Functions and Efficiency of Ciliary Swimming

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Planktonic microorganisms are ubiquitous in water, and their population dynamics are essential for forecasting the behaviour of global aquatic ecosystems. Their population dynamics are strongly affected by these organisms' motility, which is generated by their hair-like organelles, called cilia or flagella. However, because of the complexity of ciliary dynamics, the precise role of ciliary flow in microbial life remains unclear.

In terms of fluid dynamics, ciliary swimming has been analyzed by using a squirmer model. A classical squirmer model propels itself by generating surface tangential and radial velocities [1]. The velocity squirmer model has been used for investigating varieties of suspension properties, such as rheology, coherent structures and mass transport. Recently, we developed a novel squirmer model in which, instead of a velocity being imposed on the cell surface, a shear stress is applied to the fluid on a stress shell placed slightly above the cell body [2]. The shear stress expresses the thrust force generated by cilia, and the distance between the stress shell and the cell surface represents the length of the flagella. The fluid must satisfy the no-slip condition on the cell body surface. The stress squirmer model has been successful in reproducing cell-cell interactions and cell-wall interactions.

In order to understand swimming energetics, we further developed a ciliate model incorporating the distinct ciliary apparatus [3]. The hairy squirmer model revealed that over 90% of energy is dissipated inside the ciliary envelope. By using the hairy squirmer model, we found that ciliary flow highly resists an organism's propulsion, and that the swimming velocity rapidly decreases with body size; proportional to the power of minus two. Accordingly, the propulsion efficiency decreases as the cube of body length. By increasing the number of cilia, however, efficiency can be significantly improved, up to 100-fold. We found that there exists an optimal number density of cilia, which provides the maximum propulsion efficiency for all ciliates [4]. The propulsion efficiency in this case decreases inversely proportionally to body length. Our estimated optimal density of cilia corresponds to those of actual microorganisms, including species of ciliates and microalgae, which suggests that now-existing motile ciliates and microalgae may have survived by acquiring the optimal propulsion efficiency. These conclusions are helpful for better understanding the ecology of microorganisms, such as the energetic costs and benefits of multi-cellularity in *Volvocine*, as well as for the optimal design of artificial micro-swimmers.

References

[1] Blake, J., *J. Fluid Mech.*, **46**, 199-208 (1971).
[2] Ishikawa, T. et al., *J. Fluid Mech.*, **903**, A11 (2020).
[3] Ito, H., Omori, T., Ishikawa, T., *J. Fluid Mech.*, **874**, 774-796 (2019).
[4] Omori, T. Ito, H., Ishikawa, T., *Proc. Natl. Acad. Sci. U.S.A.*, in press (2020).