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POPULATION STRUCTURE OF MASU SALMON, *ONCORHYNCHUS MASOU*, IN THE SPECIES OF THE GENUS *ONCORHYNCHUS*.

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Toshio Okazaki (1990) Population structure of masu salmon, *Oncorhynchus masou*, in the species of the genus *Oncorhynchus*. *Bull. Inst. Zool., Academia Sinica* 29 (3, Supplement): 17-25. Genetic population structure of masu salmon river populations were examined by comparing to the other species of Pacific salmon (*Oncorhynchus* spp.). Obtained differences in the frequencies of alleles suggest that relatively high genetic divergence occurs among masu salmon river populations. Significant differences in allelic frequencies were also observed among proximal river populations. The magnitude of genetic divergence among river populations is relatively large among Pacific salmon. It is suggested that each river population of masu salmon has its own particular genetic traits due to their precise homing ability.

Key words: Allelic frequency, Masu salmon, *Oncorhynchus*, Population structure, Genetic distance

Many attempts have been made to find out the population structure of the fishes of the genus *Oncorhynchus* known for precise homing. The species of the genus *Oncorhynchus* spend a greater part of their life history in the ocean before they return to spawn in the freshwaters. However, the degree of dependence on freshwater varies among the species and it is considered to be closely related to their population structure. In addition to the conventional method, numerous investigations based upon biochemical genetic methods have been applied to gain a better understandings of the genetic structure of salmonid populations in recent years.

Masu salmon, *Oncorhynchus masou*, is distributed exclusively in the Far East, making a striking contrast to the other species of Pacific salmon (*Oncorhynchus* spp.) which extends widely in the freshwater along the coast of the North Pacific Ocean (Machidori and Kato, 1984).

This paper examines the biochemical population structure of masu salmon river populations by comparing it to that of chum salmon (*Oncorhynchus keta*), pink salmon (*Oncorhynchus ogorbuscha*) and remaining species. The definition of the genetric structure and maintenance of masu salmon were also described in the present paper.

MATERIALS AND METHODS

Samples of chum salmon were collected from 11 populations on the Continent of

North America and 43 river populations in Japan. Sample locations in North America are shown in Fig. 1. The details of the remaining collections were reported

