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Evolutionary Significance of the Japan Sea, a Marginal Sea, for the Shallow Marine Organisms – A Perspective From Ostracoda (Crustacea)

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Abstract - A role of the Japan Sea as a speciation field for shallow marine organisms was discussed on the basis of Ostracoda, a small Crustacea with calcified carapace. Biogeographical distributions of recent and fossil records of the closely related species showed that the Japan Sea and the Okhotsk Sea played an essential role when warm water species invaded to north to evolve into cold water species during the glacial/interglacial age of Pleistocene.

I. Introduction

The Japan Sea, which lies between Asian continent and Japanese Islands as a marginal sea, has peculiar characteristics in its topography and water mass structure. The Sea is connected to adjacent oceans by four shallow straits, all of which are shallower than 100 meters although the most part of the Sea is deep enough. The structure of the water mass of the Sea is rather complicated. The warm Tsushima Current flows into the Japan Sea from the southern strait. The warm Tsushima Current continues to slide on the surface of the Japan Sea with the thickness of approximately 200 meters around the center of the Japan Sea. Then, at the north end near Sakhalin, the warm current get to be thin and cooled enough to be heavy to sink back toward the deeper part of the sea, which eventually occupies the main part of the water body of the Japan Sea. This cool (less than 4 °C) water body has been called Japan Sea Proper Water (JSPW).

There are reports that the Japan Sea has undergone environmental changes since its appearance. Since the late Pliocene up to Recent, the cyclic environmental changes, related to glacial-interglacial eustatic sea level changes, got to be prominent. This drastic change in oceanic environments caused tremendous effects to the faunas in the Sea. For example, the benthos of the Japan Sea suffered critical damages and temporally extinguished during the transitional stages between glacial and interglacial [1, 2]. This was because the inflow of currents from both south and north decreased and the freshwater coming from the Yellow River covered the surface of the Japan Sea, which caused the stagnant condition of the Sea for a while. This is consistent with, for example, the observation that the most of the recent deep-sea fishes of the Japan Sea is pretty new to the area.

Study on mollusks [3, 4] and ostracodes [5] from the Plio-Pleistocene on the Japan Sea coast revealed that the extinction of species as well as the retreat and reentry of species have occurred in accordance with the glacial eustatic sea level changes.

On the other hand, as the data on the distribution of recent shallow marine ostracodes along the coast of Japanese Islands accumulated [6, 7, 8], it is noted that the shallow water species, especially those of intertidal species, have endemic elements related to the marine climate and the currents. The endemism are roughly exemplified as the Southern Pacific (proximal part of the warm Kuroshio current), the Middle Pacific (distal part of the warm Kuroshio), the Sea of Japan (warm Tsushima current), the Okhotsk Sea (distal part of the Tsushima current) and the northern Pacific (cold Oyashio current). A couple of sets of closely related species are found from them. If the faunas of the Japan Sea is simply caused by the reentry of the fauna from the south/north, then the endemic characters mentioned above can be not explained well. It is probable that there might be difference in response between deep and shallow water species during the glacio-eustasy because the shallow species should be able to survive the stagnant stages, unlike the deep species, with the enough dissolved oxygen condition of the surface water.

On the open coast along Pacific and Atlantic Oceans in Central-North America, speciation was said not to have occurred during glacial-interglacial cyclic environmental changes [9, 10, 11]. In this open geographical setting, speciation events were rather active during sustained, unidirectional climatic transitions, and inactive during rapid, high-frequency climatic oscillations [9]. Japan Sea seems to be a good material to check the results obtained from the open ocean whether the result is universal or conditional.

The purpose of this study is to review the distribution of shallow marine species of ostracodes around Japan, estimate the phylogeny of closely related species of some taxa, and evaluate the role of the Japan Sea, a marginal sea, for the speciation and evolution of shallow marine organisms.

II. Materials, methods and the basic data to discuss the speciation process

The taxon picked up here to mainly discuss is the 14 species of the genus *Cythere*. The data include for the recent and fossil specimens, their (paleo)geographical distribution and phylogenetic relationships, which already estimated [12] by the method of DDP [13]. The detailed phylogenetic relationship was proposed in this study on the basis of the combination of the DDP analysis, fossil records and the analysis of the morphology of sexual organs (Fig. 1). In addition to *Cythere*, the data on recent *Xestoleberis* and fossil and recent *Loxococoncha* are additionally used in the discussion.

