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Marine Biodiversity and Ecosystems

Comparative Biomechanics of Barnacle Larvae

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Time: 2019. 12. 30 Monday 14:30
Venue: Auditorium, 1st Floor, Interdisciplinary Research Building
跨領域科技研究大樓1樓演講廳
Host: Dr. Benny K. K. Chan陳國勤研究員

Doctoral Dissertation Defense Presentation

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Abstract

Adult barnacles display fascinating morphological variations and are adapted to a wide range of habitats, in some cases little morphological similarities are left in extremely modified taxa. Larval characters, such as the presence of frontal horns on nauplius larvae and the presence of an additional distinct cyprid larva in life cycle, have served to define the monophyly of this diverse group. However, the functional significance of these taxonomically important larval characters remains little understood. Barnacle nauplii swim to disperse, feed, and avoid predators. While the limbs are clearly involved in propelling their body through water and drawing food particle laden water towards their feeding apparatus, there has been few mechanistic studies showing empirical evidence of flow manipulation. By analyzing small scale hydrodynamics around swimming barnacle larvae, this thesis aimed at resolving fundamental questions on how barnacle larvae interact with surrounding water to swim and feed, and to examine the morphology-flow relationships with emphasis on the consequences of having frontal horns and transition into a distinct cyprid larva. A comparative analysis of naupliar body forms from 102 species of barnacles with geometric morphometrics shows that major variations are in aspect ratio and relative frontal horns length, which are significantly explained by larval size and trophic modes, respectively. Specifically, nauplii adopted a lecithotrophic trophic mode (non-feeding) have relatively shorter frontal horns than planktotrophic (feeding) nauplii, suggesting a possible feeding-related function.

Observation of swimming planktotrophic nauplii by particle image velocimetry technique shows that nauplii depended on feeding current generated during recovery stroke to draw particles towards body. This observation confirms the long proposed 'hypothetical' feeding flow as feasible mechanism for nauplius to swim and feed simultaneously. Compared to lecithotrophic nauplii with shorter frontal horns, planktotrophic nauplii had less backward movement during recovery stroke, which in turn help align the feeding chamber with suction current. However, the accurate feeding aided by 'anchoring effect' from having a high drag morphology with long frontal horns and tail spine was achieved at the cost of having slower swimming and higher predation risk than lecithotrophic nauplii due to pronounced fluid signal produced. To confirm the 'anchoring effect' of frontal horns, nauplii's frontal horns were experimentally ablated. Nauplii with frontal horns ablated swam with relatively higher backward movement during recovery stroke than intact nauplii, after accounting for individual variability in swimming speed. Flow paths of suction current produced by the ablated group also appeared to be straight, as oppose to the curved flow paths laterally converging to nauplius' body observed in the intact group. Analysis of flow field component perpendicular to nauplius' body axis confirmed the intact group did indeed draw water from a significantly wider area than the ablated group, which increase water clearance for food particles. Zooplankton morphology with long projecting extensions that is sub-optimal for swimming performance has long perplexed biologists. These findings support the hypothesis that such morphological traits confer feeding advantage but at the cost of swimming.

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The swimming-feeding tradeoffs has the potential to affect morphological evolution of larval form not only between taxa, but also through larval development as relative importance between swimming and feeding shift. Barnacles end larval period with a distinct non-feeding larval phase that specialized in settling onto substrate to complete their transition into sessile adults, which requires better swimming capability. Comparison of swimming between nauplii and cyprids shows that cyprids were better swimmer capable of moving more body length per beat cycle through maximizing relative duration of power stroke and asymmetry in appendages' configuration between power and recovery stroke. Given the streamlined fusiform shape and swimming kinematics, cyprids generated fluid field distinctive from that of the nauplii, and in particular with little return flow during recovery stroke. This shift to become better swimmers compromise cyprids ability to feed, highlighted the change in ecological role and requirement during development could shape larval morphology and kinematics. Notably, this change of swimming performance between nauplius and cyprid does not involve an increase in size, indicating that morphological change alone is sufficient to result in performance shift, without the switch from viscosity-dominated to inertia-dominated fluid regimes through coupled change in size and shape commonly seen during larval development of other marine invertebrates. In summary, this thesis shows that biomechanical constraints are important in shaping evolution of taxonomically important larval characters in the model system of barnacle larvae.