Sumio Minamori: the pioneer of loach speciation study

Kenji SAITOH

Tohoku National Fisheries Research Institute, Shinhama, Shiogama 985–0001, Japan; e-mail: ksaitoh@myg.affrc.go.jp

Received 2 June 1999; Accepted 16 November 1999

Dr. Sumio M i n a m o r i , Professor Emeritus, Hiroshima University was born on 10 October, 1917 in Shiwachi Village, Miyazaki Prefecture, Japan. He went to the Department of Biology, Hiroshima University of Literature and Science from 1942 to 1944. When the World War II broke out, many students were drafted into the army and sent to the battlefield. The conscription was, however, suspended upon students majoring in science and technology. Thus he did not serve in the army and was able to continue his studies.



The war situation soon became quite bad for Japan. Finally Hiroshima underwent the atomic bomb attack on 6 August, 1945. On that day he happened to be absent from Hiroshima, taking a business trip to Kyoto. If he had been in Hiroshima then, many of the modern works on loach biology would not have occurred.

After the end of the war Sumio Minamori set up his first study on loaches with his supervisor Dr. Toshijiro Kawamura at the Hiroshima University of Literature and Science. His first two works, in which he contributed as the junior author, were about some characteristics of loach hybrids.

In the spring of 1946 Sumio M i n a m o r i began to take trips for sampling loaches. The train system had been severely damaged during the war. In addition, a tremendous number of

people, disarmed soldiers, refugees, buyers of underground markets and so on rushed into the slow infrequent trains. Train cars were so crowded that people would get on and off through the windows, or they would get on the roof of the train. Inside the cars, sometimes a rope was stretched between frames of the luggage space to hang and dry diapers for babies. Under such difficult conditions he would board the train with live loaches, which for a long time were without aeration. He usually brought 20–30 loaches at a time. Because of his great care, the loaches arrived safely at his laboratory every time.

Soon after Sumio Minamori arrived at his laboratory, he made a number of experiments on loach development. These experiments include artificial ovulation, insemination, observation of morphogenesis, measurement of metabolic rate, and so on. As loaches develop very fast, he hardly took and sleep during the loach spawning season.

Soon afterwards Sumio Minamori began to make his research activities independently from Professor Kawamura. He became a lecturer in the new system of Hiroshima University. People working in the fisheries industry supported his work. By their donations he was able to run 40 outdoor aquaria for rearing loaches in Shinonome Campus of the university. From December 1950 he worked in the main campus of Hiroshima University as an associate professor of the Faculty of Science. As he changed his workplace, he again obtained funds to build and maintain 60 outdoor aquaria. These aquaria were his base until he changed his work into the genetics of *Drosophila* in the early 1960s.

One of the greatest of Sumio Minamori's works was an extensive series of hybridization experiments. He crossed 12 "local races" of loaches and analyzed hybrid deficiencies such as inviability, sterility and breakdown. Imagine the large number of aquaria necessary for only a few combinations of crosses: reciprocal crosses, control crosses, reciprocal backcrosses, and their replication for confirmation! He made a great effort to maintain his aquaria.

Spined loaches show inviability when crossed with mud loach. The extent of inviability is parallelled by variation in body size and egg size. Hybrids among spined loaches show hybrid sterility according to differences in body size and egg size.

Sumio M i n a m o r i thought that hybrid deficiencies are progressive with difference in cell sizes. They are progressive from trivial hybrid breakdown via hybrid sterility to severe hybrid inviability. Such succession is parallelled by differences in the cell size associated with temperature adaptation. Nowadays hybrid breakdown, sterility and inviability are thought to be not always progressive. They are frequently different phenomena controlled by discrete processes. The recently received wisdom is also true for loaches. Sterility between local races of different ploidy is not through physiological mechanisms but is clearly chromosomal. However, it was quite natural from a physiologist's view at that time that Sumio M i n a m o r i postulated that hybrid deficiencies are progressively associated with physiological differences.

