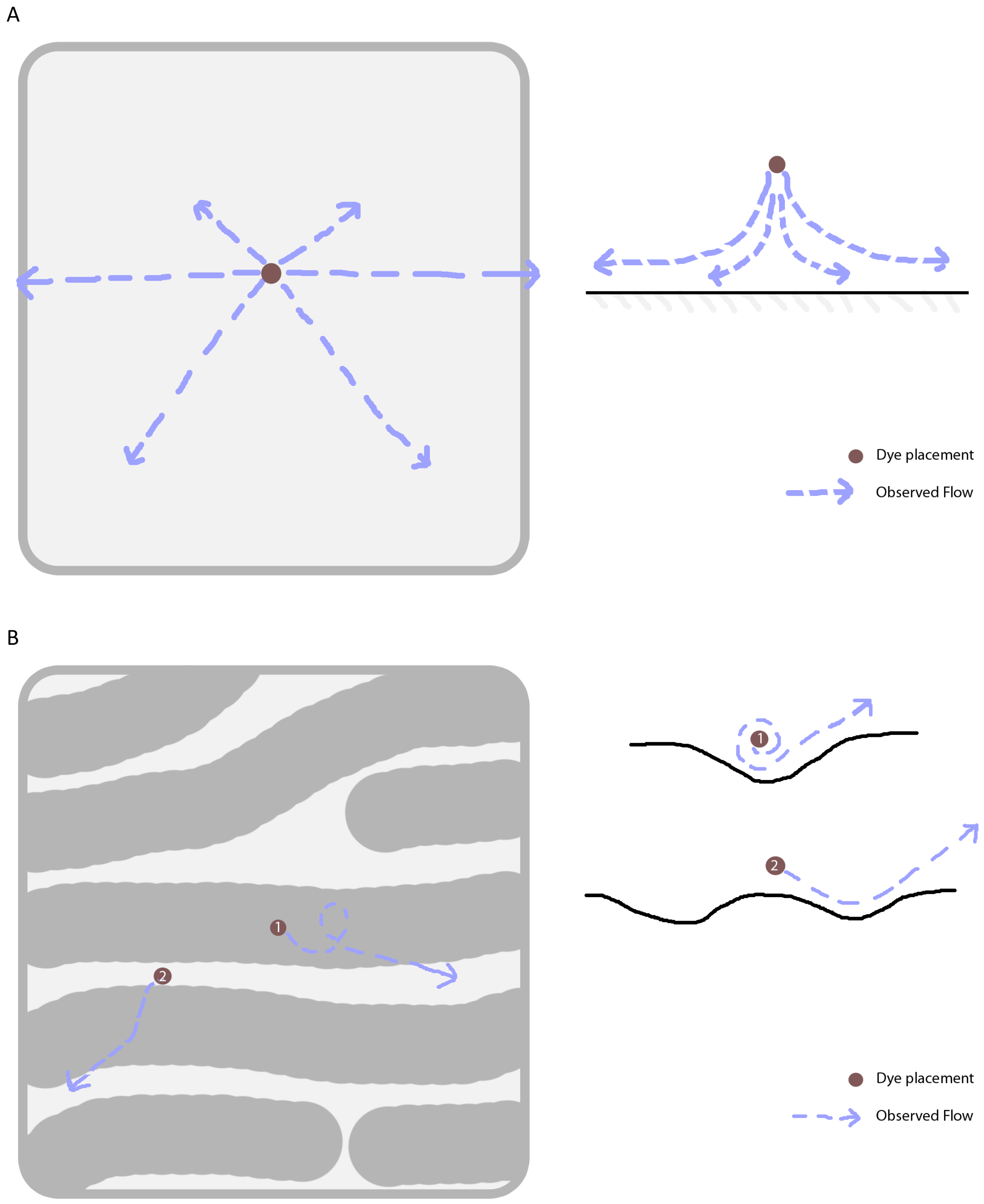
