遠洋水研報 第19号 昭和57年11月
Bull. Far Seas Fish. Res. Lab., No.19. Nov., 1982

Genetic Study on Population Structure in Chum Salmon (*Oncorhynchus keta*)

Toshio OKAZAKI*

Abstract

Salmonid fishes, which are probably most widely appreciated, consist of the genus *Oncorhynchus*, *Salmo*, *Salvelinus* and *Hucho*. Although the ecological feature such as the frequency of spawning or anadromy varies among species, they all spawn in freshwater. The species of genus *Oncorhynchus* have higher commercial value among salmonid fishes and they are made much of as one of the most important fisheries resources in the North Pacific. They spend a greater part of their life history in the ocean before they return to rivers to spawn in freshwater. Their dependence on the freshwater including their feeding is extremely low compared with other salmonid fishes. These ecological characteristics make the biomass of the genus *Oncorhynchus* large that can not be expected from the life history in freshwater alone. However, the degree of dependence on freshwater varies among the species, and it is considered to be closely related to the population structure and its maintenance.

It has received much international recognition that the state of origin of anadromous stocks has the right to manage and possess the resource of anadromous fishes including the genus *Oncorhynchus*. Accordingly the studies on the distribution and origin of salmon, the locality of populations and the migration route in and out of the territorial waters are called for more than ever. Japan, a state of origin of chum salmon, places great emphasis upon the studies of population structure of chum salmon and fishery biology because of its commercial importance as well as the people's liking for chum salmon. Subsequently, the enhancement program such as hatchery activities and egg transplantations has been put forward with remarkable endeavours.

The population structure and its maintenance, and the genetic feature of chum salmon populations which occupy the greater part of the species of genus *Oncorhynchus* distributed in Japan are examined in the current study which will form a basis for the resource management and the study of artificial propagation and transplantations in future. Morphology and tagging activities have been the major tools for the previous population studies of chum salmon, whereas in recent years the emphasis has been laid

Received Oct. 1, 1982. Contribution No.221 from the Far Seas Fisheries Research Laboratory.
* Far Seas Fisheries Research Laboratory.

on biological genetic methods which offer numerous advantages for population studies. In the current study, population analysis of chum salmon in major distribution area is made to define the population structure and genetic feature of chum salmon as a whole as well as the characteristics and the genetic structure of Japanese chum salmon. The population examined include 11 populations on the Continent of North America, three populations in the U.S.S.R. and 43 river populations in Japan. Genetic data were collected from analysis of 14 enzymes. Genetic variants were identified in 16 loci coding for ten out of the above 14 enzymes. Population analysis was made based on the phenotypic and allelic frequencies of each examined population, the average heterozygosity (H) and genetic distance (D) among the examined populations.

The results obtained are summarized as follows.

Genetic control of polymorphic loci and average heterozygosity (H)

Four isozyme systems among ten polymorphic systems, namely lactate dehydrogenase (LDH-1), α-glycerophosphate dehydrogenase (α-GDH-2), isocitrate dehydrogenase (IDH-2) and malate dehydrogenase (MDH-B) well characterized the genetic feature of each population. Two alleles are identified for the LDH-1 locus. The presence of two, five and three alleles are also identified for the α-GDH-2, IDH-2 and MDH-B loci, respectively. The average heterozygosity, indicating the genetic variability, was calculated for chum salmon river populations which ranged between 0.0319 and 0.0714. The average heterozygosity of vertebrates ranges between 1% and 15% with the average of about 10%, which indicates that the genetic variability of chum salmon is relatively low.

Genetic structure of chum salmon populations on the Continent of North America

Almost all the chum salmon stocks on the Continent of North America are maintained under natural conditions and few transplantations have been made among them. Therefore, examination of the genetic structure of North American populations may provide general insights into the population structure of chum salmon under natural conditions. The examined 11 populations in North America can be divided into the populations in Alaska and those in south of British Columbia based on the similarity of the allelic frequency at the IDH-2 and LDH-1 loci. Strong similarity of allelic frequency was observed among the tributary populations of the Fraser River and between the seasonal runs to the Yukon River.

Genetic structure of chum salmon populations in the far east regions of the U.S.S.R.

Almost all the populations of chum salmon in the U.S.S.R. are reproduced under natural conditions. However due to the difficulties in sampling, the subject for the study is confined to an area facing the Okhotsk Sea. The analysis of the collections of the coastal area of the Okhotsk Sea revealed several characteristics in the frequencies of alleles of the populations in the western part of Okhotsk centering around the Amur River and the northeastern part of Okhotsk. Significant differences are observed in the allelic frequency at the IDH-2 locus between the two populations, while both populations share a common unique feature in α-GDH-2 variation.

Genetic structure of chum salmon populations in Japan

In Japan, hatcheries are established in most rivers which have chum salmon run and therefore Japanese stocks of chum salmon are largely maintained through hatchery activities. The analysis of 43 river populations revealed geographical gradient of the allelic frequencies at the IDH-2 and LDH-1 loci in Honshu populations. 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 at middle of Iwate Prefecture on the Pacific coast and at 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 have been few transplantations to date revealed two major clusters of (1) Okhotsk and Nemuro and (2) East of Cape Erimo populations.

The presence of chum salmon regional populations

The degree of genetic isolation varies among chum salmon river populations (genetic distance ; $D=0.00003-0.00844$), while the strong genetic similarity is observed among the tributary populations within a single river system ($\bar{D}=0.00023$) and among the proximal river populations ($\bar{D}=0.00081$). It is presumed that the accumulation of the genetic intermingling for generations led to genetic similarity among river populations within one region. Therefore, it is concluded that several regional populations consisting of adjacent river populations are formed throughout the entire distribution, namely (1) western Alaska, (2) central Alaska, (3) British Columbia and northern Puget Sound, (4)

southern Puget Sound, (5) northeastern Okhotsk, (6) western Okhotsk (the Amur River), (7) Hokkaido, (8) the northern and (9) southern part on the Pacific coast of Honshu and (10) the northern and (11) southern part on the Japan Sea coast of Honshu.

Each regional population defined from the allelic frequencies has a close relation with the regional population which is assumed from the findings on distribution and migration pattern during the ocean phase. Each chum salmon regional population presumed from the result of the tagging operation and others has its unique distribution and migration pattern in the ocean and they tend to repeat the similar pattern every year with a minor fluctuation. Thus the life history of chum salmon suggests less possibility for intermingling among different regional populations than among the same regional populations. It is considered that the presence of regional population and intermingling within regional population which are indicated by continuity and discontinuity in the allelic frequency of chum salmon river populations are closely related to the above differences during their ocean phase.

The genetic structure of chum salmon in the species of genus *Oncorhynchus*

The characteristics of the genetic structure of chum salmon population can be further defined by comparing it with other species of genus *Oncorhynchus*. Six species of genus *Oncorhynchus* can be divided into two groups, namely (1) sea water dependent group (chum and pink salmon) and (2) freshwater dependent group (sockeye, coho, masu and chinook salmon). In general, the precise homing is supported for the species in the second group, which indicates the occurrence of the significant genetic divergence even among populations within a single river system or a limited area. Conversely, pink salmon shows extremely low level of the genetic divergence throughout its entire distribution. Formation of several regional populations having similar frequencies of alleles throughout its distribution makes the population structure of chum salmon distinctive among the species of genus *Oncorhynchus*. This presumably is a reflection of a close relation with the length of the freshwater phase or the degree of precision of the homing.

The effects of transplantation in chum salmon

Rivers in Japan have been heavily planted in connection with artificial propagation. However, the effects of transplantation have not been precisely evaluated and opinions

are still divided. It is confirmed through this study that the original allelic frequencies remain in the transplanted Tokachi River populations for over three generations which proves the success of the transplantations to the Tokachi River in Hokkaido. However judgning from the change in seasonal distribution of spawning run, transplantations hardly succeed in many rivers. Although many rivers in Honshu have been frequently transplanted from the rivers in Iwate, Yamagata and Hokkaido, each regional population still share a common feature in the frequencies of alleles. This raises a doubt on the effectiveness of the past transplantations. Considering distinct characteristics of each regional population such as the time of return and seaward migration of fry, it is nearly impossible to expect a good result from transplantations from latitudinally distant rivers.

Contents

Introduction

Many studies including the one by HEINCKE (1898) have been conducted to clarify the species composition and ecological feature by applying various methods for different species of fish. These studies were conducted as a basis for the study of fisheries resources which aimes at effective utilization and management of fisheries resources. The current study aimes at clarifying the temporal and spatial population structure and ecological feature of chum salmon (*Oncorhynchus keta*) which is an important species of fish in the North Pacific Ocean, through population genetics which uses genetic variations of enzymes.

Salmonid fishes are generally thought to be one of the most tasty fish and they are highly valued as the target species of fisheries. Family Salmonidae consists of the genus *Oncorhynchus, Salmo, Salvelinus* and *Hucho* and all the species in this family spawn on the gravel of stream or lake and the reproduction of salmonid fishes are maintained in the freshwater area. The species of genus *Oncorhynchus* including chum salmon are typical anadromous species which depend largely on the sea and spawn only once contrasted with other salmoind fishes. Chum salmon spends a very short period in the freshwater as pink salmon (*O. gorbuscha*) and is characterized by the highest dependency on the sea including its nutrition among the species of genus *Oncorhynchus*.

The above ecological characteristics mainly determine the stock size and the methods of fishery management of each species. To be more precise, the species of genus *Oncorhynchus* which depends largely on the sea, maintain a large biomass that can not be expected in other species which spend only in freshwater. The stock size of the species of genus *Oncorhynchus* is extremely large compared with other salmonid fishes. Approximately four hundred thousand tons of genus *Oncorhynchus* are caught annually in the North Pacific and in the rivers entering the sea. The catch of chum salmon accounts for one third of the total catch, following that of pink salmon. The catch of both species amounts to about 70% of the total catch, followed by sockeye (*O. nerka*), coho (*O. kisutch*) and chinook salmon (*O. tshawytscha*). The fish price, on the contrary, is high for sockeye and chinook salmon. Chum salmon is less appreciated in North America as it occupies a smaller portion of the total catch of the genus *Oncorhynchus* than in Japan and the U.S.S.R.

Conversely, chum salmon accounts for major portion of salmonid fishes returning to rivers and streams in Japan and its commercial value is very high. Furthermore, chum

salmon has been closely linked with the life and culture of the Japanese people. The unique eating habit and customs still subsist in many places and the legend and anecdote that have grown up around them are still told today. Chum salmon returns to many rivers in Japan from Hokkido to the middle of Honshu, but the majority returns to Hokkaido. However, chum salmon is distributed widely extending further north along the Pacific coast even to the arctic region. Fig. 1 shows that Japan corresponds to the southern limits of chum salmon distribution. Chum salmon has the most wide distribution area among the species of genus *Oncorhynchus*.

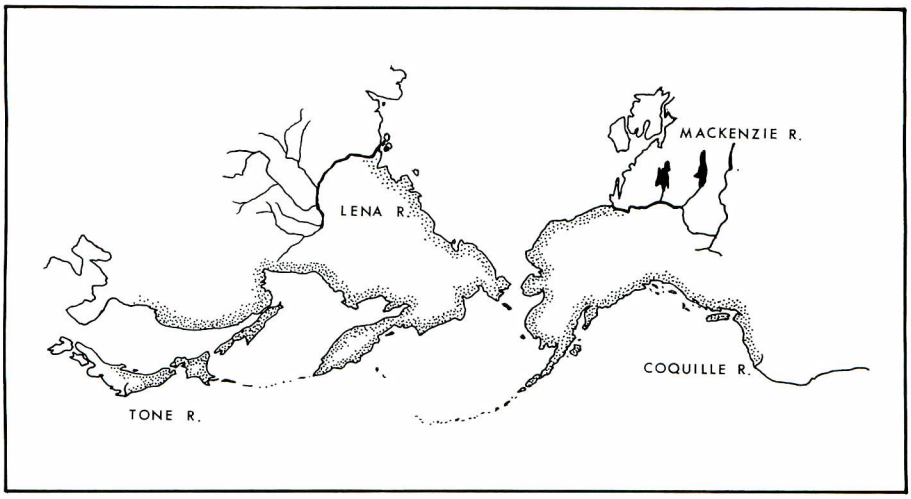


Fig. 1. Coastal distribution (stippled) of chum salmon in the North Pacific Ocean and adjacent seas (from NEAVE *et al.*, 1976).

The high sea fisheries targeted for the species of genus *Oncorhynchus* developed immensely after World War II in Japan. However various restrictions came to be imposed in recent years. Especially, a recognition of the possession of fisheries resources underwent a considerable change since the United Nations Conference on the Law of the Sea held in Geneve, 1958. Although the species of genus *Oncorhynchus* spend most of their life in the ocean, unlike the principals adopted for other fisheries resources including the highly migratory species (*i.e.* tuna, marlin……) and the sedentary species (*i.e.* crab, cod, flatfish……), the general rule was established that the state of origin of anadromous stocks has the right to possess and manage the stocks. Thus, the studies on the locality of populations and the migration route in the ocean in relation to the management and possessions of stocks in and out of territorial waters are urgently called for. Therefore,

the population study of chum salmon rises in importance in Japan which consists the state of origin of this species.

Furthermore, as the species of genus *Oncorhynchus* are reproduced in freshwater, it can be artificially managed to increase the abundance. The techniques for artificial spawning have been developed in many countries. Particularly in Japan, hatcheries are constructed in almost all the rivers that have chum salmon run and most stocks have been maintained through hatchery operations. Therefore the advanced genetic and thremmatological management which is not feasible for other marine fishes can be adopted for chum salmon in future. The genetic structure of natural river population, their mutual relation and the relation with the environment need to be clarified for the future studies of cultivable fishes.

In general, precise homing behavior is supported for salmonid fishes including chum salmon. If they indeed home with precision, then each river should have its own particular genetic populations. The population structure of salmonid fishes attracts much attention because it provides the most adequate material for the population study of fish.

Many attempts have been made to find the population structure of salmonid fishes including chum salmon. All the attempts aimed at clarifying distinct characteristics of river populations or regional populations and also grasping the distribution, migration and the state of intermingling of each regional population during their ocean phase by using these characteristics. The methods applied are as follows.

1) Tagging studies
2) Scale studies
3) Analysis of catch composition
4) Morphological studies
5) Age composition studies
6) Parasite studies
7) Studies of population genetics

Tagging studies have been most widely conducted to examine homing, migration pattern and distribution during the ocean phase. Data from tag recoveries have yielded much useful information on the distribution and migration of each chum salmon regional population in offshore waters (MANZER *et al.*, 1965 ; HARTT, 1966 ; NEAVE *et al.*, 1976). However, the defects of this method are an extremely low rate of the tag recoveries and a difference in the recovery efforts by area.

It has long been known that there are small differences in the scale patterns of

salmon of different coastal regions. These differences are expressed in the number and spacing of the ridges (circuli), apparently reflecting regional differences in growth patterns early in the life of the fish. SHEPARD *et al.* (1968) and TANAKA *et al.* (1969) examined many samples collected from major regions which have chum salmon run and they reported that distinct scale patterns were observed among the populations in different coastal regions although differences among individual rivers were not significant. Furthermore, the attempt was made to determine the places of origin of chum salmon in offshore waters by using the characteristics in scale patterns. These findings are in fairly good agreement with the results obtained from tagging experiments with a few exceptions. However, fish which could not be assigned to any region or continent amounted to more than a half of the specimen examined in offshore due to a significant overlapping of scale patterns among populations. Analysis using characteristics of scale patterns have some problems as the characteristics change significantly by year even among the population originated in the same region. The effort is still continued to improve the precision of the analysis.

The method that has been applied for chum salmon populations in the ocean phase is to analyze the distribution of the temporal and spatial density from the catch composition. It is considered that this method yields useful information on the migration pattern of each population in some areas (MANZER *et al.*, 1965). However, many populations originated in various regions are intermingling complicatedly during the ocean phase of chum salmon whereas the period and waters covered by fisheries or test sampling are limited. Thus, it is considered that there is plenty of room for improvement in this method.

On the other hand, the method using age composition, parasite and morphology could not characterize each population, because the characteristics used overlap significantly among populations (SHEPARD *et al.*, 1968).

Much effort has been made from various aspects to define the population structure of chum salmon. The results of the tagging experiments, scale studies and the analysis of catch composition indicate that the chum salmon population originating in a definite coastal region—a regional population—has its unique distribution and migration pattern in the ocean and they tend to repeat the similar pattern every year. However, the information essential to the study of the population structure of chum salmon is still lacking. This includes the question of (1) what is the degree of intermingling among river populations, (2) whether the intermingling occurs everywhere or within a limited

area and (3) how the allelic frequency is different among river or regional populations, provided there is the isolation among river populations to some extent.

The current study examines the genetic feature of chum salmon populations over an extensive geographic range of its distribution using allelic variations of enzymes as indice. The purpose of the study is to define the genetic structure and maintenance of this species. The populations examined totaled 57 populations including 11 populations on the Continent of North America, three populations in the U.S.S.R. and 43 river populations in Japan. The genetic variability of enzymes and the basis of the method for detecting variation using the zymogram technique have been defined by the recent studies (NUMACHI, 1974 ; MARKERT, 1975). Genetic data were collected from analysis of 14 enzymes. The polymorphism* was identified for 16 loci coding for ten out of the above 14 enzymes. Population analysis was made on the basis of the phenotypic and allelic frequencies of each examined population, the genetic distance (D) among examined populations and the average heterozygosity (H).

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 ($\bar{D}$=0.00023) and among the proximal river populations ($\bar{D}$=0.00081). It is presumed that the accumulation of the genetic intermingling for generations led to genetic similarity among river populations within one region. Therefore, it is concluded that several regional populations consisting of adjacent river populations are formed throughout the entire distribution. They include (1) western Alaska, (2) central Alaska, (3) British Columbia and northern Puget Sound, (4) southern Puget Sound, (5) northeastern Okhotsk, (6) western Okhotsk (the Amur River), (7) Hokkaido, (8) the northern and (9) southern part on the Pacific coast of Honshu and (10) the northern and (11) southern part on the Japan Sea coast of Honshu.

Chum salmon population is unique among the species of genus *Oncorhynchus* in having several regional populations. This characteristic presents a striking contrast to sockeye salmon and others in which the genetic isolation of river populations is more evident.

In future, the complete picture of the distribution, migration and the state of the intermingling among regional populations of chum salmon during the ocean phase will gradually emerge with the accumulation of gene frequency data. It is expected that

* A locus is here defined as polymorphic in a population if the frequency of the commonest alleles is equal to or less than 0.99.

the result of the current study will contribute greatly to the resource management of chum salmon including its application to the genetic and thremmatological management.

In genetic study the identification of origin of each individual is generally impossible and a considerable number of specimens are required to identify the differences among the populations. Furthermore, it is also impossible to identify the different populations unless the genetic differentiation is attained between them. Therefore, this method is not always pertinent to the population study.

This paper is a doctor thesis submitted to University of Tokyo.

I. Materials and methods

1. Collections and storage of samples

Samples of chum salmon mature fish, immature fish and fry are collected from extensive areas of its distribution. The number of specimens were 1,062 in North America, 164 in the coastal regions of the U.S.S.R. and 4,586 in Japan. They were taken at hatcheries or collected from the catch of local fishermen or research cruises. Whole bodies or respective tissues of fish were frozen immediately after catch, shipped to the laboratory by packing with dry ice in insulated container, and stored at −20°C. No significant changes in both the electrophoretic mobility and staining intensity of each examined enzyme were observed during the storage, and even after longer period of storage up to one year.

2. Preparation of crude extracts

Tissues of liver, heart, skeletal muscle and eyeball were used for screening. The eyeball including sclera and a part of muscle, was provided for screening without separating it to retina and other small sections. Tissue extracts of eyeball and liver were prepared by placing equal amounts of tissue and distilled water into glass tubes and blending this mixture into a paste with a glass rod. The samples were then centrifuged for five minutes at 1,000 g and the supernatants obtained were analyzed by electrophoresis. For screening of skeletal and heart muscle the cell-lysates obtained by thawing the frozen tissues were used instead of the supernatants. Various extraction media, such as distilled water and several types of buffer system gave similar results in both of extractability and electrophoretic pattern of each enzyme.

3. Electrophoresis

The supernatants or cell-lysates were subjected to starch gel electrophoresis.

After electrophoresis, the activities of 14 enzymes listed in Table 1 were identified directly on the gel by incubating in each reaction mixture.

The following three buffer systems were routinely used in the course of this study.

I) Described by NUMACHI *et al.* (1979) with slight modification based on the CLAYTON and TRETIAK (1972).

Stock solution for gel buffer (pH 7.5)

Citric acid (0.04M)

Adjusted to pH 7.5 with N-(3-Aminopropyl)-diethanolamine.

Stock solution for electrode buffer (pH 7.2)

Citric acid (0.2M)

Adjusted to pH 7.2 with N-(3-Aminopropyl)-diethanolamine.

A 1 : 20 dilution of the upper stock solution was used for gel preparation and a 1 : 5 dilution of the lower was used for the electrode buffer. During electrophoresis a constant current of 70 mA was applied to the gel.

II) Described by RIDGWAY *et al.* (1970).

Gel buffer (pH 8.5)

Tris (tris (hydroxymethyl)-aminoethane) (0.03M)

Citric acid (0.005M)

Electrode buffer (pH 8.1)

Lithium hydroxide (0.06M)

Boric acid (0.3M)

Gels were made using 99% gel buffer and 1% electrode buffer. During electrophoresis a constant voltage of 250 V was applied to the gel.

III) Described by CLAYTON and TRETIAK (1972).

Gel buffer (pH 6.1)

Citric acid (0.002M)

Adjusted to pH 6.1 with N-(3-Aminopropyl)-morpholine.

Electrode buffer (pH 6.1)

Citric acid (0.04M)

Adjusted to pH 6.1 with N-(3-Aminopropyl)-morpholine.

During electrophoresis a constant current of 70 mA was applied to the gel.

Starch gels were prepared by adding hydrolyzed starch (Electrostarch ; Electrostarch Inc., Madison, Wisconsin, U.S.A.) at a concentration of 13% to each gel buffer. This mixture was then heated to boiling and degassed with a water aspirator. The resultant

mixture was poured into a prepared frame on a glass plate and allowed to cool at room temperature during 3 to 24 hours before using. The following four different frames made of acryl were used according to purpose.

25.0×14.0×1.0 cm
25.0×14.0×0.6 cm
25.0×12.5×1.0 cm
25.0×12.5×0.6 cm

The supernatants extracts or cell-lysates soaked into filter paper wicks were placed vertically in the gel cut. A double filter paper was used to conduct the electric current from the tray of electrode buffer to the appropriate ends of the gel. An ice pack on a glass plate was placed on top of the gel and the appropriate electric current applied until the indicator dye marker reached a point 6—9 cm from the origin.

4. Staining procedures

After electrophoresis, the horizontally sliced gels of 1 mm in thickness were incubated from 15 to 60 minutes at room temperature with a reaction mixture. The components of the staining solutions used are listed in Table 1. The procedure followed the methods of SHAW and PRASAD (1970). The gel buffer (pH 8.5) of buffer system (Ⅱ) was used as stain buffer. The staining solution for Pep-LGG, PGI and PMI was prepared by adding 1% agar solution and this was overlayed on the gel.

II. Genetic basis of electrophoretic variation

1. Population study using biochemical genetic methods

In the population study using genetic methods, the allellc frequency of each population is examined by reading the genotypes directly from the phenotypes. Thus in the first place, the characteristics from which we can read the genotypes accurately and efficiently are required. Isozymes which have been used consistently throughout this study, are unique characteristics which meet the above conditions.

In the past, it was considered that in many organisms the enzyme proteins with the same catalytic activities share a single molecular form. With a progress in research, it became clear that multiple molecular forms of enzymes are commonly found not only in a single tisstue bu within sigle cells (MARKERT, 1963). Isozyme is multiple forms of enzyme arising from genetically determined difference in primary structure.

Table 1. Composition of staining solutions and buffer systems used for electrophoretic analysis of enzymes. The buffer system listed are those providing acceptable resolution for that particular enzyme. (See text for further explanation.)

Enzyme	Abbreviation	Buffer systems	NBT* PMS	Cofactor (5 mg)		Other components
Alcohol dehydrogenase	ADH	I, II, III	+	NAD	5 ml	Ethanol (95%)
Aspartate aminotransferase	AAT	II			50 mg	α-ketoglutaric acid
					100 mg	L-aspartic acid
					10 mg	Fast garnet GBC salt
α-Glycerophosphate dehydrogenase	α-GDH	I, III	+	NAD	50 mg	DL-α-glycerophosphate
Isocitrate dehydrogenase	IDH	I	+	NADP	30 mg	DL-Na-isocitrate
Lactate dehydrogenase	LDH	I, III	+	NAD	1 ml	Na-lactate (50%)
Malate dehydrogenase	MDH	III	+	NAD	200 mg	DL-Na-malate
Leucylglycylglycine Aminopeptidase	Pep-LGG	II			10 mg	O-dianisidine
					5 mg	L-amino acid oxidase
					10 mg	Peroxidase
					10 mg	DL-leucylglycylglycine
					30 ml	Agar (1%)
6-Phosphogluconate dehydrogenase	6-PGD	I, III	+	NADP	20 mg	Na-6-phosphogluconate
Phosphoglucomutase	PGM	II	+	NADP	10 units	G6PDH
					2 mg	α-D-glucose-1,6-diphosphate
					30 mg	Na-glucose-1-phosphate
Phosphoglucose isomerase	PGI	II	+	NADP	10 units	G6PDH
					5 mg	Na-fructose-6-phosphate
					30 ml	Agar (1%)
Phosphomannose isomerase	PMI	III	+	NADP	10 units	G6PDH
					100 units	Phosphoglucose isomerase
					10 mg	Ba-D-mannose-6-phosphate
					30 ml	Agar (1%)
Sorbitol dehydrogenase	SDH	II	+	NAD	100 mg	D-sorbitol
Superoxide dismutase	SOD	I, III	+			
Xanthine dehydrogenase	XDH	II	+	NAD	5 mg	Hypoxanthine

* "+" indicates the presence of both NBT (5 mg) and PMS (2 mg).

Abbreviations ;

NAD β-nicotinamide adenine dinucleotide
NADP β-nicotinamide adenine dinucleotide phosphate
NBT Nitro blue tetrazolium
PMS Phenazine methosulfate
G6PDH Glucose-6-phosphate dehydrogenase

In recent years, the combination of starch gel electrophoresis and histochemical staining procedures has resulted in the zymogram technique. The application of this method makes it easy to detect the genetic variant which brings on a change in its electrophoretic mobility or number of isozymes and provides valuable knowledge on molecular forms and genetic control of enzymes or proteins. The electrophoretic variation is the result of allelic substitutions at structual loci which causes a change of net electrical charge. The biochemical genetic methods offer a number of advantages over more conventional morphological markers in the course of population analysis in that it (1) ignores the environmental effects on the manifestation (2) provides an effective marker for over generations.

