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Genetic Features of Natural and Cultured Populations in Masu Salmon (*Oncorhynchus masou*)

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Summary

For quantifying genetic variability and differentiation of the natural and cultured masu salmon (*Oncorhynchus masou*), which has two forms, Sakuramasu (sea-run form) and Yamame (fluviatile form), enzyme polymorphism was examined by starch gel electrophoresis for a total of 21 natural and cultured populations. The screening of genetic variation at 33 presumed loci for 11 enzymes revealed no difference between Sakuramasu and Yamame. The amount of genetic variability maintained in natural river populations was higher than that of the populations maintained in culture.

The quantification of genetic differentiation revealed that the cultured populations were genetically more diversified than the natural populations. The divergence of cultured populations was assumed to be promoted by founder and/or bottleneck effect which occurred in the ancestral line of several hatcheries.

Tre distribution of masu salmon (*Oncorhynchus masou*) is confined to the Asian side including Japan. Masu salmon which spawn in fresh water can be divided into two froms, "Sakuramasu", sea-run form and "Yamame", fluviatile form, based on their life histories. Sakuramasu spend one or two winters in fresh water following hatching before they migrate to the sea. The northern population, especially that of Hokkiaido, mainly consists of the sea-run form, while almost all fish of the nouthern population are of the fluviatile form. In the northern population of Honshu, almost all females are of the sea-run form while the males are of the fluviatile form. Furthermore, artificial propagation has been successful in Sakaramasu and Yamame forms and the cultured populations have been established and maintained in fresh water ponds, during their life span.

Many studies had been done on the genetic features of natural salmonid populations over extensive geographic renges of their distribution using allelic variations of enzymes (1, 2, 3, 4, 5). Of paticular interest is the finding that the genetic distances among chum salmon river populations indicate variavility in the

degree of genetic isolation among rivers (6). Since the effect of transplantation is very little in masu salmon compared with chum salmon in Japan, they are expected to provide useful information on the genetic structure as well as on behavioural aspects of the former. Genetic variability in river populations masu salmon was identified by Okazaki (7). He reported that the proportion of polymorphic loci and the average heterozygosity were 0.48 (0.99 criterion) and 0. 056, respectively, and that significant differences were found in allelic frequencies among river populations.

The purpose of this paper is to quantify genetic variability and differentation of natural and cultured populations of masu salmon (*Oncorhynchus masou*) and discuss findings of the differences between natural and cultured population structures based on biochemical markers.

Materials and Methods

A total of 974 fishes were collected from 21 different cultured stocks of masu salmon (*Oncorhynchus masou*) which has two forms, Sakuramasu and Yamame, in several hatcheries in 1982 to 1985. The sample size, form, and names of rivers or hatcheries from which samples were obtained are given in Table 1. The fishes were classified into natural and cultured populations on the basis of whether their fry were obtained from parents returning to the river to spawn or from parents maintained in culture during their life span.

Genetic variability and genetic differentiation were quantified by using biochemical genetic markers. Polymorphism was screened electrophoretically for a total of 11 kinds of enzymes which were coded by 33 presumed loci. By applying starch gel electrophoresis (8), zymographically detectable variants were described in postulated genotypes. Gene loci were designated alphabetically from the most cathodal to the most anodal wherein duplicated loci were marked by numbers. Also the alleles were identified by alphabets consecutively from the most anodal to the most cathodal. Allele frequencies at each locus were calculated by the direct counting method.

The genetic variability within populations was quantified by measuring the proportion of polymorphic loci (p) and the average heterozygosity per individual (H). A polymorphic locus was defined as the locus at which the frequency of the most common allele was less than 0.95. The heterozygosity is calculated as $h = 1 - \Sigma qi^2$, where qi is the frequency of the ith allele at a locus, and the average heterozygosity is taken over all the loci examined. The genetic differentiation within and between natural and cultured populations as well as within and between Sakaramasu and Yamame forms were quantified by estimating the coefficient of gene differentiation, G*st* (9) and average genetic distance (10).