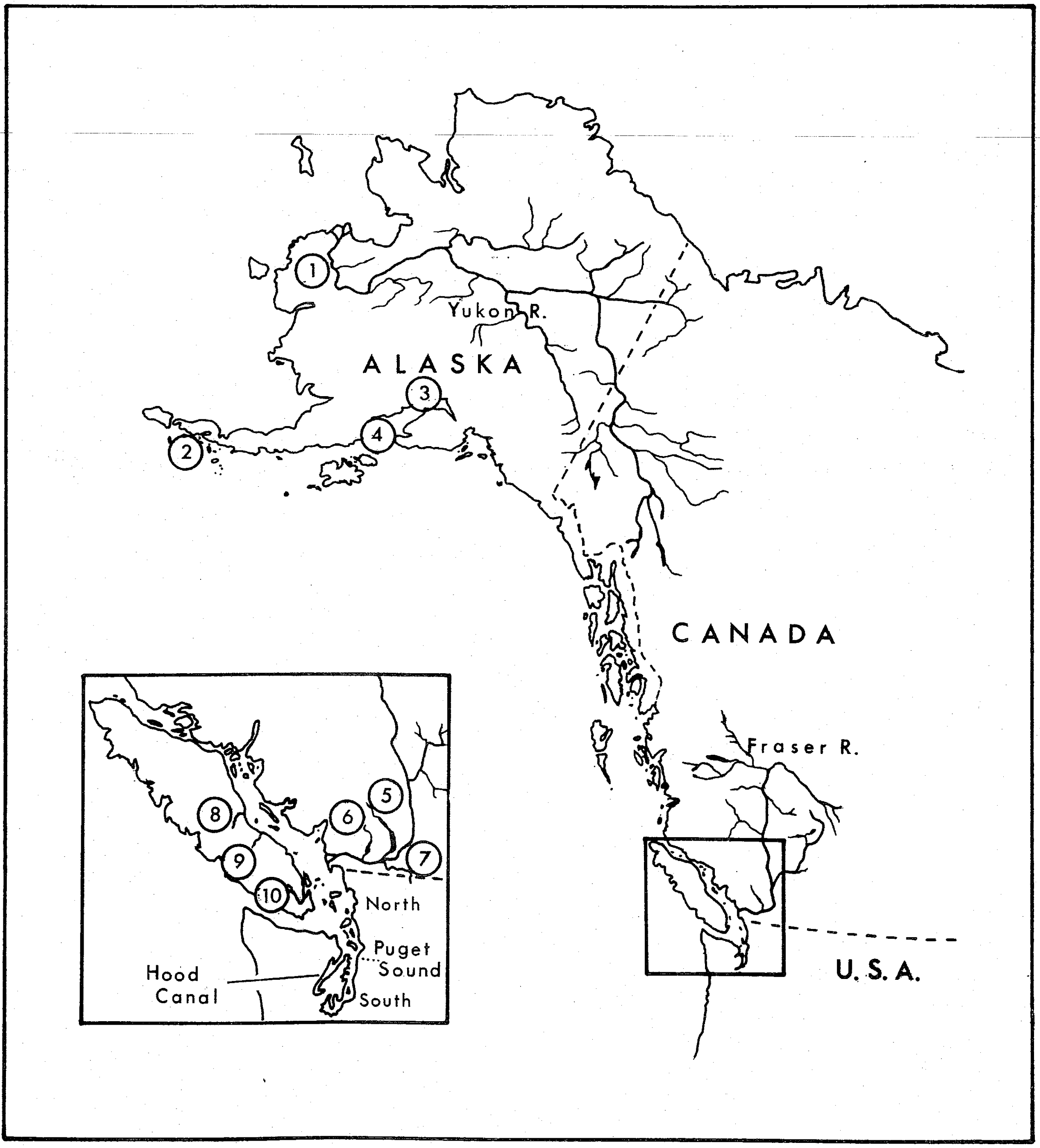

Fig. 1. Map of North America showing the sites where chum salmon were sampled. (1), Yukon River; (2), King Cove; (3), Cook Inlet (north); (4), Cook Inlet (south); (5), Harrison River; (6), Stave River; (7), Vedder River; (8), Puntledge River; (9), Qualicum River; (10), Goldstream River.

in a previous paper (Okazaki, 1982a). Samples of pink salmon were made in three rivers of Hokkaido Island, Japan during consecutive years (see Fig. 2 for locations). Sample locations of masu salmon from 18 rivers are indicated in Fig. 3 (Okazaki, 1986).

Tissues of chum and pink salmon were taken from parental fish while returning to each river, from their fry, or from parental fish returning to coastal area, separately. The specimens of masu salmon collected in Hokkaido rivers were juvenile fish. In Honshu, all of the specimens used in this study were from hatcheries. Their parents were anadromous fish which return to each river.

All kind of the specimens were frozen immediately following collection, until processed for electrophoresis. Horizontal starch gel electrophoresis was used to detect enzyme variants. Processing of samples and electrophoretic methods have been described elsewhere (May et al., 1979). Genetic data were collected from the analysis of 24-29 loci coding for 14 enzymes in chum salmon, 32 loci coding for 16 enzymes in pink salmon and 31 loci coding for 16 enzymes in masu salmon. The details of enzymes stains, the numbers of loci examined and others were mentioned in previous reports (Okazaki, 1982a; 1986).

Nei's (1972) genetic distance (*D*) measure was used to quantify the degree of similarity between populations, and then a dendrogram was constructed based on distance matrix by using UPGMA clustering

