

HYDRODYNAMICS

Modus vivendi

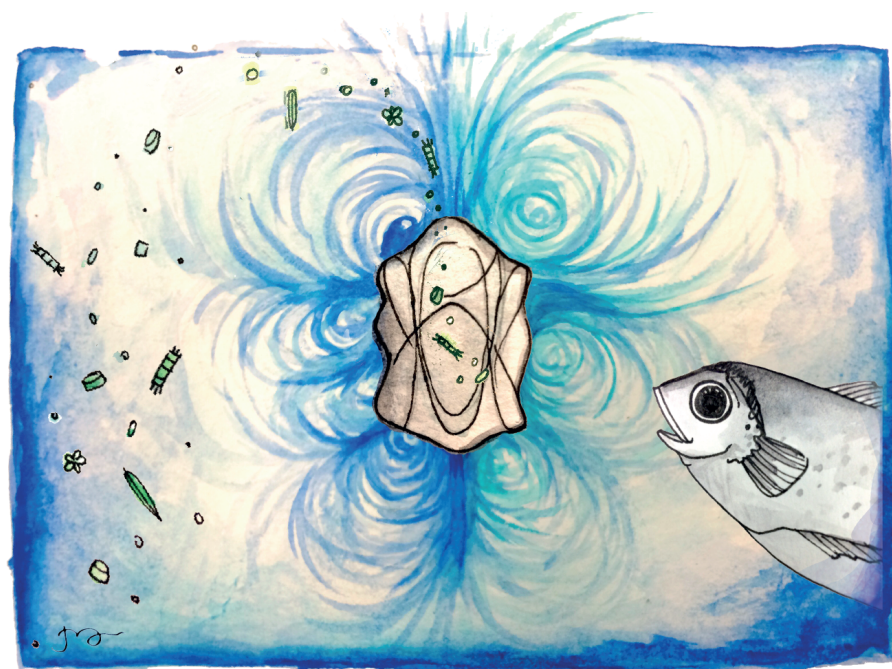
Striking visualization of the flows generated by starfish larvae in their fluid environment offers unique insight into how these organisms live. The beautiful vortices they create betray a dynamic mechanism for trading swimming off against feeding.

Vicente I. Fernandez and Roman Stocker

All aquatic organisms face an inherent difficulty: they need to balance the competing interests of migrating, feeding and avoiding predators — all mediated by their interaction with the surrounding fluid. The task is particularly challenging for those living in fluids of low Reynolds numbers, where viscosity dominates. It is perhaps not surprising then that the direct visualization of the flow fields surrounding these creatures — from micrometre-sized bacteria¹ to centimetre-scaled fish² — has proved itself to be an invaluable resource for investigating the physics underlying the behaviour of and interactions between aquatic organisms. Now, writing in *Nature Physics*, William Gilpin and colleagues have shown, using striking images and videos of the flow around bat star (starfish) larvae, that these larvae resolve a direct trade-off between swimming and feeding by switching between two different flow fields³.

Although the visualization of the flow fields generated by microorganisms has a strong track record^{1,4,5}, starfish larvae present an intriguing new subject for investigation due to their mechanism of locomotion. These larvae, approximately 1 mm in size, have dense bands of cilia that circle along the organism's periphery. Inside these bands, the closely packed, hair-like cilia beat in a directed and coordinated manner to drive the fluid along the direction of the ciliary band.

By visualizing the flow around individual starfish larvae, as depicted in the illustration, Gilpin and colleagues found that the larvae have two distinct behavioural states: swimming and feeding. During swimming, the flow field is dominated by one large vortex on each side of the larva (in the larva's frame of reference). In contrast, during feeding, portions of the ciliary band reverse direction, generating numerous smaller vortices. These additional vortices generate a feeding current by changing the path of incoming prey organisms, bringing them closer to the surface of the larva for a longer period of time. Using a classic



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mathematical model of a low Reynolds number swimmer — a so-called squirmer — the authors showed that an increase in the number of vortices is predicted to increase the feeding rate and at the same time to decrease the swimming speed. This direct trade-off between swimming and feeding is likely responsible for the larvae's intermittent behaviour.