TABLE 1. *Collection Data on Cultured Stocks of Masu Salmon*

Population	River or hatchery (origin)	Data	Number of samples	Mean of Standard length	Form
Natural population				mm	
N1	Shiribetsu (Hokkaido)	1982. 8	35	157.2	Sakuramasu
N2	Shiribetsu (Hokkaido)	1982.10	30	166.0	Sakuramasu
N3	Shiribetsu (Hokkaido)	1983.10	47	97.0	Sakuramasu
N4	Shiribetsu (Hokkaido)	1984.11	55	89.2	Sakuramasu
N5	Sykotan (Hokkaido)	1982. 7	45	146.0	Sakuramasu
N6	Hidaka (Hokkaido)	1984. 8	50	200.6	Sakuramasu
N7	Oippe (Aomori)	1982.10	34	194.2	Sakuramasu
N8	Oippe (Aomori)	1983.10	30	68.8	Sakuramasu
N9	Towada (Aomori)	1984.11	59	73.4	Sakuramasu
N10	Hasama (Miyagi)	1982. 7	70	150.7	Sakuramasu
N11	Ani (Akita)	1985.10	62	99.9	Yamame
Cultured population					
C1	Yoshokuken (Koide)	1982.10	30	211.4	Sakuramasu
C2	Yoshokuken (Koide)	1982.10	30	193.7	Sakuramasu
C	Yoshokuken (Towada)	1982.10	30	180.0	Sakuramasu
C4	Yamagata (Mogami)	1985.10	32	104.8	Sakuramasu
C5	Aomori	1983.10	99	199.6	Yamame
C6	Iwate (Kantoh)	1984. 8	50	114.4	Yamame
C7	Akita (Iwate)	1985.10	53	98.3	Yamame
C8	Akita (Ishikawa)	1985.10	54	143.5	Yamame
C9	Miyagi (Fukushima)	1982. 7	47	167.0	Yamame
C10	Yamagata (Kantoh)	1985.10	32	126.8	Yamame

Results

Distribution of Electrophoretic Variants

Among 33 presumed genetic loci, a total of 12 loci were polymorphic, the phenotypic patterns of which are shown in Fig. 1. Phenotypic expressions of variable molecules and their allelic constitution are explained below.

AAT : ATT usually exhibited three bands in liver and two bands in muscle. The former could be interpreted as a soluble form (s-AAT) and the latter as a mitochondrial form (m-AAT). The s-AAT was expressed as homodimer of B1 and B2 subunits with one heterodimer between them, indicating a dimeric structure. Variations were observed in all of 21 populations, showing six bands in heterozygotes (*B2/B2'*) which result from the association of B2 with B2′ subunit and of B1 with B2 subunits. Thus, s-AAT is controlled by two separate loci, *Aat-B1* and *Aat-B2*, which are monomorphic and polymorphic, respectively. *Aat-B2* locus indicates three alleles. The m-AAT was also expressed as homodimers of A1 and A2 subunits with no heterodimer between them. A few