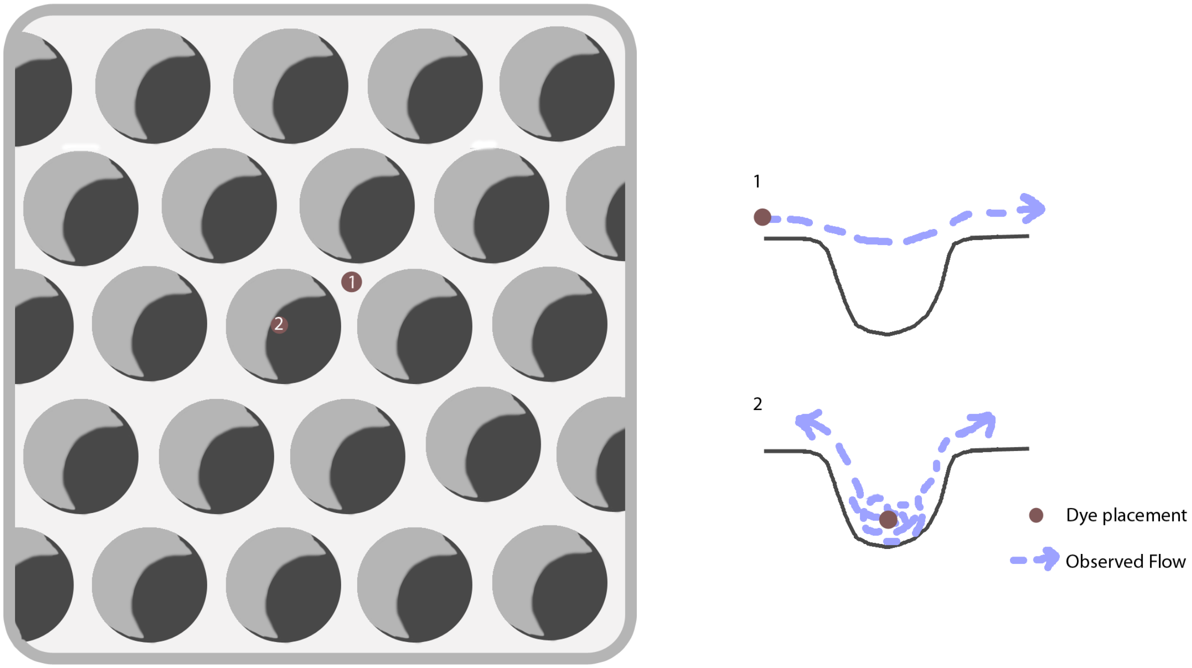