The application of this method makes it possible to grasp the genetic traits of each population and to find the degree of differences, genetic intermingling and genetic divergence among populations from a change in the frequencies of alleles.

2. Genetic traits of salmonid fishes

Salmonid fishes contain about twice as much DNA per cell and twice as many chromosomes as other clupeoid fishes, suggesting the tetraploidy hypothesis of salmonids (OHNO *et al.*, 1968). Gene duplication is observed at the most loci coding for lactate dehydrogenase (LDH ; BAILEY and WILSON, 1970), and the gene dosage of duplicate loci is also found in malate dehydrogenase (MDH-B) variations (NUMACHI *et al.*, 1972). Both lines of evidence obtained from electrophoretic analysis independently support the tetraploidy hypothesis of salmonids. However the gene duplication is not always found at entire loci and therefore, it is considered that salmonid fishes are allotetraploid.

The gene duplication at the LDH and MDH loci is found in all salmonid fishes including the genus *Salmo*, *Salvelinus* and *Hucho* to say nothing of the genus *Oncorhynchus* (OKAZAKI, 1974). It is presumed that the duplication of the entire genome (tetraploidy) occured at some previous point in their evolution in these species (OHNO *et al.*, 1968). Due consideration needs to be given to this phenomenon in investigating genetic traits of salmonid fishes.

3. Genetic control of enzymes

i. Lactate dehydrogenase (LDH ; EC, 1.1.1. 27)

Lactate dehydrogenase (LDH) is one of the best known enzymes for its genetic control and subunit structure. The five electrophoretically distinguishable LDH isozymes

of most mammals are well known to be tetramer formed by random association of two different subunits, each under the control of separate genetic loci A and B (MARKERT, 1963). LDH-A predominates in skeletal muscle, while LDH-B is predominant in heart muscle. Furthermore, many fishes have another locus for LDH, predominating in eyeball, which is designated as LDH-E (HOROWITS and WHITT, 1972). In salmonid fishes, as a result of gene duplication at the LDH-A and B loci, the LDH-A_1 and A_2 loci and the LDH-B_1 and B_2 loci arose respectively. In this report, these are designated as LDH-1 (A_2), 2(A_1), 3(B_2), 4(B_1) and 5(E) in accordance with their mobility during electrophoresis.

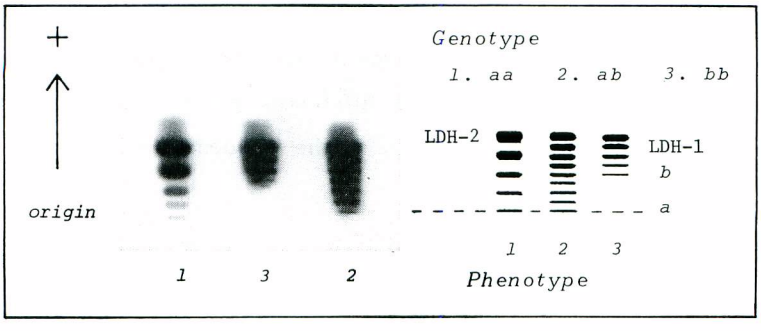


Fig. 2. Starch gel patterns of lactate dehydrogenase variants from skeletal muscle extracts in chum salmon. The number of each variant phenotype corresponds to that of genotype.

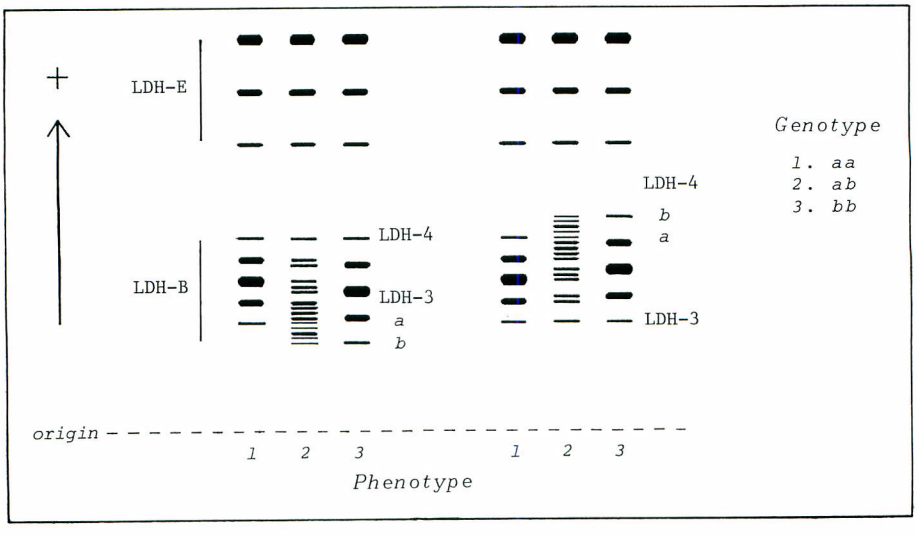


Fig. 3. Starch gel patterns of lactate dehydrogenase variants from eyeball extracts in chum salmon. The number of each variant phenotype corresponds to that of genotype.

Polymorphism for LDH-1 and 4 in chum salmon has been described by other workers (NUMACHI and SATO, 1970 ; UTTER *et al.*, 1973). LDH-3 variation was also observed through this study. However, the frequencies of the variants were extremely low except the LDH-1 locus. The LDH-1, 3 and 4 phenotypes are presented in Figs 2 and 3.

ii. Malate dehydrogenase (MDH ; EC, 1.1.1. 37)

It is known that malate dehydrogenase (MDH) contains mitochondrial and supernatant forms. Supernatant MDH, examined in this study, shows a dimeric structure in many fish species (NUMACHI, 1970). Furthermore MDH-A and B systems are identified in the supernatant MDH and they are under the control of separate genetic loci A and B (BAILEY and WILSON., 1970). MDH-A and B are predominant in liver and skeletal muscle, respectively. A three-allele polymorphism for MDH-B has been identified (NUMACHI *et al.*, 1972 ; OKAZAKI, 1981).

In diploid organisms, three genotypes occur under the presence of two alleles at a single locus. They should be distinguishable electrophoretically and typical electrophoretic phenotype of each genotype for a dimeric enzyme is (1) the three isozymes produced in the ratio of 1 : 2 : 1 for the heterozygote and (2) one isozyme with different mobility produced alone for both heterozygotes. However, the phenotypes which have inexplicable ratios of isozymes from the single locus model are present in MDH-B variation of chum salmon. It is presumed that these phenotypes occur in salmonid fishes including chum salmon resulting from the gene dosage of duplicate loci (NUMACHI *et al.*, 1972). MDH-B phenotypes reflecting three alleles and their theoretical ratios of isozymes are shown in Fig. 4. Therefore, an identification of each genotype is made considering the staining intensity (ratios of isozymes) in addition to the electrophoretic mobilities and the number of isozymes.

On the other hand, MDH-A variation was not detected throughout the examined populations.

iii. Aspartate aminotransferase (AAT ; EC, 2.6.1.1)

Three loci are coding for aspartate aminotransferase (AAT) which is a dimeric enzyme. The AAT-1 and 2 loci are predominant in skeletal or heart muscle, while the AAT-3 locus predominates in eyeball. Gene duplication has been identified for the former loci (MAY *et al.*, 1975). The presence of three alleles were found at the duplicate loci AAT-1, 2 through the examination and the phenotypes reflecting the gene dosage of

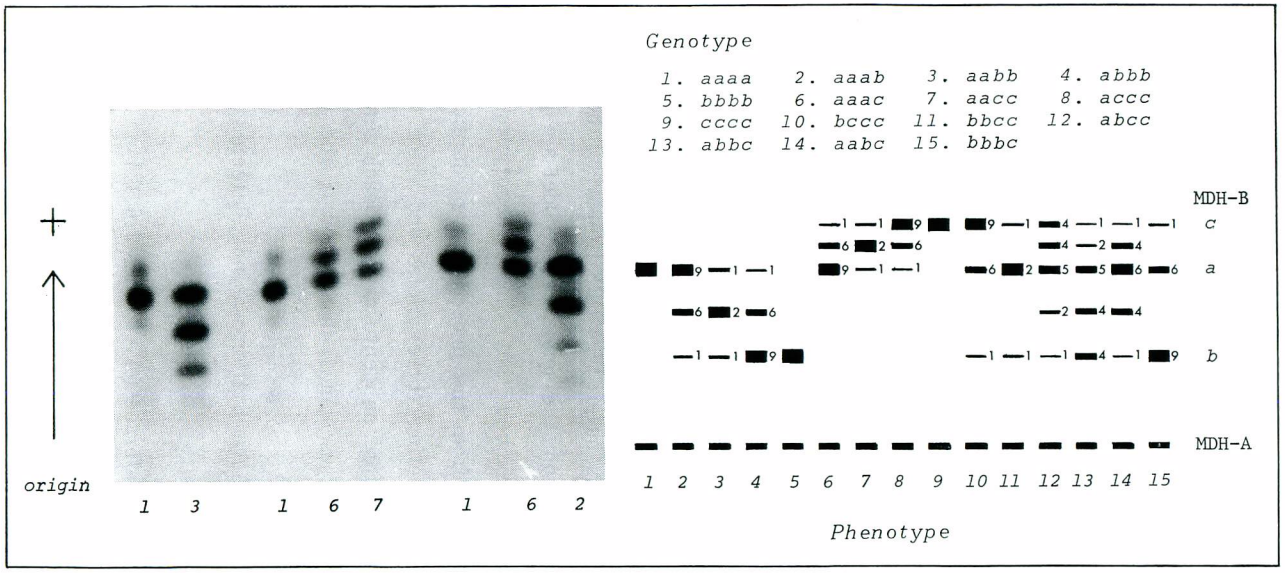


Fig. 4. Starch gel patterns of malate dehydrogenase variants from skeletal muscle extracts in chum salmon. Numerals indicate theoretical ratios of isozymes produced in each phenotype. The number of each variant phenotype corresponds to that of genotype.

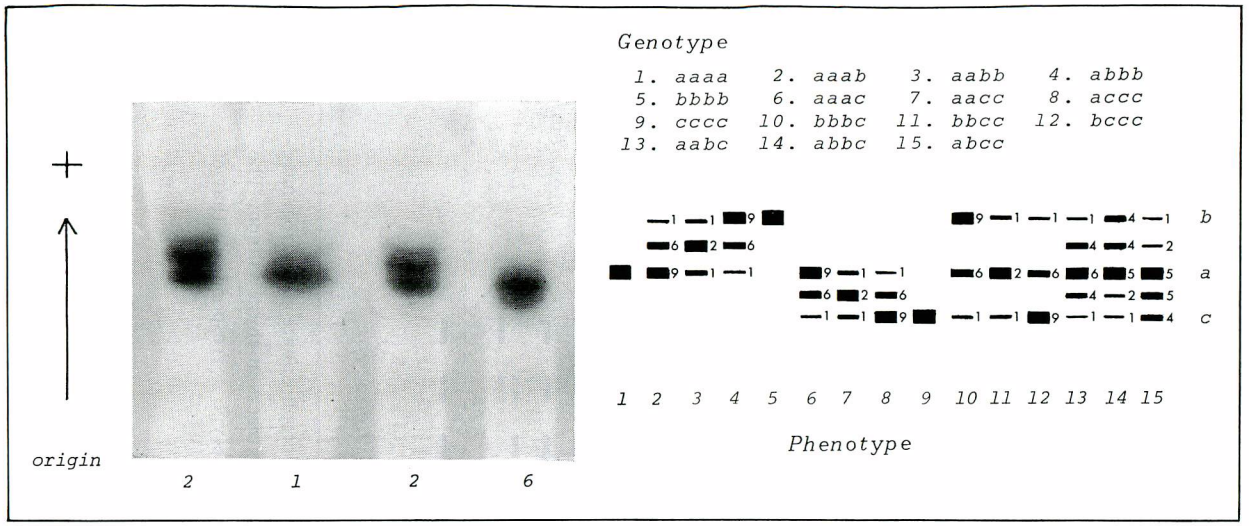


Fig. 5. Starch gel patterns of aspartate aminotransferase variants from heart muscle extracts in chum salmon. Numerals indicate theoretical ratios of isozymes produced in each phenotype. The number of each variant phenotype corresponds to that of genotype.

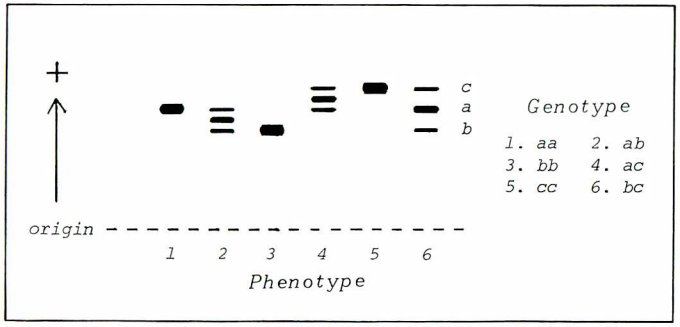


Fig. 6. Starch gel patterns of aspartate aminotransferase variants from eyeball extracts in chum salmon. The number of each variant phenotype corresponds to that of genotype.

duplicate loci were observed as well as the abovementioned MDH-B phenotypes (Fig. 5).

A three-allele polymorphism was identified for a single disomic locus AAT-3 (Fig. 6).

iv. α-Glycerophosphate dehydrogenase (α-GDH ; EC, 1.1.1.8)

The result indicates that there are three loci coding for α-glycerophosphate dehydrogenase (α-GDH). The α-GDH-3 locus, showing the highest electrophoretic mobility, predominates in heart or skeletal muscle. While α-GDH-1, exhibited at the cathodal side of the gel, and α-GDH-2 are predominant in heart muscle.

A two-allele polymorphism was identified for α-GDH-2 (Fig. 7 ; ALTUKHOV *et al.*, 1972), indicating a dimeric structure of this enzyme.

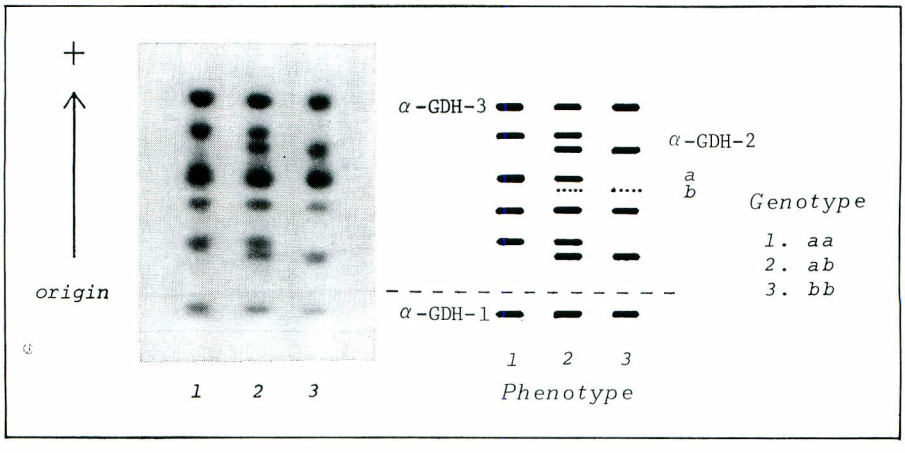


Fig. 7. Starch gel patterns of α-glycerophosphate dehydrogenase variants from heart muscle extracts in chum salmon. The number of each variant phenotype corresponds to that of genotype.

v. Isocitrate dehydrogenase (IDH ; EC, 1.1.1. 42)

Three loci are coding for isocitrate dehydrogenase (IDH). The IDH-1 and 2 loci are predominant in liver, while IDH-3 predominates in heart or skeletal muscle. A five-allele polymorphism was observed for the IDH-2 locus (Fig. 8 ; NUMACHI and OHYA, 1974a : OKAZAKI, 1978).

Polymorphism is also identified for the IDH-3 locus (Fig. 9 ; KIJIMA and FUJIO, 1979). IDH-3 phenotypes are presumed to reflect the presence of two alleles, considering the dimeric structure of this enzyme. However the possibility of the presence of gene duplication for this locus cannot be eliminated and therefore, its genetic control remains

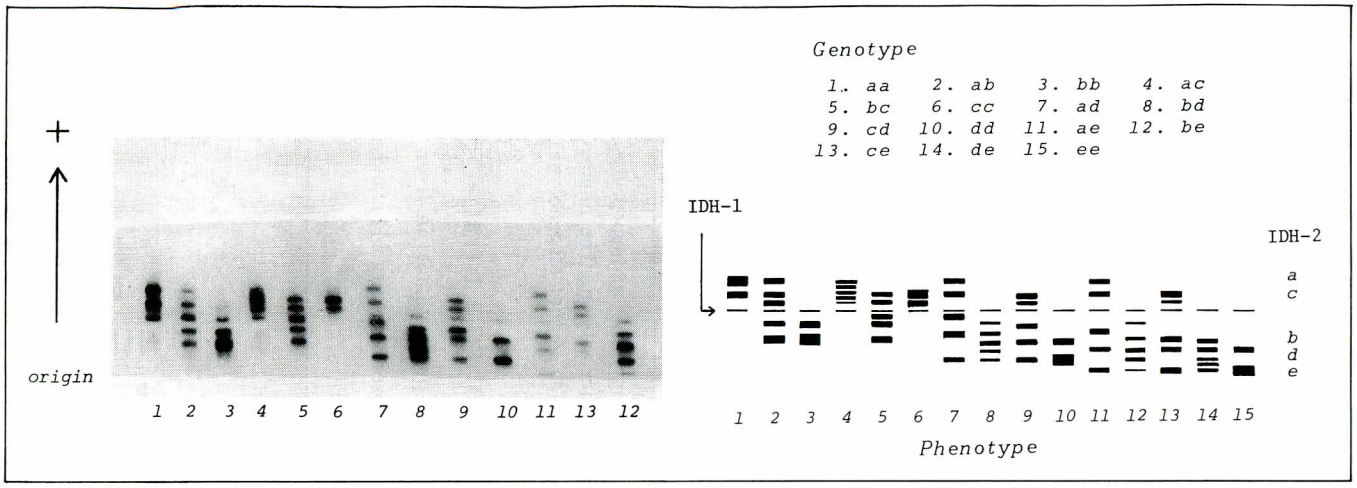


Fig. 8. Starch gel patterns of isocitrate dehydrogenase variants from liver extracts in chum salmon. The number of each variant phenotype corresponds to that of genotype.

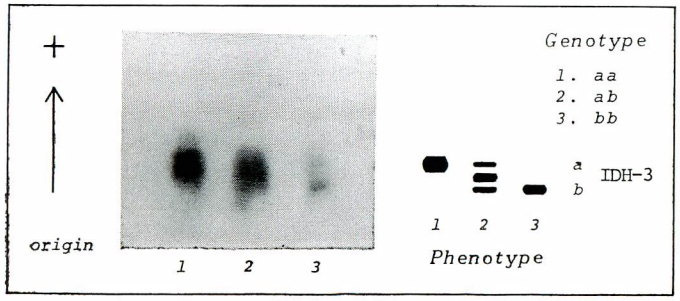


Fig. 9. Starch gel patterns of isocitrate dehydrogenase variants from skeletal muscle extracts in chum salmon. The number of each variant phenotype corresponds to that of genotype.

obscure.

vi. Leucylglycylglycine aminopeptidase (Pep-LGG ; EC, 3.4.11 or 13)

Leucylglycylglycine aminopeptidase (Pep-LGG) is active in various tissues and the variation presumably reflecting two alleles was observed (Fig. 10). Although the subunit structure of the heterozygote could not be defined on the gel, this enzyme probably has a dimeric structure.

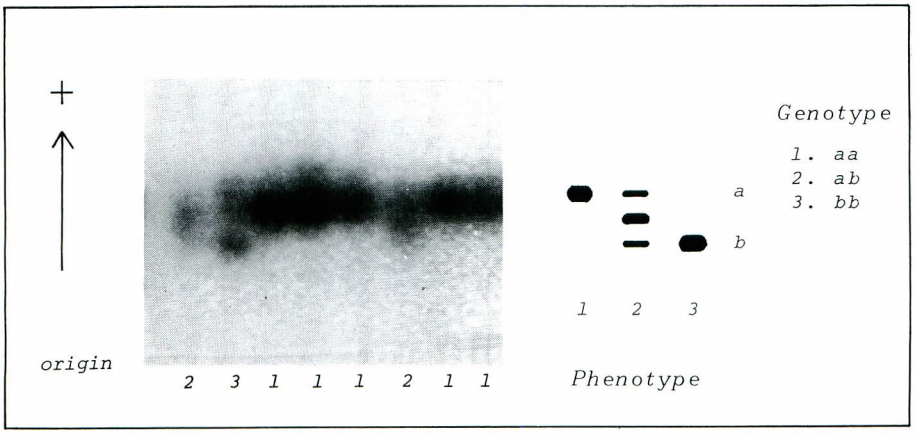


Fig. 10. Starch gel patterns of leucylglycylglycine aminopeptidase variants from eyeball extracts in chum salmon. The number of each variant phenotype corresponds to that of genotype.

vii. 6-Phosphogluconate dehydrogenase (6-PGD ; EC, 1.1.1.44)

6-Phosphogluconate dehydrogenase (6-PGD) is predominant in liver and skeletal muscle. 6-PGD variation reflecting two alleles was observed (Fig. 11) and each isozyme pattern indicates that this enzyme has a dimeric structure.

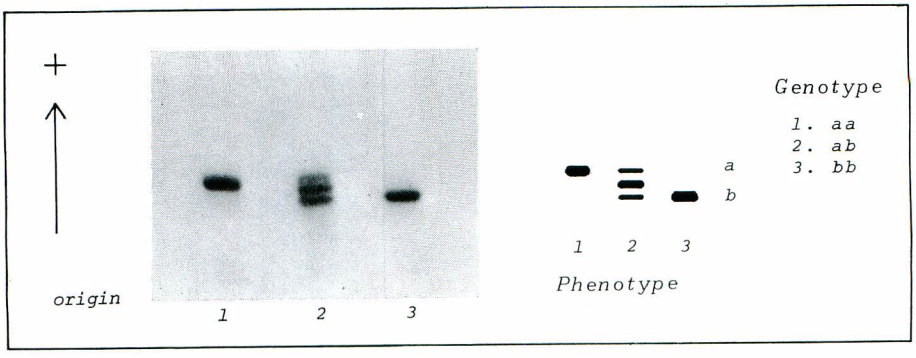


Fig. 11. Starch gel patterns of 6-phosphogluconate dehydrogenase variants from skeletal muscle extracts in chum salmon. The number of each variant phenotype corresponds to that of genotype.

viii. Phosphoglucose isomerase (PGI ; EC, 5.3.1.9)

It is indicated that phosphoglucose isomerase (PGI) is coded for by three loci. They are designated as PGI-1, 2 and 3 in accordance with their mobility during electrophoresis. PGI-1 and 2 are primarily expressed in skeletal muscle, while PGI-3 predominates in skeletal muscle and eyeball. PGI-3 variation reflecting three alleles was observed (Fig. 12) and each isozyme pattern indicates a dimeric structure of PGI.

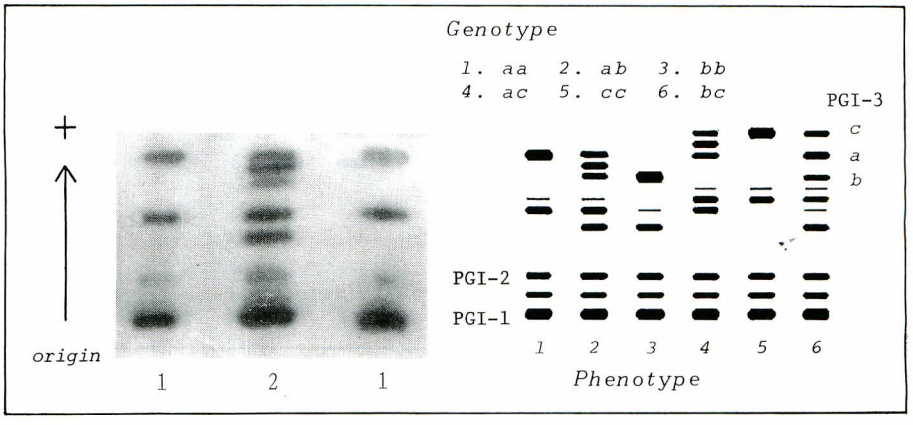


Fig. 12. Starch gel patterns of phosphoglucose isomerase variants from skeletal muscle extracts in chum salmon. The number of each variant phenotype corresponds to that of genotype.

ix. Phosphoglucomutase (PGM ; EC, 2.7.5.1)

It is known that phosphoglucomutase (PGM) has a monomeric structure in many fish species (UTTER and HODGINS, 1970 ; UTTER and HODGINS, 1972). PGM variation reflecting two alleles was observed (Fig. 13), while the frequency was extremely low.

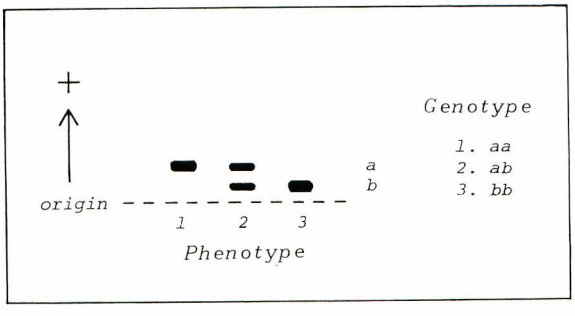


Fig. 13. Starch gel patterns of phosphoglucomutase variants from skeletal muscle extracts in chum salmon. The number of each variant phenotype corresponds to that of genotype.

x. **Phosphomannose isomerase (PMI ; EC, 5.3.1.8)**

Phosphomannose isomerase (PMI) is a monomeric enzyme as PGM and predominates in heart and skeletal muscle. PMI variation reflecting three alleles were observed (Fig.14).