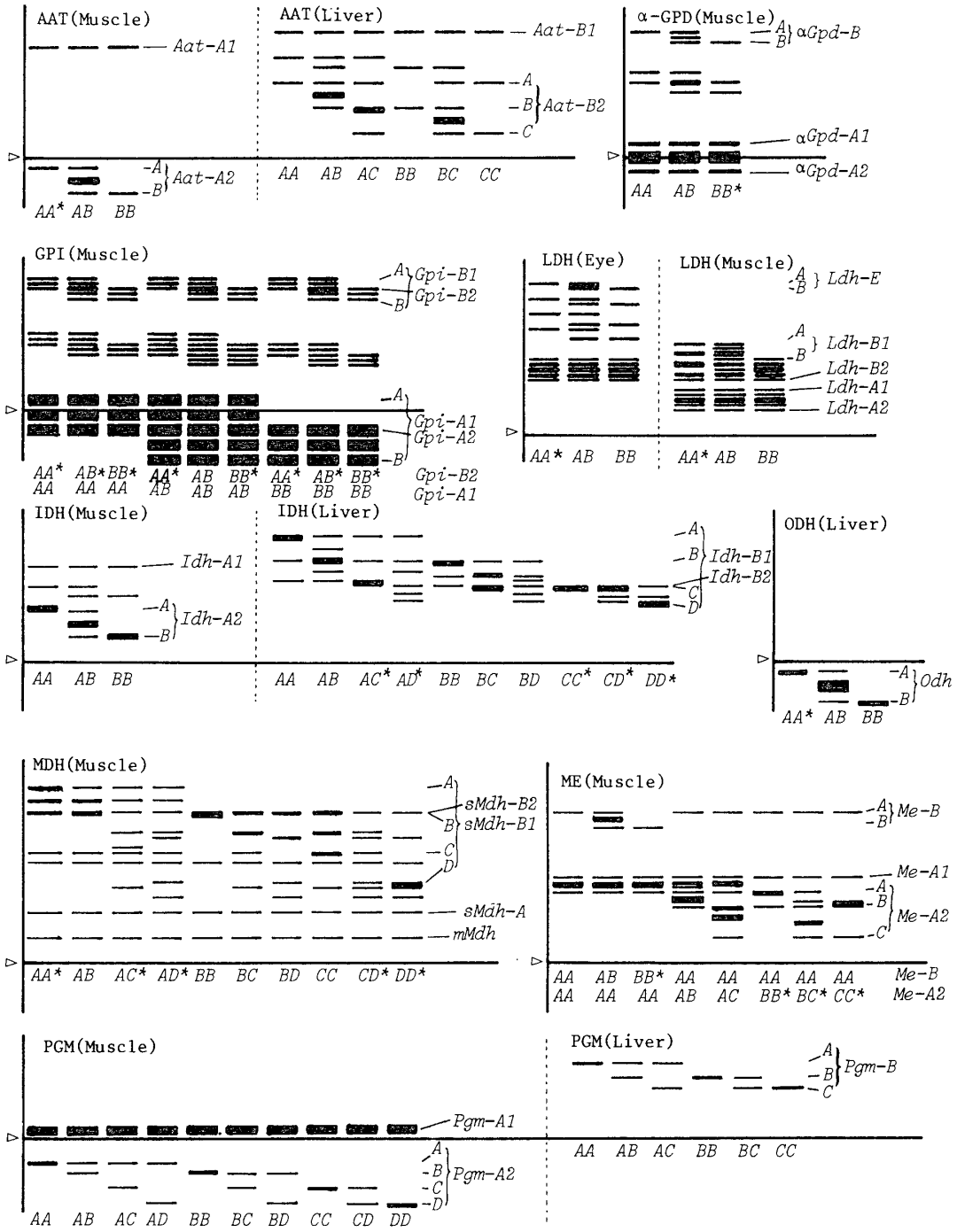

FIG. 1. Electrophretic pattersn of enzyme variations in masu salmon.
At each variable locus the locations of homomeric productions are designated by the allels that codes for it. Anode is above the origin that is shown by triangle. The genotype marked star was not observed, however the existance of genotype was estimated from other patterns and genotypes.

variants were observed in 2 of the 21 populations, which showed four bands in heterozygotes (*A2/A2'*), the homozygote (*A2'/A2'*) was not observed. Thus, m-AAT is characterized by two separate loci, *Aat-A1* and *Aat-A2*, the latter indicating two alleles.

α-GPD: α-GPD isozymes were shown to posses a dimeric structure and expressed as a six-banded phenotype in muscle. They consisted of three homdimers of A1, A2 and B subunits and of three heterodimers between them, indicating three loci, *αGpd-A1*, *αGpd-A2* and *αGpd-B*. A few variants were observed in one of the 21 populations and the phentypic pattern indicated two alleles at *αGpd-B*.

GPI: GPI showed a nine-banded phenotype in muscle. Three bands in the most anodal zone were interpreted as two homdimers of B1 and B2 suunits and one heterodimer between them. Likewise, three bands in the most cathodal zone were interpreted as two homodimers of A1 and A2 subunits with the heterodimers between them. Three bands in the middle zone are heterodimers of A1, A2, with B1 and B2 sununits. GPI is thus controlled by four subunits A1, A2, B1 and B2. In most fish, GPI is three banded, indicating a dimeric structure wiht separate gene loci *A* and *B*, coding for A and B subunits. This study reveals the duplication of the *A* and *B* loci. Variant patterns were observed in one of 21 populations where *Gpi-A1* and *Gpi-B1* loci were polymorphic while *Gpi-A2* and *Gpi-B2* loci were monomorphic.