Figure 5: Observed flow across plaster tiles (A-D). Where applicable, dye was placed at high and low points along surface. A) Flat tile: Note planar flow around tile, little turbulence; B) Furrows: water us funneled into channels, turbulent eddies in furrows direct flow outward and away from surface; C) Inset wells: zones of low flow appear in center wells, but eddies periodically wisp up dye into the water column. Closer to edges, flow moves quickly over wells, dipping inwards and creating strong eddies inside them; D) Raised bumps: Water moves quickly across top edges of bumps, slowing down closer to the base. Dye is channeled out the sides of the tile.

C


1
2
1
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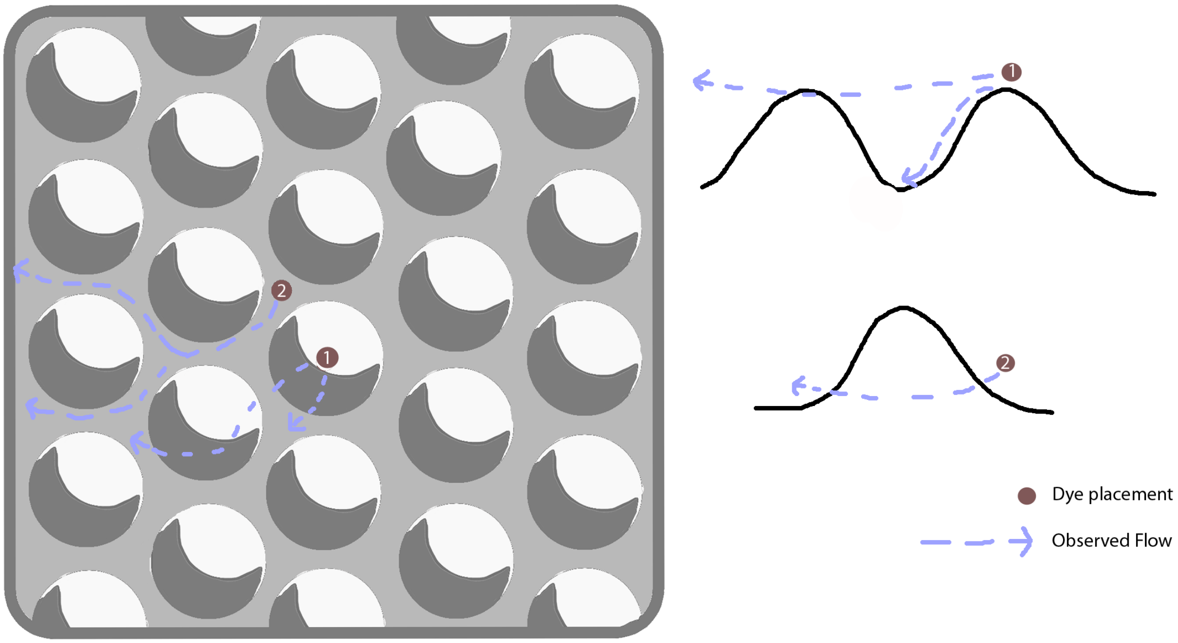
Dye placement
Observed Flow

D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Dye placement
Observed Flow

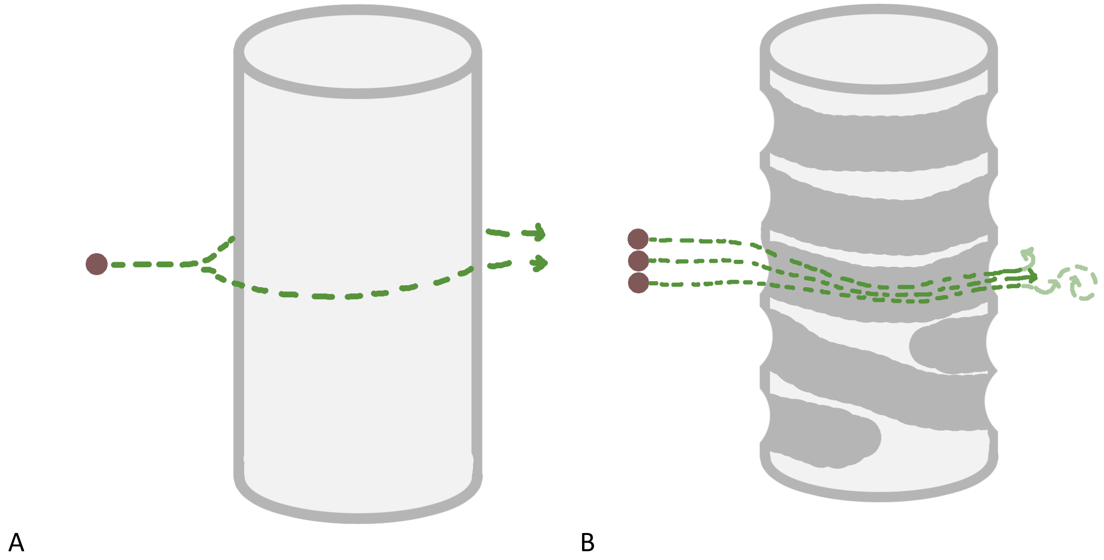
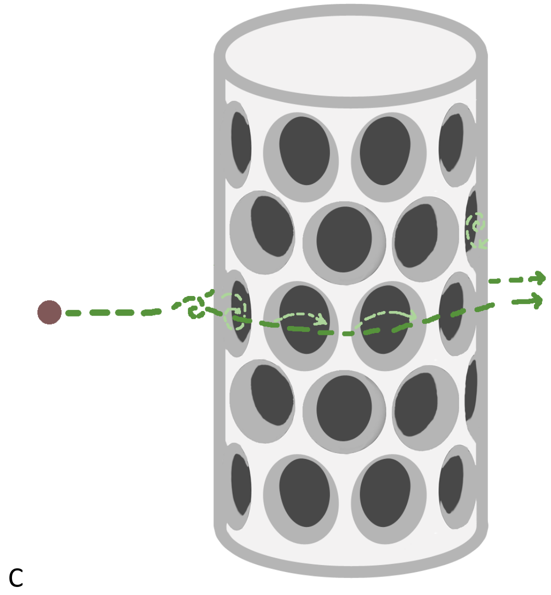


