論 文 の 内 容 の 要 旨

論文題目 **Early life-history and biogeography of animals endemic to deep-sea hydrothermal vents**

（深海熱水噴出域固有動物の初期生態および生物地理に関する研究）

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Since the first discovery of deep-sea hydrothermal vents in 1977, a number of vent fields with unique invertebrate faunas have been found at Earth's submarine plate boundaries and several intraplate hot spots.　Such faunas, characterized by high abundance and endemism of component species, are supported by the primary production of chemoautotrophic bacteria associated with hydrothermal activities.　Biogeographically, hydrothermal vent fields are ephemeral and isolated from each other, so that the component taxa are assumed to have a considerable dispersal potential.　Most animal species at hydrothermal vents are benthic as adults while they may disperse from the original location to another in the water column as pelagic larvae.　Larval dispersal thus significantly contributes to the geographic distribution, population dynamics and evolutionary processes of the vent-endemic animals.

However, surprisingly little is known as to the extent that their planktotrophic larvae migrate vertically to shallower waters to take advantages of richer food supplies and strong currents. Biological components of larvae, such as duration, rate of development, swimming behaviour and physiological tolerances, would play essential roles in the spatial patterns of larval dispersal and in determining the geographic distributions of hydrothermal-vent endemic species.　Recently, the mining of deep-sea hydrothermal deposits such as seafloor massive sulphides has become feasible, rising questions about its impact on the diversity and persistence of the animal community.　Investigation on the larval dispersal of vent-endemic animals is important not only to understand their natural history, but also to evaluate their population resilience and to integrate conservation methods into future human activities in the deep sea.

This thesis attempts to first evaluate the vertical migration of invertebrate larvae from the deep-sea hydrothermal vent for a more inclusive understanding of their dispersal, species' biogeography and evolutionary trajectories. For this purpose, the early-life history and other biological traits of the red-brood limpets and snails of Shinkailepadinae (Gastropoda: Neritimorpha: Phenacolepadidae) were explored as a model case to elucidate the biogeography of animals endemic to hydrothermal vents. The species of Shinkailepadinae inhabit exclusively the deep-sea hot vent or cold methane seep environments in low and middle latitude areas of the world. Besides their abundance and wide geographic distributions, these gastropods represent an excellent group upon which to study the larval ecology and dispersal of vent animals by virtue of the following: Embryos can be observed in transparent egg capsules; hatched planktotrophic larvae can be cultured under the atmospheric pressure; settlement sizes have been determined from the measurements of the protoconch and larval operculum.

As the Chapter 1 of the thesis, the species diversity and distributions of the Shinkailepadinae were explored by examining the conchological, anatomical and/or genetic traits of over a thousand specimens from all over the globe. Molecular phylogenetic analyses and morphological examination identified six described and 11 undescribed species from global hydrothermal fields and cold methane seeps, with a vertical range of distribution as adults from 111 m to 4,090 m and geographic range of each species up to 3,200-km across. The Chapter 2 describes the entirely novel results from the culture experiments of larvae of the vent-endemic *Shinkailepas myojinensis*. Laboratory observation of swimming behaviour and experiments on the effects of different temperatures on survival and growth strongly suggested that the planktotrophic larvae of *S. myojinensis* migrate vertically from hydrothermal vents to the photic zone upon hatching from benthic egg capsules. Population analyses using mitochondrial DNA sequences revealed a panmictic structure for *S. myojinensis* in the northwest Pacific, further corroborating the presence of long-distance dispersal in surface currents. The Chapter 3 is devoted to further confirm this discovery by analysing the larval and adult shells of three

Shinkailepas species for their oxygen isotopic compositions. This attempt, again the first for vent-endemic taxa, perfectly supported the vertical migration of larvae as an obligatory part of the species' life cycles. All settled juveniles collected from hydrothermal vent fields were found to have experienced the warm surface water during their larval period. In the Chapter 4, an attempt was made to examine if such migration and dispersal, which would surely enhance population connectivity among vent fields, are common phenomena in the entire Shinkailepadinae. The presumed basal-most species among the living members of the subfamily ('*Shinkailepas*' *briandi*) was found to have a panmictic population along the Mid-Atlantic Ridge, regardless of its wide bathymetric range that extends down to the abyssal depth of 4,090 m. Lastly, the Chapter 5 widened the scope of the present thesis to non-molluscan taxa. The geographic distributions and genetic population structures of four planktotrophic species of the shrimp family Alvinocarididae suggested that the vertical larval migration can well be a widespread phenomenon among vent endemics with planktotrophic early development. These findings on the larval migration and dispersal provide new insights into the connectivity between chemosynthetic ecosystems in hydrothermal vents, as well as between these and photosynthetic ecosystems, in both ecological and evolutionary timescales.

Based on the new evidence and exploration of previous literature, I propose that the sea surface temperature (SST) would represent a critical factor in determining the geographic distributions of vent-endemic species with a planktotrophic larval period, and in turn the faunal composition of individual vent sites and regions. Temperature optima for the larval growth of *S. myojinensis* and a vent crab *Gandalfus yunohana* (Bythograeidae) were found to coincide with SST in the geographic ranges of the two species. In addition, the vent faunas of polar regions are characterized by the lack of planktotrophs including alvinocaridid shrimps, bythograeid crabs, bathymodioline mussels and phenacolepadid gastropods, supposedly because the very low SST near the poles is difficult to cope with by their long-lived larvae. The global distribution and species richness of the Shinkailepadinae seem to add further insights into the role of surface dispersal on the biogeography of the vent fauna. Their richness shows a clear gradient with the centre of diversity in the proximity of the Coral Triangle region, with a decreasing number of species towards both east and west. Similar driving forces might have produced the high diversities of shallow-water fauna and deep-sea phenacolepadids in this region by affecting their larval dispersal in surface currents. These hypotheses provide a fundamentally new perspective on the biogeographic patterns of vent taxa, for which most previous studies have focused on the geographic and bathymetric distances, deep-sea currents and topographic continuities between individual vent fields.

Among various human activities, the exploitation of seafloor massive sulphides (SMS) is expected to make the greatest impact on the deep-sea hydrothermal vent ecosystems, which may suffer extinction of endemic species, decrease of genetic diversity and restriction of population expansion. In this regard, many vent endemics with planktotrophic early ontogeny have a wide-ranging geographic distribution and high population connectivity across the range, thus apparently less susceptible than lecithotrophs to disturbance by the exploitation of SMS and other human activities. However, the present global taxonomic revision of the Shinkailepadinae revealed that, although some species were abundant and represented by hundreds of specimens from multiple vent fields, others were much rarer and represented by a handful of individuals or even by singletons. Site-specific factors such as different chemistry and substrata at hydrothermal vents would determine the distributions and biomass of individual species, besides their dispersal capability or other biological traits. Integrated knowledge on the taxonomy, population genetics and ecology of vent taxa will continue to contribute towards the minimization of negative impacts by the exploration of hydrothermal vents.