Genetic Differentiation in Cultured Populations of Rainbow Trout (Salmo garirdneri) in Japan

Genetic Differentiation in Cultured Populations of Rainbow Trout (*Salmo garirdneri*)in Japan

Masamichi Nakajima and Yoshihisa Fujio

Department of Fishery Science, Faculty of Agriculture,
Tohoku University, Sendai 980, Japan

Summary

The amount of genetic variability and the degree of genetic differentiation in cultured stocks of rainbow trout (*Salmo gairdneri*) in Japan were examined by starch gel electrophoresis. Twenty-eight loci were analysed for 32 cultured stocks and 2 feral stocks. The proportion of polymorphic loci (P) varied from 0 to 0.214 with mean of 0.117. Heterozygosity (H) over 28 loci varied from 0 to 0.070 with a mean of 0.042. The mean genetic distance (D) which measured genetic differentiation was 0.0170.

We classified 34 stocks into four groups, Donaldson's, Selected, Native and Feral on the basis of breeding levels. Donaldson's group showed low genetic variability (H=0.029) and high genetic differentiation (D=0.0428). On the other hand, Feral group showed high geneticc variability (H=0.054) and low genetic differentiation (D=0.0030). Selected group was close to Donaldson's group and Native group to Fereal group. This phenomenon can be explained by genetic drift.

Rainbow trout (*Salmo gairdneri*) is one of the commonest species in Japanese freshwater culture fisheries. Rainbow trout has been repeatedly introduced from North America to Japan since 1877 and now cultured everywhere in Japan. Although the trout has been rleased to many rivers and lakes in Japan, examples of its going wild are few and they are called as Feral. Due to ease of artificial fertilization and its wide temperature ranges, many hatchery populations in culture have been developed. During their long maintenance, each population might have been consciously or unconsciously selected for morphological, physiological, or behavioral characters. For example, albino and non-spoted rainbow trouts have been selected from cultured stocks and new populations had been created. The famous Donaldson's strain was introduced to Japan in 1954 and 1966, and the strain has been extended to several hatcheries.

The isozyme markers are powerful tools for identifying the natural populations of rainbow trout (1, 2, 3). We used the isozyme markers to estimate the

amount of genetic variability and the degree of genetic differentiation in cultured populations of rainbow trout in Japan.

The purpose of the present work is to demonstrate the change of genetic variability and differentiation with breeding levels.

Materials and Methods

32 different cultured stocks of rainbow trout (*Salmo gairdneri*) were collected from several hatcheries and 2 feral stocks from a river and a lake from 1980 to 1987. The collection data are given in Table 1. We classified 34 stocks into four groups, Donaldson's, Selected, Native and Feral, on the basis of breeding levels. Donaldson's strain was introduced to Japan in 1954 and 1966, and the strain has been extended to several hatcheries. Selected group contains the population which had been selected for morphological, physiological and behavioral characters. Native group contains the populations which have been maintained by mass production in each hatchery. Feral group contains a few populations that have gone wild.

The isozyme markers for 12 enzymes were detected by horizontal starch gel electrophoresis. Electrophoresis and staining procedures were based on Fujio (4). Each locus is given by an italicized three-letter symbol for the enzyme and is numbered consecutively from the anodal side ; multiple alleles are designated by italicized alphabet from the anodal side. Polymorphic locus was defined as the locus at which the frequency of the most common allele was less than 0.950. The heterozygosity (H) is defined the average of h overall loci, wherein $h = 1 - \sum Xi^2$, where Xi denotes the frequency of i-th allele at the X locus.

Results and Discussion

Results of electrophoretic analysis for 32 cultured stocks and 2 feral stocks of rainbow trout demonstrated the presumed 34 loci. Of the 34 loci, polymorphism was observed in at least 10 loci, namely *Adh-2*, *αGpd-2*, *Idh-1, 2*, *Idh-3*, *Ldh-1*, *Ldh-3*, *Mdh-1, 2*, *Mdh-4*, *Pgm-2* and *Sod*. Since the phenotypic variation at *Idh-1, 2* and *Mdh-1, 2* could not be attributed to two specific loci, that were tentatively treated as tetrasomic loci. The remaining loci were monomorphic. Phenotypic patterns at these loci had been already reported by several investigators (1, 2, 3, 5, 6). The allelic frequencies at the 32 loci are given in Tables 2 and 3.