IDH: IDH isozymes were shown to possess a dimeric structure which consist of a soluble form (s-IDH) in liver and a mitchondrial form (m-IDH) in muscle. The m-IDH was commonly expressed as three bands, including two loci, *Idh-A1* and *Idh-A2*. Variant patterns were observed in 3 of 21 populations where *Idh-A2* locus indicated two alleles. Likewise, the s-IDH showed a common three-banded phenotype, including two separate loci *Idh-B1* and *Idh-B2*. Variant patterns were observed in almost all 21 populations where *Idh-B1* locus indicated four alleles.

LDH: The pattern of musu salmon showed the typical multi-banded phenotype characteristic of a tetrameric structure. The fast migrating five bands were observed in heart while the slow migrating five bands seen in muscle. The separate gene loci, *A1* and *A2*, were discovered in five molecular forms in muscle while two separate gene loci, B1 and B2, were found in heart. In eye, B1, B2 and E subunits were expressed. Variations in Ldh-B1, Ldh-E loci were observed in one of 21 populations, respectively, while Ldh-A1, Ldh-A2 and Ldh-B2 loci were monomorphic.

MDH: MDH consists of soluble (s-MDH) and mitochondrial (m-MDH) forms. The common phenotype showed four bands which was presumed to be two homodimers of A and B subunits, one heterodimer between them and m-MDH. Variant patterns were observed in 15 of the 21 populations and revealed

gene duplication of the *sMdh-B* locus, with four alleles at *sMdh-B2*. *sMdh-B2*^{B} co-migrated with *sMdh-B1*. The m-MDH exhibited a single fixed hand migrating most slowly towards the anodal side.

ME : ME was examined in muscle and liver and activity was exhibited in two zones. In the most anodal zone, a single band was observed in liver and muscle (*Me-B*). In the most cathodal zone, three hands were observed in muscel (*Me-A*), including two loci, *Me-A1* and *Me-A2*. Variations indicating three alleles at *Me-A2* and two alleles at *Me-B* were observed at 10 and at 6 of the 21 populations, respectively. However, the variations were very low in frequency and some homozygotes were not observed.

ODH : ODH was examined in liver and activity was exhibited as a single band or locus in the cathodal zone. Variations indicating 2 alleles were observed in two of the 21 populations. The variations were very low in frequency and the homozygote of the secondary allele was not observed.

PGM : PGM was examined in muscle and liver, and activity was exhibited at two zones. In the first zone (PGM-A), two bands were observed in muscle of almost all individuals. One of the bands migrated slowly towards the anode and the other towards the cathode. The two bands could be interpreted as two loci, *Pgm-A1* and *Pgm-A2*. Variations indicating 4 alleles at *Pgm-A2* were observed in 20 of the 21 populations. In the faster zone (Pgm-B), one or two banded phenotypes were observed in liver in all populations. The phenotypes indicated polymorphism at three alleles.

6-PGD and SOD : 6-PGD and SOD showed a fixed single band in muscle and liver of all individuals, respectively.

Assuming a duplicate gene loci in *αGpd-A*, *Ldh-E*, *sMdh-A*, *mMdh*, *Me-B*, *Odh*, *6Pgd*, *Pgm-B*, and *Sod*, the proportion of duplicated genes is 57.1% in masu salmon. Most of the variant alleles at the *αGpd-A*, *Gpi-A1*, *Gpi-B1*, *Idh-A1*, *Ldh-B1*, *Ldh-E*, *Me-B* and *Odh* loci do not occur universally in the species, while those of *Aat-B2*, *Idh-B1*, *sMdh-B1*, *Pgm-A2* and *Pgm-B* loci occur universally although the allelic frequencies fluctuate among populations (Tables 2 and 3).