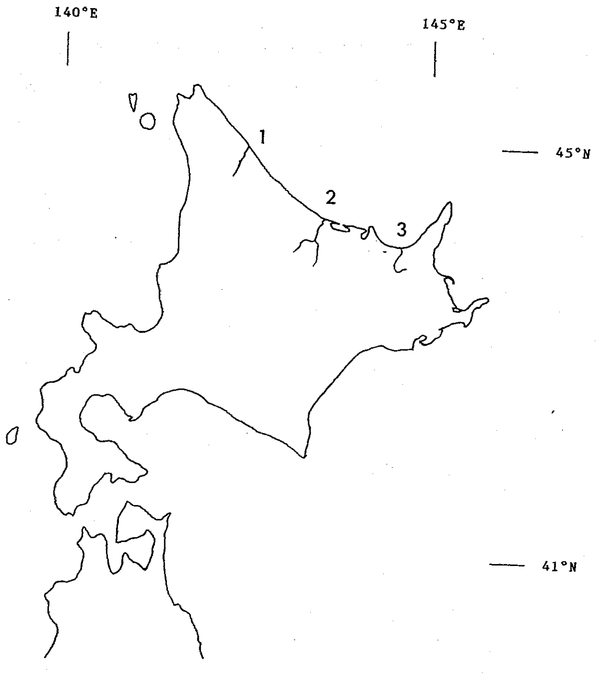

Fig. 2. Map of Hokkaido, Japan, showing the sites where pink salmon were sampled. (1), Horonai River; (2), Yuhbetsu River; (3), Shari River.

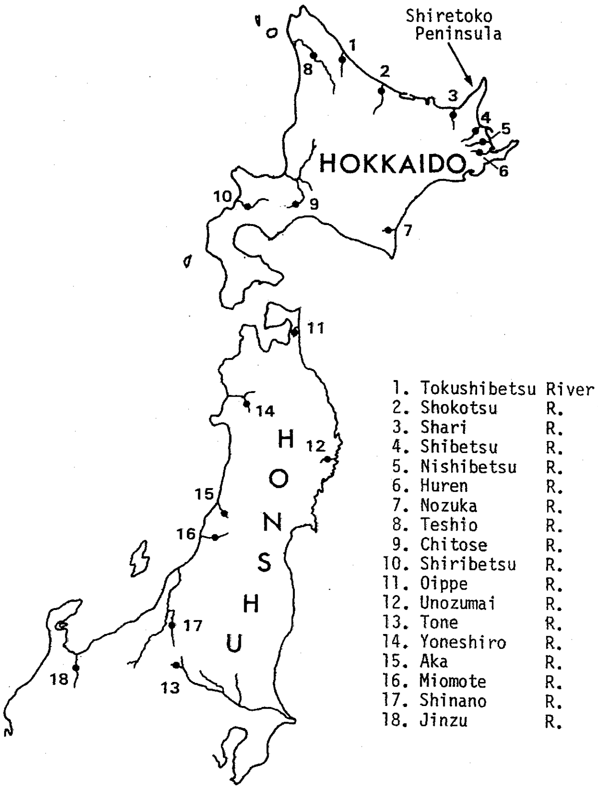

Fig. 3. Map of Japan showing the rivers where masu salmon were sampled.

method in Sneath and Sokal (1973).

RESULTS

Chum salmon

Many differences among populations are evident from comparisons of allelic frequencies at the polymorphic loci. In North America, a resulting dendrogram based on 24 loci indicates that the population structure is consistent with their geographic locations (Fig. 4). The two major clusters of (1) Alaskan and (2) Columbia and Puget Sound populations were defined for the North American chum salmon. The former cluster is further subdivided into the western Alaskan population and the central Alaskan counterpart. Likewise, the latter one is subdivided into the British Columbia and northern Puget Sound population and the southern Puget Sound counterpart. Small differences among the Fraser River collections suggest that gene flow occurs within the tributary river populations (Okazaki, 1981).

Genetic similarities were obtained from comparing 43 proximal river populations in Japnan. The genetic divergence was observed between the northern and southern populations both on the Pacific coast and the Japan Sea coast of Honshu. The division occurs in the middle of Iwate Prefecture on the Pacific coast and in the northern part of Niigata Prefecture on the Japan Sea coast. In Hokkaido, on the other hand, the distinct feature by area was not observed in the allelic frequencies of the examined river populations. However, the genetic study on river populations in the eastern part of Hokkaido where there had been few transplantations revealed two major clusters of (1) Okhotsk and Nemuro and (2) East of CapeErimo populations (Fig. 5; Okazaki, 1982b).