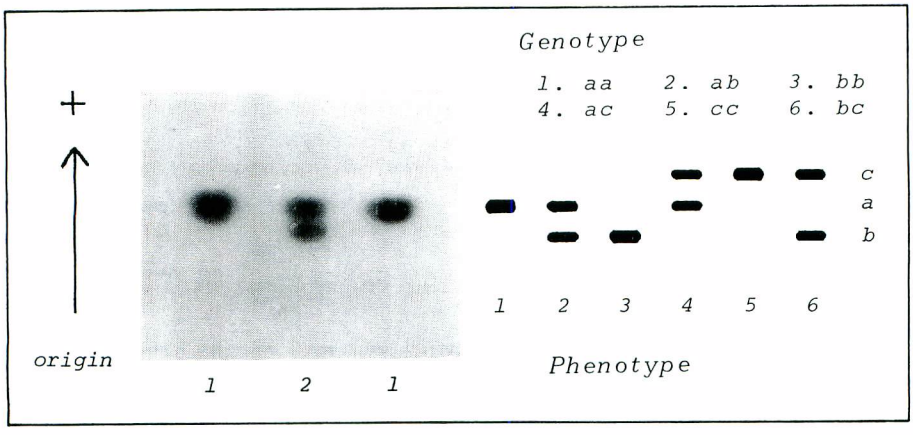


Fig. 14. Starch gel patterns of phosphomannose isomerase variants from skeletal muscle extracts in chum salmon. The number of each variant phenotype corresponds to that of genotype.

xi. **Alcohol dehydrogenase (ADH ; EC, 1.1.1.1)**
Sorbitol dehydrogenase (SDH ; EC, 1.1.1.14)
Superoxide dismutase (SOD ; EC, 1.15.1.1)
Xanthine dehydrogenase (XDH ; EC, 1.2.3.2)

No variation was observed in the above enzymes throughout the examined populations.

Sorbitol dehydrogenase (SDH) has a tetrameric structure in many organisms and it is reported that the SDH locus is duplicated in rainbow trout (*Salmo gairdnerii* ; ENGEL *et al.*, 1970). It is also known that alcohol dehydrogenase (ADH) and superoxide dismutase (SOD) show a dimeric structure in many organisms, including salmonid fishes (UTTER *et al.*, 1974). Therefore, it is presumed that each enzyme of chum salmon has a similar feature. However, the exact number of loci involved and the subunit structure cannot be determined as no genetic variation was observed.

Tissue distribution, number of alleles and others of each enzyme are listed in Table 2.

Table 2. Enzyme stained for, locus designation, tissue distribution and number of alleles.

Enzyme	Locus designation (if multiple)	Tissue distribution	Alleles	Report in
ADH		L	-	
AAT	1,2	H,M	3	MAY *et al.*, 1975
	3	E	3	SEEB and WISHARD, 1977
α-GDH	1	H	-	
	2	H	2	ALTUKHOV, 1975
	3	H,M	-	
IDH	1	L	-	
	2	L	5	NUMACHI and OHYA, 1974a
	3	M	2	KIJIMA and FUJIO, 1977
LDH	A 1	M	2	NUMACHI and SATO, 1970
	2	M	-	
	B 3	E,H,M	2	OKAZAKI, 1981
	4	E,H,L,M	2	UTTER *et al.*, 1972
	E 5	E	-	
MDH	A 1,2	L	-	
	B 3,4	H,M	3	NUMACHI *et al.*, 1972
Pep-LGG		E,H,M	2	OKAZAKI, 1981
6-PGD		L,M	2	SEEB and WISHARD, 1977
PGM		M	2	OKAZAKI, 1981
PGI	1	M	-	
	2	M	-	
	3	E,M	3	OKAZAKI, 1981
PMI		E,H,M	3	SEEB and WISHARD, 1977
SDH		L	-	
SOD		L	-	
XDH		L	-	

- Monomorphic
E=eye, H=heart, L=liver, M=muscle

III. Genetic structure of chum salmon populations in North America

Chum salmon are distributed extensively on the Pacific coast of North America. It plays an important role among the species of genus *Oncorhynchus*. However in view of its taste, it is less appreciated than sockeye or chinook salmon in North America. The eminent feature of chum salmon populations in North America is that they are

reproduced and preserved under the natural environments. Although hatcheries were constructed recently in some rivers in British Columbia and Washington, the artificial spawning occupies only a small portion in the total spawning. Furthermore, hardly any transplantations have been made so far. Therefore, an examination of the genetic structure of North American populations may provide general insights into the structure of natural populations of chum salmon.

Samples of 11 populations were collected from 10 locations of rivers and coasts (Fig. 15), which represent major areas of chum salmon run in North America and the allelic frequencies were compared among these collections. All the samples collected by

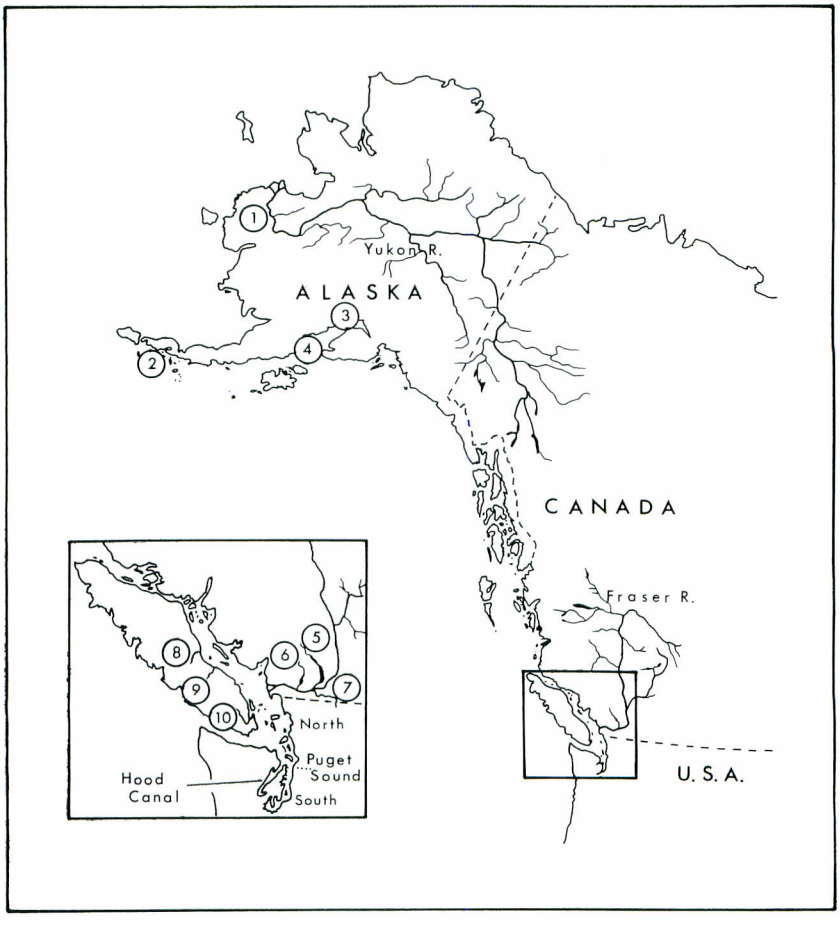


Fig. 15. Map of North America showing the sites where chum salmon were sampled. (1) Yukon River, (2) King Cove, (3) Cook Inlet (north), (4) Cook Inlet (south), (5) Harrison R., (6) Stave R., (7) Vedder R., (8) Puntledge R., (9)Qualicum R., (10) Goldstream R.

hand seine or spear in Britich Columbia were parental fish after spawning except the Qualicum River collection. Parental fish in the Qualicum River were collected during the process of artificial spawning at the hatchery. Alaskan samples were collected from local fishermen at the mouth of the Yukon River or along coastal areas where developed gonads and nuptial coloration or hooked snout indicated that the fish were destined for imminent spawning in the immediate vicinity.

In result, common feature was observed in the frequencies of alleles among each regional population in North America. A strong similarity was also found in the frequencies of alleles within the tributary populations of a single river system and proximal river populations. Both lines of evidence strongly suggest that the genetic intermingling is occuring among the proximal river populations to say nothing of tributary populations (OKAZAKI, 1981). It is detailed in the following section.

1. Biological characteristics

Chum salmon are distributed in North America from the Mackenzie River entering the Arctic Ocean, southward through the Bering Sea and the North Pacific Ocean to the Coquille River in Oregon. The rivers with large runs are located within an area extending from the Yukon River entering the Bering Sea through British Columbia to the northern part of Washington (SHEPARD *et al.*, 1968). Large differences in the abundance of chum salmon are found between North America and Asia including Japan and from the catch statistics it is postulated that the latter has an abundance about four times as large as the former (NEAVE *et al.*, 1976). Therefore, the ratio of chum salmon to all the species of genus *Oncorhynchus* in North America is smaller than in Asia.

Some diversities are observed in biological features of North American chum salmon as they are distributed widely from north to south. To cite an instance, northern runs spawn as early as June and timing gradually becomes later as distribution extends southward to mid-winter in some southern populations (ATKINSON *et al.*, 1967 ; ARO and SHEPARD, 1967).

The distribution and migration of North American chum salmon are confined to the northeastern Pacific Ocean and it is considered that the populations which migrate beyond 180° longitude are very few (NEAVE *et al.*, 1976). These characteristics of North American chum salmon present a striking contrast to Asian chum salmon which migrate beyond the northeastern Pacific Ocean to as far as the Gulf of Alaska.

Table 3. Gene frequencies at each locus in 14

Location	Collectcd date	Sample size	AAT-1,2			AAT-3			α-GDH-2		IDH-2				IDH-3	
			a	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*a*	*b*	*c*	*d*	*a*	*b*
Yukon River (Emmonak ; summer run)	Jul. 13,79	150	.952	.043	.005	—	—	—	.874	.126	.483	.479	.038	.000	.867	.133
Yukon R. (Emmonak ; fall run)	Aug. 7,79	100	.931	.051	.018	—	—	—	.918	.082	.419	.535	.040	.005	.839	.161
King Cove	Aug. 2,79	85	.934	.066	.000	—	—	—	.961	.039	.500	.414	.056	.031	.882	.118
Cook Inlet (north)	Jul. 21,79	80	.914	.086	.000	.761	.239	.000	.790	.210	.500	.410	.077	.013	.803	.197
Cook Inlet (south)	Jul. 23,79	80	.954	.046	.000	—	—	—	.747	.253	.477	.432	.053	.038	.830	.170
Puntledge R.	Nov. 28,78	100	.918	.082	.000	.745	.255	.000	.950	.050	.615	.270	.055	.060	.946	.054
Qualicum R.	Nov. 27,78	100	.926	.074	.000	.698	.302	.000	.945	.055	.667	.266	.026	.042	.967	.033
Goldstream R.	Nov. 29,78	87	.890	.110	.000	.649	.351	.000	.953	.047	.601	.274	.024	.101	.915	.085
Harrison R.	Nov. 21,78	80	.850	.150	.000	.734	.266	.000	.963	.038	.640	.260	.040	.060	.907	.093
Stave R.	Nov. 22,78	100	.850	.150	.000	.643	.357	.000	.940	.060	.677	.187	.056	.081	.906	.094
Vedder R.	Nov. 23,78	100	.825	.175	.000	.675	.314	.010	.928	.072	.697	.207	.035	.061	.893	.107
Puget Sound (north)			.884	.116	.000	.706	.293	.000	—	—	.644	.256	.019	.082	—	—
Puget Sound (south)			.878	.122	.000	.727	.273	.000	—	—	.478	.332	.151	.038	—	—
Hood Canal			.901	.098	.000	.748	.253	.000	—	—	.545	.293	.112	.050	—	—

Gene frequencies in Puget Sound(north and south)and Hood Canal were calculated by weighting

2. Genetic feature of regional populations

Allelic frequencies at 14 polymorphic loci in the examined populations were listed in Table 3. Many differences among populations are evident from comparisons of allelic freqencies at the polymorphic loci. The frequency of the *Idh-2-a* allele is much higher than that of the *b* allele in British Columbia populations while intermediate and similar frequencies of both alleles are observed in Alaskan populations. All Alaskan populations are polymorphic for the LDH-1 locus while only two variant individuals were seen in all of the Canadian samples. Alaskan populations are further characterized by particularly low frequencies of the *Idh-2-d* allele which was not observed in the summer run of the Yukon River. Cook Inlet populations were distinguishable from all other groups by higher frequencies of α-GDH-2 variation and much lower frequencies of Pep-LGG variants, which indicates further division of Alaskan populations into the population in western Alaska facing the Bering Sea and those of central Alaska facing the Gulf of Alaska. Significant differences among areas were not observed at the remaining polymorphic loci although

populations of chum salmon in North America.

LDH-1		LDH-3		LDH-4		MDH-B			Pep-LGG		6-PGD		PGI-3			PGM		PMI		
a	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*c*	*a*	*b*	*a*	*b*	*a*	*b*	*c*	*a*	*b*	*a*	*b*	*c*
.846	.154	1.000	.000	1.000	.000	1.000	.000	.000	.883	.117	.970	.030	1.000	.000	.000	1.000	.000	.953	.047	.000
.750	.250	1.000	.000	1.000	.000	1.000	.000	.000	.865	.135	.975	.025	1.000	.000	.000	1.000	.000	.933	.067	.000
.929	.071	1.000	.000	1.000	.000	1.000	.000	.000	.842	.158	.982	.018	.988	.000	.012	1.000	.000	.940	.060	.000
.949	.051	1.000	.000	1.000	.000	1.000	.000	.000	.988	.013	1.000	.000	1.000	.000	.000	1.000	.000	.956	.044	.000
.974	.026	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	.981	.019	.000
.990	.010	.990	.010	.990	.010	1.000	.000	.000	.768	.232	1.000	.000	.995	.005	.000	1.000	.000	.915	.085	.000
1.000	.000	1.000	.000	.990	.010	1.000	.000	.000	.790	.210	1.000	.000	1.000	.000	.000	.995	.005	.885	.115	.000
1.000	.000	1.000	.000	1.000	.000	1.000	.000	.000	.822	.178	1.000	.000	1.000	.000	.000	1.000	.000	.849	.151	.000
1.000	.000	1.000	.000	1.000	.000	1.000	.000	.000	.878	.122	.994	.006	1.000	.000	.000	1.000	.000	.863	.138	.000
1.000	.000	1.000	.000	1.000	.000	.988	.008	.005	.805	.195	.990	.010	.995	.005	.000	1.000	.000	.860	.140	.000
1.000	.000	1.000	.000	.995	.005	1.000	.000	.000	.726	.274	.995	.005	1.000	.000	.000	1.000	.000	.910	.085	.005
1.000	.000	1.000	.000	1.000	.000	1.000	.000	.000	—	—	.994	.006	1.000	.000	.000	1.000	.000	.829	.171	.000
.997	.003	1.000	.000	1.000	.000	1.000	.000	.000	—	—	.981	.019	1.000	.000	.000	1.000	.000	.763	.237	.000
.998	.002	1.000	.000	1.000	.000	.999	.000	.001	—	—	.990	.010	1.000	.000	.000	1.000	.000	.821	.181	.000

the data published by SEEB and WISHARD (1977) by sample size.

the patterns of distribution for some loci (*e.g.*, AAT-1, 2 ; PMI ; IDH-3) suggested that additional structuring may become evident upon further sampling. The remaining 12 loci which are not listed in Table 3 were monomorphic for all the populations examined.

The combined data indicate that river populations in each area share a common genetic feature and that two major clusters of (1) Alaskan and (2) British Columbia and Puget Sound populations were defined for North American chum salmon. The former is further subdivided into populations in western Alaska and those in central Alaska. Likewise, the latter is subdivided into the populations in British Columbia and northern Puget Sound and those in southern Puget Sound. Thus, it is indicated from the genetic traits that throughout chum salmon distribution there are what may be called regional populations each consisting of several proximal river populations.

The absence or extremely low frequency of MDH-B variation is observed in all North American populations, which distinguish North American chum salmon from Japanese counterpart in which the polymorphism is observed at this locus at a constant rate, as discussed in the later section.

3. Genetic feature of river populations

i. Genetic feature among subpopulations within a single river system

The chum salmon runs returning to the Yukon River have been separated into two groups on the basis of their time of return (GILBERT, 1922). Fish of the summer run, which is more abundant and returns to the river from early June to mid-July are smaller and mature rapidly upon reaching freshwater to spawn in the lower reaches of the river. The autumn run fish, returning from late July through early September, are larger and spawn in the upper sections of the river (Alaska Dept. Fish and Game, 1978).

Samples of the Yukon River were collected at the river mouth (Emmonak) in July and August coinciding with the time of summer and autumn runs. Allelic frequencies were similar between runs where only LDH-1 had a difference of fairly low significance ($\chi^2=5.37$; $p<.05$). Both populations are characterized by low frequencies of the *Idh-2-d* allele unlike other Alaskan populations. It is assumed that the similarities within and between runs persist through some degree of gene flow among populations.

Both the summer and autumn runs of the Yukon River were sampled at the river mouth and therefore, almost certainly reflected mixtures of populations returning to different areas upstream. However, phenotypic frequencies of both collections conformed to Hardy-Weinberg expectations which would not be expected if highly divergent allelic frequencies occurred among populations within the two runs ; it is therefore assumed that similar allelic frequencies exist among component populations of each run. Thus, only minimal differences exist between the two runs in spite of different timing, spawning locations and body size.

Similarly, differences among the Fraser River collections are small although the three tributary rivers (Harrison, Stave and Vedder), represent half of the total chum salmon return to the Fraser River (Canada Dept. Fisheries, 1963). The only significant difference occurs between the Harrison and Vedder Rivers at the Pep-LGG locus ($\chi^2=12.11$: $p<.01$). These similarities within the Fraser River collections suggest that gene flow occurs within the Fraser River tributary populations.

ii. Genetic feature among proximal river populations

The genetic similarity is observed not only among subpopulations within one river system but also among proximal river populations. All the rivers examined in British Columbia enter the Strait of Georgia and their river mouths are located proximately.

The British Columbia population share the common trait in their allelic frequency which distinguish them from other populations. A large difference in the frequency of the *Idh-2-a* allele is observed between the northern and southern populations of Puget Sound which is close to the southern limits of chum salmon distribution on the Continent of North America (SEEB and WISHARD, 1977).

All the populations examined have been reproduced naturally and therefore, it is presumed that some degree of intermingling among proximal river populations is inevitable even under the natural environments.

4. Genetic similarity among populations

In the following section, genetic relationship among the populations in Alaska and British Columbia including Washington populations is examined based on genetic distance.

According to NEI (1975), genetic distance (D) between the populations, X and Y, is given by

$$D = -\log_e I,$$

where

$$I = J_{XY}/\sqrt{J_X \cdot J_Y}$$

is the normalized identity of genes between X and Y. I is called the genetic identity and given by

$$J_X = \sum_j \sum_i (x_{ij})^2/r$$

$$J_Y = \sum_j \sum_i (y_{ij})^2/r$$

$$J_{XY} = \sum_j \sum_i x_{ij} \cdot y_{ij}/r \qquad (r : \text{number of examined loci}),$$

where x_{ij} and y_{ij} are the frequencies of the i^{th} allele at the j^{th} locus in X and Y populatlons. Should X and Y populations share the same frequencies at all loci, the genetic distance is given by $D=0$. Conversely if they do not share the common allele, the value becomes $D=\infty$.

Genetic distances among North American populations were estimated based on 24 loci examined in common (Table 4), and a dendrogram was constructed by unweighted paired-group method (Fig. 16 ; SNEATH and SOKAL, 1973). The dendrogram indicates a structuring of populations that conforms to their geographic locations. The two major clusters of (1) Alaskan and (2) British Columbia and Puget Sound populations were defined for North American chum salmon. The former is further subdivided into the western Alaskan regional population and the central Alaskan counterpart. Likewise, the

Table 4. Estimates of genetic distance among 14 populations of chum salmon in North America based on gene frequencies at 24 loci.

	Yukon R. (autumn)	King Cove	Cook I. (north)	Cook I. (south)	Punt-ledge R.	Qualic-um R.	Gold-stream R.	Har-rison R.	Stave R.	Vedder R.	Puget S. (north)	Puget S. (south)	Hood Canal
Yukon River (summer)	.00060	.00049	.00079	.00085	.00256	.00312	.00337	.00406	.00526	.00533	.00399	.00389	.00307
Yukon R. (autumn)		.00192	.00237	.00263	.00509	.00586	.00578	.00655	.00806	.00814	.00653	.00564	.00525
King Cove			.00010	.00022	.00100	.00149	.00156	.00209	.00301	.00313	.00208	.00220	.00138
Cook Inlet (north)				.00023	.00093	.00148	.00152	.00185	.00277	.00273	.00205	.00211	.00133
Cook Inlet (south)					.00130	.00189	.00210	.00278	.00380	.00383	.00278	.00297	.00196
Puntledge R.						.00014	.00033	.00055	.00080	.00101	.00050	.00186	.00062
Qualicum R.							.00034	.00054	.00072	.00102	.00034	.00205	.00073
Goldstream R.								.00023	.00048	.00089	.00008	.00119	.00036
Harrison R.									.00017	.00030	.00017	.00148	.00065
Stave R.										.00022	.00031	.00208	.00104
Vedder R.											.00074	.00295	.00170
Puget Sound (north)												.00135	.00049
Puget Sound (south)													.00036

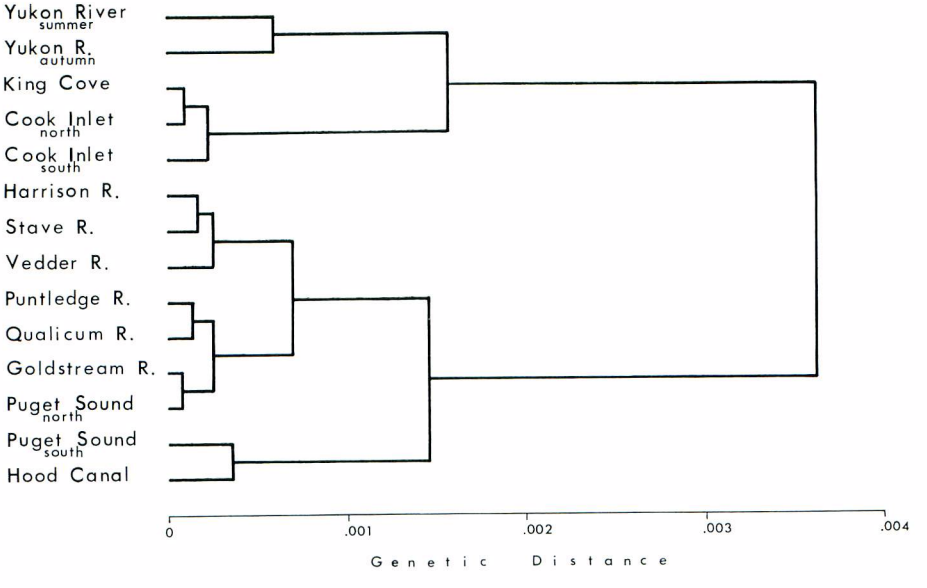


Fig. 16. Dendrogram drawn from indices of genetic distance among 14 populations of chum salmon in North America.

latter is subdivided into the British Columbia and northern Puget Sound regional population and the southern Puget Sound counterpart.

Because of a limited number of the examined populations and the lack of the collections from southeastern Alaska and northern British Columbia which have large chum salmon runs, the current study does not cover the full range of chum salmon distribution on the Continent of North America. However, it is presumed at least that North American chum salmon are divided into the abovementioned four regional populations.

IV. Genetic structure of chum salmon populations in the far east regions of the U.S.S.R.

Russian chum salmon is distributed extensively from the Lena River entering the Arctic region southward through the Bering Strait, the Kamchatka Peninsula and Primore to the river dividing North Korea from the U.S.S.R. (BERG, 1948). Chum salmon is also found on the east coast of the Korean Peninsula and the southern part of the peninsula is considered to be the southern limits of the distribution in Asia (CHOI, 1978). Although the information available on chum salmon distributed in the Arctic region is limited, it is presumed that the rivers with large runs are confined to an area extending from the Anadyr area facing the Bering Sea through the Kamchatka Peninsula to the Amur River or Sakhalin (SANO, 1967).

The abundance of Russian chum salmon stocks is large following that of pink salmon and the quantitative ratio of chum salmon to the entire species of genus *Oncorhynchus* is high unlike in North America. Therefore, in the U.S.S.R., the commercial importance of chum salmon is great compared with other species of genus *Oncorhynchus*.

Much endeavor has been made for the enhancement activities. Some hatcheries were constructed in Sakhalin, the Amur River and the southern Kuril Islands (SANO, 1967). Transplantations have been also attempted particularly in the Kola Peninsula facing the Barents Sea where no indigenous chum salmon is distributed (SURKOV and SURKOVA, 1968). However, these activities produced little effect on the natural populations which are distributed extensively. Thus almost all the populations are reproduced under natural conditions in the U.S.S.R.

Although the author was unable to collect any specimens from Russian rivers, the specimens collected along the coast of the Okhotsk Sea in the U.S.S.R. through Japanese research activities were used for genetic analysis in this study. After the establishment of the 200 nautical mile fishery zone of the U.S.S.R. in 1977, any researchl activities by

Japanese vessels within this zone have been prohibited. Although some informations were obtained on the genetic feature of chum salmon populations returning to the coastal area of the Okhotsk Sea including the Amur area, the information is still insufficient due to the unavailability of the river collections. However, several characteristics in allelic frequency which distinguish Russian chum salmon from North American and Japanese chum salmon are clarified (OKAZAKI, 1979).

1. Biological characteristics

Chum salmon originating in the Far East regions of Asia are grouped into two major categories, summer chum populations and autumn chum populations on the basis of their time of return. The coastal runs of summer chums occur somewhat earier than those of autumn chums. They approach the coast during the period from the end of May or June to August and enter spawning streams during the period from July to the end of August or September. Autumn chums approach the coast from September on and migrate into streams mostly during October through December (SANO, 1967). Summer chums return from the Arctic region, through the Kamchatka Peninsula and Okhotsk to the Amur River, northern Sakhalin and the northern Kuril Islands. On the other hand, autumn chums return to area further south and their geographical distribution extend from the Amur River, southern Sakhalin and the southern Kuril Islands, to Primore and Japan.

Although both summer chums and autumn chums return to the Amur River, some differences are observed between them. For instance, Autumn chums are larger and return to the upper and middle sections of the river in contrast to summer chums which return to the lower sections (SANO, 1967). These characteristics are similar to those of summer and autumn runs of the Yukon River which were previously discussed. It is of interest that the populations in these large rivers remotely situated have a similar phenomenon. The number of summer chums has decreased substantially in recent years and the abundance of autumn chums exceeds that of summer chums.

It is known from the tagging experiments that autumn chums originating in the Far East regions of Asia except the Amur River population, migrate widely throughout much of the North Pacific and Bering Sea as far as east as the western Gulf of Alaska. Conversely summer chums which originate in western Kamchatka and the northern coasts of the Okhotsk Sea rarely migrate to waters beyond 180° longitude and they spend most of their ocean phase in the waters of the western North Pacific Ocean. It is also known that the migration pattern of autumn chums in the Amur River during the ocean phase

is essentially the same with that of the above summer chums (NEAVE *et al.*, 1976). Accordingly the term "summer" or "autumn chum salmon" has been used based on the difference in the time of return. Some summer chum salmon migrate northward to the Okhotsk Sea through the waters off the Pacific coast of northern Japan from spring to early summer. They are called "tokishirazu" in Japan (HIRANO, 1969).