Although the *Idh-1, 2* and *Mdh-1, 2* loci are reported to be controlled by two disomic loci (7), we could not assign the two loci separately. However, we found that the phenotypic variation in some of the populations deviated from the expected values calculated by a tetrasomic model (Table 4). Specially, almost all individuals in the D-1 population were of the AAA'A' phenotype, indicating that the normal and variant alleles were at either *Mdh-1* or *Mdh-2*, respectively. If

TABLE 1. *Collection Data on Cultured and Feral Stocks of Rainbow Trout*

Hatchery Location	Strain (Origin)	Data		Number of Individuals	Standard Length Mean±SE (mm)
Danaldson's Group					
D- 1 Nikko	Donaldson	Aug.	1982	30	273.333±2.231
D- 2 Aomori	Donaldson	Oct.	1983	100	188.846±1.580
D- 3 Iwate	Donaldson	Aug.	1984	15	318.000±5.903
D- 4 Hokkaido	Donaldson	Sep.	1986	53	108.755±1.111
D- 5 Shizuoka	Donaldson	Mar.	1987	50	211.860±2.312
D- 6 Miyazaki	Donaldson	May.	1987	55	85.655±1.016
Selected Group					
S- 1 Nikko	Albino	Aug.	1982	27	229.926±4.933
S- 2 Aichi	Non-spoted	Oct.	1983	30	160.133±1.369
S- 3 Akita	Non-spoted	Oct.	1985	52	73.885±1.264
S. 4 Nagano	IHN resistant	Oct.	1986	54	241.870±1.707
S- 5 Saitama	IPN resistant	Dec.	1986	50	177.060±2.685
S- 6 Yoshida	IPN sensitive	Dec.	1986	49	194.327±1.505
S- 7 Saitama	IPN sensitive	Dec.	1986	51	170.314±1.055
Native Group					
N- 1 Fukushima	Inawashiro	Apr.	1980	16	162.237±4.689
N- 2 Nikko	Kumagaya	Aug.	1982	30	240.833±3.269
N- 3 Nikko	Nikko	Aug.	1982	30	236.167±2.707
N- 4 Miyagi	Miyagi	Jul.	1982	75	125.907±2.466
N- 5 Miyagi	Togatta	Jul.	1982	31	181.548±1.886
N- 6 Aichi	Aichi	Jud.	1983	30	190.867±2.403
N- 7 Aomori	Aomori	Oct.	1983	58	157.690±1.155
N- 8 Aomori	Aomori	Nov.	1984	63	127.683±1.684
N- 9 Iwate	Nagano	Aug.	1984	50	105.380±1.612
N-10 Miyagi	Miyagi	Aug.	1985	43	241.442±3.641
N-11 Yamagata	Yamagata	Oct.	1985	33	126.545±1.496
N-12 Aomori	Nagano	Oct.	1985	50	167.980±0.684
N-13 Nagano	Nagano	Jun.	1985	56	225.804±2.473
N-14 Akita	Akita	Oct.	1985	83	54.463±0.712
N-15 Nagano	Nagano	Oct.	1986	60	109.050±1.710
N-16 Miyagi	Miyagi	Aug.	1986	80	40.813±0.416
N-17 Hokkaido	Hokkaido	Oct.	1986	53	106.736±1.391
N-18 Aomori	Yamanashi	Jun.	1986	101	100.584±1.211
N-19 Miyazaki	Miyazaki	May.	1987	54	79.481±0.791
Feral Group					
F- 1 Akita	Akita(Oga)	Oct.	1985	14	101.571±9.122
F- 2 Aomori	Aomori(Iwasaki)	Oct.	1986	50	185.640±1.504