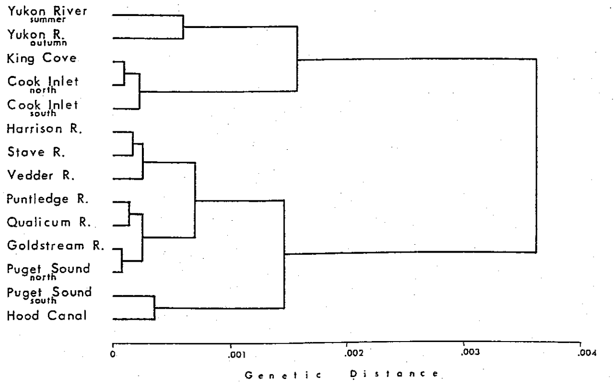

Fig. 4. Dendrogram drawn from indices of genetic distance among fourteen populations of chum salmon in North America.

Though the degree of genetic isolation varies among chum salmon river populations, regional populations which are indicated by continuity and discontinuity in the frequencies of alleles in river populations were observed throughout its range (Fig. 5; Okazaki, 1983).

Pink salmon

Pink salmon attracts much attention because of its rigid two-year life cycle which has led to a complete isolation of even- and odd-year populations. Reflecting the above, observed differences in allelic frequencies within broodlines among three rivers were quite small. On the other hand, significant differences were observed between broodlines even in the same river system. A resulting dendrogram clearly indicated that greater genetic divergence occurred between the two-year class populations even in the same river system than among proximal river populations within the same year class (Fig. 6; manuscript in preparation).

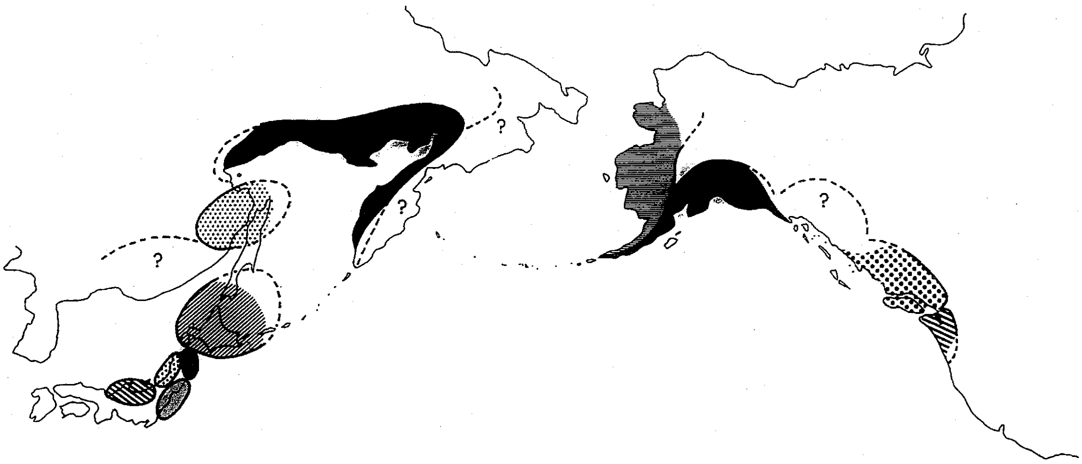

Fig. 5. Schematic diagram of regional chum salmon populations defined by gene frequency data.

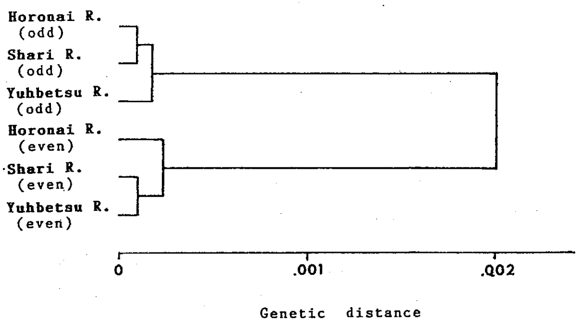

Fig. 6. Dendrogram drawn from indices of genetic distance among Horonai, Yuhbetsu and Shari river populations of pink salmon in Japan.