Genetic Differentiation and Variability within and between Natural and Cultured Populations

The degree of genetic differentiation among populations of the masu salmon measured by Gst and D is presented in Table 4. Gst measures the proportion of gene diversity between populations to gene diversity in the total population. The genetic distance (D) can be regarded as the estimate of net codon differences between populations (10). The table showed that no genetic differentiation between Sakuramasu and Yamame cound be found, although the genetic constitution of populations was not unifom. The overall mean of D, 0.012, equal to that within Sakuramasu and Yamame, respectively. Thus, the magnitude of genetic

TABLE 2. *Allele Frequencies of 11 Natural Populations of Masu Salmon at 14 Loci with Observed Variation*

Locus	Allele	N1	N2	N3	N4	N5	N6	N7	N8	N9	N10	N11
Aat-A2	*A*	0	0	0.130	0	0	0	0	0	0	0	0
	B	1.000	1.000	0.870	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Aat-B2	*A*	0.414	0.333	0.375	0.217	0.389	0.390	0.267	0.367	0.595	0.211	0.333
	B	0.371	0.350	0.325	0.585	0.478	0.610	0.333	0.633	0.310	0.578	0.625
	C	0.215	0.317	0.300	0.198	0.133	0	0.400	0	0.095	0.211	0.042
Gpi-A1	*A*	0	0	0	0	0	0	0.150	0	0	0	0
	B	1.000	1.000	1.000	1.000	1.000	1.000	0.850	1.000	1.000	1.000	1.000
Gpi-B1	*A*	1.000	1.000	1.000	1.000	1.000	1.000	0.950	1.000	1.000	1.000	1.000
	B	0	0	0	0	0	0	0.050	0	0	0	0
Idh-A2	*A*	1.000	1.000	1.000	1.000	1.000	1.000	0.883	1.000	1.000	1.000	1.000
	B	0	0	0	0	0	0	0.117	0	0	0	0
Idh-B1	*A*	0.172	0.138	0.108	0.043	0.200	0.135	0	0.031	0.063	0	0.050
	B	0.813	0.862	0.892	0.870	0.767	0.823	0.967	0.922	0.830	1.000	0.830
	C	0.015	0	0	0.065	0.033	0.042	0.033	0.047	0.107	0	0.120
	D	0	0	0	0.022	0	0	0	0	0	0	0
Ldh-B1	*A*	0	0	0	0	0	0	0	0	0.025	0	0
	B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.975	1.000	1.000
Ldh-E	*A*	0	0	0	0.073	0	0	0	0	0	0	0
	B	1.000	1.000	1.000	0.927		1.000	1.000	1.000	1.000	1.000	1.000
sMdh-B1	*A*	0	0	0	0	0	0	0	0	0.008	0	0
	B	0.928	0.966	0.947	0.962	0.822	0.623	1.000	0.967	0.975	0.545	0.783
	C	0.072	0.034	0.053	0.038	0.178	0.367	0	0.033	0.017	0.455	0.217
	D	0	0	0	0	0	0.010	0	0	0	0	0
Me-A2	*A*	1.000	1.000	0.947	1.000	0.967	0.960	1.000	0.967	1.000	1.000	0.867
	B	0	0	0.053	0	0.033	0.040	0	0.033	0	0	0.083
	C	0	0	0	0	0	0	0	0	0	0	0.050
Me-B	*A*	1.000	1.000	1.000	0.991	0.878	0.930	1.000	1.000	1.000	1.000	0.992
	B	0	0	0	0.009	0.122	0.070	0	0	0	0	0.008
Odh	*A*	0	0	0	0	0	0	0	0	0.051	0	0.067
	B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.949	1.000	0.933
Pgm-A2	*A*	0.629	0.650	1.660	0.664	0.600	0.530	0.650	0.767	0.992	0.745	0.603
	B	0.071	0.167	0.138	0.100	0.056	0	0.133	0.133	0	0	0
	C	0.200	0.150	0.202	0.236	0.344	0.470	0.217	0.100	0.008	0.245	0.397
	D	0.100	0.033	0	0	0	0	0	0	0	0.010	0
Pgm-B	*A*	0.429	0.217	0.119	0.188	0.167	0.531	0.233	0.019	0.110	0.282	0.189
	B	0.014	0.017	0.013	0	0.011	0	0	0	0	0	0
	C	0.557	0.766	0.868	0.812	0.822	0.469	0.767	0.981	0.890	0.718	0.811

Aat-A1, *Aat-B1*, *αGpd-A1*, *αGpd-A2*, *αGpd-B*, *Gpi-A2*, *Gpi-B2*, *Idh-A1*, *Idh-B2*, *Ldh-A1*, *Ldh-A2*, *Ldh-B2*, *sMdh-A*, *sMdh-B2*, *mMdh*, *Me-A1*, *6Pgd*, *Pgm-A1*, *Sod* are monomorphic.

differentiation of the Sakuramasu form is considered to be equal to that of the Yamame form. It can also be said that there are no differences, genetically, between Sakuramasu and Yamame.