From his extensive hybridization experiments Sumio M i n a m o r i concluded that three nominal spined loach species, Cobitis taenia japonica (C. taenia), C. t. striata (C. striata) and C. biwae, are species complexes comprising a number of biological species. The striated spined loach (striata complex) was especially intensively studied and divided into three species: large, middle and smaller "races". The biological species concept was established in the 1950s by Ernst M a y r and his colleagues among a school of the new synthetic theory of evolution. Sumio Minamori's works were contemporary with this revolution in biological thinking. Thus he was at the frontier in biological science, the most exciting field of study.

From the words of Sumio Minamori, a field of scientific research should have its particular intended goal, materials and methodology. As for speciation, the goal is the elucidation of mechanisms and processes of stability, change and splitting of species. Natural populations comprising species are the materials for that study. Both descriptive and experimental methods are useful for the study of speciation. Because of the species definition as reproductively isolated entities, establishment of physiological isolation is then the most important aspect of speciation.

From this viewpoint Sumio M i n a m o r i made more extensive work on physiology of developmental stages, which is also one of his greatest works. He studied several developmental characteristics to delineate temperature adaptation in development. Local races which lay smaller eggs show high temperature tolerance, high respiratory and developmental rates but low growth rate. The Q₁₀ values of these parameters in those races are larger indicating adaptation to higher temperatures because of presumed higher energy demand at higher temperatures. Though experiments at lower temperatures were not possible for him, he made a reasonable assumption that local races with lower Q₁₀ values adapt to lower temperatures because of possible residual activity at extremely low temperatures.

When two diverged genomes come in contact by hybridization, incompatibility between nucleus and egg cytoplasm arises. Sumio M i n a m o r i discussed if such incompatibility is a source of hybrid inviability. He concluded that physiological isolation is a by-product of adaptation to different temperatures.

Sumio M i n a m o r i also made the important observation that larvae hatched from the same litter are smaller at higher temperatures. This means that the differentiation rate is accelerated more than growth rate at higher temperatures. Growth retardation becomes so severe at the lethal temperature that embryos become inviable. From this observation, combined with analysis of other developmental parameters, he considered that loaches diverged about their body size and egg size by the genetic assimilation of an acquired character. In other word, adaptation to different temperatures in loaches, which caused their speciation, is a shift of developmental canalization.

While Sumio M i n a m o r i succeeded in obtaining the direct evidence for mechanistic factors of isolation, what did other Japanese or world ichthyologists do about studies of speciation? Unfortunately, Sumio Minamori published most of his important works about loaches in a localized journal, a university bulletin. Many ichthyologists could not easily gain access his papers. Sumio Minamori's works on loach speciation had only very small impacts on ichthyologists views at that time. Moreover, after the finding of diploid-tetraploid complexes, a great misunderstanding had prevailed on Japanese ichthyologists that all hybrid sterility phenomena can be explained by chromosomal mechanisms. Ichthyologists, in Japan at least, were so underdeveloped that they could not evaluate his works properly until recently. Thus most of so-called speciation studies dealing with morphology, ecology, and even DNA sequencing should be simply regarded as description of differentiation patterns associated with speciation. There have been many works which invoke speciation from inadequate viewpoints except those by Sumio Minamori. His conclusion that reproductive isolation establishes itself as a by-product of adaptation is now not very much novel, but it is surprising that his studies were made more than 40 years ago!

Sumio M i n a m o r i retired from Hiroshima University in March, 1981. He now lives peacefully in a small town near Hiroshima. I hope this short introduction can be an opportunity for a re-evaluation of Sumio M i n a m o r i and his works.