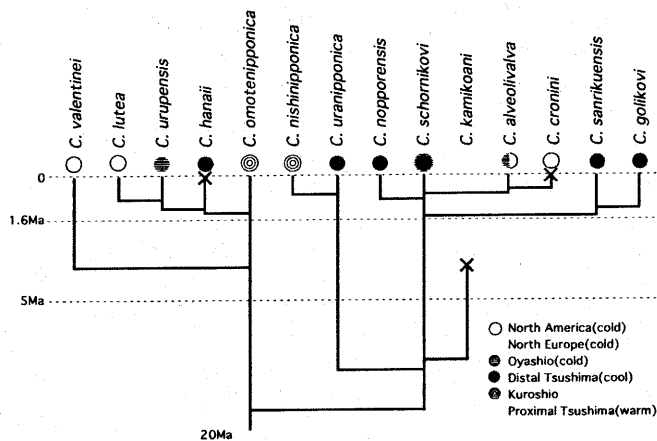


Fig.1. Phylogeny and geographical distribution of *Cythere*

III. Speciation in the Japan Sea during Pre-glacial/interglacial environmental changes

The genus *Cythere* was originally an endemic genus to Japan and adjacent areas. Therefore, the estimate of detailed phylogeny is not as complicated as for the most cosmopolitan taxa. Since the first *Cythere*, *C. omotenipponica* (Kuroshio species) has appeared in Miocene in the paleo-Kuroshio area, only 4 out of 14 species have newly appeared during Miocene and Pliocene, the duration of some fifteen million years. These are *C. schornikovi* (originally Distal Tsushima species), *C. uranipponica* (Distal Tsushima species), *C. kamikoaniensis* (extinct Distal Tsushima species) and *C. valentinei* (North America cold water species). It is noteworthy that all these descendant's habitats were in the northern or northward Japan Sea. All speciation events seem to have happened in or through the Japan Sea. Although the number is low, these five species constitute the three major species group of *Cythere* into which all 14 species are eventually classified. Therefore it is concluded that the basic species to later form the major species group already evolved during this duration, but the diversity of *Cythere* species was not yet enough high.

IV. Speciation in the Japan Sea during glacial/interglacial environmental changes

Within a geologically short interval of 1.6 million years of Pleistocene-Recent, 9 new species have evolved to make the total species number into 14. These are *C. hanaii* (originally Distal Tsushima species), *C. urupensis* (Oyashio species), *C. lutea* (North America and North Europe species), *C. nopporensis* (Distal Tsushima species), *C. sanrikuensis* (Distal Tsushima species), *C. golikovi* (Distal Tsushima species), *C. alveolivalva* (Oyashio and North America species), *C. cronini* (extinct North America species) and *C. nishinipponica* (Kuroshio species). The speciation happened very actively during Pleistocene, an age of glacial/interglacial, which is inconsistent with the observation from the open ocean in the Central-North America [9, 10, 11]. Four species of the *C. omotenipponica* species group, which evolved during Pleistocene, are very closely related each other. The recent geographical distribution of the four species is expected to indicate the process of the speciation of this group because of the short interval after the speciation events. The geographical distribution (Figs. 2, 3) shows that the each species has own independent territory although it is partly overlapped; *C. omotenipponica* (Southwestern Pacific coast and Southern Japan Sea coast), *C. hanaii* (fossil; Northern Japan Sea coast, Living; Southern Japan Sea coast), *C. urupensis* (Kuril Islands coast) and *C. lutea* (North America and North Europe coast). Their habitats are geographically arranged from south to north in correspondent with the order of evolutionary appearance.