M. Nakajima and Y. Fujio

TABLE 2. *Allele Frequencies for*

Locus	Allele	D-1	D-2	D-3	D-4	D-5	D-6
Aat-1		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	30	15	53	50	55
Aat-2		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	30	15	53	50	55
Acp-1		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	30	15	53	50	55
Acp-2		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	30	15	53	50	55
Acp-3		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	30	15	53	50	55
Adh-1		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	30	15	53	50	55
Adh-2	A	0	0	0	0	0	0
	B	1.000	1.000	1.000	1.000	1.000	1.000
	N	30	30	15	53	50	55
Ak-1		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	30	15	53	50	55
Ak-2		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	30	15	53	50	55
αGpd-1		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	100	15	53	50	55
αGpd-2	A	0	0	0	0.557	0	0.100
	B	1.000	1.000	1.000	0.443	1.000	0.900
	N	30	100	15	53	50	55
αGpd-3		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	100	15	53	50	55
Idh-1, 2	A	N.T.	0	0.117	0.001	0	0
	B		0.822	0.666	0.797	0.679	0.814
	C		0.178	0.217	0.029	0.174	0.018
	D		0	0	0.173	0.147	0.159
	E		0	0	0	0	0.009
	N		94	15	52	50	55
Idh-3	A	0	0	0	0.991	0.420	0.491
	B	1.000	1.000	1.000	0.009	0.580	0.509
	N	30	100	15	52	50	55
Idh-4		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	100	15	53	50	55
Ldh-1	A	0	0.265	0.033	0	1.000	0.718
	B	1.000	0.735	0.967	1.000	0	0.282
	N	30	100	15	53	50	55
Ldh-2		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	100	15	53	50	55
Ldh-3	A	0	0	0	0	0	0.155
	B	1.000	1.000	1.000	1.000	1.000	0.845
	N	30	100	15	53	50	55

Donaldson's, Selected and Feral Groups

S-1	S-2	S-3	S-4	S-5	S-6	S-7	F-1	F-2
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000.	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
0	0	0	0	0	0	0	0.107	0
1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.893	1.000
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
0	0	0	0	0.110	0	0	0.179	0.030
1.000	1.000	1.000	1.000	0.890	1.000	1.000	0.821	0.970
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
N.T.	N.T.	0	0.014	0	0	0	0.018	0.012
		0.772	0.769	0.945	1.000	0.955	0.964	0.744
		0.079	0.014	0.055	0	0.005	0.018	0.024
		0.149	0.203	0	0	0.040	0	0.220
		0	0	0	0	0	0	0
		52	54	50	49	51	14	41
1.000	0.317	0.308	0.425	0.790	0.714	0.755	0.536	0.688
0	0.683	0.692	0.575	0.210	0.286	0.245	0.464	0.312
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
0.981	0.800	0.808	0.648	0.940	0.959	0.971	1.000	0.936
0.019	0.200	0.192	0.352	0.060	0.041	0.029	0	0.064
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
0	0	0	0	0	0	0	0	0
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50

TABLE 2.

Locus	Allele	D-1	D-2	D-3	D-4	D-5	D-6
Ldh-4		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	100	15	53	50	55
Ldh-5		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	100	15	53	50	55
Mdh-1, 2	A	0.492	0.493	0.633	0.952	0.595	0.913
	B	0	0	0	0.024	0.285	0.073
	C	0.508	0.507	0.367	0.024	0.120	0.014
	N	30	100	15	53	50	55
Mdh-3		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	100	15	53	50	55
Mdh-4	A	0	0	0	0	0	0
	B	1.000	1.000	1.000	1.000	1.000	1.000
	C	0	0	0	0	0	0
	N	30	100	15	53	50	55
Me-1		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	100	15	53	50	55
Me-2		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	30	15	53	50	55
Me-3		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	30	15	53	50	55
Me-4		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	30	15	53	50	55
6-Pgd		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	30	15	53	50	55
Pgm-1		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	100	15	53	50	55
Pgm-2	A	1.000	1.000	1.000	0.269	0.980	0.909
	B	0	0	0	0.731	0.020	0.091
	N	30	100	15	53	50	55
Pgm-3		1.000	1.000	1.000	1.000	1.000	1.000
	N	30	100	15	53	50	55
Sod	A	0	0.517	0	0.349	0	0.655
	B	1.000	0.483	1.000	0.651	1.000	0.345
	C	0	0	0	0	0	0
	N	30	100	15	53	50	55
	P	0	0.071	0	0.107	0.036	0.214
	H	0	0.032	0.002	0.054	0.019	0.070
	A	1.000	1.071	1.036	1.143	1.071	1.214