Publications by Sumio Minamori on loach speciation studies

- KAWAMURA, T. & MINAMORI, S.,1947: Studies on hybrids in the family Cobitidae. I. On the intergeneric hybrids between Misgurnus anguillicaudatus, ♀ and Cobitis biwae, ♂, C.taenia striata, ♂ and C. taenia japonica, ♂. Seibutu, 2:149–152 (in Japanese).
- KAWAMURA, T. & MINAMORI, S., 1947: Studies on hybrids in the family Cobitidae. II. On the color pattern of intergeneric hybrids. Zool. Mag., 57:63-64 (in Japanese).
- MINAMORI, S.,1950a: Reciprocal hybrids between Misgurnus anguillicaudatus and Cobitis taenia striata, with special reference to sterility of females. Coordinat. Com. Res. Genet., 1:7-13 (in Japanese, with English abstract)
- MINAMORI, S.,1950b: Isolating mechanisms in the striated spinous loach, Cobitis taenia striata. J. Sci. Hiroshima Univ., [B1], 11:55-59.
- MINAMORI, S.,1951a: Hybridization and classification in spinous loaches. Jpn. J. Ichthyol., 1:215-225 (in Japanese, with English abstract).
- MINAMORI, S.,1951b: The lethal phenomena in the second generation of the spinous loach hybrid. J. Sci. Hiroshima Univ., [B1], 12:57-66.
- MINAMORI, S., 1952: Physiological isolation in Cobitidae. I. Two races of the striated spinous loach with special reference to the difference in their embryonic respiration. J. Sci. Hiroshima Univ., [B1], 13:199–212.
- MINAMORI, S., 1953a: Problems on the origin of physiological isolation. Seibutsugakkaishi Hiroshima, 5:52-62 (in Japanese).
- MINAMORI, S.,1953b: Physiological isolation in Cobitidae. II. Inviability of hybrids between the mud loach and some local races of spinous loaches. J. Sci. Hiroshima Univ., [B1], 14:125-149.
- MINAMORI, S.,1954: Temperature adaptation of some local races of striated spinous loach. *Jpn. J. Ecol.*, 4:66-68 (in Japanese, with English abstract).
- MINAMORI, S.,1955a: Temperature adaptation in development. Seibutsugakkaishi Hiroshima, 6:13-22 (in Japanese).
- MINAMORI, S.,1955b: Physiological isolation in Cobitidae. III. Hybrid sterility and hybrid breakdown in contact regions of two races of the striated spinous loach. *Jpn. J. Genet.*, 30:243-251.
- MINAMORI, S.,1955c: Local races of spinous loaches. Bull. Biogeogr. Soc. Jpn., 16-19:278-282.
- MINAMORI, S.,1956a: Physiological isolation in loaches. In: Komai, T. & Sakai, K. (eds.), Population Genetics. Baifukan, Tokyo: 163–167 (in Japanese, with English abstract).
- MINAMORI, S., 1956b: Physiological isolation in Cobitidae. IV. Speciation of two sympatric races of Lake Biwa of the striated spinous loaches. *Jpn. J. Zool.*, 12:89–104.
- MINAMORI, S.,1957a: Physiological isolation in Cobitidae. V. Sterility of the hybrids between the mud loach and six races of spinous loaches. J. Sci. Hiroshima Univ., [B1], 17:55-64.
- MINAMORI, S.,1957b: Physiological isolation in Cobitidae. VI. Temperature adaptation and hybrid inviability. J. Sci. Hiroshima Univ., [B1], 17:65-119.
- MINAMORI, S.,1957c: Speciation in relation to temperature and body size. Biol. Sci. Tokyo, 9:80-85 (in Japanese).
- MINAMORI, S., 1957d: Adaptation. Seibutsugakkaishi Hiroshima. 7:17-22 (in Japanese).
- MINAMORI, S., 1957e: Speciation. Seibutsugakkaishi Hiroshima, 9:40-47 (in Japanese).
- MINAMORI, S.,1960: Speciation in the case of the striated spinous loach. Biol. Sci. Tokyo, 12:72-74 (in Japanese).
- MINAMORI, S.,1962: Variation in respiratory enzymes of embryos in the loach fishes. *Jpn. J. Genet.*, 37:462-473.
- MINAMORI, S., 1964: A comparative study of the activity of hepatopancreas catalase in theloach fishes. Jpn. J. Zool., 14:231–246.
- MINAMORI, S., 1984: Speciation in spinous loaches. The Freshwater Fishes, 10:19-24 (in Japanese).