Chum salmon of southern Sakhalin and the southern Kuril Islands are included in Japanese populations in a broader sence, as the tagging experiments and the time of return indicate that their migration pattern is similar to that of Japanese chum salmon (NEAVE *et al.*, 1976).

2. Genetic feature of regional populations

Sample locations and dates of collections are identified in Fig. 17. All the specimens were taken from the catch collected on research cruise of 'the Oyashio maru' a research vessel of Hokkaido University in the northern Okhotsk Sea during the late summer of 1976. Two distinct maturity classes were apparent among fish of both sexes collected in the research area (Fig. 18). The fish of one group had heavier gonad weights and were

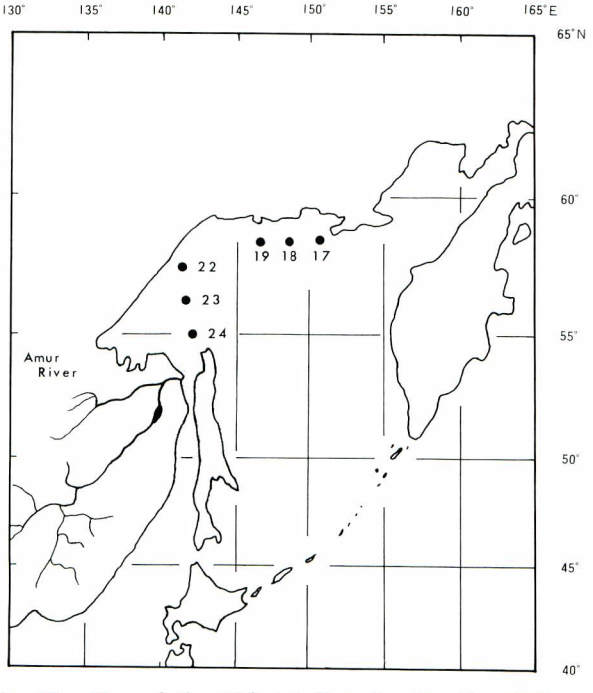


Fig. 17. Map of the Okhotsk Sea showing the stations (●) from which chum salmon were sampled in August, 1976. Numerals indicate the date of collection.

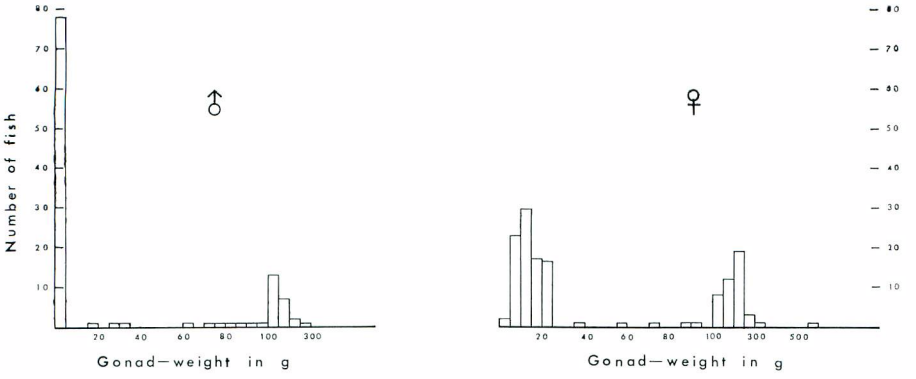


Fig. 18. Gonad weight frequency distributions of chum salmon caught in the northern and western area of the Okhotsk Sea in middle and late August, 1976.

developing obvious external characteristics of imminent spawning such as nuptial coloration and hooked snouts. Fish of the second group had much lighter gonad weights and were obvious not destined to mature and return to their natal areas during the approaching season (TAKAGI, 1961). The mixing ratio of mature and immature fish differs among the examined specimens and the frequency of occurrence of the immature fish was higher at the stations in north. Particularly at three stations west of 144°E longitude, almost all of the specimens were immature.

The allelic frequencies of the Okhotsk Sea collections are listed in Table 5. The immature samples were further divided according to their capture east or west of 144°E longitude ($\chi^2=13.23$; $p<.01$). Particularly significant differences were observed in the relative frequencies between the *Idh-2-a* and *b* alleles. The eastern population have the higher frequency of the *Idh-2-b* allele relative to that of the *Idh-2-a* allele which occurs predominantly in other populations. The western population of immature samples were

Table 5. Gene frequencies at five loci in populations of chum salmon caught in the northern and western area of the Okhotsk Sea in middle and late August, 1976.

Population	Collected date	Sample size	α-GDH-2		IDH-2				LDH-1		MDH-B			6-PGD	
			a	*b*	*a*	*b*	*c*	*d*	*a*	*b*	*a*	*b*	*c*	*a*	*b*
Mature	Aug. 22-24,76	51	.825	.175	.480	.333	.118	.069	.925	.075	.990	.000	.010	.962	.038
Immature															
west of 144°E	Aug. 22-24,76	35	.806	.194	.531	.313	.093	.063	—	—	.993	.000	.007	.986	.014
east of 144°E	Aug. 17-19,76	78	.753	.247	.404	.481	.083	.032	—	—	.997	.003	.000	.986	.014

statistically indistinguishable from the mature samples ($\chi^2 \leqq 0.97$; $p > .05$) suggesting that these fish originated in the same area.

It is presumed from the maturity index and external characteristics of imminent spawning such as nuptial coloration and hooked snouts that the examined mature population are destined to return to the U.S.S.R. In the following section, we will discuss where this population is destined for. The result of tagging experiments and differences in migration pattern and time of return suggest the presence of four regional populations, namely the Amur River, the northern coasts of the Okhotsk Sea, western Kamchatka and southern Sakhalin and the southern Kuril Islands, in the coastal area of the Okhotsk Sea in the U.S.S.R. (NEAVE *et al.*, 1976). Furthermore, summer and autumn races are identified in the Amur River as mentioned earlier.

A few migration routes to these areas proposed by KONDO *et al.* (1965), include a fairly direct route to north along the eastern coast of Sakhalin and a slightly circular, counterclockwise route around the Okhotsk Sea. It is assumed that summer chums of the Amur River take the former route, while autumn chums take the latter. Chum salmon destined for the northern coasts of the Okhotsk Sea is presumed to take both routes. On the other hand, a direct route passing the straits in the northern Kuril Islands is expected to be taken by chum salmon returning to western Kamchatka (Fig. 19).

The ratio of mature fish in the Okhotsk Sea collections as well as the gonad weights tends to increase proceeding south to the mouth of the Amur River. Conversely, almost all the collections in the northern stations in the waters off the northern coasts of the Okhotsk Sea, were predominantly immature fish which were apparently a year away from spawning.

The time of return of chum salmon to each area is

	beginning		end
western Kamchatka	June	15—August	10
the northern coasts of the Okhotsk Sea	June	25—August	20
the Amur River (summer run)	June	15—July	30
the Amur River (autumn run)	September	5—September	15

according to KAGANOVSKI (1955). The sampling was made in late August when most chum salmon destined for the northern coasts of the Okhotsk Sea already returned, while autumn runs started to the Amur River. The above as well as the fact that the chum stocks in the Amur River dominate in the western coasts of the Okhotsk Sea indicates

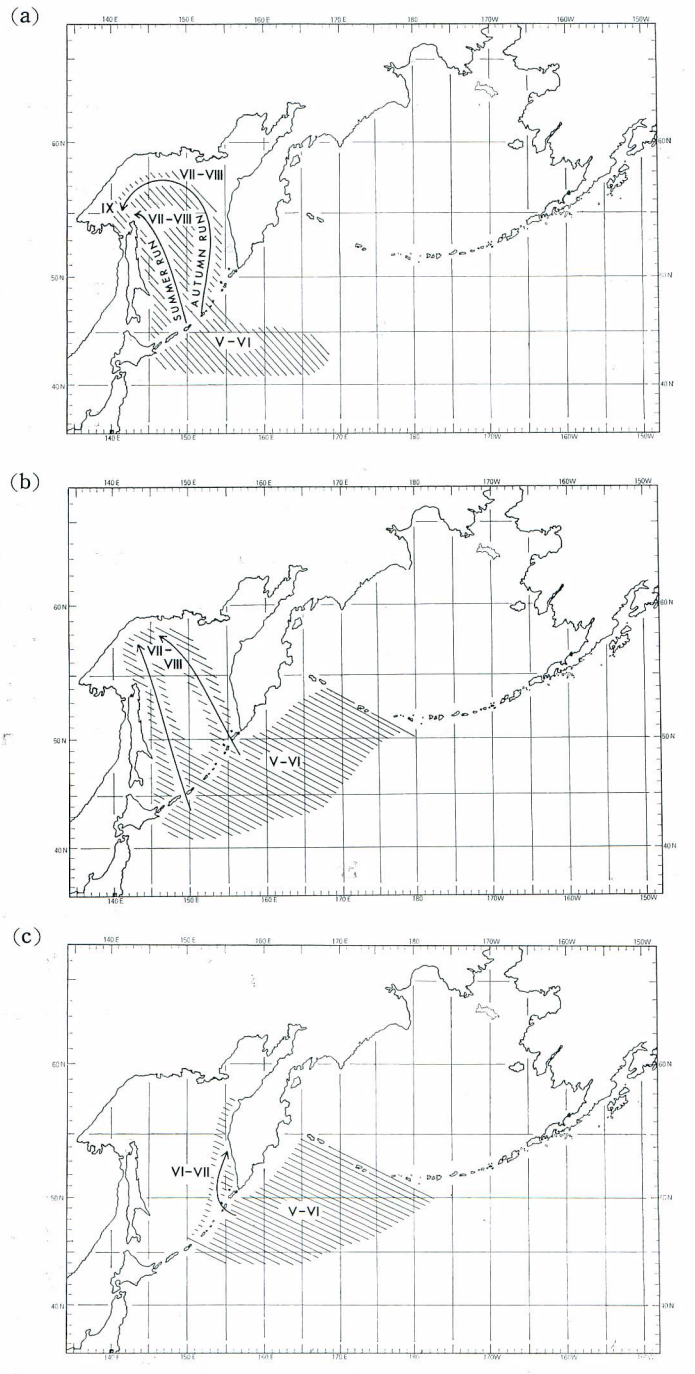


Fig. 19. Estimated areas of distribution and migration routes of chum salmon from (a) the Amur River and vicinity, (b) the northern coasts of the Okohtsk Sea and (c) western Kamchatka (from KONDO *et al.*, 1965). (V) May, (VI) June, (VII) July, (VIII) August, (IX) September.

that the mature population is primarily destined for imminent spawning in the Amur River.

The immature population which were caught in the waters west of 144°E longitude and were statistically indistinguishable from the mature samples is also presumed to originate in the Amur River. The distribution of immature chum salmon is not limited to the examined waters but rather extends widely in the Okhotsk Sea during summer (MISHIMA, 1970). These factors indicate that some of the immature fish originating in the coasts of the Okhotsk Sea, migrate to the Okhotsk Sea before they attain maturity.

Although it is difficult to specify the origin of the immature population which was collected in the waters east of 144°E and shows distinct genetic feature, a higher frequency of the *α-Gdh-2-b* allele as well as the area of capture indicates that these fish were not of Japanese origin. The minimal tagging data of immature fish in the past indicate that these fish were more likely to be from the coastal areas of the Okhotsk Sea except the Amur area, such as the northern coasts of the Okhotsk Sea or western Kamchatka (NEAVE *et al.*, 1976).

All Okhotsk Sea populations are highly polymorphic for the α-GDH-2 locus. The polymorphism, although not at high frequencies, was also observed at MDH-B in contrast with North American chum salmon. Besides the predominant *a* allele, the *Mdh-B-c* allele was present in the western Okhotsk (the Amur River) regional population and the *b* allele was present in the northeastern Okhotsk regional population. However, the frequencies of both the *Mdh-B-b* and *c* alleles were low. Significant differences between the two regional populations were observed at the frequencies of the *Idh-2-a* and *b* alleles as mentioned earlier. However the frequency of the *Idh-2-c* allele is higher than that of the *Idh-2-d* allele in both populations. It is reverse in the most of Japanese river populations and therefore, this can distinguish the Japanese population from the Russian population.

The gene frequency data of Russian chum salmon are insufficient and the only data we can use are those by ALTUKHOV (1975) and Utter (unpublished). ALTUKHOV (1975) reported the allelic frequency of the river populations in the far east regions of the U.S.S.R., however the number of populations examined is limited and the examined locus is restricted to LDH and MDH. According to this report, the polymorphism was found at the LDH-1 locus in all the examined populations including one river population in eastern Kamchatka and the frequency of the *Ldh-1-a* allele ranges between 0.80 and 0.96. All the examined populations are also polymorphic for the MDH-B locus and the

Mdh-B-c allele was present in the southern Kuril Islands populations while the *b* and *c* alleles were present in southern Sakhalin populations. The frequencies of both alleles were low and were less than 0.05. The polymorphism is observed at LDH-1 and MDH-B in Russian populations over an extensive geographic range.

Although UTTER investigated only the Kalininka River population in the south-western part of Sakhalin, he examined loci other than LDH-1 and MDH-B. Juvenile specimens taken at the hatchery were used for the examination. According to the report, each allelic frequency at the IDH-2 locus is $a=0.70$, $b=0.27$, $c=0.00$ and $d=0.03$, indicating significant differences from the populations in the Amur River and the north-eastern coasts of the Okhotsk Sea. The genetic feature of this population seems somewhat similar to that of Japanese chum salmon in that the frequency of the *Idh-2-c* allele is extremely low. Although it is based on a limited number of populations and loci, it is assumed that southern Sakhalin populations whose distribution and migration pattern during the ocean phase are very similar to those of Japanese chum salmon have the frequencies of alleles similar to Japanese populations.

Due to the insufficiency of gene frequency data of Russian populations, only a characteristic of a limited loci were pointed out here without further examining their genetic structure.

V. Genetic structure of chum salmon populations in Japan

The distribution of Japanese chum salmon extends from Hokkaido in north to the middle of Honshu in south which corresponds to the southern limits of chum salmon distribution in Asia. Chum salmon stock in Japan is largely maintained through hatchery activities, which makes Japanese populations distinct from the populations in North America or the U.S.S.R. Almost all the rivers in Japan have been planted due to frequent transplantations associated with artificial propagation. Therefore due consideration needs to be given to the effects produced on the frequencies of alleles of the native stocks.

In this chapter, the population structure of Japanese chum salmon as well as its genetic feature is examined. The parental fish returning to each river or their fry are used as specimens and the analysis is made on 43 river populations throughout the entire distribution of Japanese chum salmon. As a result a common feature was observed in the frequencies of alleles of each river population both on the Pacific coast and the Japan Sea coast. Furthermore, the study on genetic similarity revealed two major clusters of the northern and southern regional populations on both coasts 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. On the other hand, the distinct feature by area was not observed in the allelic frequencies of the examined populations in Hokkaido. This presumably is a result of frequent transplantations among rivers. However, when comparison is made within the rivers in the eastern part of Hokkaido where there has been few transplantations to date, similar allelic frequencies are observed among proximal populations. Although a strong influence of transplantations is conceivable, it appears that the allelic frequencies of Japanese chum salmon are similar among proximal river populations.

Although frequent transplantations of chum salmon have been made in Japan, only a few follow up researches were made after the transplantation. In the following section, the trend of planted populations is examined taking the Tokachi River as an example. In addition, the result of other transplantations is compared and their effects are also discussed.

The population structure of maturing chum salmon, approaching rivers, was examined from both the tagging experiments and gene frequency data. The result indicates that each shoal distributed in the waters off the southern Kuril Islands in autumn was composed of the chum salmon in returning to the proximal rivers at approximately the same time.

1. Biological characteristics

It is considered that the southern limits of the distribution of Japanese chum salmon are the Tone River on the Pacific coast and near Yamaguchi Prefecture on the Japan Sea coast (SANO, 1966). Chum salmon seldom returns to rivers south of these limits (KIMURA, 1981). The rivers with large chum salmon runs are confined to an area from Hokkaido to Fukushima Prefecture on the Pacific coast and from Hokkaido to Toyama Prefecture on the Japan Sea coast. Chum salmon runs to the rivers in further south are relatively small.

Almost all the stocks of Japanese chum salmon have been maintained through hatchery operations and it is considered that few river populations are maintained naturally. Hatchery operations have a long history in Japan commenced since the late 19th century and hatcheries have been established in almost all rivers which have chum salmon run. Japanese rivers are relatively small and the streams which provide suitable condition for spawning and rearing of salmonid fishes continue to decrease due to water pollution and stream bed modifications including dam constructions. Under the present

conditions, the hatchery operations are considered to be an indispensable and appropriate means to ensure the reproductions of chum salmon stocks.

In addition to chum, pink and masu salmon (*O. masou*) also return to Japanese rivers, while their abundance is extremely small compared with that of chum salmon. Therefore the ratio of chum salmon in the species of genus *Oncorhynchus* cannot bear comparison with that in North America or in the U.S.S.R. Therefore chum salmon is an important species in the Japanese fisheries.

Chum salmon runs to Japanese rivers begin in September and end in January in the average year and therefore, they are categorized in autumn chum salmon as previously mentioned. Japanese chum salmon is known for its large migration extending to the eastern North Pacific Ocean including the Gulf of Alaska (NEAVE *et al.*, 1976).

2. Genetic feature of regional populations and their genetic structure

i. Hokkaido

Sample locations and allelic frequencies of 14 rivers in Hokkaido are shown in Fig. 20 and Table 6. Hokkaido is divided by five capes and rivers situated in between these capes make up one 'area' (Fig. 20). This unit of 'area' well reflects the ecological feature of chum salmon. For example, chum salmon population in different area is distinguishable by different returning period.

the East of Cape Erimo area	late September	—	late October
the west of Cape Erimo area	early October	—	late November
the Japan Sea area	early October	—	late October
the Nemuro area	middle November	—	early December
the Okhotsk area	late November	—	middle December

However, the distinct feature by area was not observed in the allelic frequencies of the examined river populations. This presumably is a result of frequent transplantations among rivers. However, when comparison is made within the rivers in the eastern part of Hokkaido where there has been few transplantations to date, similar allelic frequencies were also observed among proximal populations. It is particularly noteworthy that the *Idh-2-e* and *Mdh-B-c* alleles which are absent in the East of Cape Erimo area and other areas are present in the Okhotsk and Nemuro areas. Furthermore similar timing of runs is observed between these adjoining areas. These similarities in the frequencies of alleles as well as in timing of runs indicate a considerable amount of gene flow within the two areas.

On the other hand, significant differences ($\chi^2 = 20.48—39.09$; $p < .01$) were detected at the IDH-2 locus between the Tokachi River population in the East of Cape Erimo area and the Kushiro or Bekanbeushi River population also in the East of Cape Erimo area. Incidentally the Kushiro River population bears close resemblance to the Bekanbeushi River population. This result corresponds well with NUMACHI and OHYA (1974b) and suggests that even among rivers in the same area having similar timing of runs, the degree of gene flow varies according to the distance between river mouths.

A dendrogram was drawn from indices of genetic distance among eight river populations in eastern Hokkaido based on 22 loci examined in common (Table 7 ; Fig. 21). This also indicates genetic similarity among river populations in the Okhotsk and Nemuro areas.

Therefore, a distinct feature by geographical location was not observed in the frequencies of alleles in Hokkaido river populations with an exception of a few areas.

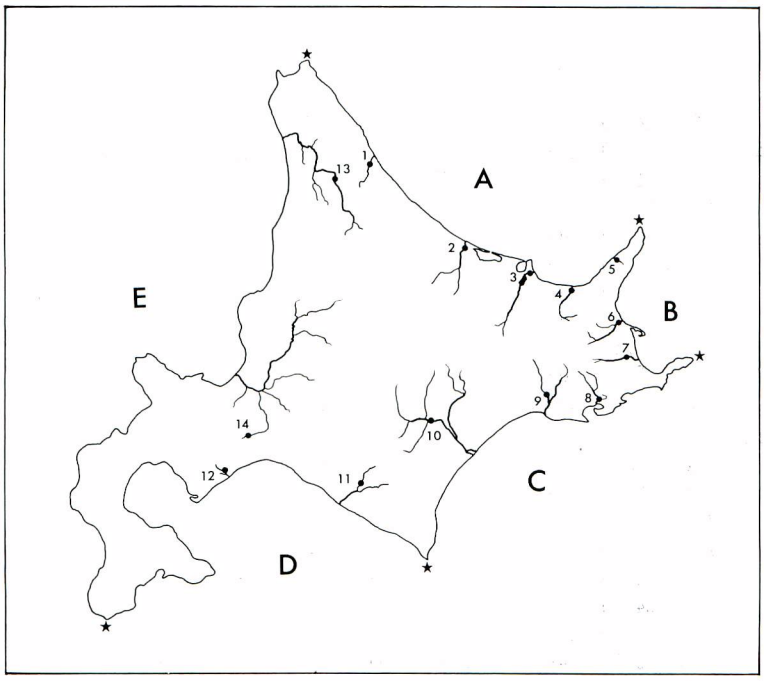


Fig. 20. Map of Hokkaido showing the rivers where chum salmon were sampled. (1) Tokushibetsu River, (2) Yubetsu R., (3) Abashiri R., (4) Shari R., (5) Iwaobetsu R., (6) Shibetsu R., (7) Nishibetsu R., (8) Bekanbeushi R., (9) Kushiro R., (10) Tokachi R., (11) Shizunai R., (12) Shikifu R., (13) Teshio R., (14) Chitose R. A) Okhotsk area, B) Nemuro area, C) East of Cape Erimo area, D) West of Cape Erimo area, E) Japan Sea area. ★) Boundary of each area.

Table 6. Gene frequencies at each locus in 43

River	Collected date	Sample size	AAT-1, 2		AAT-3		α-GDH-2		IDH-2				
			a	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*c*	*d*	*e*
Hokkaido													
Tokushibetsu	Apr. 79	100 (J)	—	—	—	—	—	—	.527	.287	.027	.160	.000
Yubetsu	Nov. 25, 77	100(M)	—	—	—	—	.990	.010	.480	.395	.025	.080	.020
Abashiri	Nov. 27, 77	100(M)	—	—	—	—	.985	.015	.490	.381	.046	.062	.021
Shari	Nov. 26, 77	100(M)	—	—	—	—	.985	.015	.439	.408	.061	.082	.010
Iwaobetsu	Apr. 79	100 (J)	—	—	—	—	—	—	.433	.346	.019	.202	.000
Shibetsu	Nov. 29, 77	100(M)	—	—	—	—	.970	.030	.505	.414	.020	.056	.005
Nishibetsu	Dec. 1, 77	99(M)	—	—	—	—	.975	.025	.469	.388	.026	.102	.015
Bekanbeushi	Oct. 14, 77	100(M)	—	—	—	—	.985	.015	.510	.272	.000	.218	.000
Kushiro	Oct. 13, 77	100(M)	—	—	—	—	.920	.080	.515	.318	.020	.146	.000
Tokachi	Oct. 12, 77	100(M)	—	—	—	—	.985	.015	.530	.435	.010	.025	.000
Shizunai	Apr. 79	100 (J)	—	—	—	—	—	—	.526	.417	.000	.058	.000
Shikifu	Apr. 79	100 (J)	—	—	—	—	—	—	.539	.344	.006	.110	.000
Teshio	Apr. 79	91 (J)	—	—	—	—	—	—	.539	.402	.010	.049	.000
Chitose	Oct. 15, 77	100(M)	.944	.056	.701	.299	.975	.025	.606	.328	.010	.056	.000
Honshu													
Pacific coast													
Oirase	Mar. 3, 81	100 (J)	—	—	.600	.400	—	—	.739	.250	.000	.011	.000
Mabechi	Feb. 26, 81	100 (J)	—	—	.672	.328	—	—	.644	.316	.017	.023	.000
Hei	Mar. 14, 80	92 (J)	—	—	.774	.226	—	—	.703	.279	.017	.000	.000
Tsugaruishi	Mar. 14, 80	100 (J)	—	—	.582	.418	—	—	.663	.320	.006	.012	.000
Origasa	Mar. 14, 80	100 (J)	.979	.021	.779	.221	—	—	.680	.280	.020	.020	.000
Ohzuchi	Mar. 14, 80	100 (J)	—	—	.717	.283	—	—	.663	.308	.029	.000	.000
Katagishi	Mar. 14, 80	100 (J)	—	—	.679	.321	—	—	.638	.259	.011	.092	.000
Ohkawa	Mar. 80	100 (J)	—	—	.673	.327	—	—	.631	.363	.006	.000	.000
Kitakami	Mar. 80	100 (J)	—	—	.750	.250	—	—	.626	.351	.011	.011	.000
Ukedo	Feb. 7, 80	100 (J)	—	—	—	—	—	—	.583	.383	.000	.033	.000
Kido	Feb. 8, 81	100 (J)	—	—	.646	.354	—	—	.500	.486	.000	.014	.000
Same	Feb. 8, 81	100 (J)	—	—	.855	.145	—	—	.491	.491	.000	.019	.000
Naka	Feb. 8, 81	100 (J)	—	—	.813	.188	—	—	.558	.416	.006	.019	.000
Japan Sea coast													
Iwaki	Mar. 17, 81	100 (J)	—	—	.616	.384	—	—	.717	.250	.011	.022	.000
Oirase	May. 2, 80	100 (J)	—	—	—	—	—	—	.414	.414	.092	.080	.000
Omono	Mar. 80	100 (J)	—	—	—	—	—	—	.432	.414	.074	.080	.000
Nishime	Mar. 80	99 (J)	—	—	.548	.452	—	—	.412	.551	.022	.015	.000
Naso	Mar. 31, 80	100 (J)	—	—	—	—	—	—	.544	.412	.044	.000	.000
Gakko	Mar. 24, 80	96 (J)	—	—	—	—	—	—	.380	.598	.000	.022	.000
Nikko	Mar. 80	100 (J)	—	—	—	—	—	—	.475	.467	.042	.017	.000
Aka	Dec. 3, 80	49(M)	1.000	.000	.804	.196	1.000	.000	.394	.521	.053	.032	.000
Miomote	Mar. 79	100 (J)	—	—	.707	.293	—	—	.489	.447	.011	.053	.000
Shinano	Mar. 12, 80	100 (J)	—	—	—	—	—	—	.646	.268	.018	.067	.000
Kurobe	Feb. 81	100 (J)	—	—	.636	.364	—	—	.655	.275	.035	.035	.000
Kado	Mar. 4, 80	100 (J)	—	—	.587	.413	—	—	.630	.250	.016	.103	.000
Hayatsuki	Feb. 23, 81	100 (J)	—	—	.661	.339	—	—	.687	.247	.049	.016	.000
Jintsu	Feb. 81	100 (J)	—	—	.730	.270	—	—	.617	.300	.072	.011	.000
Shoh	Feb. 81	100 (J)	—	—	.506	.494	—	—	.621	.328	.023	.029	.000
Tedori	Oct. Nov. 79	103(M)	—	—	—	—	.985	.015	.597	.272	.097	.034	.000

M=mature J=juvenile

river populations of chum salmon in Japan.

