

# 日本の淡水域におけるオオクチバスの形態変異とその遺伝的特徴

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## Morphological Variabilities and Genetic Structures of Largemouth Bass *Micropterus salmoides* in Japanese Fresh Waters

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**Abstract:** A population of largemouth bass, *Micropterus salmoides*, in Kaminamazugoshi Reservoir, Japan, having specialized morphological characteristics, was examined morphologically and genetically, and compared with other Japanese populations. Morphologically, the Kaminamazugoshi population differed significantly from the others, although character variances of the former tended to be less. Genetic peculiarities observed in all of the populations examined suggested that the numbers of initially-released individuals were small. The Kaminamazugoshi population, in particular was considered to have arisen from a very small number of individuals, characterized by chance by some specialized morphological features, because it showed no genetic variability at any locus.

**Key words:** *Micropterus salmoides*; Morphology; Genetics; Isozyme

Largemouth bass, *Micropterus salmoides* (Perciformes: Centrarchidae), is a fresh-water fish originating from the southeast North American Continent<sup>1-9</sup>. From early times, It has been familiar as food and target for sport fishing<sup>1,4,6,7,9-11</sup>. Since it is able to adapt to various environments, it has been transplanted all over the world, including Central and South America, Europe, Africa and Asia including Japan<sup>1,2,4,5,9,11-15</sup>.

Largemouth bass were initially introduced into Japan in 1925 by an enterpriser of Tetsuma Akaboshi; Individuals from Santa Rosa, California, were released into Ashi Lake, Kanagawa Prefecture<sup>1,14-21</sup>. Thereafter, additional introductions to Ashi Lake were made from Pennsylvania and Minnesota in 1972<sup>15,18</sup>. At first, the transplanted largemouth bass populated only Ashi Lake, as time being, they also appeared in other lakes, reservoirs and rivers in various regions in Japan<sup>14,15,17-19</sup>.

Although largemouth bass populations seemed to decline after World War II<sup>17,18,20</sup>, since the

1970's, the species has been well established over much of Japan<sup>20,22-23</sup>. In 1988, it had been recorded from all prefectures, except Hokkaido and Iwate<sup>24</sup> (recently it was also found in Iwate<sup>25-27</sup>). The reason why the population extended the distribution in Japan is believed to be chaotic often release mainly by lure anglers<sup>14,15,19,20,22,23,28</sup>.

Recently, a largemouth bass population with an unusual appearance was discovered at Kaminamazugoshi Reservoir, Takamatsu, Kagawa Prefecture. Individuals were characterized by greater body depth, shorter pectoral fins, a more greenish body color, and an indistinct and intermittent body lateral stripe (Fig. 1). These features differed from those of other largemouth bass populations in Japan (Fig. 1) and the native populations inhabiting North America<sup>2-4,6-9</sup>.

Morphological and genetic comparisons of the Kaminamazugoshi form were made with the other largemouth bass populations in Japan, and possible features pertaining to its origin were discussed.

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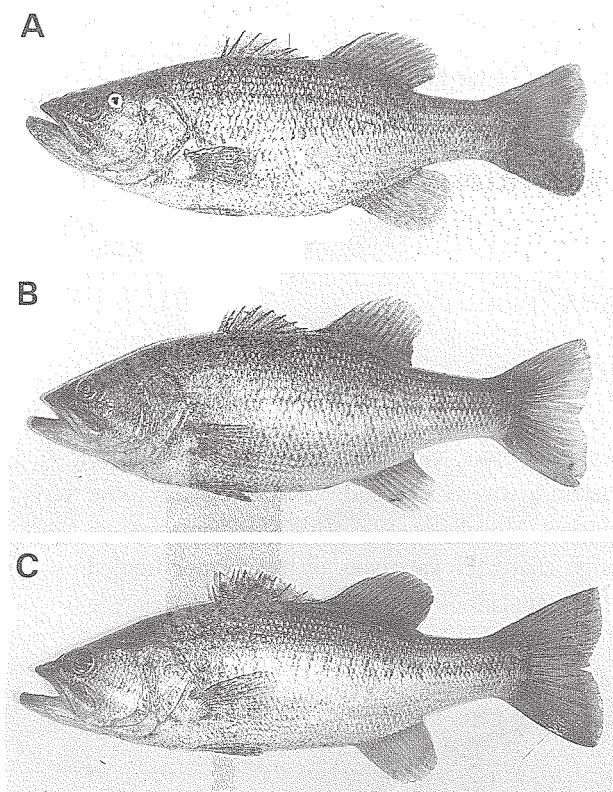


Fig. 1. General aspects of a largemouth bass (*Micropterus salmoides*) from Kaminamazugoshi Reservoir, showing a specialized appearance, compared with "normal" largemouth bass (represented by an individual from Hachiman Reservoir). A: Specimen from Kaminamazugoshi Reservoir (TL 223.6 mm); B: Kaminamazugoshi Reservoir (TL 330.0 mm); C: Hachiman Reservoir (TL 257.7 mm).

