Mathematical Biology: A Personal Journey

Nanako Shigesada

My favorite subjects in high school were mathematics and physics. In 1960, I entered Kyoto University and majored in physics. I gave up another option, pure mathematics, since I was rather interested in real natural phenomena. I took a graduate course in statistical mechanics under the supervision of Prof. Ei Teramoto, who was well known for his innovative work in high-polymer physics. Under his influence, I studied diffusion-controlled reactions in liquid for my PhD thesis.

In 1969, when Teramoto moved to the newly founded Department of Biophysics at Kyoto University, I was luckily hired as an assistant professor in his new lab. In the same year, student protests broke out throughout Japan. With no exception, the campus of Kyoto University was filled with the clamor of demonstrations almost every day. After the student strife finally subsided in the early 1970s, the campus was left with an air of apathy all over. However, there also arose among students strong anticipations for exploring new fields beyond the boundaries of traditional academic disciplines. Leading such trends, Teramoto launched a laboratory for mathematical biology, the first of its kind in Japan. Since then it has served as an important center for those aspiring to his high aim for the subsequent two decades.

Many ambitious students gathered there: Norio Yamamura, Hisao Nakajima, Kohkichi Kawasaki, Yoh Iwasa, Toshiyuki Namba, Masahiko Higashi, and even John Milton, who joined from Canada under the JSPS invitation fellowship. They engaged in enthusiastic discussions and seminars, literally day and night. The Teramoto lab eventually grew into a lively salon for interdisciplinary exchanges with additional participants, such as Prof. Masaya Yamaguti and his student Masayasu Mimura from the Applied Mathematics Department in Faculty of Engineering, and researchers from the fields of ecology and agriculture. Participants introduced hot topics such as bifurcation theory, chaos or singular perturbation theory from the mathematical field, and the ESS game theory, adaptive strategy and evolutionary biology from the ecological field. Every day I was excited to learn new things, either about mathematics that I had used to yearn for or about the marvelous behaviors and evolution of organisms that I had been largely ignorant of.

On one of those days, I received another strong impact by reading a book Diffusion and Ecological Problems as written in Japanese by Akira Okubo (1975). (Its English edition was published first in 1980 and then in 2001 as the expanded second edition coauthored with S. Levin.) In this book, Okubo introduced studies of biological diffusion done by a number of Japanese entomologists. I was particularly impressed by the environmental density theory proposed by Masaaki Morisita. He quantitatively evaluated the population pressure due to interference between individual animals by ingenious experiments using antlions. On the basis of his data, I demonstrated in collaboration with Kawasaki and Teramoto in 1979 that the population pressure can be formulated by nonlinear diffusion equations. Encouraged by this outcome, I wanted to learn directly from Okubo and made a sabbatical visit with him at SUNY, Stony Brook, in 1979.

Okubo kindly arranged opportunities for me to meet his friends working on mathematical biology. First, he introduced me to Simon Levin by taking me to Cornell University at Ithaca. I can still remem-

ber Akira and Simon exchanging joyous conversations over happenings in mathematical biology in the US. Judging from what I heard from them, the field of mathematical biology in those days seems to have been still in the rising phase. Simon then introduced me to his student, Peter Kareiva, who had been measuring flight paths of butterfly at that time. Peter took me to his cabbage field and enthusiastically told how his experiment was going. Our discussions started there culminated in a joint article on the "correlated random walk" as published in 1983.

When I returned to Kyoto, Teramoto had been thinking about providing young Japanese scientists with an arena for international exchanges. In cooperation with M. Yamaguti and S. Levin, he organized the International Symposium on Mathematical Biology in Kyoto in 1985. He invited many world-class experts, including V. Capasso, C. Clark, D. Cohen, O. Diekmann, J. Gillespie, L. Ginsberg, A. Goldbeter, S. Kauffman, S. Levin, R. May, H. Meinhardt, R. Miura, A. Okubo, G. Oster, H. Othmer, L. Ricciardi, J. Rinzel, R. Rosen, L. Segel, and G. Sugihara. The symposium indeed gave immeasurable impacts to all participants, young and old alike.

Meanwhile, I gradually focused my interests on the spatial ecology of biological invasions. As a representative classical work in this field, Fisher (1936) and Skellam (1951) had used a reaction-diffusion equation to demonstrate that the range front of invasive species advances at a constant speed. This clear-cut result vividly exemplifies the beauty and power of mathematical modeling. However, there remained two essential problems, as Akira taught me in New York. First, the environment was assumed as homogeneous in the Fisher model. How would the spreading speed be affected if the environment were heterogeneous as is often the case in nature? Thus, I studied with Kawasaki and Teramoto the range expansion of invasive species into periodic patchy environments by using an RDE of the Fisher type. We discovered that a species succeeding in invasion expands its range in a spatio-temporal pattern termed "traveling periodic wave", and we obtained a mathematical formula for the spreading speed. Second, various field observations have shown that the rate of the spread of invasive species is not necessarily constant, but often tends to accelerate with time. To explain this phenomenon, I constructed together with Kawasaki and Takeda a stratified diffusion model, which assumes that a small proportion of individuals sporadically makes a long-range dispersal, while the remaining majority undergo ordinary random diffusion. Compiling these results with a series of my preceding studies, I published a monograph on invasion in Japanese in 1992.

In 1992, I moved to Nara Women's University. Soon after that, a letter arrived from Robert May, to my great surprise, inviting me to publish an updated English version of my Japanese book as part of the Oxford series in Ecology and Evolution. This turned out to have been mediated by a kind recommendation of my book to May by Joel Cohen, who once visited me and saw a draft of that book in 1990 when I was in Kyoto. Although the original Japanese book was authored by me, the English version was coauthored by Kohkichi Kawasaki, since most of its content had been worked out by indispensable collaborations with him.

In February 1996, both Ei Teramoto and Akira Okubo passed away. In the same year, I happened to be organizing an international symposium on mathematical biology in Kyoto. Thus I switched it to a memorial conference dedicated to them. We deeply missed their warm and selfless humanity on top of their love for and foresight in science. In Nara, I continued to develop theories of biological invasion by cooperating with my students - Noriko Kinezaki, among others - and many colleagues such as Fugo Takasu, K. Kawasaki, Kazuro Iwata, and so on. We also investigated the epidemic spread of the pine wilt disease in Japan with field researchers Katsumi Togashi, Yoich Kishi and Kazuyoshi Futai. Moreover, I hosted several foreign visitors, including Hal Caswell, Horst Malchow, and Sergei Petrovskii, and enjoyed fruitful discussions and collaborations with them.

In 2005, I retired from Nara Women's University and moved to Doshisha University, where I worked until 2012. Fortunately, there I was able to converse daily with Kawasaki, who had been working at the same university. Consequently, we succeeded in solving some of our pending problems.

In 2013, I was awarded the Okubo Prize. I feel so honored and humbled to be selected for the prize crowned with the name of Okubo. As a whole, my personal journey has been blessed with countless lucky encounters with great mentors, colleagues and students. I would like to express my heartfelt thanks to all of them. My new email address is: nshigesa@oak.dti.ne.jp