IDH-3		LDH-1		MDH-B			Pep-LGG		6-PGD		PGI-3			PGM		PMI	
a	*b*	*a*	*b*	*a*	*b*	*c*	*a*	*b*	*a*	*b*	*a*	*b*	*c*	*a*	*b*	*a*	*b*
—	—	.918	.082	.985	.015	.000	1.000	.000	1.000	.000	1.000	.000	.000	.993	.007	1.000	.000
—	—	.947	.053	.980	.013	.008	1.000	.000	.995	.005	1.000	.000	.000	1.000	.000	1.000	.000
—	—	.874	.126	.975	.023	.003	1.000	.000	.985	.015	1.000	.000	.000	1.000	.000	.990	.010
—	—	.854	.146	.970	.028	.003	1.000	.000	.985	.015	1.000	.000	.000	1.000	.000	.995	.005
—	—	.949	.051	.986	.014	.000	1.000	.000	.993	.007	1.000	.000	.000	1.000	.000	1.000	.000
.820	.180	.849	.151	.983	.008	.010	1.000	.000	.985	.015	.995	.005	.000	.995	.005	.985	.015
.885	.115	.843	.157	.977	.020	.003	.995	.005	.980	.020	1.000	.000	.000	1.000	.000	.954	.046
.919	.081	.890	.110	.960	.040	.000	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	.990	.010
—	—	.903	.097	.968	.033	.000	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	.990	.010
.831	.169	.829	.171	.973	.028	.000	.986	.014	.985	.015	1.000	.000	.000	1.000	.000	.965	.035
—	—	.915	.085	.990	.007	.003	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	.975	.025
—	—	.911	.089	.975	.025	.000	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	1.000	.000
—	—	.871	.129	.997	.003	.000	1.000	.000	.978	.022	1.000	.000	.000	.995	.005	1.000	.000
.969	.031	.882	.118	1.000	.000	.000	.985	.015	.980	.020	.995	.000	.005	1.000	.000	.995	.005
.954	.046	.787	.213	.997	.003	.000	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	.970	.030
.990	.010	.878	.122	.989	.011	.000	.945	.055	1.000	.000	1.000	.000	.000	1.000	.000	.980	.020
.993	.007	.846	.154	.986	.014	.000	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	.938	.063
.987	.013	.932	.068	.979	.021	.000	.995	.005	1.000	.000	1.000	.000	.000	1.000	.000	.944	.056
.975	.025	.837	.163	.995	.005	.000	.995	.005	1.000	.000	1.000	.000	.000	1.000	.000	.951	.049
.977	.023	.925	.075	.985	.015	.000	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	.932	.068
.971	.029	.922	.078	.990	.010	.000	1.000	.000	.985	.015	1.000	.000	.000	1.000	.000	.968	.032
1.000	.000	.938	.063	.995	.005	.000	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	.913	.087
.994	.006	.919	.081	.995	.005	.000	1.000	.000	1.000	.000	1.000	.000	.000	.994	.006	.981	.019
—	—	.896	.104	.980	.020	.000	1.000	.000	.995	.005	1.000	.000	.000	1.000	.000	1.000	.000
.995	.005	.833	.167	.993	.008	.000	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	.955	.045
.994	.006	.850	.150	.998	.003	.000	1.000	.000	1.000	.000	.975	.025	.000	1.000	.000	1.000	.000
.980	.020	.950	.050	.960	.040	.000	1.000	.000	1.000	.000	.995	.005	.000	1.000	.000	.950	.050
.975	.025	.811	.189	.990	.010	.000	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	.975	.025
—	—	.940	.060	1.000	.000	.000	1.000	.000	.990	.010	1.000	.000	.000	1.000	.000	1.000	.000
—	—	.793	.207	.988	.013	.000	1.000	.000	.990	.010	1.000	.000	.000	1.000	.000	.995	.005
—	—	.920	.080	.990	.010	.000	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	1.000	.000
—	—	.875	.125	.993	.008	.000	1.000	.000	1.000	.000	.995	.005	.000	1.000	.000	1.000	.000
—	—	.833	.167	.987	.013	.000	1.000	.000	1.000	.000	1.000	.000	.000	1.000	.000	1.000	.000
—	—	.817	.183	.990	.010	.000	1.000	.000	.980	.020	.995	.005	.000	1.000	.000	.995	.005
.939	.061	.872	.128	1.000	.000	.000	1.000	.000	.969	.031	1.000	.000	.000	1.000	.000	.969	.031
.959	.041	.895	.105	.992	.008	.000	1.000	.000	.989	.011	1.000	.000	.000	1.000	.000	.929	.071
—	—	.880	.120	.995	.005	.000	1.000	.000	.995	.005	1.000	.000	.000	1.000	.000	1.000	.000
.990	.010	.590	.410	.995	.005	.000	1.000	.000	.965	.035	.990	.010	.000	1.000	.000	1.000	.000
.984	.016	.705	.295	1.000	.000	.000	.990	.010	.995	.005	1.000	.000	.000	.995	.005	.980	.020
.995	.005	.633	.367	1.000	.000	.000	.990	.010	.990	.010	.990	.010	.000	1.000	.000	.985	.015
.989	.011	.790	.210	.985	.013	.003	1.000	.000	1.000	.000	.975	.025	.000	1.000	.000	.979	.021
.965	.035	.612	.388	.995	.005	.000	.995	.005	1.000	.000	.985	.015	.000	1.000	.000	.990	.010
.943	.057	.816	.184	1.000	.000	.000	.995	.005	.995	.005	.986	.000	.014	1.000	.000	1.000	.000

Table 7. Estimates of genetic distance among 14 populations of chum salmon in Hokkaido based on gene frequencies at 22 loci.

	Yubetsu R.	Abashiri R.	Shari R.	Iwaobetsu R.	Shibetsu R.	Nishibetsu R.	Bekanbeushi R.	Kushiro R.	Tokachi R.	Shizunai R.	Shikifu R.	Teshio R.	Chitose R.
Tokushibetsu River	.00054	.00060	.00092	.00038	.00090	.00078	.00021	.00008	.00142	.00070	.00016	.00076	.00057
Yubetsu R.		.00028	.00049	.00048	.00051	.00062	.00106	.00040	.00092	.00018	.00026	.00043	.00076
Abashiri R.			.00012	.00088	.00010	.00017	.00098	.00036	.00032	.00024	.00027	.00016	.00049
Shari R.				.00092	.00020	.00016	.00118	.00059	.00044	.00051	.00058	.00040	.00101
Iwaobetsu R.					.00123	.00094	.00051	.00039	.00192	.00091	.00055	.00121	.00147
Shibetsu R.						.00016	.00129	.00061	.00013	.00024	.00044	.00008	.00051
Nishibetsu R.							.00092	.00048	.00032	.00044	.00050	.00035	.00077
Bekanbeushi R.								.00020	.00178	.00124	.00046	.00127	.00110
Kushiro R.									.00099	.00049	.00008	.00056	.00054
Tokachi R.										.00043	.00076	.00024	.00067
Shizunai R.											.00025	.00016	.00045
Shikifu R.												.00031	.00031
Teshio R.													.00026

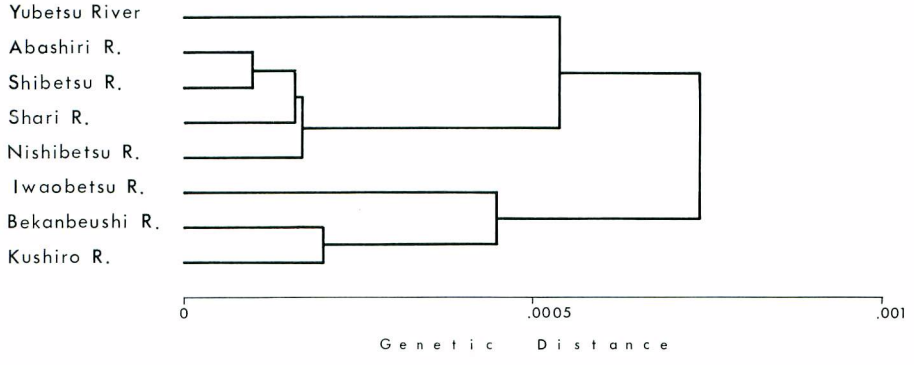


Fig. 21. Dendrogram drawn from indices of genetic distance among eight river populations of chum salmon in the eastern part of Hokkaido.

ii. Honshu

Sample locations and allelic frequencies of 29 rivers in Honshu are shown in Fig. 22 and Table 6. A distinct feature was found in the frequencies of alleles between the northern and southern populations in Honshu. In the following section, the genetic structure of the river populations on the Pacific and the Japan Sea coasts is discussed.

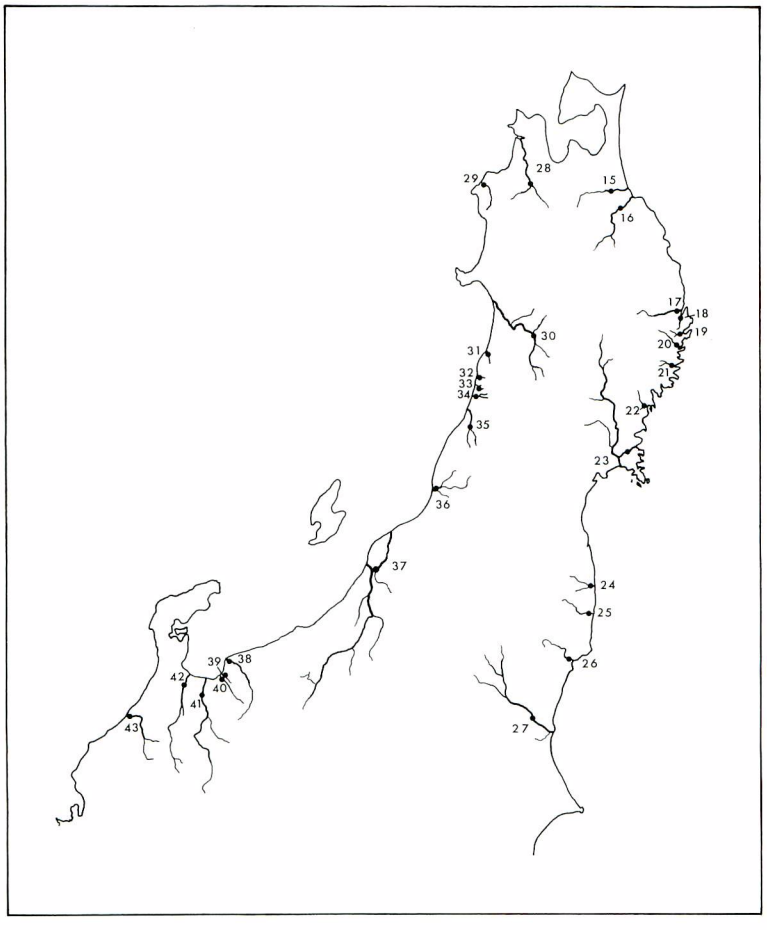


Fig. 22. Map of Honshu showing the rivers where chum salmon were sampled. (15) Oirase River, (16) Mabechi R., (17) Hei R., (18) TsugaruishiR., (19) Origasa R., (20) Ohzuchi R., (21) Katagishi R., (22) Ohkawa R., (23) Kitakami R., (24) Ukedo R., (25) Kido R., (26) Same R., (27) Naka R., (28) Iwaki R., (29) Oirase R., (30) Omono R., (31) Nishime R., (32) Naso R., (33) Gakko R., (34) Nikko R., (35) Aka R., (36) Miomote R., (37) Shinano R., (38) Kurobe R., (39) Kado R., (40) Hayatsuki R., (41) Jintsu R., (42) Shoh R., (43) Tedori R.

a. The Pacific coast

A common feature of the Pacific coast populations was high frequency of the *Idh-2-a* allele. Geographical gradient of this allelic frequency was observed and the frequency tends to be lower proceeding southward (Fig. 23). The cline was also found for the frequency of the *Ldh-1-a* allele (Fig. 24). The frequency shows the highest

value in the middle of Iwate Prefecture and tends to decrease as proceeds both north and south. This result agrees well with KIJIMA and FUJIO (1979). However, the cline of allelic frequency for the IDH-3 locus was not observed in the current study.

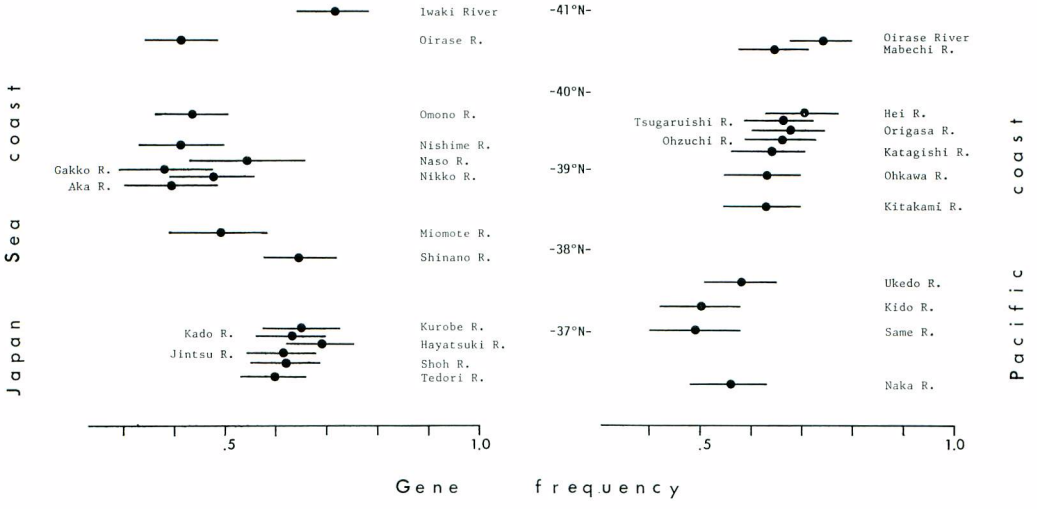


Fig. 23. Distribution of allelic frequencies and 95% confidence intervals of the *Idh-2-a* allele in river populations on the Pacific and the Japan Sea coasts of Honshu.

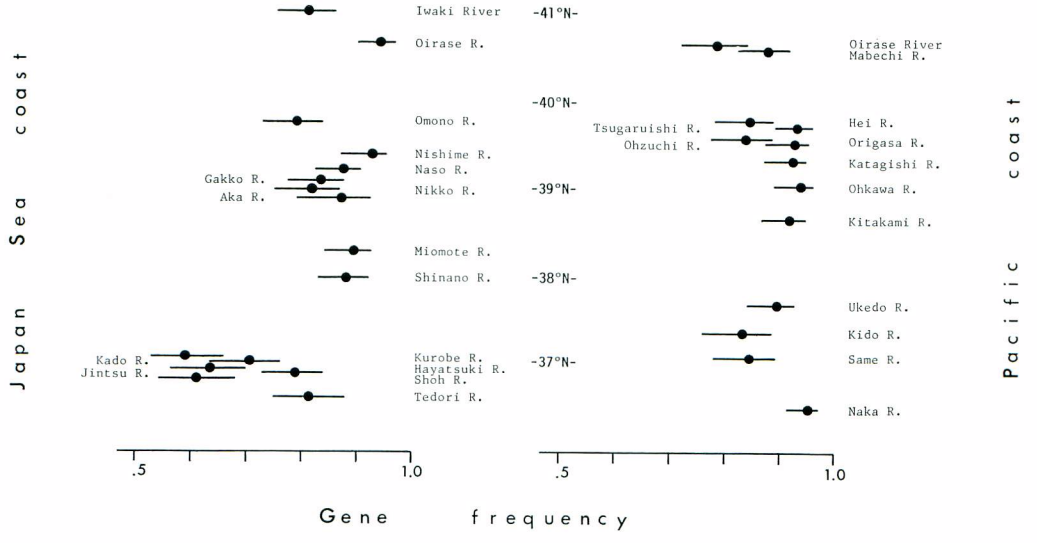


Fig. 24. Distribution of allelic frequencies and 95% confidence intervals of the *Ldh-1-a* allele in river populations on the Pacific and the Japan Sea coasts of Honshu.

Following the same procedure applied to river populations in Hokkaido, a dendrogram was drawn from indices of genetic distance based on 22 loci (Table 8 ; Fig. 25). This defines two major clusters of (1) northern and (2) southern populations divided by the central part of Iwate Prefecture, excepting the Mabechi River in Aomori Prefecture.

Table 8. Estimates of genetic distance among 13 populations of chum salmon on the Pacific coast of Honshu based on gene frequencies at 22 loci.

	Mabechi R.	Hei R.	Tsugaru-ishi R.	Origasa R.	Ohzuchi R.	Katagi-shi R.	Ohkawa R.	Kitaka-mi R.	Ukedo R.	Kido R.	Same R.	Naka R.
Oirase River	.00087	.00028	.00131	.00025	.00122	.00128	.00180	.00137	.00163	.00278	.00309	.00283
Mabechi R.		.00041	.00034	.00030	.00038	.00044	.00059	.00026	.00039	.00146	.00152	.00093
Hei R.			.00044	.00004	.00036	.00064	.00072	.00061	.00093	.00203	.00237	.00154
Tsugaruishi R.				.00050	.00003	.00031	.00014	.00015	.00047	.00176	.00192	.00053
Origasa R.					.00043	.00054	.00078	.00055	.00079	.00179	.00206	.00152
Ohzuchi R.						.00035	.00014	.00021	.00059	.00183	.00205	.00066
Katagishi R.							.00062	.00038	.00061	.00221	.00225	.00101
Ohkawa R.								.00024	.00055	.00136	.00161	.00039
Kitakami R.									.00015	.00118	.00116	.00041
Ukedo R.										.00072	.00064	.00034
Kido R.											.00014	.00095
Same R.												.00098

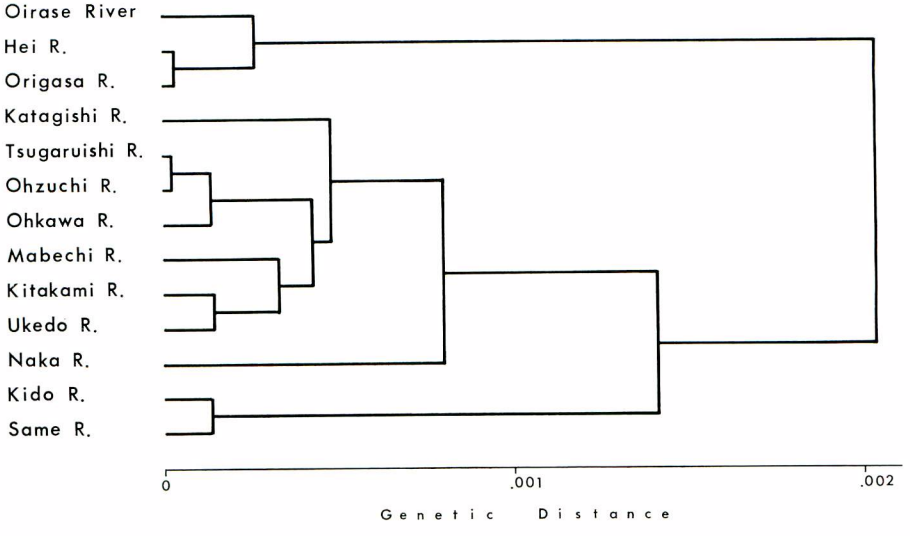


Fig. 25. Dendrogram drawn from indices of genetic distance among 13 river populations of chum salmon on the Pacific coast of Honshu.

b. The Japan Sea coast

The cline for the frequency of the *Idh-2 a*-allele was also observed for chum salmon river populations on the Japan Sea coast. The frequency shows the lowest value in the south of Yamagata Prefecture and tends to increase as proceeds both north and south (Fig. 23). The eminent feature was an extremely low frequency of the *LDh-1-a* allele in the rivers south of Toyama Prefecture (Fig. 24).

A dendrogram was drawn likewise for each river population on the Japan Sea coast from indices of genetic distance based on 22 loci (Table 9 ; Fig. 26). This clearly indicates two independent clusters of (1) northern and (2) southern populations divided by the northern part of Niigata Prefecture. The degree of the divergence was higher on the Japan Sea coast than on the Pacific coast. The result shows that the population of the Iwaki River situated northernmost is included in the southern population group. The allelic frequencies for the IDH-2 and LDH-1 loci of the Iwaki River population were extremely different from that of the proximal river populations in Aomori and Akita Prefectures on the Japan Sea coast. In terms of the genetic distance, the population is more close to those in the eastern part of Aomori Prefecture and the northern part of Iwate Prefecture on the Pacific coast ($\overline{D}=0.00019$).

Table 9. Estimates of genetic distance among 16 populations of chum salmon of the Japan Sea coast based on gene frequencies at 22 loci.

	Oirase R.	Omono R.	Nishime R.	Naso R.	Gakko R.	Nikko R.	Aka R.	Miomote R.	Shinano R.	Kurobe R.	Kado R.	Hayatsuki R.	Jintsu R.	Shoh R.	Tedori R.
Iwaki River.	.00387	.00277	.00493	.00159	.00561	.00256	.00449	.00261	.00043	.00252	.00088	.00158	.00043	.00226	.00058
Oirase R.		.00104	.00069	.00081	.00167	.00103	.00065	.00066	.00208	.00782	.00453	.00706	.00253	.00649	.00205
Omono R.			.00136	.00078	.00115	.00026	.00073	.00092	.00201	.00375	.00207	.00358	.00129	.00274	.00124
Nishime R.				.00098	.00044	.00078	.00026	.00069	.00332	.00844	.00566	.00793	.00338	.00672	.00331
Naso R.					.00160	.00036	.00093	.00045	.00086	.00467	.00246	.00393	.00082	.00362	.00080
Gakko R.						.00069	.00039	.00127	.00441	.00719	.00534	.00717	.00370	.00547	.00390
Nikko R.							.00042	.00057	.00189	.00413	.00252	.00386	.00125	.00301	.00136
Aka R.								.00052	.00315	.00693	.00460	.00661	.00278	.00544	.00273
Miomote R.									.00159	.00610	.00331	.00539	.00172	.00478	.00174
Shinano R.										.00405	.00150	.00303	.00061	.00354	.00043
Kurobe R.											.00085	.00019	.00210	.00019	.00265
Kado R.												.00054	.00074	.00071	.00092
Hayatsuki R.													.00141	.00031	.00188
Jintsu R.														.00162	.00015
Shoh R.															.00221

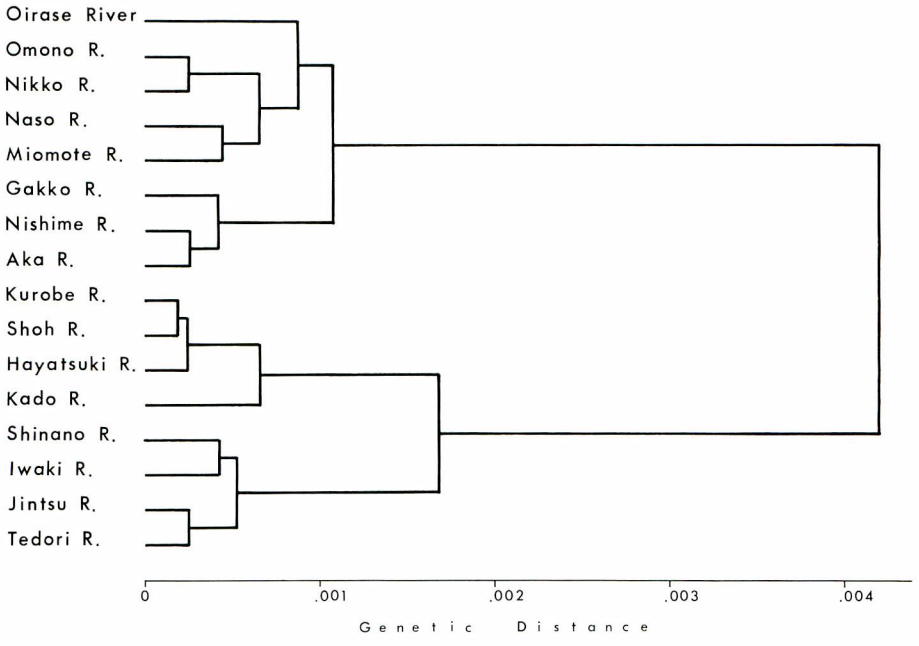


Fig. 26. Dendrogram drawn from indices of genetic distance among 16 river populations of chum salmon on the Japan Sea coast of Honshu.

It is worthwhile to note that even among the chum salmon river populations distributed in such a small area, geographical differences were observed in the frequencies of alleles. Fig. 27 shows resulting Japanese chum salmon regional populations presumed from the genetic feature.

Other biological characteristics of the regional populations presumed on the basis of the frequencies of alleles and of their river populations, and in particular its relation to the time of return are discussed. Chum salmon returns to rivers approximately the same period every year and this timing has a very unique trend both on the Pacific coast and on the Japan Sea coast of Honshu. MACHIDORI (1978) reports that on the Japan Sea coast the time of return tends to be later proceeding southward to the border of Yamagata and Niigata Prefectures where the trends reverses and runs to streams further to the south again tend to return earlier (Fig. 28). He ascribes this phenomenon to the adaptation made by parental fish so that fry may migrate seaward at an appropriate time in the region close to the southern limits of chum salmon distribution. In this particular region, life of the chum salmon can be directly endangered by high sea temperature. Although the time of return is deferred proceeding south throughout its entire distribution, this adjustment alone cannot sustain the race. Therefore the time of

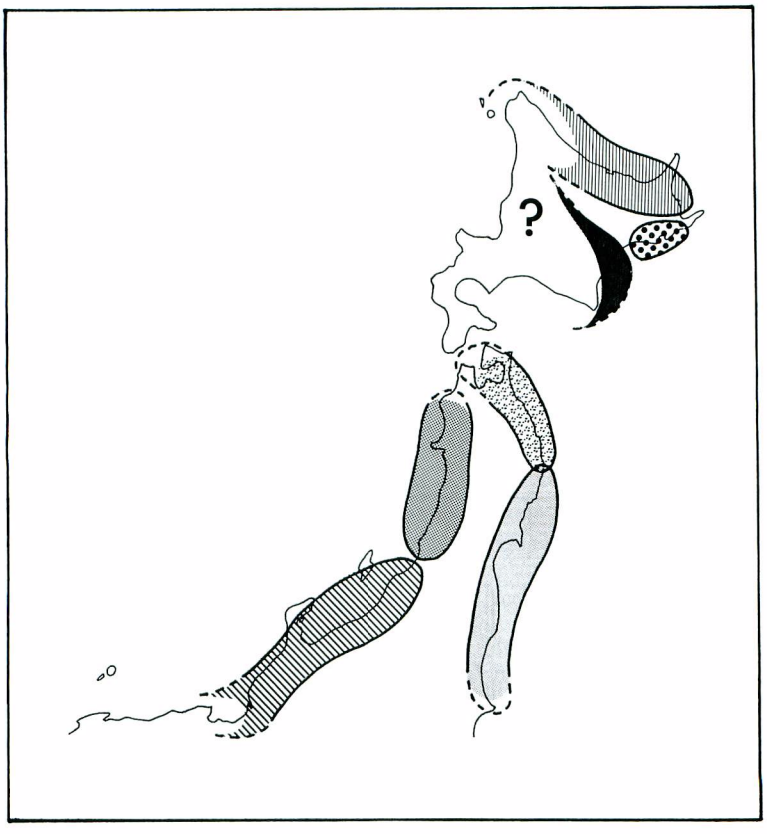


Fig. 27. Schematic diagram of regional chum salmon populations in Japan defined by gene frequency data.

return has to be advanced so that fry can safely migrate to sea in early spring while the coastal sea temperature still stands low.