The estimate of Gst in the cultured populations is about 3 times larger than that in the natural populations reflecting a higher a higher magnitude of genetic differentiation in cultured compared to the natural populations.

TABLE 3. *Allele Frequemcies of 10 Cultured Populations of Masu Salmon at 10 Loci with Observed Variation*

Loci	Allele	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10
Aat-A2	*A*	0	0	0.150	0	0	0	0	0	0	0
	B	1.000	1.000	0.850	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Aat-B2	*A*	0.968	0.983	0.900	0.063	0.344	0.122	0.396	0.202	0.096	0.094
	B	0.032	0.017	0.050	0.937	0.423	0.827	0.557	0.769	0.638	0.891
	C	0	0	0.050	0	0.233	0.051	0.047	0.029	0.266	0.015
αGpd-B	*A*	0	0.033	0	0	0	0	0	0	0	0
	B	1.000	0.967	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Idh-A2	*A*	1.000	1.000	1.000	1.000	0.825	1.000	1.000	0.991	1.000	1.000
	B	0	0	0	0	0.175	0	0	0.009	0	0
Idh-B1	*A*	0.483	0.433	0.100	0	0.750	0	0	0	0.138	0.016
	B	0.517	0.567	0.900	0.804	0.215	1.000	0.981	0.963	0.755	0.984
	C	0	0	0	0.196	0.035	0	0.019	0.037	0.107	0
	D	0	0	0	0	0	0	0	0	0	0
sMdh-B1	*A*	0	0	0	0	0	0	0	0	0	0
	B	0.936	0.884	1.000	0.828	1.000	1.000	1.000	0.907	0.789	1.000
	C	0.064	0.116	0	0.172	0	0	0	0.093	0.211	0
	D	0	0	0	0	0	0	0	0	0	0
Me-A2	*A*	0.871	0.900	0.800	0.875	0.975	1.000	1.000	1.000	1.000	1.000
	B	0.129	0.100	0.200	0.125	0.025	0	0	0	0	0
	C	0	0	0	0	0	0	0	0	0	0
Me-B	*A*	1.000	1.000	1.000	1.000	0.981	1.000	1.000	1.000	0.911	1.000
	B	0	0	0	0	0.019	0	0	0	0.089	0
Pgm-A2	*A*	0.661	0.717	1.000	0.516	0.750	0.850	0.754	0.686	0.711	0.641
	B	0.081	0.150	0	0.313	0.094	0	0.189	0.200	0	0.313
	C	0.258	0.133	0	0.161	0.156	0.150	0.057	0.114	0.289	0.046
	D	0	0	0	0	0	0	0	0	0	0
Pgm-B	*A*	0.387	0.397	0.100	0.188	0.373	0.330	0.387	0.259	0.213	0.078
	B	0	0	0	0	0.149	0	0	0	0.011	0
	C	0.613	0.603	0.900	0.812	0.478	0.670	0.613	0.731	0.776	0.992

Aat-A1, *Aat-B1*, *αGpd-A1*, *αGpd-A2*, *Gpi-A1*, *Gpi-A2*, *Gpi-B1*, *Gpi-B2*, *Idh-A1*, *Idh-B2*, *Ldh-A1*, *Ldh-A2*, *Ldh-B1*, *Ldh-B2*, *Ldh-E*, *sMdh-A*, *sMdh-B2*, *mMdh*, *Me-A1*, *Odh*, *6Pgd*, *Pgm-A1*, *Sod* are monomorphic.