N : Number of individuals   N.T. : Not tested
A : Number of alleles per locus

continued

S-1	S-2	S-3	S-4	S-5	S-6	S-7	F-1	F-2
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000	0.742	0.899	0.907	0.950	1.000	0.936	1.000	0.898
0	0	0.063	0.042	0.045	0	0	0	0.066
0	0.258	0.038	0.051	0.005	0	0.064	0	0.036
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
0	0	0	0	0	0	0	0	0
1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.893	1.000
0	0	0	0	0	0	0	0.107	0
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
0.907	0.800	0.942	0.815	0.730	0.724	1.000	0.857	0.745
0.093	0.200	0.058	0.185	0.270	0.276	0	0.143	0.255
27	30	52	54	50	49	51	14	50
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
27	30	52	54	50	49	51	14	50
0.630	0.232	0.106	0.491	0.360	0.286	0.010	0.321	0.230
0.370	0.768	0.894	0.509	0.640	0.714	0.990	0.679	0.770
0	0	0	0	0	0	0	0	0
27	30	52	54	50	49	51	14	50
0.071	0.143	0.143	0.143	0.179	0.107	0.036	0.179	0.143
0.024	0.050	0.037	0.062	0.053	0.046	0.016	0.059	0.048
1.107	1.143	1.143	1.143	1.179	1.143	1.107	1.179	1.179

H : Heterozygosity   P : Proportion of polymorphic loci

TABLE 3. Allele frequencies

Locus	Allele	N-1	N-2	N-3	N-4	N-5	N-6	N-7	N-8
Aat-1		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	75	31	30	58	63
Aat-2		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	75	31	30	58	63
Acp-1		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	75	31	30	58	63
Acp-2		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	75	31	30	58	63
Acp-3		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	75	31	30	58	63
Adh-1		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	75	31	30	58	63
Adh-2	A	0	0	0	0	0	0	0	0
	B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	75	31	30	58	63
Ak-1		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	75	31	30	58	63
Ak-2		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	75	31	30	58	63
αGpd-1		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	75	31	30	58	63
αGpd-2	A	0	0	0	0	0.100	0	0	0.079
	B	1.000	1.000	1.000	1.000	0.900	1.000	1.000	0.921
	N	16	30	30	75	31	30	58	63
αGpd-3		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	75	31	30	58	63
Idh-1,2	A	N.T.	N.T.	0.054	N.T.	N.T.	N.T.	N.T.	0
	B			0.795					0.822
	C			0.009					0.178
	D			0.153					0
	E			0					0
	N			28					59
Idh-3	A	0.625	0.426	0.267	0.660	0.450	0.317	0.383	0.452
	B	0.375	0.574	0.733	0.340	0.550	0.683	0.617	0.548
	N	16	30	30	75	31	30	58	63
Idh-4		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	75	31	30	58	63
Ldh-1	A	1.000	1.000	1.000	0.840	1.000	0.817	1.000	0.960
	B	0	0	0	0.160	0	0.183	0	0.040
	N	16	30	30	75	31	30	58	63
Ldh-2		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	75	31	30	58	63
Ldh-3	A	0	0	0	0	0	0	0	0
	B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	30	65	31	30	58	63

for Native Groups.