This presumably brought about considerable differences in biological characteristics such as the adaptability for high sea temperature between the populations in north and that in the southern limits of the distribution. Based on the genetic data, the chum salmon populations on the Japan Sea coast were separated into two groups, one returning to rivers south of the Shinano River and the other returning to rivers north of the Miomote River in Niigata Prefecture. This boundary coincides with a point of inflection of timing. The same trend in timing is observed on the Pacific coast. The point of inflection occurs in the middle of Iwate Prefecture where unlike on the Japan Sea coast (Fig. 28), both the rivers with early run and those with later run are distributed within a limited area. Rivers with early runs are from north, the Omoto, Sekiguchi, Origasa and Unozumai Rivers, in between which lies the Tsugaruishi and Ohzuchi Rivers with

later runs. The genetic data also divides the runs on the Pacific coast into the northern and southern regional populations at a point close to the Tsugaruishi and Origasa Rivers. Furthermore early runs returning to the Hei and Origasa Rivers were included in the northern group and the later runs returning to the Tsugaruishi and Ohzuchi Rivers were included in the southern group.

An extremely close relation was observed between the time of return and the genetic structure of chum salmon river populations both on the east and the west coasts of Honsbu. This indicates that genetic structure also proves chum salmon population returning to rivers south of the inflection point of timing to be independent.

The point of inflection on the east coast is in somewhat different latitude from that on the west coast and it occurs to the north of the point of inflection on the west coast. Generally run on the Pacific coast proceeds runs on the Japan Sea coast by 20 to 30 days (Fig. 28). These phenomena are closely related to difference in environment between the two coasts. For instance, coastal sea temperature on the Japan Sea coast tends to be higher than on the Pacific coast from the end of September to November when parental fish start to return and conversely it tends to be lower on the Japan Sea coast in the region close to the southern limits of the distribution from January to February when fry migrate to sea (Japan Hydrographic Association, 1978).

The cline was observed between the east and the west coasts of Honshu for the frequency of the *Idh-2-a* allele. The cline for the allelic frequency is well known in many organisms and several factors including adaptability of gene to the environment are considered to be relevant (KOEHN, 1969 ; MOON and HOCHACHKA, 1972). In case of the observed cline for the *Idh-2-a* allele of each river population in Honshu, the trend of variation on the Pacific coast is reverse from that on the Japan Sea coast. Therefore it is hard to ascribe this phenomenon to the different adaptability of this allele. Although it is presumably related to the effects of many years of straying to proximal rivers, the cause have not yet been determined.

3. Genetic intermingling among river populations by transplantations

Chum salmon has been frequently transplanted among many rivers in Japan. However the information is not available on the actual effects of transplantation on the abundance of planted river. Chum salmon has been most frequently transplanted to the rivers in Honshu, particularly close to the southern limits of the distribution where the stock size is small. As there are only few rivers with sufficient amount of eggs to supply in Honshu, the main sources of eggs have been the rivers in Hokkaido in addition to a very few

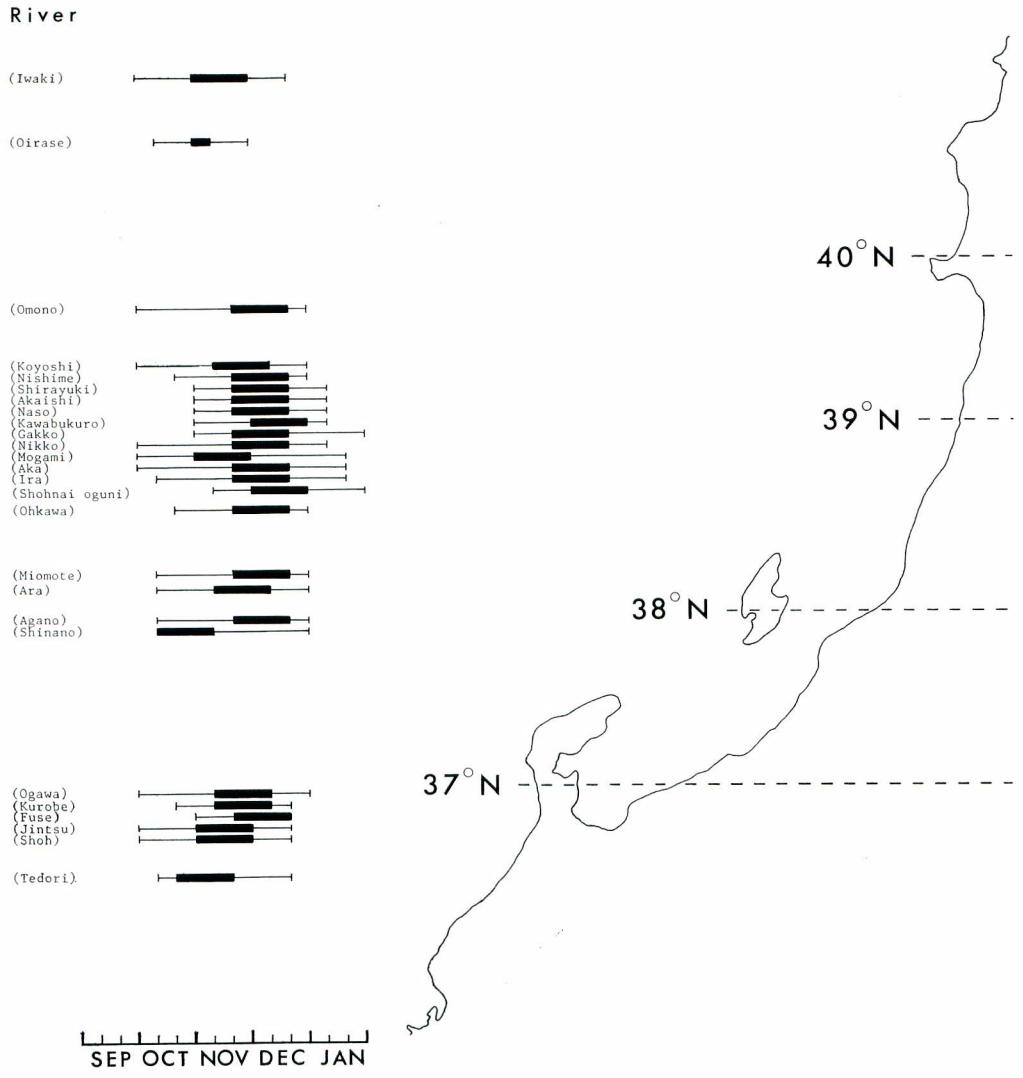
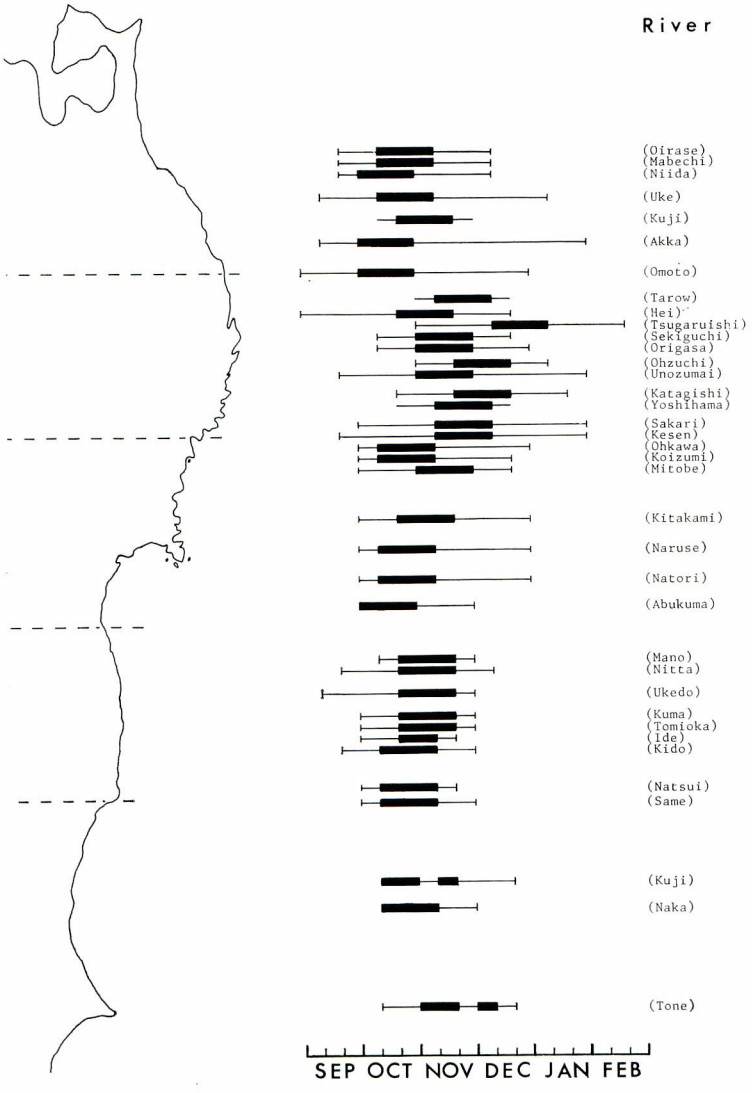


Fig. 28. Geographical distribution of the time of return and its peak period in Salmon and Trout Resource Conservation Association, 1976).

rivers in Iwate and Yamagata Prefectures. Eggs have been transferred to rivers with small stock size every year. However, the donor stream is not always the same as the supply and demand fluctuate yearly. Donor streams are not even recorded with accuracy in some rivers. Despite many years of large-scale transplantations, the trend of particular increase in returns was hardly observed. The question remains as to whether the planted stock did in effect return to new rivers and contribute to reproduction. Not a few rivers are even considered to be barely sustaining a certain level of returns by continuing to



chum salmon on the Pacific and the Japan Sea coasts of Honshu (from Japan

introduce large number of eggs every year.

In the following section, the trend of planted populations in some rivers is discussed by comparing the seasonal distribution of spawning run before and after the transplantation. In the Ohkawa River of Miyagi Prefecture, a new late peak was temporarily established three and four years after transplantation of fish of a late run from the Ohzuchi River. The late peak again appeared another three and four years later (Nose, 1970). A general characteristic of many salmonid fishes, including chum salmon, is their

definite timing. In general, since the original timing tends to persist in the transplanted fish, they seem to be quite conservative with this trait. The second peak of chum salmon run to the Ohkawa River is probably a reflection of the transplantation, as chum salmon generally return to rivers as four and five year old fish. However, this late peak eventually disappeared, and it is not clear to what extent the transplanted stock ultimately contributed to the reproduction of the Ohkawa River.

In general the change in seasonal distribution of spawning run resulting from transplantation tends to disappear eventually as in the Ohkawa River, and it is extremely rare that this change persists for a long period. However a new late peak established after transplantations is still present in the Omoto, Hei and Origasa Rivers in Iwate Prefecture (SHIRAHATA, 1976). Chum salmon eggs of a late run in the Tsugaruishi River have been transferred to the Omoto River since 1967, and a change in seasonal distribution of spawning run has been observed since 1971 (Fig. 29). Namely, a new late peak is established from mid-December to mid-January besides the usual peak in October. In recent years, the abundance of the late run exceeds by far that of the early run.

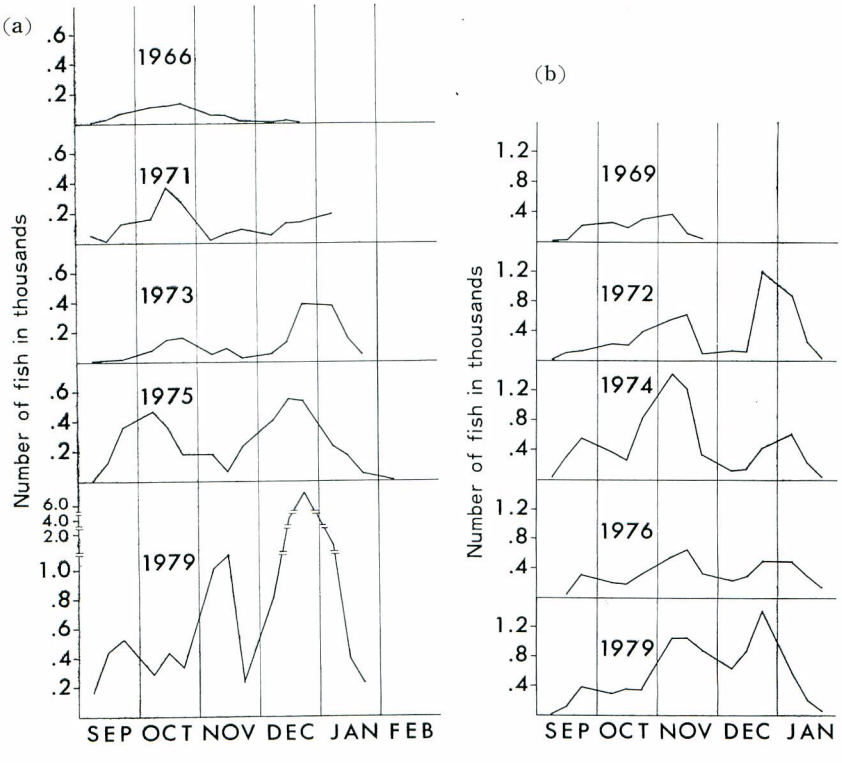


Fig. 29. Seasonal abundance of chum salmon catch in (a) the Omoto and (b) the Hei Rivers.

Therefore it is presumed that transplantations increased the abundance of chum salmon in these three rivers. However, as a large amount of eggs in the Tsugaruishi River and others have been transferred to these rivers every year, it is doubtful whether the transplanted stock in effect repeats the reproduction effectively. It is a question of a great interest what sort of change would occur in the seasonal distribution of spawning run, should the transplantation be interrupted.

On the other hand, the Tokachi River in Hokkaido still shows a change in seasonal distribution of spawning run even after the interruption of transplantation. The Tokachi River is known for having a large chum salmon run and supplied a great number of eggs to other rivers every year. Consequently, few transplantations have been done until large number of eggs of a late run was transferred from the Abashiri and Yubetsu Rivers in the Okhotsk area at the end of 1970 (Table 10). The chum salmon run to the Tokachi River usually begins in early September and the trend of seasonal distribution of spawning run exhibits a single peak in late September or early October. However, a new late peak has appeared in December since 1973, except in 1975 (Fig. 30). It is worthwhile to note that this late peak corresponds in timing with the runs of the Abashiri and Yubetsu Rivers. It is known that chum salmon returning to the rivers in Hokkaido are predominantly three and four year old fish and it is also recognized that 95% of the fish returning to the Abashiri and Yubetsu Rivers are composed of these year classes (unpublished data, Fishery Agency of Japan). These returns correspond exactly with returns that would be expected from three and four year old fish resulting directly from the 1970 transplantations to the Tokachi River (as outlined in Fig. 31) ; and therefore, an absence of a late run in 1975 stands to reason.

Table 10. Summary of chum salmon egg transplants during 1970 and 1971. Number represents thousands of eggs.

Area transplanted	Donor stream		
	Tokachi River	Abashiri River	Yubetsu River
Tokachi River	—	4,773 (1970)	5,324 (1970)
Abashiri River	4,373 (1970)	—	0
Yubetsu River	4,470 (1970) 4,919 (1971)	0	—
Shari River	4,401 (1971)	0	0

The frequencies of alleles were compared between the collections of the early run and late run of 1977 (Table 11), which revealed significant differences in the allelic frequencies of the IDH-2 locus ($\chi^2=18.85$; $p<.01$). It is particularly noteworthy that the *Idh-2-e* allele which only appears in most of the river populations in the Okhotsk and Nemuro areas was present in the late peak of the Tokachi River, but not in the early peak of the Tokachi River (Table 6). The data presented to this point independently indicate thate the late peak of the Tokachi River run is a direct result of 1970 transplan-

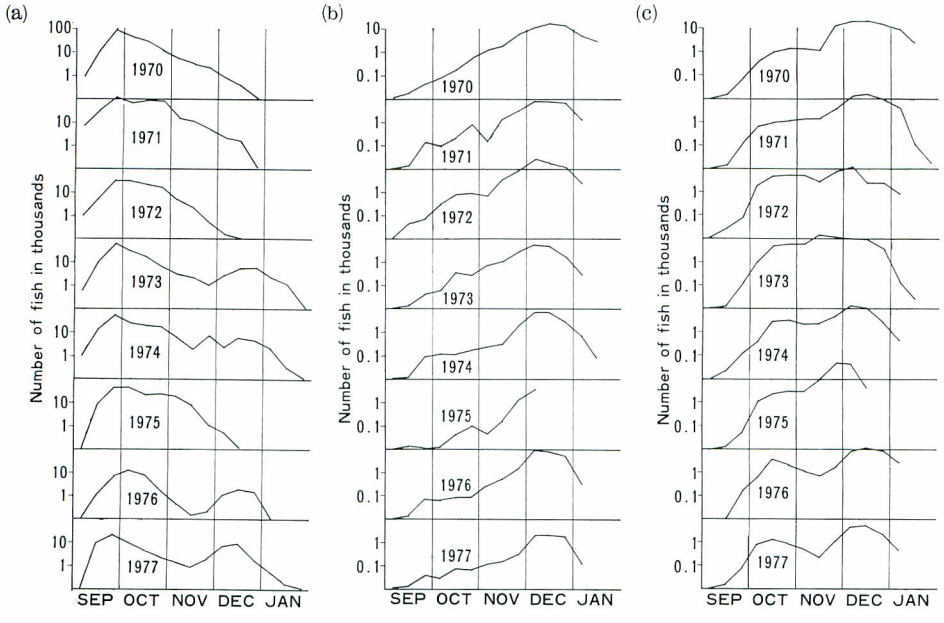


Fig. 30. Seasonal abundance of chum salmon catch in (a) the Tokachi, (b) the Yubetsu and (c) the Abashiri Rivers from 1970 to 1977.

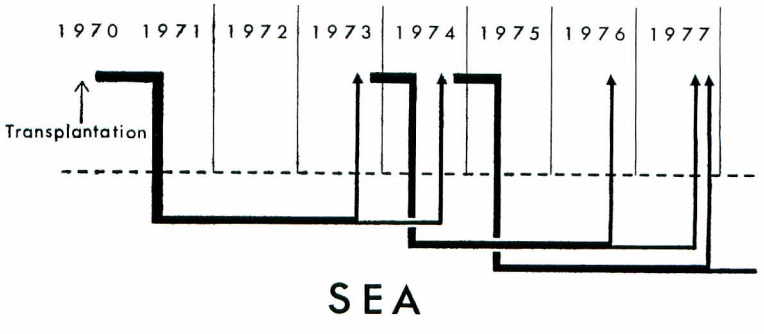


Fig. 31. Schematic model of the relation between returning year and age composition of the transplanted chum salmon in the Tokachi River.

Table 11. Gene frequencies at four loci in each river population of chum salmon involved in the transplantations to the Tokachi River.

River name	Collected date	Sample size	IDH-2					6-PGD		MDH-B			α-GDH-2	
			a	*b*	*c*	*d*	*e*	*a*	*b*	*a*	*b*	*c*	*a*	*b*
Tokachi R.	Oct. 12, 77	100	.530	.435	.010	.025	.000	.985	.015	.973	.028	.000	.985	.015
Tokachi R.	Nov. 24, 77	60	.408	.442	.075	.042	.033	.992	.008	.996	.004	.000	1.000	.000
Shari R.	Nov. 26, 77	100	.439	.408	.061	.082	.010	.985	.015	.970	.028	.003	.985	.015
Abashiri R.	Nov. 27, 77	100	.490	.381	.046	.062	.021	.985	.015	.975	.028	.003	.985	.015
Yubetsu R.	Nov. 25, 77	100	.480	.395	.025	.080	.020	.995	.005	.980	.013	.008	.990	.010

tations from the Abashiri and Yubetsu Rivers (OKAZAKI, 1978). The transplantation produced the third generation in 1977 as indicated in Fig. 31, yet the transplanted populations still retain the frequencies of alleles considerably different from those of the native populations. Both lines of evidence suggest that the two populations do not intermingle easily within such a short period of time as a few generations.

The reciprocal transplantations were made at the same time from the Tokachi River to the rivers entering the Okhotsk Sea including the Abashiri and Yubetsu Rivers (Table 10). However, an eminent change was not observed in their seasonal distribution of spawning run as indicated in Fig. 30. A few years after the transplantation, the transplanted Tokachi River fish did approach the Okhotsk Sea streams as adult in considerable number preceding the regular run, but were harvested by the set net fishery so that they did not contribute significantly to subsequent generations. In contrast, the set net fishery of the estuary of the Tokachi River closes early in November when the catch decreases. Thus the transplanted fish from the Okhotsk Sea rivers, whose spawning peak occurs after this time, returned in sufficient number to continue the transplanted lineage for another generation. Therefore we should not overlook the fact that not only the adaptation of chum salmon to a new environment but also fisheries will affect the effects of transplantations.

The change in seasonal distribution of spawning run resulting from transplantation tends to disappear eventually unless the transplantation is made continually. This phenomenon is presumed to be a result of actual loss of this run caused by their inadaptability to a new environment, or merely a change in their time of return due to the hybridization with the native run. The two peaks are still identified in the Tokachi River even ten years after the transplantations. Thus the continued study of the chum salmon runs returning to the Tokachi River through the use of genetic markers provides a model for

the general study of transplanted salmonid populations.

However, monitoring the success of transplantations by time of return alone is not possible if the transplanted and native stocks do not differ with regard to this trait. Gene frequency data, on the other hand, permit monitoring of the relative success of transplanted runs having similar timing to native runs if differences of allelic frequencies exist for the two groups, and if data pertaining to these differences are available prior to transplantation. These data will permit continued monitoring of possible changes occurring in these populations relative to their genetic makeup.

The effects of transplantation have not been precisely evaluated. In the following section, the actual effects of the transplantations in the past are discussed. General characteristic of annual chum salmon runs returning to different rivers is their definite timing. This trait of distinct timing tends to persist in the transplanted fish as noted in the above. This indicates that these traits acquired for the purpose of efficient reproduction in particular river would not easily alter in a different environment. A good example of this is a later run of the Tokachi River which still keeps the original timing after three generations have passed since the transplantation. River populations even in a relatively small area of Honshu acquired various traits well adapted to their environment. If ineed these traits would hardly change after transplantation, reproduction in a different environment will become very inefficient particularly when a difference is significant. Physical environment such as temperature in river or coastal area and sunshine usually differs more between north and south than between east and west. These factors cumulatively indicate that it is nearly impossible to expect a good result from transplantation from latitudinally distant rivers. Effective transplantation probably requires eggs from proximal rivers. However, rivers in and close to the southern limits of chum salmon distribution do not have sufficient number of eggs and the main source of supply has been rivers in Iwate, Yamagata and Hokkaido. The observed genetic divergence between the northern and southern groups both on the Pacific coast and on the Japan Sea coast raises a doubt on the effectiveness of the past transplantations. The same doubt is also raised as cline was observed in some of the allelic frequencies despite the large-scale transplantations carried out in many rivers in Honshu to date.

On the other hand in Hokkaido, almost all the eggs are transferred from rivers in Hokkaido. Transfer is in a way from rivers in east to those in west and vice versa with a few exceptions. Unlike in Honshu, a phenomenon presumed to be a result of transplantation such as the absence of distinct genetic feature within regional populations was

observed in the structure of river populations in Hokkaido. As the period of time and scale of transplantation are different, it is not appropriate to readily compare Hokkaido populations with Honshu populations. Neverthless the difference in effects of transplantation between the two is presumed to be significant.

A donor stream in most cases has been chosen merely according to a supply and demand situation of eggs, and little attention has been paid to qualitative differences of eggs. In future, eggs most suited to a river should be selected for more effective transplantations.

4. Population structure of chum salmon in spawning migration

Japanese chum salmon migrate widely throughout much of the North Pacific as far as the Gulf of Alaska and the most of them return to rivers as three or four year old fish. It is assumed from the tagging experiments that Japanese chum salmon is distributed in the Bering Sea or the waters along the Aleutian Islands in summer and they migrate southward along the coast of the Kuril Islands in autumn (HIRANO, 1969 ; NEAVE *et al.*, 1976). The population structure of chum salmon in spawning migration arouses the interest, because it represents limited geographic origin compared with chum salmon in the open sea which consist of mixture of individuals representing diverse geographic origins and differing states of maturity.

It is known that mature chum salmon is distributed in the waters off the southern Kuril Islands in autumn and according to the tagging experiments, all the recoveries were made along the Japanese coasts (YONEMORI *et al.*, 1975). YONEMORI *et al.* (1975) proposed on the basis of these data that the chum salmon is mainly the mature population returning to Hokkaido or Honshu within the next few months.

The survey using 'the Hokko-maru', a research vessel of Fisheries Agency of Japan also identified the population of mature chum salmon in the said waters. Developed gonads and nuptial coloration or hooked snouts indicated that the fish were destined for imminent spawning. The researches operated between September 25th and October 7th, 1975 and October 13th through October 27 th, 1976. Research gear of both cruises were gillnets for research operations and longlines for tagging operations.