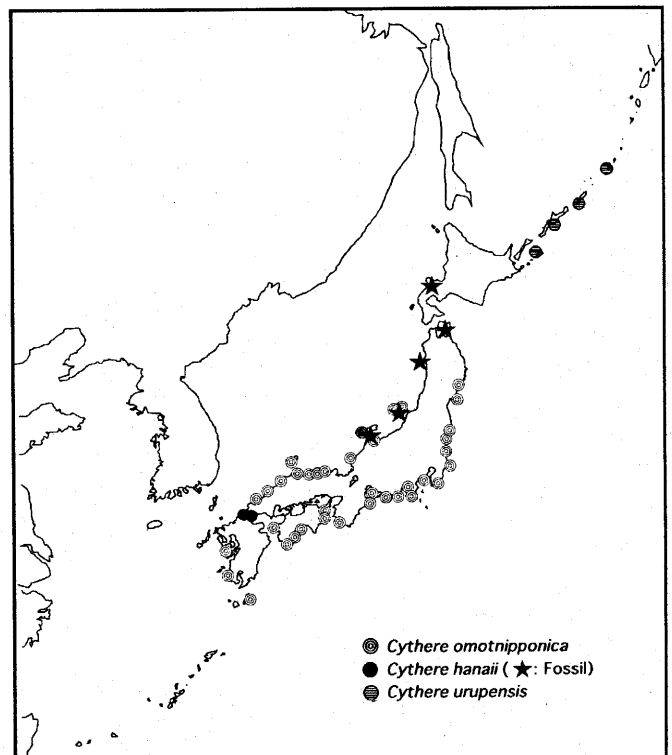


Fig.2. Distribution of *Cythere omotenipponica* species group around Japan

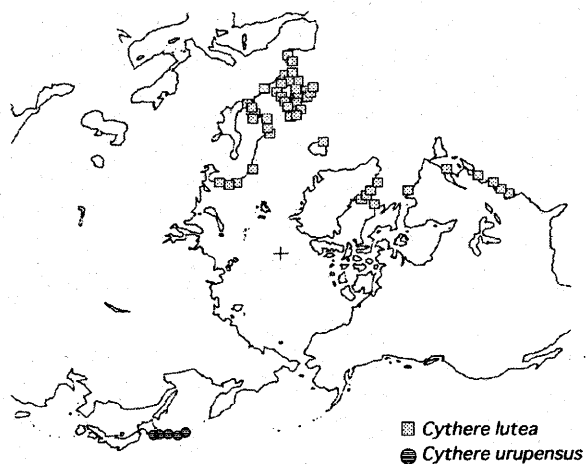


Fig.3. Distribution of *Cythere omotenipponica* species group

When we think the oceanic environmental change during the late Pliocene-Pleistocene, glacial eustacy and the topographical setting around Japanese Islands would easily contribute to the isolation of the population of marine organisms (Fig. 4). During an interglacial period, the warm water species (i.e. *C. ostenippocica*) entered and prevailed in the Japan Sea. Then this deme, a local population, was isolated under the following glacial period because the Sea was easily closed down. Under the cooler conditions some could survive only through mutations to be a variety or a new species (i.e. *C. hanaii*). Then, in the next warm interglacial stage, the new species that had adapted to the cooler conditions was able to invade to the north, the Okhotsk Sea. The Okhotsk Sea was also easily isolated from the Japan Sea during the following glacial period, and some of the species (*C. hanaii*) had survived through mutation to be the second new species (*C. urupensis*). The second new species (*C. urupensis*) moved to the coast of Kuril Islands, a colder area with Oyashio current, in the following interglacial period. The second new species (*C. urupensis*) succeeded in proceeding toward north and passed through the Bering Strait to spread over the North Europe and North America. In the course of this spreading, the third new species (*C. lutea*) has appeared.

A point of this model is that when warm water species invade northward to evolve to be new cold water species, they must pass the Japan Sea to be cool water species first. The direct invasion from southern Pacific to northern Pacific is not acceptable from the data of *Cythere*. The diversification of *Cythere* never has happened without Japan Sea. If this is true, the Japan Sea and the Okhotsk Sea play an essential role for the speciation of shallow marine organisms. This is still a schematic model and need to be further examined in the future.

Other species-groups of *Cythere* support this model. *C. schornikovi*, originally a Distal Tsushima species, produced *C. alveolivalva* (Oyashio and North America species) and *C. cronni* (extinct North America species).

Most speciation processes that occurred in the northern Japan for other genera seem to be consistent with the result of *Cythere*, although they are still under investigations. *Xestoleberis*, for example, is a typical cosmopolitan tropical-subtropical genus, but has its only cold water species in the northern Japanese Islands that evolved through Japan Sea and Okhotsk Sea [14].

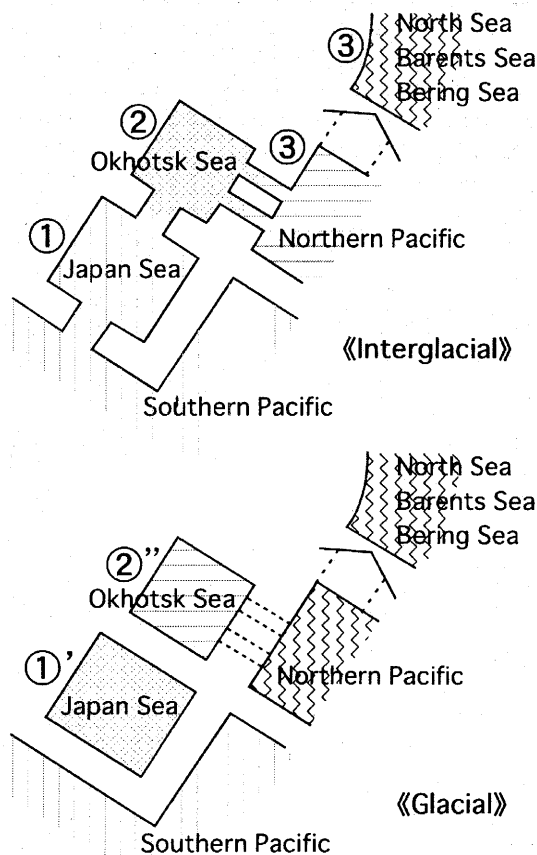


Fig.4. "Pomp Effect of Marginal Seas" model for Speciation.

V. Discussion and conclusions

The evolution that produced the basic species of a certain genus could happen during Pliocene, probably earlier than late Pliocene, the age before glacial-interglacial sea level changes occurred. This is exemplified by the evolution of *Puriana* [10] and *Loxoconcha* [15]. The sustained unidirectional climatic warming might be required in this case. Then the modified speciation occurred during the Pleistocene of rapid, high-frequency climatic oscillations only if the habitats were easily isolated between glacial and interglacial ages. The Japan Sea and the Okhotsk Sea are, thus, essential for the modified speciation in the glacial/interglacial Pleistocene age.

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