Table 5 shows the estimates for the proportion of polymorphic loci (P) ranging from 0.091-0.182, average heterozygosity (H) ranging 0.026-0.074, and number of alleles per locus ranging for 1.18 to 1.36. The amount of genetic variability within cultured population is smaller than within natural populations. A decrease in the number of alleles per locus was remarkable in the cultured populations. Furthermore, allelic frequencies at *Aat-B2* and *Idh-B1* loci fluctuated more significantly in cultured than in natural populations as shown in Fig. 2.

Discussion

The present work estimated the proportion of the duplicated gene loci in

TABLE 4. *Gene Diversity and Gene Differentation among Natural and Cultured Populations of Masu Salmon*

	No. of populations	HT	Hs	GST	Mean of D
Within Sakuramasu	14	0.064	0.057	0.109	0.012±0.001
Within Yamame	7	0.063	0.051	0.190	0.009±0.001
Between Sakuramasu and Yamame					0.012±0.001
Within natural populario n	11	0.064	0.059	0.078	0.006±0.000
Within cultured population	10	0.064	0.049	0.238	0.017±0.002
Between natural and cultured population					0.012±0.001
Overall mean	21	0.065	0.054	0.169	0.012±0.001

masu salmon to be 57%. Salmonid fish have been demonstrated to be in a diploid-tetraploid relationship and postulated to have decended from a tetraploid ancestor (11, 12, 13, 14). The behavior of our isozyme systems confirm the hypothesis that the masu salmon is a tetraploid species in the process of diploidization just like chum salmon (13). However, the proportion of the duplicated gene in masu salmon is lower than in chum salmon (80%).

Assuming that genetic change was stable throughout the process of population subdivision, the genetic distance obtained between Sakuramasu and Yamame could be regarded as a measure of lack of genetic differentiation between them. However, the genetic constitution of the populations was not uniform. Thus, without distinction between Sakuramasu and Yamame, these could just be treated as masu salmon. The mean of the H estimates obtained for the present natural populations was equal to that obtained for the 6 river populations of the masu salmon (0.056) (7) but lower than that obtained for the 37 river populations of the chum salmon (0.097) (15).

The quantity of genetic differentiation, G*st*, for the natural populations is either equal or higher than those obtained for the natural populations of other salmonid species (Table 6), while that for the cultured populations is higher. The divergence of cultured populations is assumed to be promoted by founder and/or bottleneck effects which occurred in the ancestral line of several hatcheries. Such circumstances are considered responsible for a decrease in the number of alleles par locus and for lower heterozygosity in the cultured populations.

Higher genetic differentiation for natural river populations of the masu salmon compared to chum salmon can be a consecuence of the lack or very small degree of transplantation which activity might have occurred in higher frequency in different river populations of chum salmon.

Since the knowledge of the available genetic resources are not-well-documented, an extensive survey of natural populations is expected to provide

TABLE 5. *Genetic Variability within Natural and Cultured Populations of Masu Salmon*

Population	Proportion of polymorphic loci (P)	Average heterozygosity (H)	Number of alleles per locus
Natural population			
N1	0.152	0.065	1.303
N2	0.121	0.056	1.273
N3	0.212	0.061	1.303
N4	0.182	0.057	1.364
N5	0.182	0.072	1.333
N6	0.182	0.074	1.273
N7	0.182	0.065	1.273
N8	0.091	0.035	1.242
N9	0.121	0.038	1.303
N10	0.152	0.056	1.182
N11	0.213	0.070	1.333
Mean	0.163	0.059	1.289
Cultured population			
C1	0.152	0.057	1.212
C2	0.152	0.058	1.242
C3	0.152	0.034	1.182
C4	0.182	0.056	1.212
C5	0.152	0.074	1.333
C6	0.091	0.030	1.212
C7	0.091	0.043	1.182
C8	0.121	0.045	1.242
C9	0.182	0.066	1.273
C10	0.091	0.026	1.182
Mean	0.137	0.049	1.227
Overall mean	0.150	0.054	1.260