Masu salmon

Many differences among populations were evident from comparisons of allelic frequencies at the polymorphic loci. However no alleles which characterize specific river populations located in a given area were not observed. From the result of *t* test, highly significant differences were observed in 150 combinations out of 190 combinations at the *PGM-1* (Phosphoglucomutase) locus. Furthermore, the greater part of them were significant at the 1% level.

Nei's genetic distance among examined 20 populations was calculated using 31 loci. The obtained values ranged from 0.0003 to 0.0091 with the average of 0.0028. Based upon the above distance data a dendrogram was constructed (Fig. 7). A clear structuring of populations that conforms to their geographic locations was not evident. But the examined populations appeared to be roughly divided into two geographic groups at the Shiretoko Peninsula of Hokkaido except for a few river populations: (1) the rivers entering the Strait of Nemuro and the Pacific Ocean, (2) the rivers entering the Okhotsk Sea and the Japan Sea (Okazaki, 1986).

DISCUSSION

Various population structure is observed in the examined three species of the genus *Oncorhynchus.*

Almost all the chum salmon stocks on the Continent of North America were maintained under the natural condition when the analysis was made. Hereby, it is

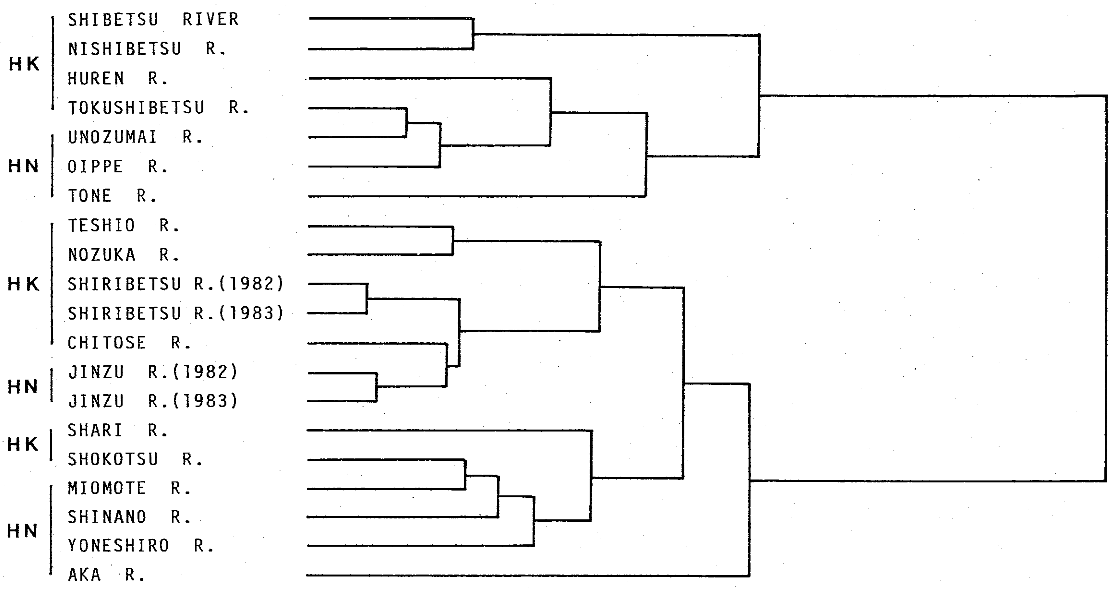

Fig. 7. Dendrogram drawn from indices of genetic distance among twenty populations of masu in Japan. HK, Hokkaido; HN, Honshu.

presumed that some degree of intermingling among proximal river populations in chum salmon is inevitable even under the natural environments. In Japan, chum salmon are mostly maintained through hatchery activities. Furthermore, due to frequent transplantations associated with artificial propagation, almost all the rivers have been planted. Through the current analysis, several regional populations were observed. Although the effects of transplantation have not been precisely evaluated, the above raises a doubt on the effectivenese of the past transplantations (Okazaki, 1982b).

The degree of genetic isolation varies among chum salmon river populations (*D*= 0.00003–0.00844), while the strong genetic similarity is observed among the tributary populations within a single river system (*D*= 0.00023) and among the proximal river populations (*D*= 0.00081). It is presumed that the accumulation of the genetic intermingling for generations led to genetic similarity among river populations within one region.

