# Gravitactic Swimming of the Planula Larva of the Coral Acropora: Quantitative Description of Vertical Straightforward Swimming and Hairpin Turn, and Investigation into the Mechanism

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This thesis focuses on vertical straightforward swimming and hairpin turn of the planula larva of the reef-building coral *Acropora tenuis* and argues mechanisms of this unique behavior based on quantitative analyses of gravikinetic and gravitactic aspects.

Processes of dispersal and recruitment of acroporids' larvae have been understood in a simple scheme: eggs of acroporid corals are buoyant, and the resultant planula larvae gradually consume light lipids to go down to the seabed to settle down on appropriate substrata after dispersion mostly by horizontal advection in the ocean. However, it was found that about 10% proportion of the planulae migrate almost vertically between top and bottom with fairly straight trajectories, although most of the planulae stay exclusively at either the top or the bottom of the rearing tank. Planulae sometimes switched their swimming direction via a sharp turn in a hairpin-like trajectory (hereinafter referred to as "hairpin turn") between the opposite directions. Vertical swimming is expected to provide a new insight for dispersal and recruitment. In addition, vertical straightforward swimming and quick switching of swimming direction against gravity vector are considered to be a novel gravitactic swimming of aquatic invertebrates.

To quantify this vertical swimming in detail, we constructed a magnifying imaging device that can observe the shape and axis of the body. For recording, a thin chamber with an inner dimension of 100H × 100W × 3D mm made of glass plates separated by a 3 mm-thick silicon rubber spacer was used. The recorded video images were analyzed frame by frame using an image analysis software. The planula has a spheroidal shape of approximately 1mm in length and 0.4mm in width, and swims with their aboral-end in front with rotation around the fore-aft axis (rolling) and rotation around the axes perpendicular to the fore-aft axis (yawing/pitching) by beating cilia on the overall body surface. These rotational components caused planulae to swim along a helical trajectory. In contrast to horizontal swimming in a petri dish, which showed frequent changes of swimming directions and of speeds from 0 to 2 mm $s^{-1}$, vertical swimming was straight, and its speeds were stable and high as 2.44 ± 0.39 mm $s^{-1}$ in upward swimming and 2.10 ± 0.39 mm $s^{-1}$ in downward swimming on average. The hydrodynamic estimation of the larval body density calculated from the ascent speed of the motionless larvae that were treated by removal of cilia was 1.0176×103 kg·m-3, which was 0.25% lighter than seawater. This can be explained by the large amount of light lipids in the planula body. A comparison of the propulsion speed calculated from the swimming speed and the ascent speed statistically proved that the propulsion speed of the downward swim was significantly faster than the propulsion speed of the upward swim. These results suggest that planulae make a greater effort of propulsion in the downward direction than in the upward direction. In addition, most of the motionless larvae that were treated by removal of cilia oriented thin posterior (oral) end toward upward during floatation. This suggested that downward torque mainly works in larvae during vertical swimming due to the bias in the density distribution in the body (heavy anterior and light posterior). This was thought to fit the larva's purpose of going to the seabed to settle.

The hairpin turns were performed for tens of seconds between the longer-lasting straightforward swimming in opposite directions. Maximum turning rates of the swimming direction were –0.29 ±0.11 rad $s^{-1}$ and 0.28 ± 0.11 rad $s^{-1}$ on average, for downward and upward turns, respectively. Three hypotheses were investigated as the mechanism of hairpin turn: (1) shift of the center of mass of the larval body, (2) shift of the reaction center of hydrodynamic stress, and (3) change in ciliary movement. Regarding hypotheses (1) and (2), the distance among the centers of three forces which are acting on the body of an aquatic microorganisms due to gravitational acceleration; gravity, buoyancy, and hydrodynamic stress, was estimated by measuring the maximum rotation speed of each of the turning larvae. It suggested that a hairpin turn may occur due to a slight shift of center of forces. Plasticity of the larval tissue geometry could allow sufficient separation of the centers of forces to work together to generate gravitactic-orientation torque and, therefore, abrupt changing of the gravitactic swimming direction. The shift of the center of mass would be possible if the light lipid, wax ester, moved slightly within all cells simultaneously. The shift of the reaction center of hydrodynamic stress would be possible by changing the fore-aft asymmetry of the larval body shape. Preliminary measurements of the widths of the anterior and posterior ends on one individual planula suggested that there is a possibility of morphological changes. Regarding hypothesis (3), changes in ciliary motility, the water flow around a larva which reflected ciliary movement differed between the inside and outside of the hairpin turn trajectory. Since neuropeptide controls ciliary movement, neuronal control of ciliary movement may be involved in hairpin turns. Thus, larvae that swim straightforward vertically drawing a spiral trajectory are expected to be in a state where the torque derived from the spiral produced by the three rotating components and the torque derived from gravity are balanced. It was expected that a hairpin turn would begin when the torque equilibrium was disrupted by any one or more of the center of mass shift or the change of fore-aft asymmetry of the larval body shape on one individual planula or the change in ciliary motion. Future research is expected to test these hypotheses.

When planulae were put into a larger setup (400H × 200W × 3D mm), they could continue to travel even 40 cm upward or downward along nearly straight swimming paths. In the oceanic water column, which frequently has a static water mass structure, the planula may be able to travel vertically over longer distances than expected. During dispersal, vertical swimming will allow coral larvae to reach the seabed quickly and to depart from unfavored substrates to the sea surface for the next attempt at dispersal and settlement. This scheme provides a new insight into dispersal and recruitment of coral larvae. Thus, the unique bimodal gravitactic behavior of planula larvae are highly worth investigating not only in gravitational biology and biomechanics but also in ecology.