## Materials and Methods

Collection and treatment data for specimens used in this study are shown in Table 1. Seven largemouth bass populations in total were selected: Inba lake, Chiba Pref.; Oshio Reservoir, Gunma Pref.; Ikehara Reservoir, Nara Pref.; Biwa Lake, Shiga Pref., and Hachiman, Manno, Kaminamazugoshi Reservoirs, in Kagawa Pref. (Fig. 2).

Body proportions measured are shown in Fig. 3. Body width (BW) and interorbital width (IOW)

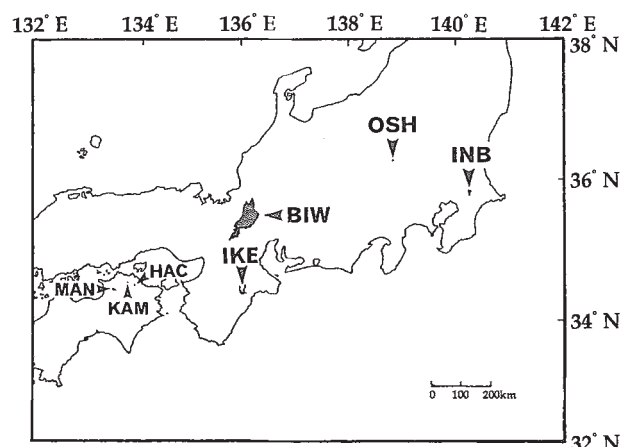


Fig. 2. Collection localities of largemouth bass. For locality abbreviations, see Table 1.

Table 1. Sampling data of largemouth bass specimens examined

Locality (Abbreviation)	Inba Lake (INB)	Oshio Reservoir (OSH)	Ikehara Reservoir (IKE)	Biwa Lake (BIW)
Date of collection	Dec. 19, 1992	Aug. 25, 1992	Nov. 4, 1992	Dec. 1992
Number of individuals	22 <sup>M)</sup> (7 <sup>G)</sup>	19 <sup>M)</sup> (6 <sup>G)</sup>	6 <sup>M)</sup> (2 <sup>G)</sup>	21 <sup>M)</sup> (8 <sup>G)</sup>
Method of sampling	Surround net	Hook and line	Hook and line	Cast net
Size range (TL, mm)	152.4-345.0	167.0-292.0	272.0-475.0	101.6-176.8
Average size (TL, mm)	305.3	213.6	339.6	131.3
Locality (Abbreviation)	Hachiman Reservoir (HAC)	Manno Reservoir (MAN)	Kaminamazugoshi Reservoir (KAM)	
Date of collection	Nov. 19-20, 1989	Oct. 25, 1992	Oct. 20-27, 1991	
Number of individuals	88 <sup>M)</sup>	74 <sup>G)</sup>	66 <sup>M)</sup>	
Method of sampling	Surround net	Surround net	Lure fishing	
Size range (TL, mm)	121.0-462.0	Unmeasured	135.0-378.0	
Average size (TL, mm)	221.2	Unmeasured	250.4	
Date of collection	Nov. 7, 1992	May 2-25, 1992	Mar. 19, 1993	
Number of individuals	24 <sup>G)</sup>	6 <sup>M)</sup> (4 <sup>G)</sup>	38 <sup>M)</sup> (7 <sup>G)</sup>	
Method of sampling	Hook and line	Lure fishing	Surround net	
Size range (TL, mm)	Unmeasured	159.8-381.0		
Average size (TL, mm)	Unmeasured	316.4		

<sup>M)</sup> Number of individuals used for morphological analysis.

<sup>G)</sup> Number of individuals used for genetic analysis.

were also measured. The methods for measurements and counts followed Hubbs and Lagler<sup>3)</sup>. The length measured are expressed as percentages of standard length or head length. Vertebrae were counted from radiographs. Gill rakers on the right side of the first gill arch were counted by separating the upper and lower limbs. The raker located at the angle of the gill arch was included in the lower limb counts.

Isozymes detected by horizontal starch-gel electrophoresis were used as genetic markers. The experimental techniques were based mainly on Taniguchi and Okada<sup>29)</sup>, using a citric acid-aminopropylmorpholine buffer (pH 6.0) system. Gene nomenclature and expression of alleles follows Yokogawa and Seki<sup>30)</sup>.