The daily sample size and gene frequency variation for the IDH-2 and MDH-B loci are listed in Tables 12 and 13. Daily fluctuations of the allelic frequencies among these fish correlated with known frequencies of some Hokkaido populations. In the 1975 collection, the *Mdh-B-c* allele that is characteristic of the populations of the Okhotsk or Nemuro area was absent while a high frequency was observed at the *Idh-2-d* allele that is

characteristic of the Kushiro or Bekanbeushi Rivers. It is therfore postulated that these mature fish captured in 1975 originated predominantly in rivers east of Cape Erimo. This conclusion is supported by the tag recoveries of 1975 which occurred predominantly east Cape Erimo within ten days following tagging (Fig. 32). Also, the peak of timing of these runs (from late September to late October) coincides with the timing of these tag recoveries while runs to the Okhotsk or Nemuro area return later (from mid-November to mid-December). These data indicate that the main population returning to the Okhotsk or Nemuro area does not yet migrate to the research waters during this period (from late September to early October).

The timing of the 1976 research cruise was about three weeks later than that of

Table 12. Gene frequencies at the IDH-2 and MDH-B loci in populations of chum salmon caught in the waters off southern Kuril Islands in late September and early October, 1975.

Collected date		Sep. 29	Sep. 30	Oct. 2	Total
Sample size		37	4	28	69
IDH-2	*a*	.554	(.750)	.500	.543
	b	.297	(.250)	.429	.348
	c	.027		.000	.014
	d	.122		.071	.094
	e	.000		.000	.000
MDH-B	*a*	.962	(1.000)	.964	.965
	b	.038		.036	.035
	c	.000		.000	.000

The gene frequency of the collection less than twenty is given in parenthesis.

Table 13. Gene frequencies at the IDH-2 and MDH-B loci in populations of chum salmon caught in the waters off southern Kuril Islands in middle and late October, 1976.

Collected date		Oct. 13	Oct. 14	Oct. 15	Oct. 17	Oct. 19	Oct. 20	Oct. 24	Oct. 25	Oct. 27	Total
Sample size		65	22	66	42	6	74	5	5	3	288
IDH-2	*a*	.515	.455	.432	.417	(.583)	.419	(.800)	(.700)	(.333)	.460
	b	.369	.386	.470	.417	(.333)	.459	(.200)	(.300)	(.333)	.418
	c	.054	.023	.023	.012	(.083)	.054			(.167)	.038
	d	.062	.136	.076	.155		.068			(.167)	.083
	e	.000	.000	.000	.000		.000				.000
MDH-B	*a*	.981	1.000	.971	.976	(.958)	.980	(1.000)	(1.000)	(.833)	.978
	b	.019	.000	.026	.018	(.042)	.017				.018
	c	.000	.000	.004	.006		.003			(.017)	.004

The gene frequency of the collection less than twenty is given in parenthesis.

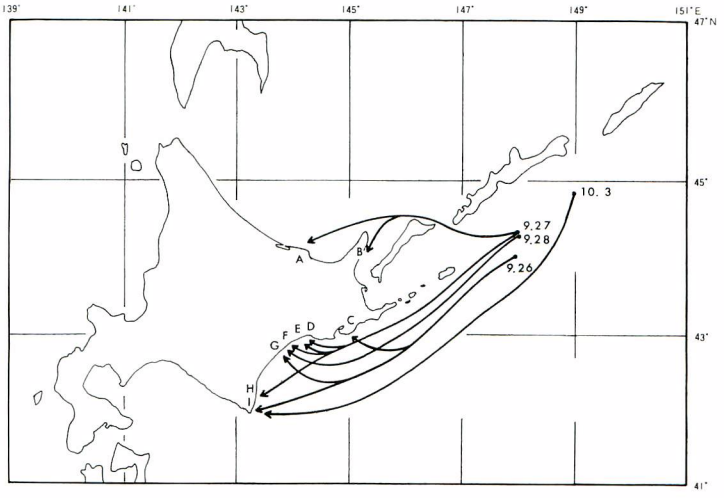


Fig. 32. Tag recoveries and their assumed migratory route from the tagging in the waters off the southern Kuril Islands in late September and early October, 1975.
A) Tokoro, B) Rausu, C) Hamanaka, D) Kushiro, E) Shiranuka, F) Uraboro, G) Toyokoro, H) Hiroo, I)Erimo.
Numerals indicate the date of tagging.

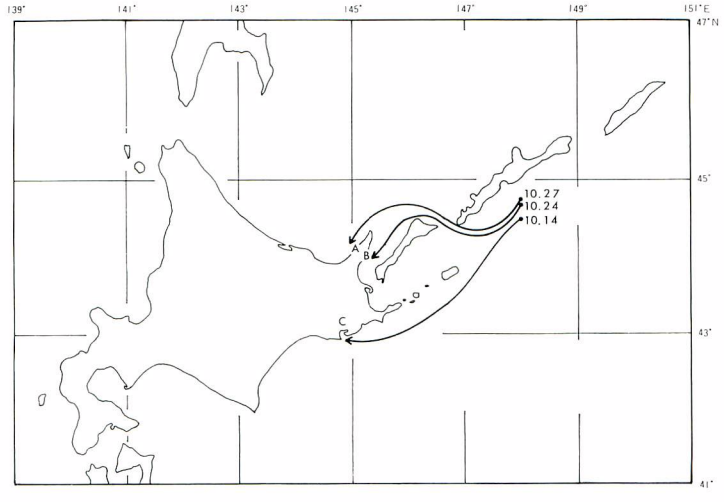


Fig. 33. Tag recoveries and their assumed migratory route from the tagging in the waters off the southern Kuril Islands in October, 1976.
A) Utoro, B) Rausu, C) Akkeshi.
Numerals indicate the date of tagging.

1975. A decrease of the frequency of the *Idh-2-a* and an increase in the frequency of the *Idh-2-b* alleles was noted following the first day's collection (Table 13). In addition, the *Mdh-B-c* allele (which was absent in these collections of 1975) began to appear towards the middle of collections. These shifts in allelic frequency coupled with the later timing of the collections suggest that salmon of the Okhotsk or Nemuro area were entering the reserch area. The minimal tagging data of 1976 also tend to support these conclusions (Fig. 33). The allelic frequencies of longline catches of October 14th indicate a high frequency of the *Idh-2-d* allele, which typifies populations of the Kushiro and Bekanbeushi Rivers. One of the fish tagged that day was recovered on the shore of Akkeshi near the mouth of the Bekanbeushi River. Another tag recovery occurred at Utoro on the coast of Okhotsk from a fish tagged on October 27th ; the electrophoretic data of this date indicate the presence of the *Mdh-B-c* allele which typifies this area.

The data presented to this point indicate that chum salmon population during their spawning migration is composed of subpopulations returning to the proximal rivers at about the same time. Although the research area for both 1975 and 1976 were almost identical, there were large daily fluctuations of CPUE and of allelic frequencies, which suggest that several mature subpopulations that rapidly replace one another are moving through this area (OKAZAKI, 1979).

The above characteristics of the population structure of chum salmon in their spawning migration also indicate that proximal river populations are liable to intermingle one another.

VI. Genetic characteristics of chum salmon regional populations

1. Genetic variability in chum salmon

i. Average heterozygosity (H) of chum salmon

The degree of average genetic variation at many loci is compared for each examined chum salmon population using average heterozygosity (H) which shows the proportion of heterozygotes per locus. The average heterozygosity of chum salmon river populations ranged between 0.0319 and 0.0714, which is slightly lower than that of other vertebrate species. This indicates that the genetic valiability of chum salmon is relatively low.

Average heterozygosities in North American populations based on 28 loci are presented in Table 14. However the populations in Washington are excluded here, since their allelic frequencies are estimated from mixed river populations and not from a single

population. The estimates are similar among the studied populations and they range between 5% and 7%. Although it is difficult to make comparison uniformly when the number of loci examined or type of loci used is different, the average heterozygosities of vertebrates range between 1% and 15% with the average of about 10% (NEI, 1975). The value tends to be larger in invertebrates and NEI (1975) attributes this to a large difference of population size between them.

Table 14. Average heterozygosities of chum salmon populations in North America based on 28 loci.

Area	Population	Average heterozygosity
Alaska	Yukon River (summer)	0.0638
	Yukon R. (autumn)	0.0714
	King Cove	0.0598
	Cook Inlet (north)	0.0623
	Cook Inlet (south)	0.0538
British Columbia	Puntledge R.	0.0579
	Qualicum R.	0.0532
	Goldstream R.	0.0621
	Harrison R.	0.0618
	Stave R.	0.0687
	Vedder R.	0.0697
Mean (unweighted)		0.0622

Average heterozygosity of chum salmon has been already reported both by ALTUKHOV *et al.* (1972) and ALLENDORF and UTTER (1978) who estimate it to be 3.2% and 4.5% respectively. Both figures are lower than the estimate obtained from the current study. This is probably due to the dependence of average heterozygosity on the number of loci examined and type of loci used. ALLENDORF and UTTER (1978) estimated this value based on 30 loci, the 24 loci of which are used in the current study and another six are monomorphic. If we use another six monomorphic loci in addition to the examined 24 loci used in the current study for the estimation, the value decreases from 6.2% to 5.1%. Thus, average heterozygosity will fluctuate by the number of loci examined and type of loci used when the estimation is made on the basis of relatively small number of loci. Therefore it is not appropriate to readily compare the estimates obtained through different methods.

The average heterozygosities of Japanese chum salmon populations estimated on the basis of 22 loci are given in Table 15. The estimates of the examined populations range between 3% and 5% which is relatively low compared with those of North American chum salmon populations. This is probably a reflection of the absence of polymorphic

loci such as AAT-1, 2 and α-GDH-2 in the examined 22 loci. The comparison based on the same loci is discussed in the following section.

Table 15. Average heterozygosities of chum salmon river populations in Japan based on 22 loci.

Hokkaido	Average hetero-zygosity	Honshu			
		Pacific coast	Average heterozygosity	Japan Sea coast	Average heterozygosity
Tokushibetsu	0.0381	Oirase	0.0362	Iwaki	0.0372
Yubetsu	0.0362	Mabechi	0.0410	Oirase	0.0352
Abashiri	0.0444	Hei	0.0391	Omono	0.0471
Shari	0.0471	Tsugaruishi	0.0356	Nishime	0.0324
Iwaobetsu	0.0372	Origasa	0.0388	Naso	0.0359
Shibetsu	0.0442	Ohzuchi	0.0349	Gakko	0.0376
Nishibetsu	0.0505	Katagishi	0.0360	Nikko	0.0433
Bekanbeushi	0.0449	Ohkawa	0.0348	Aka	0.0415
Kushiro	0.0423	Kitakami	0.0319	Miomote	0.0423
Tokachi	0.047_4	Ukedo	0.0358	Shinano	0.0340
Shizunai	0.035^9	Kido	0.0412	Kurobe	0.0493
Shikifu	0.0381	Same	0.0377	Kado	0.0466
Teshio	0.0380	Naka	0.0395	Hayatsuki	0.0463
Chitose	0.0372			Jintsu	0.0457
				Shoh	0.0482
				Tedori	0.0412
Unweighted mean	0.0415	Uuweighted mean	0.0371	Unweighted mean	0.0415
Grand mean (unweighted) 0.0400					

2. Genetic variability of each regional population and its divergence

The characteristics of the frequencies of alleles of each river population or regional population were already discussed. In this section it is made clear that the regional populations included in such a large unit of population as the North American or the Asian population share the common trait in the frequencies of alleles. The genetic variability of chum salmon is also examined for each hierarchical population such as river or regional population using average heterozygosity. It indicates that a large part of the genic variation at the protein level exists within river populations and interpopulational gene variation (between river populations or regional populations) is rather small.

Although each chum salmon population has its own feature in the frequencies of alleles as already described, the common gene composition was found throughout the whole

distribution area. Each population had approximately the same allele at all the examined loci with the mere difference occurring in the frequency. Furthermore the type of allele which appears predominantly was almost common to all the populations. These findings lead to the conclusion that the genetic diversity in chum salmon regional populations is merely a difference in the frequency of alleles at each locus, like many other organisms (NEI, 1975).

Table 16. Analysis of gene diversity among chum salmon regional populations of North America based on 28 loci.

Area	No. of populations	H_T	H_S	G_{ST}
Western Alaska	2	0.0678	0.0676	0.0027
Central Alaska	3	0.0598	0.0586	0.0194
Alaska (total)	5	0.0636	0.0622	0.0222
Fraser River	3	0.0671	0.0667	0.0060
British Columbia	6	0.0627	0.0622	0.0081

In this section, the degree of genetic divergence among populations and among regional populations is examined based on average heterozygosity following NEI's method (1975). The result obtained for the population on the Continent of North America based on 28 loci is presented in Table 16, where H_T is the gene diversity in the total population measured by total allelic frequency of all the examined populations. And H_S is the gene diversity within river populations estimated by unweighted mean average heterozygosity of each river population D_{ST} is the average gene diversity between river populations and expressed as

$$H_T - H_S = D_{ST}.$$

The relative magnitude of gene differentiation among river populations is measured by

$$G_{ST} = \frac{D_{ST}}{H_T} = \frac{H_T - H_S}{H_T},$$

and this value is called the coefficient of gene differentiation.

Lower values of G_{ST} in the populations of western Alaska, Fraser system and British Columbia indicate that the degree of gene differentiation is extremely low among these populations. Conversely a higher degree of gene differentiation was observed in the populations of central Alaska. This is probably attributed to the following ; (1) the specimens were collected from coastal catch, so that it reflects mixtures of populations returning to different rivers, and (2) sampling locations are scattered over central Alaska.

In the following section, it is discussed how the genic variation is apportioned within and between the regional populations or river populations. The gene diversity among North

American populations is shown in Table 17. In Alaska, due to a limited number of populations in western and central Alaska coupled with a low level of divergence between the western and central Alaskan regional populations, they were treated as one regional population. H_S is the gene diversity in the regional population measured by the total allelic frequency of all the examined populations in a given region. D_{CS} and G_{CS} correspond to the aforementioned D_{ST} and G_{ST}. $\bar{D}_m$ is given by

$$\bar{D}_m = sD_{CS}/(s-1) \quad (\text{s : number of examined populations}),$$

and this measure is an estimate of minimum net codon differences between regional populations and independent of the gene diversity within river populations.

Table 17. Analysis of gene diversity and degree of gene differentiation in chum salmon regional populations of North America based on 28 loci.

Area	No. of populations	H_S	H_C	D_{CS}	$\bar{D}_m$	G_{CS}
Alaska	5	0.0636	0.0622	0.0014	0.0018	0.0222
British Columbia	6	0.0627	0.0622	0.0005	0.0006	0.0081
Mean (unweighted)		0.0632	0.0622	0.0010	0.0012	

This indicates the higher gene differentiation among the Alaskan regional population, as the value of $\bar{D}_m$ is higher in Alaskan population than in British Columbia population. By using the unweighted mean gene frequencies for 11 populations in Alaska and British Columbia, the total average heterozygosity (H_T) of North American populations can be estimated as 0.0648. On the other hand, the estimates of H_C and D_{CS} are 0.0622 and 0.0010, respectively. Therefore, D_{ST} is estimated to be 0.0016. Thus, 96.0% (H_C/H_T) of the gene diversity in North American chum salmon populations exists within rivers, while the gene diversities between rivers within regional populations (D_{CS}/H_T) and between regional populations (D_{ST}/H_T) are 1.5% and 2.5% respectively.

Table 18. Analysis of gene diversity among chum salmon regional populations of Japan based on 22 loci.

Area	No. of populations	H_T	H_S	G_{ST}
Hokkaido	14	0.0420	0.0415	0.0112
Honshu				
Pacific coast (north)	3	0.0382	0.0380	0.0034
Pacific coast (south)	9	0.0373	0.0364	0.0239
Total	13	0.0381	0.0371	0.0270
Japan Sea coast (north)	8	0.0399	0.0394	0.0130
Japan Sea coast (south)	7	0.0456	0.0445	0.0254
Total	16	0.0437	0.0415	0.0517

Following the same procedure as was applied to North American chum salmon, gene diversities of Japanese regional populations are estimated based on 22 loci (Table 18). The Mabechi and Iwaki Rivers in the northern part of Honshu are excluded here, because they were included in the southern group according to the dendrogram (Figs. 25 and 26). This indicates that larger gene diversity occurs among the populations in Honshu, particularly on the Japan Sea coast than in Hokkaido. The relatively small gene diversity within the northern regional population on the Pacific coast of Honshu is probably attributed to the insufficient number of populations examined in this region.

The total average heterozygosity (H_T) of 43 river populations in Japan becomes 0.0418, following the same procedure that was applied to North American populations. Thus, 97.1% (H_C/H_T) of the gene diversity in Japanese populations exists within rivers and the gene diversities between rivers within regional populations (D_{CS}/H_T) and between regional populations (D_{ST}/H_T) are 1.9% and 1.0%, respectively (Table 19). Because of the limited number of populations in the northern regional population on the Pacific coast of Honshu and a low level of divergence between the northern and southern regional populations on the Pacific coast of Honshu, they were treated as one regionl population. This conforms well with the result obtained for North American populations based on 28 loci.

Table 19. Analysis of gene diversity and degree of gene differentiation in chum salmon regional populations of Japan and North America based on 22 loci.

Area	No. of populations	H_S	H_C	D_{CS}	D_m	G_{CS}
Alaska	5	0.0471	0.0460	0.0011	0.0014	0.0234
British Columbia	6	0.0492	0.0487	0.0005	0.0006	0.0102
Mean (unweighted)		0.0482	0.0474	0.0008	0.0010	
Hokkaido	14	0.0420	0.0415	0.0005	0.0005	0.0119
Honshu						
Pacific coast	13	0.0381	0.0371	0.0010	0.0011	0.0262
Japan Sea coast (north)	8	0.0399	0.0394	0.0005	0.0006	0.0125
Japan Sea coast (south)	7	0.0456	0.0445	0.0011	0.0013	0.0241
Mean (unweighted)		0.0414	0.0406	0.0008	0.0009	
Grand mean (unweighted)		0.0437	0.0429	0.0008	0.0009	

In order to examine the gene diversity throughout the entire distribution, the average heterozygosities including those of North American chum salmon are estimated based on 22 loci examined in common (Table 19). This also indicates that the value of average

heterozygosity (H_S) tends to be lower in Japanese populations than in North American populations. This is probably due to a large difference in geographical extent of the examined populations between the two. Furthermore it is presumed that many years of artificial spawning, resulting in a small ratio of mating individuals to total run, affects the genetic variability of Japanese chum salmon. Both the values of D_{CS} and $\bar{D}_m$ indicate large genetic divergence among Honshu populations, particularly on the Japan Sea coast (Table 19). It is presumed that the reason for large genetic divergence within such a small geographic area is the presence of a unique population adapted to the southern limits of chum salmon distribution in this region. Genetic divergence among the populations close to the southern limits is also observed on the Continent of North America, where a large difference in allelic frequency is observed between the northern and southern populations in Puget Sound (Fig. 16 and Table 3).

The total average heterozygosity (H_T) from unweighted mean gene frequencies of 54 examined populations in North America and Japan was 0.0439. Thus, 97.7% (Hc/H_T) of the gene diversity throughout the distribution exists within rivers, while the gene diversities between rivers within regional populations (D_{CS}/H_T) and between regional populations (D_{ST}/H_T) are merely 1.8% and 0.5%. A similar result is reported by Lewontin (1972) for the human race. He concluded that a large part of the genic variation in man exists within small units of populations and the interpopulational gene variation is rather small. It is presumed that this conclusion holds also for other organisms.

The presence of several regional populations and their genetic differentiation have been confirmed from the genetic traits. The comparison of the gene frequency data of each regional population revealed that the regional populations included in such a large unit of population as the North American or the Asian population share the common trait in the frequencies of alleles. Although there is no genetic information available for the populations in southeastern Alaska or an area facing the Bering Sea in the U.S.S.R., the common feature in polymorphism for MDH-B was observed both among the Asian and North American populations. To be precise, polymorphism was observed at a constant rate in the Asian population, whereas in the North American population polymorphism for MDH-B was hardly detected. The presence or absence of LDH-1 variation or frequencies of the *Idh-2-a, d* alleles *etc.* can further subdivide the populations on the Continent of North America into several regional populations. Likewise, the Asian population can be subdivided into the Russian population and the Japanese population based upon the observed differences in the frequencies of the *Idh-2-c,d* or *α-Gdh-2-b* alleles. These two populations

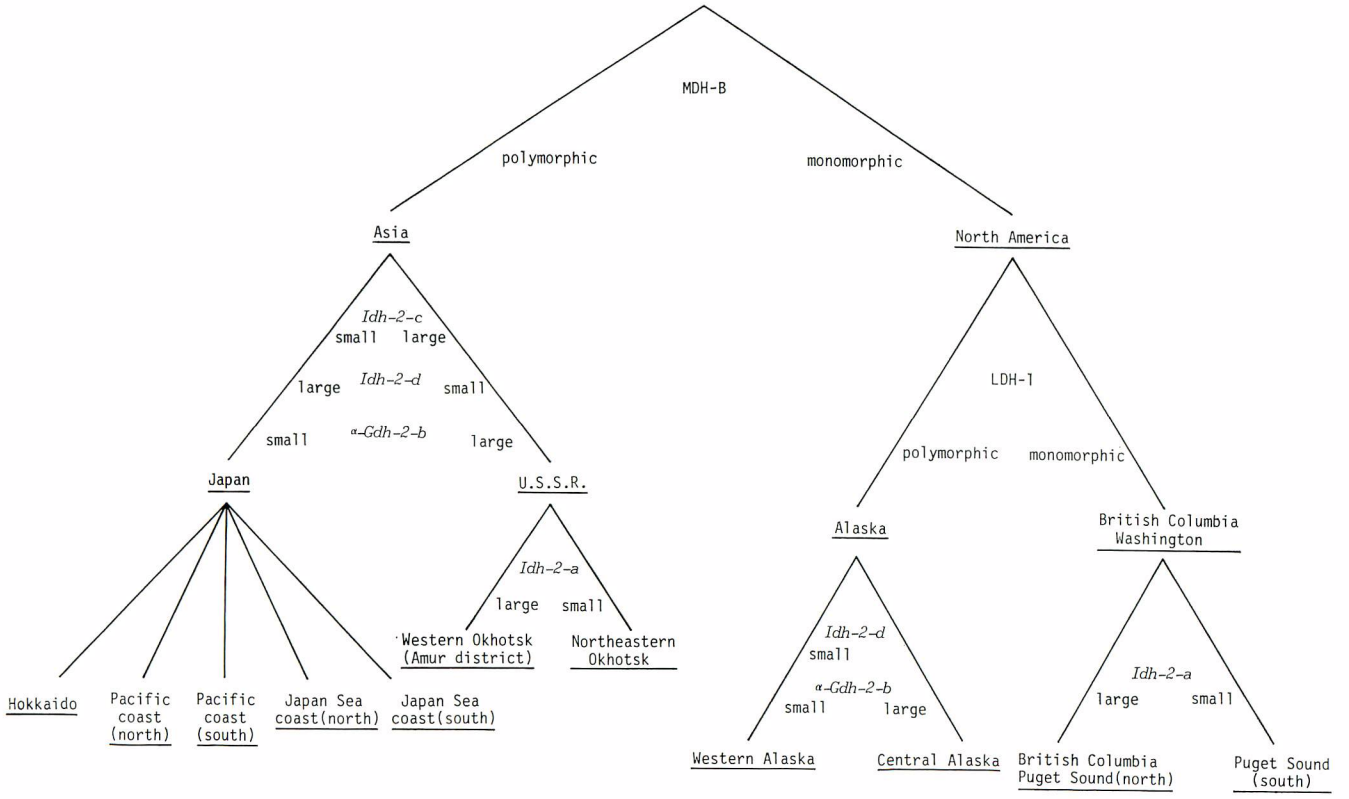


Fig. 34. Key to the regional chum salmon populations defined by genetic traits.

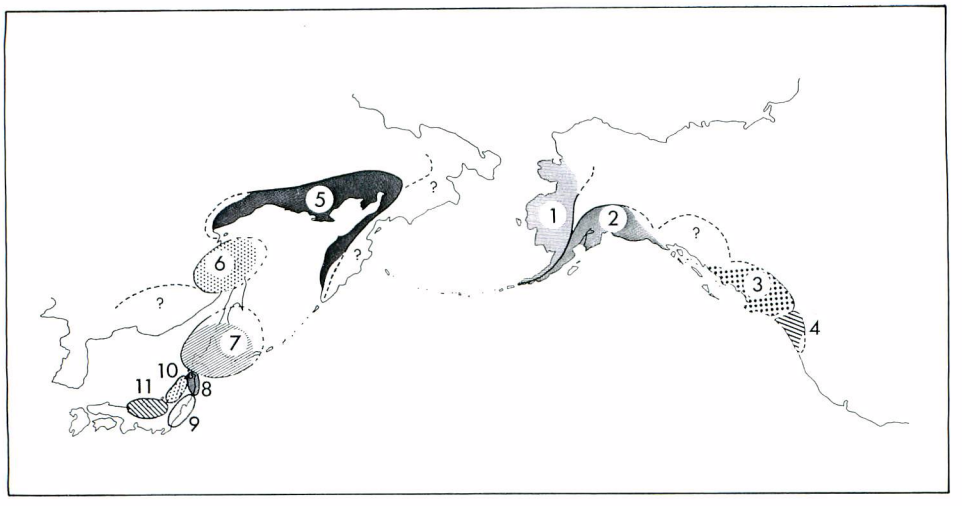


Fig. 35. Schematic diagram of regional chum salmon populations defined by gene frequency data.
(1) western Alaska, (2) central Alaska, (3) British Columbia and northern Puget Sound, (4) southern Puget Sound, (5) northeastern Okhotsk, (6) western Okhotsk (the Amur River), (7) Hokkaido, (8) the northern and (9) southern part on the Pacific coast of Honshu and (10) the northern and (11) southern part on the Japan Sea coast of Honshu.

Fig. 36. Schematic diagram of regional chum salmon populations presumed from the tagging experiments (from NEAVE *et al.*, 1976).

were further subdivided into several regional populations.

The regional populations and their genetic traits postulated from the thus far obtained findings are shown in Figs. 34 and 35.

Findings on distribution and migration pattern during the ocean phase, obtained from the result of tagging experiments also suggest the formation of several regional populations throughout chum salmon distribution area (Fig. 36). This result seems to be closely related to the genetically postulated regional populations.

3. Formation of regional population

The presence of regional population and intermingling within regional population which are indicated by continuity and discontinuity in the frequencies of alelles in chum salmon river populations have been discussed. In this section, the homing of chum salmon as well as the formation of regional population is examined from the result of the past tagging experiments and it is also discussed that the characteristics of homing and the migration routes are closely related to the formation of regional population.

SAKANO (1960) reported the result of the recovery of the parental fish which were released as finclipped fry in a total of two million in the Tokoro River in the Okhotsk area and the Chitose River in the Japan Sea area of Hokkaido from 1951 to 1955. According to this report, most of chum salmon released in the Tokoro River were recovered in the Tokoro River or around its river mouth and 98% of the chum salmon recovered in rivers were found in the natal stream. Strayings that were observed extended from the Nishibetsu River in the Nemuro area to the Teshio River in the Japan Sea area. On the contrary, strayings of chum salmon released in the Chitose River amount to as high as 10% and extended as far as to Niigata Prefecture.

