BOUNDARY ELEMENT ANALYSIS OF PROPULSIVE FORCE AND TORQUE OF A DINOFLAGELLATE *SYMBIODINIUM*

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Summary Swimming motion of a dinoflagellate *Symbiodinium* is analyzed with the boundary element method (BEM) and high-speed video observation. Our observation shows that a transverse flagellum produces thrust and that there is a membrane between the transverse flagellum and the cell body. BEM analysis reveals that this membrane produces thrust as much as that of an observed cell. The model with no membrane produces little thrust.

INTRODUCTION

Dinoflagellates swim using two kinds of flagella: a transverse flagellum encircling the cell and a longitudinal one trailing perpendicular to the transverse flagellum. Role of each flagellum is, however, not clarified quantitatively. It is partly because of the diversity in the species of dinoflagellates, and partly because of the difficulty in observing their swimming motion. It has been reported that some kinds of dinoflagellates use their transverse flagella to rotate around their length axes, while they use longitudinal ones for their translational swimming [1]. On the other hand, LeBlond et al. have proposed propulsive mechanism of dinoflagellates by transverse flagella [2]. Miyasaka et al. observed the swimming motion of *Prorocentrum minimum* cells with a high-speed video to obtain detailed shape and motion of transverse and longitudinal flagella [3]. Their swimming motion has recently analyzed by using the resistive force theory, resulting in propulsive thrust by a transverse flagellum [4]. The boundary element method (BEM), which can be adapted to arbitrary cell shapes, may be used for details of swimming motion of dinoflagellates. In this study, role of a transverse flagellum in swimming motion of a dinoflagellate *Symbiodinium* is investigated by using BEM analysis, where the cell is modeled according to the observation.

METHODS

Cell Model

Detailed structure and characteristic swimming motion of *Symbiodinium* cells are observed by a high-speed camera and an electron microscope. A cell body is dumbbell-shaped and slightly elongated into the longitudinal direction as shown in Fig. 1. A transverse flagellum seems to have a helical shape, with the helical axis forming a circle around the cell body. In this electron micrograph, a membrane can be seen between the cell body and its helical transverse flagellum. The size of a cell body is approximately 10 μm and the radius of helical flagellum is 1 μm.

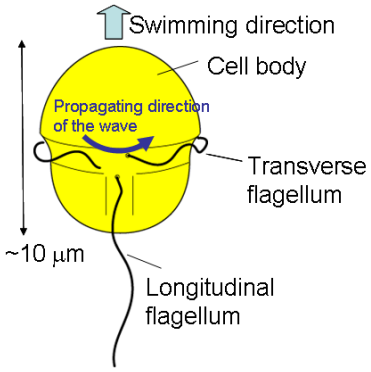

Fig. 1. Illustration of a *Symbiodinium* cell.

In order to investigate roles of each flagellum, we observed the swimming motion of *Symbiodinium* cells without either flagellum. Transverse and longitudinal flagella can be removed by sonication and a vortex mixer, respectively. A *Symbiodinium* cell can swim translationally despite lack of its longitudinal flagellum, while it only change its direction at the same position and does not swim forward without its transverse flagellum.

High-speed movie reveals that the transverse flagellum has a left-handed helical form, the wave of which propagates right viewed from the swimming direction, seeming that there is no deformation of its waveform. Speed of propagating wave is 6.5 turns around the body per 1 second. Translational swimming speed is 180 μm/s in average.

The cell model in this study was constructed based on the observed result above. In our model a transverse flagellum was represented as a left-handed helix around the equator of the sphere, with pitch of 1/7 turns around the body. Three-dimensional representation of the membrane is shown in Fig. 2. All of the seven wider parts of the membrane are tilted in the same way. It is expected that when the helical wave propagates to the direction as indicated by the arrow in Fig. 2, these wider parts of the membrane produce thrust perpendicular to this paper, indicated in the figure. Little thrust will be produced if there is a transverse flagellum alone and no membrane.