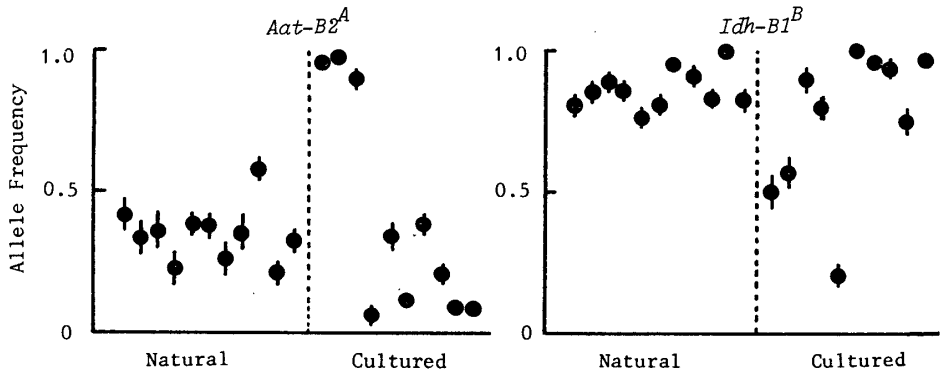

FIG. 2. Fluctuation of allele frequencies at *Aat-B2* and *Idh-B1* loci in Cultured population. Solid line indicates the standard error.

TABLE 6. *Summary of the Levels of Genetic Diversity in Salmonid Fishes*

Spesies	Number of populations	Number of loci	HT	Hs	GST	Reference
Cultured population						
Oncorhynchus masou	9	33	0.064	0.049	0.238	The present study
Natural population						
Oncorhynchus masou	12	33	0.064	0.059	0.078	The present study
	6	31	0.061	0.056	0.082	Okazaki (7)
Oncorhynchus nerka	18	26	0.046	0.044	0.043	Grant *et al.* (16)
	7	24	0.028	0.026	0.071	Wilmot and Burger (2)
Oncorhynchus gorbuscha	25	12	0.099	0.095	0.040	Beacham *et al.* (5)
Oncorhynchus keta	37	16	0.100	0.097	0.030	Kijima (6)
	28	10	0.156	0.153	0.019	Beacham *et al.* (3)

useful information on the genetic structure including homing and will determine in detail the genetic changes that may possibly occur with domestication.

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References

1) Ryman, N., *Aquaculture*, **33**, 1 (1983)
2) Wilmot, L.R., and Burgar, C.V., *Tras. Am. Fish. Soc.*, **114**, 236 (1985)
3) Beachm, T.D., Withler, R.E., and Gould, A.P., *Can. J. Fish. Aquat. Sci.*, **42**, 437 (1985)
4) Ryman, N., and Ståhl, G., *Can. J. Fish. Aquat. Sci.*, **38**, 1562 (1981)
5) Beacham, T.D., Withler, R.E. and Gould, A.P., *Can. J. Fish. Aquat. Sci.*, **42**, 147 (1985)
6) Kijima, A., *Doctor thesis*, Tohoku Univ. (1980) (in Japanese)
7) Okazaki, T., *Marine Ranching Program. Progress Report on Masu Salmon Production*, **3**, 131 (1983) (in Japanese)
8) Fujio, Y., "*Study on Genetics Characteristics of Fish and Shell-Fishes in Isozymic Analysis.*" Tohoku univ. (1984) (in Japanese)
9) Nei, M., *Proc. Nat. Acad. Sci. USA.*, **70**, 3321 (1975)
10) Nei, M., *Amer. Naturalists.*, **106**, 283 (1972)
11) Ohno, S., "*Evolution by Gene Duplication*" Springer-Verlag, New York (1970)
12) Allendorf, F.W., Utter, F.M., and May, B.P., "*Isozyme IV Genetics And Evolution*" ed. by C.L. Market, Academic Press, New York, p. 415 (1975)
13) Fujio, Y., and Imura, T., *Fish. Genet. and Breed. Sci.*, **4**, 13 (1979) (in Japanese)
14) Kijima, A., and Fujio, Y., *Tohoku. J. Agr. Res.*, **31**, 159 (1980)
15) Kijima, A., and Fujio, Y., *Bull. Japan. Soc. Sci. Fish.*, **45**, 287 (1979)

16) Grant, W.S., Milner, G.B., Kranowski, P., and Utter, F.M., *Can. J. Fish. Sci.*, **8**, 1236 (1980)