# Evolutionary ecology of complex sexual systems in marine animals

Kota Sawada

Doctor of Philosophy

Department of Evolutionary Studies of Biosystems
School of Advanced Sciences
SOKENDAI (The Graduate University for Advanced Studies)

Marine animals are not only diverse taxonomically, but also represent ecological diversity different from terrestrial ones, in many aspects which evolutionary ecologists are interested in. In this thesis, I focus on the evolutionary ecology of sexual systems among marine animals.

Sexual system is a distribution of male and female functions within a population or a species. I studied more complex systems than simple systems like dioecy, simultaneous hermaphroditism, protogyny and protandry. Here, complex systems are defined as mixtures of more than one simple systems, for example, androdioecy (the coexistence of gonochoristic males and hermaphrodites), gynodioecy (females and hermaphrodites), trioecy (males, females and hermaphrodites) and bi-directional sex change (the combination of protandry and protogyny) They offer unique opportunities to study sexual system evolution. Since it is widely accepted that the evolution of sexual systems is primarily affected by mating systems, I hypothesized that different sexuality within a complex sexual system can be explained by spatiotemporal fluctuation of mating systems. The broad aim of this thesis is to test this hypothesis. I studied androdioecy of barnacles and bi-directional sex change in fishes as case studies to gain insight into the evolution of sexual systems in general.

Barnacles have diverse sexual systems, including hermaphroditism, androdioecy and dioecy. I collected crab-symbiotic barnacles *Octolasmis unguisiformis*, in Okinawa and Amami, and examined their sexual system using histological observations. As a result, conspecific-attached individuals were dwarf males, while crab-attached individuals were simultaneous hermaphrodites. Thus the species is androdioecious. I also demonstrated the difference of life history between dwarf males and hermaphrodites, by comparing the size at maturation. The existence of dwarf males in this species supported a theoretical prediction that small mating groups favor dwarf males, since the mating group size (the number of hermaphrodites per host) in this species is small and up to 4. Then I statistically tested the contribution of neighboring individuals to fertilization and the correlation between sex ratio and mating group size. While the presence of dwarf males significantly increased the possibility of brooding by hermaphrodites, the presence of other matured hermaphrodites did not. The male function of hermaphrodites should be examined more. I found no significant correlation between mating group size and the frequency of dwarf males. These results may indicate that different factors affect within- and cross-species patterns of barnacle sexuality. A comprehensive approach incorporating both patterns, as well as detailed works on larval settlement behavior and the mechanism of sex determination, is strongly required.

Bi-directional sex change in fishes, or reversed sex change in basically protogynous species, is induced by the cohabitation of multiple males. The subordinate males usually change sex into females. Since most of them are polygynous, subordinate males may benefit from dispersal to keep being dominant, rather than sex change. I studied why and when subordinate males prefer sex change over dispersal. I constructed a theoretical model of decision making and predicted that low density and risk of dispersal favor sex change, supporting the previous hypotheses. It is also predicted that sex change is more favorable for smaller males, under realistic assumptions. The possibility of unified framework to understand both hermaphroditic and gonochoristic animal societies were discussed.

I conducted a long-term (3 years) field survey on a bi-directionally sex changing goby *Trimma caesiura* in Okinawa, and demonstrated bi-directional sex change based on morphological observations. A large fluctuation of population density and sex ratio was also observed, suggesting that temporal low density caused by fluctuation promotes sex change. However, the rarity of observed despite drastic fluctuation indicates the presence of alternative tactics, other than sex change, to adopt the change of social conditions. Although sex-specific growth rate was proposed as a key factor in the evolution of bi-directional sex change in other species of gobies, I found no significant difference of growth rate between the sexes, calling for the need to examine the growth pattern in other hermaphroditic gobies.

In summary my studies generally supported the effect of mating systems on sexual system evolution. However, I found that other factors such as life history (growth and maturation), dispersal (larval and adult) and social dominance are also important to understand the evolution of diverse sexual systems. I integrated different approaches, that is, histology, specimen-based comparison, theoretical modeling and long-term field survey, demonstrating the potential of such integration to study sexual systems in marine animals with limited available information.