In the pink salmon population of North America, many authors indicated similarity in the frequencies of alleles within a year-class in a given area but also an occurrence of significant divergence between year-classes even in the same river (Johnson, 1979; McGregor, 1983). According to Johnson (1979), allelic similarity was observed in the population covering North America to Asia. Furthermore, synchronized fluctuation in allelic frequencies at some loci between odd- and even-year populations was observed through the range (manuscript in preparation). The above evidence suggests that considerable genetic intermingling is occurring extensively among pink salmon river populations. Thus it is suggested that pink salmon does not possess precise homing ability.

The obtained allelic frequencies varied among the examined masu salmon populations, although a loose structuring of populations that conforms to their geographic locations was observed. The observed loose clustering of the population is presumably related to their migration patterns in the ocean (Okazaki, 1986). The obtained levels of the genetic distance suggest that relatively high genetic divergence occurs among masu salmon river populations. In particular, significant differences in allelic frequencies were also observed among proximal river populations. Recently, quite precise homing ability was shown for masu salmon from the results of tagging experiments (Mayama, 1985). The above result suggests that each river population of masu salmon has its own particular genetic traits due to precise homing ability.

The characteristics of the genetic structure of masu salmon population can be further defined by comparing it with other species of the genus *Oncorhynchus*. According to the dependence on freshwater in early life stage, six species of the genus *Oncorhynchus* can be devided into following two groups:

Freshwater dependent group – sockeye (*O. nerka*), coho (*O. kisutch*), masu and chinook salmon (*O. tshawytscha*).
Sea water dependent group – chum and pink salmon.

Four species of genus *Oncorhynchus* included in the first group such as sockeye salmon and others spend a certain period of time after hatching in freshwater with a few exceptions. This period varies according to the species, but extends to as long as four to five years at the longest. Conversely chum salmon and pink salmon migrate to sea shortly after hatching and the period of time they spend in freshwater is considerably shorter compared to the freshwater dependent species. In particular, the downstream migration of pink fry begins immediately on emergence from the gravel and the freshwater phase is even shorter than that of chum salmon. On the supposition that the relative strength of the imprinting of natal stream during the early stage depends on the relative length of time in freshwater during the early stage, some takes a view that the first group has the ability to identify the natal stream more precisely than the second group (Semko, 1954).

The genetic population structure of the remaining three species of sockeye, chinook and coho salmon has been studied by many authors. The genetic sturucture of each species and the homing which supposedly linked closely with the genetic structure are presumed in the followings.

Regarding the homing of sockeye salmon, Foerster (1968) and Hartman and Raleigh (1964) report from the results of tagging experiments that sockeye salmon can even identify their originating tributaries to say nothing of their natal streams. With respect to the genetic divergence among sockeye river populations, Grant et al. (1980) confirmed the considerable differences in the frequencies of alleles even among the tributary populations within the same water system. Significant differences among river populations or seasonal runs were also observed in chinook and coho salmon (Utter et al., 1989; Wehrhahn and Powell, 1987).

Various population structure is observed in the species of the genus *Oncorhynchus*. The characteristics in population structure and the homing are closely related. It is presumed that the precision of the homing depends largely upon the life history of fish including the freshwater phase in the early stage.

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櫻鮭屬 *Oncorhynchus* 之櫻鮭 *Oncorhynchus mosou* 的族羣結構

岡崎登志夫

本研究在以與太平洋鮭魚魚種相互比較的方式來探討生活河流中的櫻鮭 *Oncorhynchus masou* 遺傳學上的族羣結構。所獲有關對偶基因頻度分布的差異顯示，在櫻鮭的河流族羣間，遺傳上的分化程度相當大。此類差異也出現在生存於河流中點的族羣之間。在衆太平洋鮭魚魚種中，這些櫻鮭河流族羣間的遺傳分化程度有偏高的現象。文中並認爲：可能是由於具有精確地返回原產地的能力，這些不同河流族羣的櫻鮭乃得以保有其特別的遺傳型質。