N-9	N-10	N-11	N-12	N-13	N-14	N-15	N-16	N-17	N-18	N-19
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
0	0	0	0	0	0	0	0	0	0	0
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
30	43	33	50	56	83	60	80	53	101	54
0.048	0	0	0.080	0.036	0	0	0.006	0.057	0.139	0.011
0.952	1.000	1.000	0.920	0.964	1.000	1.000	0.994	0.943	0.862	0.989
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
N.T.	0	0	0	0.005	0	0.022	0	0.011	0	0
	0.720	0.867	0.915	0.830	0.730	0.767	0.848	0.898	0.781	0.832
	0.262	0.133	0.085	0.005	0.020	0	0.004	0.011	0.013	0.168
	0.017	0	0	0.160	0.250	0.211	0.148	0.080	0.206	0
	0	0	0	0	0	0	0	0	0	0
	42	32	50	56	83	60	80	53	101	54
0.786	0.660	0.167	0.459	0.634	0.521	0.183	0.545	0.519	0.559	0.784
0.214	0.340	0.833	0.541	0.366	0.479	0.817	0.455	0.481	0.441	0.216
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
0.929	0.840	0.652	0.880	0.687	0.780	0.942	0.930	1.000	0.990	0.861
0.071	0.160	0.348	0.120	0.313	0.220	0.058	0.070	0	0.010	0.139
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
0	0	0	0	0	0	0.025	0.056	0.009	0.134	0.046
1.000	1.000	1.000	1.000	1.000	1.000	0.975	0.944	0.991	0.866	0.954
50	43	33	50	56	83	60	80	53	101	54

M. Nakajima and Y. Fujio

TABLE 3.

Locus	Allele	N-1	N-2	N-3	N-4	N-5	N-6	N-7	N-8
Ldh-4		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	75	31	30	30	58	63
Ldh-5		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	75	31	30	30	58	63
Mdh-1,2	A	0.906	0.992	0.927	0.983	0.792	0.850	0.958	0.730
	B	0	0	0	0	0	0	0	0.008
	C	0.094	0.008	0.073	0.017	0.208	0.150	0.042	0.262
	N	16	30	75	31	30	30	58	63
Mdh-3		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	75	31	30	30	58	63
Mdh-4	A	0	0	0.027	0	0	0	0	0
	B	1.000	1.000	0.973	1.000	1.000	1.000	1.000	0.992
	C	0	0	0	0	0	0	0	0.008
	N	16	30	30	31	30	30	58	63
Me-1		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	75	31	30	30	58	63
Me-2		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	75	31	30	30	58	63
Me-3		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	75	31	30	30	58	63
Me-4		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	75	31	30	30	58	63
6-Pgd		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	75	31	30	30	58	63
Pgm-1		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	75	31	30	30	58	63
Pgm-2	A	1.000	1.000	1.000	1.000	1.000	0.933	0.550	0.857
	B	0	0	0	0	0	0.067	0.450	0.143
	N	16	30	75	31	30	30	58	63
Pgm-3		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	N	16	30	75	31	30	30	58	63
Sod	A	0	0.517	0.236	0.258	0.379	0.433	0.150	0.063
	B	1.000	0.483	0.764	0.742	0.621	0.567	0.850	0.937
	C	0	0	0	0	0	0	0	0
	N	16	30	75	31	30	30	58	63
	P	0.036	0.071	0.071	0.107	0.107	0.143	0.107	0.143
	H	0.013	0.034	0.032	0.038	0.031	0.051	0.043	0.036
	A	1.036	1.071	1.071	1.107	1.071	1.143	1.107	1.179

N : Number of individuals N.T. : Not tested H : Heterozygosity
P : Proportion of polymorphic loci A : Number of alleles per lobus

heterozygosity at the *Mdh-1, 2* was calculated by $h = 1 - \sum X i^4$, a danger of overestimating the heterozygosity exists. Therefore, we omitted the obtained results in muscle-MDH and Liver-IDH for the calculation of genetic variability

continued

N-9	N-10	N-11	N-12	N-13	N-14	N-15	N-16	N-17	N-18	N-19
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
0.839	0.927	0.894	0.920	0.942	0.949	0.913	0.931	0.901	0.963	0.716
0.137	0	0	0.040	0.022	0.024	0.025	0.016	0.014	0.035	0.157
0.024	0.073	0.106	0.040	0.036	0.027	0.062	0.053	0.085	0.002	0.127
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
0	0	0.182	0	0	0	0	0	0	0	0
1.000	1.000	0.818	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
0	0	0	0	0	0	0	0	0	0	0
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
0.655	1.000	1.000	0.740	0.714	0.728	0.875	0.640	0.689	0.782	0.818
0.345	0	0	0.260	0.286	0.272	0.125	0.360	0.311	0.218	0.182
50	43	33	50	56	83	60	80	53	101	54
1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
50	43	33	50	56	83	60	80	53	101	54
0.083	0.236	0.227	0.160	0.554	0.335	0.183	0.169	0.462	0.386	0.463
0.917	0.764	0.773	0.830	0.446	0.665	0.817	0.831	0.538	0.614	0.537
0	0	0	0.010	0	0	0	0	0	0	0
50	43	30	50	56	83	60	80	53	101	54
0.143	0.107	0.107	0.179	0.143	0.143	0.143	0.179	0.143	0.179	0.143
0.041	0.056	0.039	0.055	0.067	0.060	0.035	0.053	0.055	0.064	0.053
1.179	1.179	1.107	1.214	1.179	1.143	1.179	1.214	1.179	1.214	1.214