The squirmer model, in which a prescribed tangential surface velocity creates a flow around the organism, has a long tradition in aiding the study of locomotion of microscopic organisms and the trade-offs they face. Stokeslet models offer an alternative, based on a superposition of fundamental singularities that are solutions of the linear equations of fluid mechanics at low Reynolds numbers (Stokes equations). These models are frequently used when the fluid is forced in specific locations, as in the case of microorganisms with small numbers of flagella. In contrast, the squirmer model decomposes the surface velocity into a superposition of modes with

increasing spatial complexity. As the authors showed, the feeding and swimming flows of starfish larvae open an interesting direction for further fundamental research on squirmers, as flow states that are biologically very different are well captured by the combination of a few modes. This work on starfish larvae fits into a backdrop of efforts to find what constitutes optimal feeding under different conditions and for different types of microswimmers^{6,7}. In several cases, the observed morphology or behaviour is close to the optima predicted theoretically⁶ for feeding or swimming.

The conclusions from Gilpin and colleagues depart somewhat from previous theoretical studies using squirmer models, which found that non-swimming modes — such as those responsible for the extra vortices in larvae — do not contribute as much to feeding as the swimming mode⁷. It will be interesting to follow the resolution of this discrepancy, and understand whether it lies in the constraints (such as a fixed-energy budget) on the organism, in the nature of


the modelled prey, or elsewhere. It is also possible that the larval behaviour does not represent optimal feeding, due to additional biological and ecological pressures.

One such biological pressure known to also affect the flow fields generated by microorganisms, and not considered by Gilpin and colleagues, is predation. As recently demonstrated for other zooplankton through the use of similar hydrodynamic techniques, feeding currents can increase the hydrodynamic footprint of an organism and thereby increase the chances that it is detected by predators with mechanosensory systems⁸. In copepods, differing predation pressures may explain the variety of feeding strategies, which include both stationary feeding (similar to the starfish larvae) and cruising feeding. For starfish larvae, predators include fish that often have mechanosensing capability via their lateral line system and may therefore cause the larvae to sacrifice efficiency in feeding in order to restrict the spatial or temporal extent of the flow disturbance. It thus seems likely that the need to evade predators may also play a role in determining the flow fields produced by starfish larvae.

Gilpin and colleagues also provide new insight into a fundamental principle of ciliary fields. A classical theorem in topology — the ‘hairy ball’ theorem⁹ — states that it is impossible to have a completely smooth vector field on

a sphere, or equivalently to perfectly comb a hairy ball. This means that the typical surfaces covered by cilia, often close to spheres or ellipsoids, must have defects where the direction of the flow driven by surface cilia abruptly changes. The consequences of these defects have been observed on coral surfaces, which are also covered by cilia, to generate a prominently vortical structure to the millimetre-scale flow fields induced by the corals, considerably enhancing mass transport¹⁰. In their work with the quasi one-dimensional ciliary bands of starfish larvae, Gilpin and colleagues directly observed surface flow discontinuities where the beating direction of the ciliary band reversed. At these interfaces where the flow is either converging or diverging, individual cilia are crushed together or pulled apart and do not seem to beat with their neighbours (but may help to capture prey). The observation of ciliary movement at defect locations could provide impetus to modellers working on hydrodynamic coordination of individual cilia, by providing an example of how this coordination can break down.

We are reminded by exploratory voyages such as *Tara Oceans*¹¹ about the astonishing diversity of small planktonic organisms still being uncovered even in our modern times. The multitude of shapes and behaviours observed in such studies highlights the individual-level

interactions that these species’ have with their environment, underpinning their crucial roles in the oceans’ food-web and biogeochemical cycles. Modern laboratory and visualization techniques are adept at probing the often beautiful small-scale flows that these organisms generate. They represent a powerful way to gain access to this microscale world and to understand the physical principles that govern and constrain life at these scales. 

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