Figure 6: Flow around cylinders. Brown dot is location of dye injection. Green line tracks path of dye. Light green lines note areas of turbulence. A) Smooth cylinder; Flow is consistent with no visible turbulence except in the leeward side of the cylinder. B) Furrowed cylinder: Water appeared to funnel into the grooves and created greater turbulence in the leeward side than the control, smooth cylinder. C) Inset wells: Prominent eddies form in the depressions, particularly on the front and leeward-facing wells. Flow is unidirectional into wells on the sides parallel to flow. Little turbulence extends leeward of the cylinder aside from the wells.



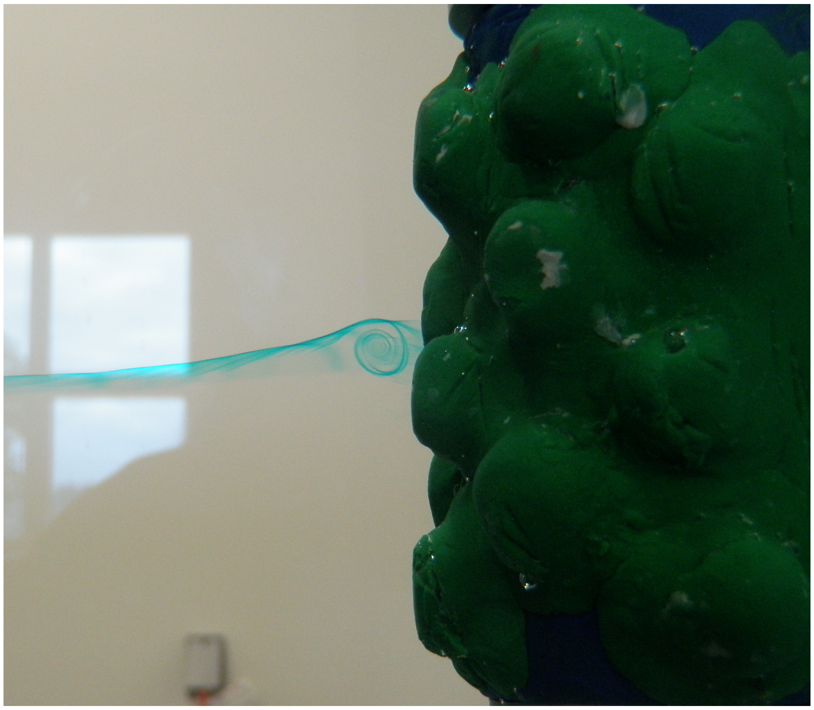


Figure 7: Turbulence on the front edge of the verrucose cylinder. Turbulence forms in the crux of three verrucae, and spiral flow extends around the sides, deflecting away from elevated bumps. Turbulence is high on the leeward side.