and distance. Accordingly, 28 loci were used after this analysis.

The proportion of polymorphic loci (P) varied from 0 to 0.214 with a mean of 0.117. The average number of alleles per locus (A) varied from 1.00 to 1.21

TABLE 4. *Phenotypic Distribution at the Idh-1,2 and Mdh-1,2 Loci*

| Locus | Stocks | No. of Tested | Phenotype | | | | | Frequency | | G |
			AAAA	AAAA'	AAA'A'	AA'A'A'	A'A'A'A'	qA	qA'	
Idh-1, 2	D- 2	94	79	14	1	0	0	0.957	0.043	0.2
			(79.0)	(14.0)	(0.9)	(0.0)	(0.0)			
	S- 5	50	39	11	0	0	0	0.945	0.055	1.9
			(39.9)	(9.3)	(0.8)	(0.0)	(0.0)			
	N- 8	59	19	38	2	0	0	0.822	0.178	18.5*
			(27.0)	(23.3)	(7.6)	(1.1)	(0.0)			
	N-11	32	15	17	0	0	0	0.867	0.133	8.9*
			(18.1)	(13.0)	(1.8)	(0.3)	(0.0)			
	N-12	50	33	17	0	0	0	0.915	0.085	5.2
			(35.1)	(13.0)	(1.8)	(0.1)	(0.0)			
	N-19	52	22	25	5	0	0	0.832	0.168	3.4
			(25.0)	(20.1)	(6.1)	(0.8)	(0.0)			
Mdh-1, 2	D- 1	30	0	0	29	1	0	0.492	0.508	50.6*
			(1.8)	(7.3)	(11.2)	(7.7)	(2.0)			
	D- 2	100	3	4	83	7	3	0.493	0.507	90.5*
			(5.9)	(24.3)	(37.5)	(25.7)	(6.6)			
	S- 2	30	14	1	15	0	0	0.742	0.258	31.4*
			(9.1)	(12.7)	(6.6)	(1.5)	(0.1)			
	N- 4	75	57	14	4	0	0	0.927	0.073	3.1
			(55.3)	(17.5)	(2.1)	(0.1)	(0.0)			
	N- 6	30	17	8	5	0	0	0.850	0.150	2.7
			(15.7)	(11.1)	(2.9)	(0.3)	(0.0)			
	N-11	33	19	14	0	0	0	0.894	0.106	5.4
			(21.1)	(10.0)	(1.8)	(0.1)	(0.0)			

A presents common allele and A'variant allele.

Number in parenthesis presents expected number.

* shows a significant difference.

with a mean of 1.13. Heterozygosity (H) varied from 0 to 0.070 with a mean of 0.042. In the four groups based on breeding levels, heterozygosity (H) was 0.029 with a range of 0 to 0.070 in Donaldson's group, 0.041 with a range of 0.016 to 0. 062 in Selected group, 0.045 with a range of 0.013 to 0.067 in Native group, and 0.054 with a range of 0.048 to 0.059 in Feral group. The value of mean heterozygosity in Native and Feral group is close to the values of 0.058 (1) and 0.053(6) in natural populations of North America. This suggests that there is no significant difference in genetic variability between natural and introduced ppulations, while the selected cultured populations have a remarkable tendency to decrease in genetic variability. The virtual lack of significant difference in genetic variability between natural and introduced populations can be explained by the mass propagation maintained in each hatchery. On the other hand, the decrease of genetic variability can be explained by founder effect and/or bottleneck, because the selection has a tendency to diminish in population size during

