

論文の内容の要旨

論文題目 Evolutionary history, species diversity and biogeography of amphidromous neritid gastropods in the Indo-West Pacific

(インド・西太平洋域における両側回遊性アマオブネ科腹足類の進化史および種多様性と生物地理に関する研究)

氏名 福森 啓晶

In tropical and subtropical regions worldwide, numerous continental and oceanic islands exist and many such islands have freshwater streams. Island streams are generally smaller than continental rivers, having higher gradients and shorter distances from headwaters to stream mouth. These streams are too short, thus in tropics they become raging torrents during the rainy season, while during drought they may be dried up. Such environmental conditions present a serious problem for primary freshwater animals that spend the whole lives in streams and rivers, even if they could somehow colonize the islands by rare, stochastic dispersal events. Amphidromous animals, on the other hand, flourish there.

Many fish, crustaceans and gastropod molluscs in the island streams have an amphidromous life cycle; (1) their larvae are swept downstream to the sea, (2) feed on phytoplankton and grow up, and (3) settle at the river mouth; (4) metamorphosed benthic juveniles migrate upstream. Despite the limnic habitat of the adult, these amphidromous species are thought to have potential to disperse and colonize other island streams with the marine larval period and high fecundity; amphidromy indeed is the most prevalent life history strategy in low-latitude island streams. However, fundamental studies on their natural history are still badly needed as the first step in elucidating the formation and maintenance mechanisms and in promoting conservation of the freshwater ecosystems on tropical and subtropical islands.

The aim of the present thesis is to elucidate the natural history of limnic species of the gastropod family Neritidae (Neritimorpha: Neritoidea) as model taxa for understanding the role and importance of amphidromy in low-latitude islands by taking the following three approaches. Evolutionary systematics: Phylogeny, morphological diversification and habitat shifts are inferred from the Bayesian and likelihood analyses of mitochondrial and nuclear DNA sequences. Larval ecology and evolution: Global patterns of settlement size and larval duration are explored to understand their dispersal capability and recruitment in consideration with phylogenetic and ecological backgrounds. Taxonomy: Species taxonomy and biogeography in the Indo-West Pacific are assessed and revised based on the morphological and genetic characters of comprehensively accumulated samples and museum specimens including type material.

In the Chapter 2, I present the first comprehensive, well-supported phylogeny of the superfamily Neritoidea based on four gene sequences (ca. 4 kbp in total) from 60 species representing most living genera. Bayesian and likelihood reconstruction not only confirms the repeated invasions of the freshwater realm by marine ancestors but also indicate multiple reinvasions of the sea from limnic habitats. A very plausible explanation for such unusual reversal in habitat shifts is the ontogenetically euryhaline nature of amphidromous animals. Morphological traits that would be adaptive in the amphidromous life cycle have also been acquired in parallel. The most striking case concerns four independent losses of shell coiling and functional operculum to better facilitate upstream migration, resulting in the near-identical appearance of the polyphyletic *Septaria*.

Body size during larval development is among the most important attributes of aquatic animals. The optimal size for changing form or habitat may vary according to ecological traits of species, while phylogenetic constraints also play a significant role. The major goal of the Chapter 3 is to reveal the global patterns in the settlement size of

planktotrophic larvae in the Neritimorpha. Taking the unique advantages of the group where the size at various ontogenetic stages can be rigorously estimated by measuring adult opercula, I provide the most comprehensive data on the settlement size of any aquatic invertebrate groups in terms of taxonomic sampling and coverage of different habitats. Eighty-eight species show only negligible intraspecific variation and considerable interspecific differences in the settlement size, particularly between genera or families. The settler size is determined primarily by phylogenetic constraints, while parallel acquisitions of smaller sizes are suggested exclusively in four independent clades (two living and two extinct) of amphidromous snails with a marine larval period followed by a limnic adult phase. The smaller size may be adaptive in avoiding abortive dispersal through shorter metamorphic competence time, particularly with a sufficiently long delay period. This delay period also seems to obscure the possible correlation between the settlement size and geographic distribution range of neritimorph species, both fully marine and amphidromous.

The Chapter 4 is devoted to recognize and classify all neritid species in the limnic environments of the tropical to subtropical Indo-West Pacific islands through meticulous investigation on their morphology and mitochondrial COI sequences. Eighty-six species are identified among 462 sequenced individuals; of these, only four species near the equator hatch as benthic juveniles and spend the whole life in freshwater. Most of amphidromous neritids show small intraspecific genetic diversity despite their wide geographic ranges, suggesting high levels of dispersal as seen in marine confamilials. Indeed, the comparison of species compositions between two distant geographic regions demonstrates high faunistic homogeneity: 22 out of 39 Japanese species are also found in the ca. 6,000-km apart Solomon Islands and Vanuatu. Summary of the compiled locality data reveals that species richness peaks in the Coral Triangle and declines with increasing distance from this region, both latitudinally and longitudinally, again corresponding with the pattern for marine taxa. The Neritidae as well as many other amphidromous animal lineages with their origins in the tropics may have rapidly changed distribution ranges according to the fluctuating climate and shaped the present-day regional diversity almost entirely by dispersal but rarely by speciation through small-scale vicariance.

Seasonal natural disturbances are characteristic of tropical streams, so that the extinction or decrease of local population may happen frequently over evolutionary and ecological timescales. The presence of numerous larvae in the sea, however, seems to allow them to reoccupy in vacant habitats and result in high sympatric and syntopic diversity through “intermediate” disturbance on metapopulation. Further accumulation

of ecological data on stream animals on low-latitude islands, which has been greatly enabled for the Neritidae by the present study, is needed for evaluating this hypothesis on the driving and maintenance mechanisms of the species diversity.