The result indicates that most chum salmon return to their natal streams with precision. However, we must also take into account the possibility of overestimating the homing precision, since the effort of recovery tends to concentrate in and close to natal streams in the tagging experiments. The effort of recovery in this experiment was concentrated in Hokkaido, particularly in the rivers and coasts of the Okhotsk and the Japan Sea areas, and it seems that there were little interest in the coastal regions of Honshu. Neverthless four strays (as high as 10% of the total recoveries in rivers) were recovered in Niigata Prefecture which suggests that actual rate of straying is probably higher than 10%. There is a limit to a strict estimation of homing precision by the finclipping experiments alone, due to effects of regeneration of clipped fin or actual loss

of fin under the natural environments and the lack of uniformity of the recovery effort.

Although the homing is supported in general, the above result suggests that the genetic impact of straying upon each river population is large should the 2% to 10% of straying is repeated for generations.

Each chum salmon regional population presumed from the result of the tagging operation and others has its unique distribution and migration pattern in the ocean and they tend to repeat the similar pattern every year with a minor fluctuation. The distinct distribution and migration pattern of each regional population are closely related to the environment of each population. To be more precise, river temperature or coastal temperature from spring to summer in each district put restriction on the timing of seaward migration of chum salmon fry. It also restricts hatching as well as the timing of return and spawning of parental fish. Subsequently, fry in adjacent rivers migrate seaward at about the same period every year, as the physical environment in limited area is similar. Chum salmon fry after reaching river mouth, temporarily stay in coastal waters and then gradually migrate to the open sea. However as their swimming ability is insufficient, they might be affected by a current and others. This is also presumed from the appearance of the juvenile chum salmon of each regional population in a specified water in the following spring every year. Afterward, they spend from two to four years in the ocean and each regional population is known for having distinct distribution and migration route during their ocean phase (NEAVE *et al.*, 1976). This is probably related with the constant seasonal change of the structure of the sea water or distribution of forage organisms.

The life history of chum salmon suggests less possibility for intermingling among different regional populations than among the same regional populations. In other words, the straying of chum salmon occurs in a limited area. This trait of chum salmon is reflected in the presence of regional populations observed throughout its distribution. To be more precise, it can be construed that the present regional populations with respective genetic traits were formed as the genetic intermingling of adjacent chum salmon river populations occurred succesively within a certain limited geographic range.

From the above, the homing of chum salmon in the strict sence of the term, is the trait of chum salmon to return to rivers in a set area centering on its natal stream.

VII. Genetic structure of chum salmon in the species of genus *Oncorhynchus*

The characteristic of the genetic structure of chum salmon population can be further defined by comparing it with other species of genus *Oncorhynchus*. In this section the

population structure of chum salmon in the species of genus *Oncorhynchus* is clarified and it is also pointed out that the early stage of the life history and the homing are closely related to this structure.

Six species of genus *Oncorhynchus* can be divided into the following two groups from the characteristics observed during the early stage of their life histories.

Sockeye salmon	(*O. nerka*)	(1) freshwater dependent group
Coho salmon	(*O. kisutch*)	
Masu salmon	(*O. masou*)	
Chinook salmon	(*O. tshawytscha*)	
Chum salmon	(*O. keta*)	(2) sea water dependent group
Pink salmon	(*O. gorbuscha*)	

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 and pink salmon migrate to sea shortly after hatching and the period of time they spend in freshwater is considerably shorter compared with the freshwater dependent species. 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 ; VERNON, 1962). The genetic structure of each species of genus *Oncorhynchus* and the homing which is supposedly linked closely with the genetic structure are examined in the following.

Regarding the homing of sockeye salmon, FOERSTER (1968) and HARTMAN and RALEIGH (1964) reported from the results obtained from the tagging experiments that sockeye salmon can even identify their originating tributaries to say nothing of their natal streams. FOERSTER (1968) examined the homing of sockeye salmon in the Cultus Lake of the Fraser River system by marking the whole of two successive smolt migrations and reported that possible strays ammounted to only 0.59% of the run. HARTMAN and RALEIGH (1964) carried out displacement experiments by replacing pre-spawned adult sockeye which once returned to tributary rivers entering Brook's Lake, Alaska and reported that almost all of them returned to the same tributaries. According to the tagging experiments, sockeye salmon can identify even their tributaries with precision. However due to the lack of the sufficient research in streams other than those examined, the strayings to other streams

cannot be totally denied.

With respect to the genetic divergence among sockeye salmon river populations, there is a report by GRANT *et al.*, (1980) who examined three river systems entering Cook Inlet in Alaska. They confirmed the considerable differences in the frequencies of alleles even among the tributary populations within the same water system based on six polymorphic loci. The following is the genetic distance among the sockeye tributary populations estimated on the assumption that the 18 monomorphic loci are used in addition to the six already exmined polymorphic loci in order to compare this result with that of chum salmon populations examined on the basis of 24 loci in chapter three.

Kasilof River system (among five tributary populations)

$$D=0.00010-0.00058 \ (\bar{D}=0.00030)$$

Kenai River system (among four tributary populations)

$$D=0.00139-0.00904 \ (\bar{D}=0.00440)$$

Susitna River system (among four tributary populations)

$$D=0.00143-0.01134 \ (\bar{D}=0.00437)$$

The above figures differ considerably from the genetic distance estimated for the chum salmon tributary populations of the Fraser River system on the basis of the examined 24 loci ($\bar{D}=0.00023$) and they are as high as the genetic distance between the chum salmon populations in Alaska and those in British Columbia ($\bar{D}=0.00341$).

Both lines of evidence independently indicate that intermingling rarely occurs among the sockeye tributary populations.

The homing of coho salmon is confirmed from the result of tagging experiments (FOERSTER and RICKER, 1953). SHAPOVALOV and TAFT (1954) examined the intermingling between adjacent two river populations in central California, and they reported that possible strays amounted to 14.9% to 26.8%. However, the mouths of the examined rivers are closed frequently in spring and summer by sand bars and it is presumed that this might have caused such high straying. Since few tagging experiments have been conducted on a wide range, the degree of precision of the homing is not sufficiently known.

Although there is not sufficient amount of information available on the genetic structure and feature of coho salmon, UTTER *et al.* (1970) and MAY (1975) reported the gene frequency data of the river populations distributed from the Fraser River to the Columbia River. The number of loci examined in their reports was limited, but significant differences were found in the frequency of the transferrin (Tf) alleles by area. Three alleles (*a*, *b* and *c*) are present at this locus, while the *Tf-a* allele predominates and its

frequency amounts to 0.79 to 1.00 in the tributary populations of the Columbia and Fraser Rivers. On the other hand, the *Tf-c* allele is predominant among 10 river populations distributed between these two rivers and its frequency ranges from 0.37 to 0.75. Furthermore, the relatively low frequency of the *Tf-a* allele ranging from 0.15 to 0.37, indicates significant differences from the populations in the Columbia and Fraser Rivers. The distance between the mouth of the Columbia River and that of the Fraser River is merely 350 km in a straight line. It is distinctive that a large difference in the frequencies of alleles occurs within such a small area.

Although the number of loci or areas examined is limited, the above figures suggest that coho salmon population is composed of extremely divergent populations by each small area. Furthermore, tributary populations within one river system or river populations within a limited area seem to have common frequencies of alleles in contrast to the population structure of sockeye salmon.

Chinook salmon is known for having more than two seasonal runs in many rivers and the number of runs tends to be greater in the rivers in south (Mason, 1965). Each seasonal run has different spawning time and freshwater phase (Fry, 1961), which suggests that chinook salmon population even within a single river system may consist of several sub-populations.

Since the tagging experiments have not been conducted extensively and in sufficient number, little information is available on the homing of chinook salmon. MAJOR *et al.* (1978) reviewed a series of mark-recovery experiments involving Columbia River hatchery fish of the 1961—65 brood years and reported that straying amounted to 8.4%. They pointed out that the actual rate of straying probably was appreciably less than 8.4%, because many of these 'strays' were fish which had been taken in other hatcheries and some might leave and continue their research for their true home stream. RICH and HOLMES (1929) and SNYDER (1931) examined the homing of transplanted chinook salmon and reported that all the recoveried fish although the number is small showed the precise homing to their planted streams.

Genetic information available on chinook salmon population is also limited to those in Washington and the Columbia River. UTTER *et al.* (1973a) examined the chinook salmon river populations distributed from Puget Sound to the Columbia River and they found a conspicuous difference in the allelic frequency at the SOD locus between the summer and winter runs. Furthermore, significant differences were also observed in the allelic frequency at the SOD locus among each tributary population of the summer and autumn runs to the

Columbia River and two types of different allele exist in the tributary populations (KRISTIANSSON and MCINTYRE, 1976). It is also known that there are significant differences in the frequencies of alleles at the PGI-2 locus between the coastal and non-coastal populations of the autumn runs returning to the rivers in Washington (UTTER *et al.*, 1976).

The above indicates that significant genetic differentiation occurs among seasonal runs and among tributary populations of chinook salmon within a single river system, hence it is presumed that chinook salmon has very complex subpopulations even within a limited area or in the same river. These lines of evidence suggest that intermingling hardly occurs among seasonal runs or among tributary populations of chinook salmon.

Masu salmon spend one or two winters in freshwater following hatching before their seaward migration and their life history is similar to that of coho salmon (HIKITA, 1956). Unlike other species of genus *Oncorhynchus*, the distribution of masu salmon is confined to the Asian side including Japan (TANAKA, 1965). Since the effect of transplantation is very little in masu salmon compared with chum salmon, they are expected to provide useful information on the genetic structure including the homing. However at present, the information is seldom available.

On the contrary, pink salmon have less dependency on the freshwater throughout their life history compared with other species discussed earlier. In general, the spawning grounds of pink salmon are in the lower section of rivers, but in some instances the spawning takes place in stream-mouth areas of tidal influence (HUNTER, 1959). The downstream migration of fry begins immediately on emergence from the gravel and the freshwater phase is even shorter than that of chum salmon, making the dependence on the freshwater the least among the species of genus *Oncorhynchus*. The rigid two-year life cycle of pink salmon has led to a complete isolation of even- and odd-year populations.

The tagging and other experiments have been carried out extensively to study the homing of pink salmon. However, the data accumulated to date can lead to various conclusions on the precision of the homing and no uniform view has been obtained.

The tagging experiments conducted by PRITCHARD (1939) in British Columbia from 1931 to 1936 suggests the precise homing of pink salmon. BAMS (1976) carried out an experiment in British Columbia, comparing an introduced pure donor stock with a hybrid stock created by crossing females from the donor with males of the local residual stock. Large differences occurred in returns to the river between them, that is the former showed less precise homing than the latter. Thus he suggests the presence of lacally adapted paternal genes in each river. On the other hand VERNON (1962) reported that several

hundred pink salmon were found in Fraser River tributaries in 1959 although none were found in these same tributaries two years early. MERRELL (1962) also reports a similar case in Alaska.

Furthermore the result obtained from the introduction of pink salmon in the region where there were no indigenous populations draws much attention. Eggs in British Columbia have been transferred to the rivers in Newfoundland, Canada since 1959. According to the result in 1967 when the return was most numerous, 98% of pink salmon recovered in rivers were found in the natal stream. However straying was also observed and some even wandered to a distance of 1,000 km from the natal stream (BLAIR, 1968). During the period of 1956 to 1959 the Russians transferred pink salmon eggs from Sakhalin Island to the rivers in the Kola Peninsula facing the Barents and White Sea and annual return of parental fish has been observed since 1960 (SURKOV and SURKOVA, 1968 ; SURKOVA, 1970). In 1960, the location of recoveries of pink salmon extended from Norway, Iceland to England. Therefore, AZBELEV and YAKOVENKO (1963) postulated that pink salmon apparently have the least precise homing among the species of genus *Oncorhynchus*.

Although opinion is divided on the homing of pink salmon, a similar result is obtained from the genetic studies. ASPINWALL (1974) reported that the frequencies of alleles at the α-GDH and MDH loci are similar within the odd- or even-year class populations, while they are different between two year-classes. Thus he pointed out that each of the year-classes could be considered a single panmictic population.

JOHNSON (1979) reported an interesting feature of the population structure of pink salmon from the extensive geographic surveys of genetic variation covering North America to Asia. According to his report, a striking similarity was confirmed in the frequencies of alleles within a year-class as a result of his investigation using six polymorphic loci. Conversely significant genetic divergence is observed between year-classes even in the same river. The estimate of genetic distance among the even-year class populations is low ($\bar{D}$=0.00150) even on the basis of six polymorphic loci alone over an extensive area of Alaska to Asia. Furthermore, in order to compare the genetic divergence with that of the aforementioned sockeye and chum salmon, the author calculated on the assumption that the 18 monomorphic loci are used in addition to the six polymorphic loci already examined in this report. The genetic distance among the even-year class populations is extremely low ($\bar{D}$=0.00032) over an extensive area of Alaska to Asia. Likewise, the genetic distance between year-classes on the Kodiak Island of Alaska is 0.00189. Therefore, in pink salmon greater genetic divergence occurs between year-classes within a limited area than among

river populations within a year-class over an extensive area.

It may not be appropriate, to readily compare the above figures with those of chum salmon when the number of loci examined is limited, however the degree of genetic divergence among the even-year class populations over an extensive geographic range is as small as that among chum salmon tributary populations within the same water system ($\overline{D}=0.00023$). This suggests that considerable genetic intermingling is occurring extensively among pink salmon river populations. Thus it is evident from the genetic aspect of the study that pink salmon is least precise in its homing among the species of genus *Oncorhynchus*.

Various population structure is observed in the species of 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. Formation of several regional populations having similar frequencies of alleles throughout its distribution makes the population structure of chum salmon distinctive among the species of genus *Oncorhynchus*.

On the other hand, the difference of the population structure among these species hamper the population study using biochemical genetic methods. Biochemical genetic methods are an effective tool for conducting a population study of sockeye, coho and chinook salmon whose tributary populations or proximal river populations show great divergence. However, an application of this method alone will not produce satisfactory results when an object for the population study is chum salmon distributed in a limited area, since the genetic differentiation among proximal river populations is considerably low. Conversely, when an object for the study is chum salmon over an extensive area such as the North Pacific Ocean where various stocks originating from different area are intermingling, the distribution or mixing ratio of each regional population in offshore waters can be accurately estimated by comparing the allelic frequencies of each regional population, since chum salmon has several regional populations consisting of adjacent river populations which share similar frequencies of alleles. However, biochemical genetic methods have little effect on the population study of sockeye salmon and others in offshore, since highly divergent allelic frequencies occur even among tributary populations within a single river system and thus, innumerable standard populations shoud be present throughout their entire distribution. It is also difficult to apply this method to the population study of pink salmon, since the genetic differentiation among the populations distributed over an extensive area is low. Effectiveness of the biochemical genetic methods depends largely upon the

geographic area subjected for investigation due to various characteristics of the population structure of the species of genus *Oncorhynchus*.

The population structure of chum salmon has been examined from the genetic aspect in this study. It is pointed out that biochemical genetic methods are sometimes ineffective in some species of genus *Oncorhynchus*. Therefore, it is evident that biochemical genetic methods are not always useful tool for the population study of fish. When we apply this method to the population study, various conditions need to be met. For example, there should be a difference in the allelic frequency among the populations to be examined and a considerable number of specimens are also required for the analysis since the identification of the origin for each individual is generally impossible.

At least, biochemical genetic methods advance the population study of chum salmon. The results of the current population study will come in useful for effective transplantations as well as for the genetic management of chum salmon stocks.

Acknowledgements

The author would like to express his sincere gratitude to Dr. Kazuhiro MIZUE, the ex-Professor of Ocean Research Institute, University of Tokyo for his guidance and encouragement. The author is deeply indebted to Dr. Ken-ichi NUMACHI, Assoc. Professor of Otsuchi Marine Research Center, University of Tokyo for making this study possible and for his kind advice in the preparation of the manuscript. The author is also indebted to Messrs. Osamu SANO, Kenji TAKAGI, Jun ITOH, Seiji MACHIDORI and Dr. Shigeru ODATE of the Far Seas Fisheries Research Laboratory, Fisheries Agency of Japan for their support and interest in the course of the work and Dr. Fred M. UTTER of the U.S. National Marine Fisheries Service, NOAA, for his valuable advice as well as for providing a laboratory. Appreciation is given to Dr. Ikuo IKEDA, the director of the Far Seas Fisheries Research Laboratory for his valuable advice on the content of the manuscript. Grateful acknowledgement is to Dr. Tetsuo KOBAYASHI, Mr. Shin-ichi ABE, Dr. Osamu HIROI and Mr. Hiroshi MAYAMA of Hokkaido Salmon Hatchery, Fisheries Agency of Japan for their kind advice and good offices for the sampling in Hokkaido.

Thanks are due to many generous people for their help in the sample collections : Dr. Robby A. BAMS of Pacific Biological Station, Environment Canada ; Mr. Don J. BUXTON and other members of the Canada Department of Fisheries ; Mr. Alan KINGSBERY and other members of the Alaska Department of Fish and Game ; Mr. Hidetaka IWASAKI of Nichiro Pacific Co., Ltd. in Seattle ; Dr. Kenji SHIMAZAKI, Faculty of Fisheries, Hokkaido University ;

Mr. Yukio NAGAHORA of Fisheries Experimental Station of Iwate Prefecture ; Mr. Yoshiya TAKAHASHI of Japan Sea Regional Fisheries Research Laboratory, Fisheries Agency of Japan ; Mr. Ken-ichi KAWASAKI of Fisheries Experimental Station of Toyama Prefecture ; Mr. Masahide KAERIYAMA of Fisheries Experimental Station of Miyagi Prefecture ; the crew of 'the Hokko-maru' Fisheries Agency of Japan, and 'the Oyashio-maru' Hokkaido University.

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サケ（*Oncorhynchus keta*）の集団構造に関する遺伝学的研究

岡崎登志夫

摘　要

サケ科魚類は，サケ属（*Oncorhynchus*），ニジマス属（*Salmo*），イワナ属（*Salvelinus*），イトウ属（*Hucho*）から構成されており，これらは降海性や産卵回数などの生態的特性に様々なちがいがあるが，共通して河川や湖沼で産卵する。このうちサケ属の各種は，産業的に高い価値をもち，北太平洋域での最も重要な魚類資源として国際的に重視されている。サケ属は生活史の過半を海洋で過した後，遡河して産卵するが，餌料をもふくめて淡水域への依存度が他のサケ科魚類に比べてはるかに低い。このような生態的特性により，サケ属各種は淡水域のみの生活では期待できない生物量をもっているが，淡水域依存性はサケ属各種の間でも異なり，これが各種の集団構造や維持にも大きくかかわっていると考えられる。

典型的遡河性魚類であるサケ属の資源の帰属と管理権は母川国にあるとする国際的認識が一層明確になり，これに関連して領海内外でのサケの分布と帰属，集団の局地性，回遊路の研究が一層厳しく要求されている。サケ（*O. keta*）の母川国である日本では，国民の嗜好と産業的重要性もあいまって，この魚種の集団研究と資源生物学的研究がますます重要となり，また人工ふ化放流と稚魚の移植による資源増大策が従来にも増して大きな努力で進められている。

本研究は我が国のサケ属魚類資源の過半を占めるサケを対象とし，資源管理と今後におけるふ化放流と移植の研究の基礎として，集団の構成と維持，各集団の遺伝的特性について研究したものである。ここでいう集団とは，従来一般にはいわゆる系統群あるいは系群と呼ばれてきたものである。サケの系統群研究は，これまでは主に形態学的に，あるいは標識放流法によって数多く研究されている。本研究では，北米大陸の11河川系，ソ連の3地方および日本の43河川の集団を材料にして，この種の主要分布域をカバーして集団分析を行ない，集団構成と集団遺伝学的特性，そのなかにおける日本の河川にそ上するサケ集団とその特徴および構成を明確にした。遺伝学的研究のために分析した酵素は14種類，そのうち集団分析に利用した多型的酵素と遺伝子座はそれぞれ10種類および16種類である。集団の分析は，各河川集団サンプルにおける表現型度数，遺伝子度数，集団間の遺伝的距離（*D*），平均ヘテロ接合体率（*H*）の検討によって行なった。その結果，得られた主要な知見を要約すれば下記の通りである。

遺伝的多型と遺伝的支配および平均ヘテロ接合体率　多型が見出された10酵素のうち，特に乳酸脱水素酵素（LDH-1），α-グリセロリン酸脱水素酵素（α-GDH-2），イソクエン酸脱水素酵素（IDH-2）およびリンゴ酸脱水素酵素（MDH-B）の4つのアイソザイム系が，サケ各集団の遺伝的組成を良く特徴づけていた。4量体の酵素であるLDH-1では関与している2つの対立遺伝子が，また2量体であるα-GDH-2，IDH-2およびMDH-Bに関与している各遺伝子座にはそれぞれ2，5，3の対立遺伝子が認められた。

一方，22～28遺伝子座について変異性を示す平均ヘテロ接合体率を求めた結果，サケ河川分集団では0.0319～0.0714を得た。この値は他の脊椎動物で求められた値と比較してやや低めであり，サケの変異性はそれ程高くないということになる。

アメリカ大陸における河川分集団の遺伝的組成　北米大陸の各河川では，本種の大部分は天然条件下で維持されており，河川間での移植等の人為的な影響も無視することができるため，天然状態におけるサケ河川分集団の構造を研究するうえで格好な素材を提供している。検討した11河川系の集団はIDH-2，LDH-1等の遺伝子組成の類似性で，アラスカとブリティシュ・コロンビア（B.C.）州以南に大別できた。また，フレーザー河の支

流分集団間，ユーコン河のそ上時期が異なる2つの分集団間で共に，遺伝子組成に極めて高い近似性が認められた。

ソ連極東地区河川分集団の遺伝的組成　ソ連のサケも，その大部分は天然条件下で再生産されているが，種々の制約のため本研究ではオホーツク海に面する地域のみをその対象とした。オホーツク海沿岸からの漁獲物を用いて分析した結果，オホーツク海の西岸（アムール）地方とその他のオホーツク海沿岸地域を起源とする集団の遺伝的特徴が明らかになった。両集団では，IDH-2 等の遺伝子組成に相異が認められた反面，*a*-GDH-2 に関しては共通して他の地域とは大きく異なる遺伝子組成をもっていた。

北海道・本州北部河川分集団の遺伝的組成　我が国では，サケがそ上するほぼすべての河川にふ化場が設置されており，資源の大部分が人工ふ化放流によって維持されている。43河川分集団について分析した結果，本州では IDH-2 と LDH-1 の遺伝子組成に地理的な勾配があり，太平洋側では岩手県中部を，また日本海側では新潟県北部を境にした南北の集団間で，その遺伝的組成に分化があることが明らかになった。一方，北海道内では遺伝子組成に地域による明瞭な差は認められないものの，他河川からの移植が比較的少なかった道東方面に限れば，根室半島を境にしてオホーツク・根室海区と襟裳以東海区の河川分集団間に特徴的な遺伝的差異が認められた。

サケ地方集団の存在　このように，サケの各河川分集団は遺伝的に様々な程度（遺伝的距離：$D=0.00003$～0.00844）に独立しているが，同一河川内の支流分集団間（$\overline{D}=0.00023$）や地理的に近接した集団間（$\overline{D}=0.00081$）にも遺伝的に高い共通性が認められた。これらの河川分集団間では，ある程度の遺伝的混合が毎世代蓄積された結果，共通の遺伝的組成を持つに至ったと考えた。そして，地理的に近接した幾つかの河川分集団からなる地方集団が，西部アラスカ，中央アラスカ，ピュジェット・サウンド北部を含むB．C．州，ピュジェット・サウンド南部，オホーツク海北東部，同西部（アムール），本州太平洋側北部，同南部，本州日本海側北部，同南部および北海道の各地域で形成されていると結論した。

また，遺伝的な特徴からみたこれらの地方集団と，サケの海洋生活期における分布・回遊パターンから推定されている地方集団との間には，密接な関連が認められた。海洋生活期中のサケは，一定の地域内の河川にそ上する集団ごとに毎年ほぼ決まった水域を回遊することが，標識放流試験によって明らかにされてきた。しかも，この回遊パターンは地方集団ごとに異なっているため，地方集団間では地方集団内に比べて海洋中で混合を生じる可能性はより少ないものとみられる。サケ河川分集団の遺伝的組成にみられる連続性と不連続性で示される地方集団の存在と地方集団内での混合は，このような海洋における回遊経路のちがい等とも密接に関係していると考えた。

サケ属魚類におけるサケ集団の遺伝的特性　サケ集団にみられるこの遺伝的構造は，他のサケ属魚類と比較することによって，その特徴をさらに明確にすることができる。サケ属の6魚種については，発生初期の生活史の特徴から海洋依存型（サケおよびカラフトマス（*O. gorbuscha*））と淡水依存型（ベニザケ（*O. nerka*），ギンザケ（*O. kisutch*），マスノスケ（*O. tshawytscha*）およびサクラマス（*O. masou*））の2つのグループに分けられ，一般に後者は母川への厳密な回帰性が支持されており，一水系内あるいは小地域内の分集団間にも極めて高い遺伝的分化が認められている。これに対して，カラフトマスは広い分布域全体を通じても，遺伝的な分化は極めて小さいという特徴を持つ。分布域を通じて遺伝的に特徴のある幾つかの地方集団から構成されているサケの集団構造は，サケ属の中でも特徴的であり，淡水生活期間の長短や母川への回帰性の程度等と密接に関連した結果であると考えた。

サケの移植効果　我が国の大部分の河川では，他河川からの移植を経験しているが，移植群のその後の動向については必ずしも明らかではなく，その実際の効果についても様々な議論がある。北海道の十勝川では，本研究を通じて移植後3世代を経ても移植群はなお従来の遺伝的組成を保持しているのが認められ，移植群の十勝川への定着が確認された。しかし，他の多くの河川では移植後のそ上数曲線に現われる変化からみる限り，移植群の定着を示唆する例は少ない。特に，本州では山形県，岩手県あるいは北海道の諸河川から極めて頻繁に移植が行なわれてきたにもかかわらず，なお各地方集団には共通する遺伝的な特徴が認められていることからみても，

移植の実際の効果はなお明らかでない。地域ごとに異なるそ上時期や稚魚の降海時期等他の生物的特性を考慮に入れると，南北に距離を隔てた河川からの移植効果は高くないとも考えられた。

集団構造に関する知見の蓄積と遺伝的な指標を利用することによって，今後は効果的な移植方法の確立や移植効果の的確な判定が可能になるものと考えられた。