TABLE 5. *Mean Genetic Distance within and among Four Groups*

Group	Donaldson's	Selected	Native	Feral
Donaldson's	0.0428 (0.0000-0.0872)			
Selected	0.0347 (0.0009-0.0933)	0.0108 (0.0008-0.0293)		
Native	0.0372 (0.0022-0.0894)	0.0086 (0.0006-0.0365)	0.0071 (0.0000-0.0226)	
Feral	0.0373 (0.0063-0.0666)	0.0062 (0.0002-0.0132)	0.0051 (0.0014-0.0157)	0.0030

Number in the parenthesis presents the range

maintenance.

The degree of genetic differentiation was measured by genetic distance (8) and the results are presented in Table 5. The genetic distance (D) among 34 stocks varied from 0 to 0.0933 with a mean of 0.0170. The smallest value was that between N-4 and N-10, and the largest was that between D-4 and N-3. The mean genetic distance was the largest within Donaldson's group and the smallest within Feral group. There is no tendency for any correlation between genetic distance and sampling location or strain. The greatest mean genetic distance was that between Donaldson's with Native and Feral group and the smallest was that between Feral with Native and Selected group. It indicates a significant difference between Native cultured populations in Japan and Donaldson's strain. The mean genetic distance between groups were smaller than that obtained within Donaldson's group.

Genetic variability and distance are summarized in Table 6. As shown in Table 6, Donaldson's group showed low genetic variability and high genetic differentiation. On the other hand, Feral group showed high genetic variability and low genetic differentiation. Selected group was close to Donaldson's group

TABLE 6. *Summary of Genetic Variability and*
Distance in Rainbow Trout of Japan

Group	Mean Heterozygosity	Mean Genetic Distance
Donaldson's	0.029 (0.000-0.070)	0.0428 (0.0000-0.0872)
Selected	0.041 (0.016-0.062)	0.0108 (0.0008-0.0293)
Native	0.045 (0.013-0.067)	0.0071 (0.0000-0.0226)
Feral	0.054 (0.048-0.059)	0.0030
Overall mean	0.042 (0.000-0.070)	0.0170 (0.0000-0.0933)

Number in parenthesis presents the range

and Native group to Feral group.   It indicates that higher genetic differentiation shows lower genetic variability in cultured populations.   This phenomenon can be explained by the levels of breeding.   Both the amount of genetic variability and degree of genetic differentiation in the cultured populations depend on many factors, such as selection, population size, mixture and culture technique.   It is possible that a relatively small number of individuals produced a large number of offspring in each cultured stock.   If a population is consciously selected, the population number used for propagation is usually small.   The new population established by selection has a tendency for loss and fixation of alleles which are at low frequencies in the parental population.   Thus, the genetic differentiation would progress with the division of the population by genetic drift.   A more detail study about the mechanisms of maintaining polymorphism in cultured populations is warranted.

Acknowledgements

References

1) Allendorf, F.W., *"Genetic variability in a species possessing extensive gene duplication : Genetic interpretation of duplicate loci and examination of genetic variation in populations of rainbow trout."* Ph.D. Thesis, Univ. of Washington (1975)

2) Campton, D.E., and Utter, F.M., *Can. J. Fish. Aquat. Sci.*, **42**, 110 (1985)

3) Campton, D.E., and Johnston, J.M., *Trans. Am. Fish. Soc.*, **114**, 782 (1985)

4) Fujio, Y., *"Study of genetic characteristics of fish and shellfishes in isozymic analysis."* Nosuisho Tokubetsu Shiken (1984) (in Japanese)

5) Guyomard, R., *Gan. J. Genet. Cyttol.*, **23**, 33 (1981)

6) Fisher, P.W., Browne, D., Cameron, D.G., and Vyse, E.R., *Trans. Am. Fish. Soc.*, **111**, 312 (1982)

7) Allendorf, F.W., Utter, F.M., and May, B.P., *"Isozyme IV. Genetics and Evolution"* ed. by C.L. Markert, Academic Press, New York, 415 (1975)

8) Nei., M., *Amer. Natur.*, **106**, 283 (1972)