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Boudary element analysis

The numerical method was based on boundary element analysis, which is detailed in Ref. [5]. Because the Reynolds number of the associated fluid motion is 10^{-3}, the fluid motion is therefore governed by the Stokes equation. Both the cell body and membrane are assumed to be rigid bodies and rotate relative to each other, though the membrane does not actually rotate but the helical wave only propagates.

RESULTS

We compare the swimming speed of our cell model with that of the observed cell. We refer the swimming distance in one turn of the membrane as thrust rate. Figure 3 shows the thrust rate for cell models with various radii of helical membrane *r*. Observed thrust rate is 25 μm/turn in average, which is similar as calculated results.

In order to confirm existence of a membrane between a transverse flagellum and a cell body, we calculate the thrust rate of our cell model without a membrane (only the transverse flagellum). The model without membrane has thrust rate of only 3.0 μm/turn.

The obtained results above are based on the assumption that the rigid cell body and membrane rotate relative to each other, different from an actual *Symbiodinium* cell. Nevertheless, calculated thrust rate is in agreement with the observed result. With respect to the thrust, there is no difference between our model and actual motion because it is velocity of the elements of the membrane to the ambient fluid that contributes propulsive thrust of the cell. It can be said that our model cell has proper dimensions.

With respect to the rotation rate of cell body, there is considerable difference between our observation and simulation. In the simultaneous observation from two orthogonal directions, when a *Symbiodinium* cell swims by using its transverse flagellum, a cell body and transverse flagellum rotate in the same direction. Especially in the vicinity of a surface, the cell body never rotates. In contrast, the angular velocity of the cell body is much larger than that of the membrane in our calculation. A longitudinal flagellum may play a role of balancing in torque. It also may be important that the membrane expands and contracts with the propagation of its helical wave, producing a flow field on the membrane.

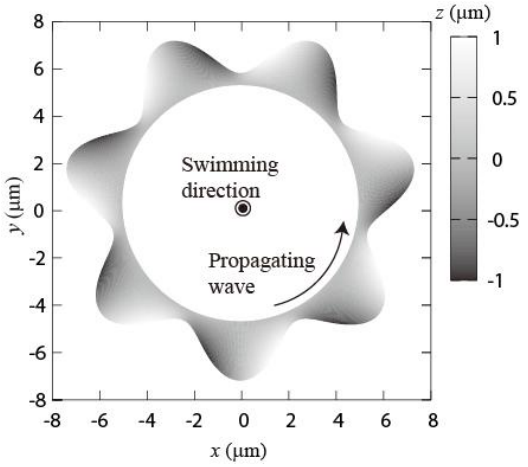

Fig. 2. Three-dimensional representation of the membrane.

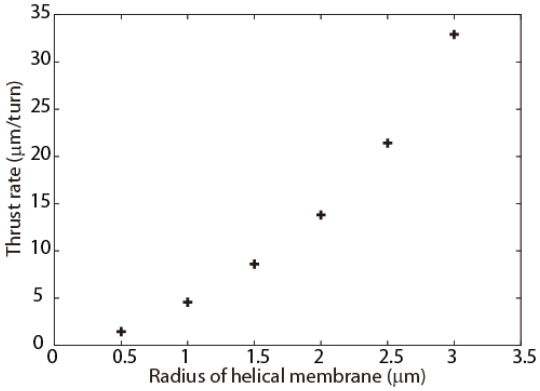

Fig. 3. Thrust rate of cell models with various sizes of radius of helical membrane.

CONCLUSION

Swimming motion of a dinoflagellate *Symbiodinium* is investigated by using BEM method and high-speed video observation. A model membrane assumed between a cell body and a transverse flagellum explains a mechanism of thrust by the propagation of helical wave of a transverse flagellum. This calculation result together with the experimental one clearly demonstrates the existence of membrane between a transverse flagellum and a cell body.

References

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