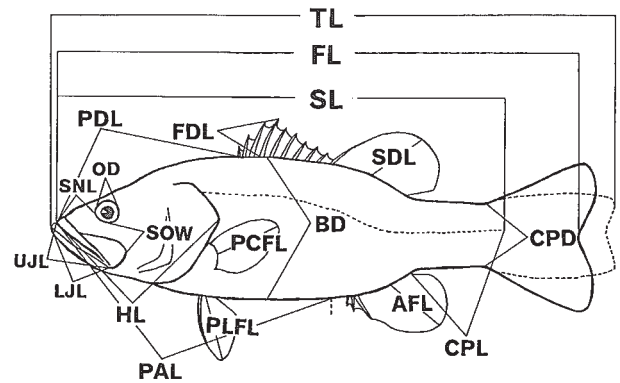


Fig. 3. Body measurements taken. TL: total length; FL: fork length; SL: standard length; PAL: pre-anus length; BD: body depth; CPL: caudal peduncle length; CPD: caudal peduncle length; PDL: pre-dorsal length; FDL: first dorsal fin length; SDL: second dorsal fin length; AFL: anal fin length; PCFL: pectoral fin length; PLFL: pelvic fin length; HL: head length; SNL: snout length; OD: orbital diameter; SOW: sub-orbital width; UJL: upper jaw length; LJL: lower jaw length.

Table 2. Average values of morphological characters of largemouth bass populations examined

Population <sup>1</sup>	INB	OSH	IKE	BIW	HAC	MAN	KAM
Total length <sup>2</sup>	121.64	122.09	121.33	123.62	122.78	122.11	121.26*
Fork length <sup>2</sup>	116.77	116.53	117.17	118.38	117.74	117.45	115.79*
Pre-anus length <sup>2</sup>	61.42	60.33	61.76	61.25	60.62	59.09	63.70*
Body depth <sup>2</sup>	32.91	30.00	29.79	31.62	30.80	27.59	34.64*
Body width <sup>2</sup>	17.70	16.92	17.00	15.75	16.98	15.78	18.56*
Caudal peduncle depth <sup>2</sup>	12.88	12.20	12.34	12.46	13.08	12.20	13.50*
Caudal peduncle length <sup>2</sup>	22.46	21.65	23.04	21.88	22.93	23.25	22.93
Pre-dorsal length <sup>2</sup>	39.85	40.33	41.14	41.72	39.81	40.15	40.35*
First dorsal fin length <sup>2</sup>	7.36	7.84	7.03	9.81	8.27	8.39	6.48*
Second dorsal fin length <sup>2</sup>	13.94	12.97	12.14	13.04	14.02	13.47	12.95
Anal fin length <sup>2</sup>	13.15	13.54	11.98	12.82	15.05	14.27	13.56
Pectoral fin length <sup>2</sup>	18.27	17.46	18.17	17.52	18.20	18.23	16.64*
Pelvic fin length <sup>2</sup>	15.24	15.63	14.93	16.65	15.92	16.18	14.69*
Head length <sup>2</sup>	34.69	34.74	35.29	35.52	35.10	34.67	33.93*
Snout length <sup>3</sup>	25.92	26.68	26.67	25.57	26.85	26.92	27.56*
Orbital diameter <sup>3</sup>	15.84	16.38	15.46	22.10	17.09	16.10	15.43*
Interorbital width <sup>3</sup>	26.23	26.77	27.50	26.25	25.18	26.01	28.87*
Sub-orbital width <sup>3</sup>	20.28	19.47	22.24	14.02	16.80	19.97	21.17
Upper jaw length <sup>3</sup>	49.41	48.03	50.16	46.00	48.00	48.51	50.01
Lower jaw length <sup>3</sup>	51.91	50.71	53.65	48.32	50.33	51.14	52.91
Dorsal fin spines	10.05	10.00	10.05	10.62	10.29	9.95	9.66*
Dorsal fin soft rays	12.00	12.96	12.05	11.88	12.09	12.80	11.89
Anal fin spines	3.00	2.96	2.81	2.99	2.82	2.86	2.98
Anal fin soft rays	10.00	11.12	10.00	10.00	9.93	10.83	9.75
Pectoral fin soft rays	14.05	14.28	13.76	14.91	14.27	14.24	14.59
Pelvic fin spines	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Pelvic fin soft rays	5.00	5.00	5.00	5.00	5.00	5.00	5.00
Pored scales on lateral line	61.59	62.64	63.52	63.85	63.85	63.44	61.77
Scales above lateral line	7.50	7.56	7.76	8.30	7.68	7.65	7.20*
Scales below lateral line	14.45	15.44	15.14	16.46	16.06	14.70	13.89*
Gill rakers (upper limb)	1.68	2.48	2.19	2.20	2.01	1.97	1.80
Gill rakers (lower limb)	6.45	5.92	7.00	7.44	6.03	7.24	6.73
Gill rakers (total)	8.14	8.40	9.19	9.64	7.03	9.21	8.52
Vertebrae	31.82	31.80	32.20	32.45	31.99	31.65	31.70

<sup>1</sup> Refer to abbreviations in Table 1.

<sup>2</sup> Percentage of standard length.

<sup>3</sup> Percentage of head length.

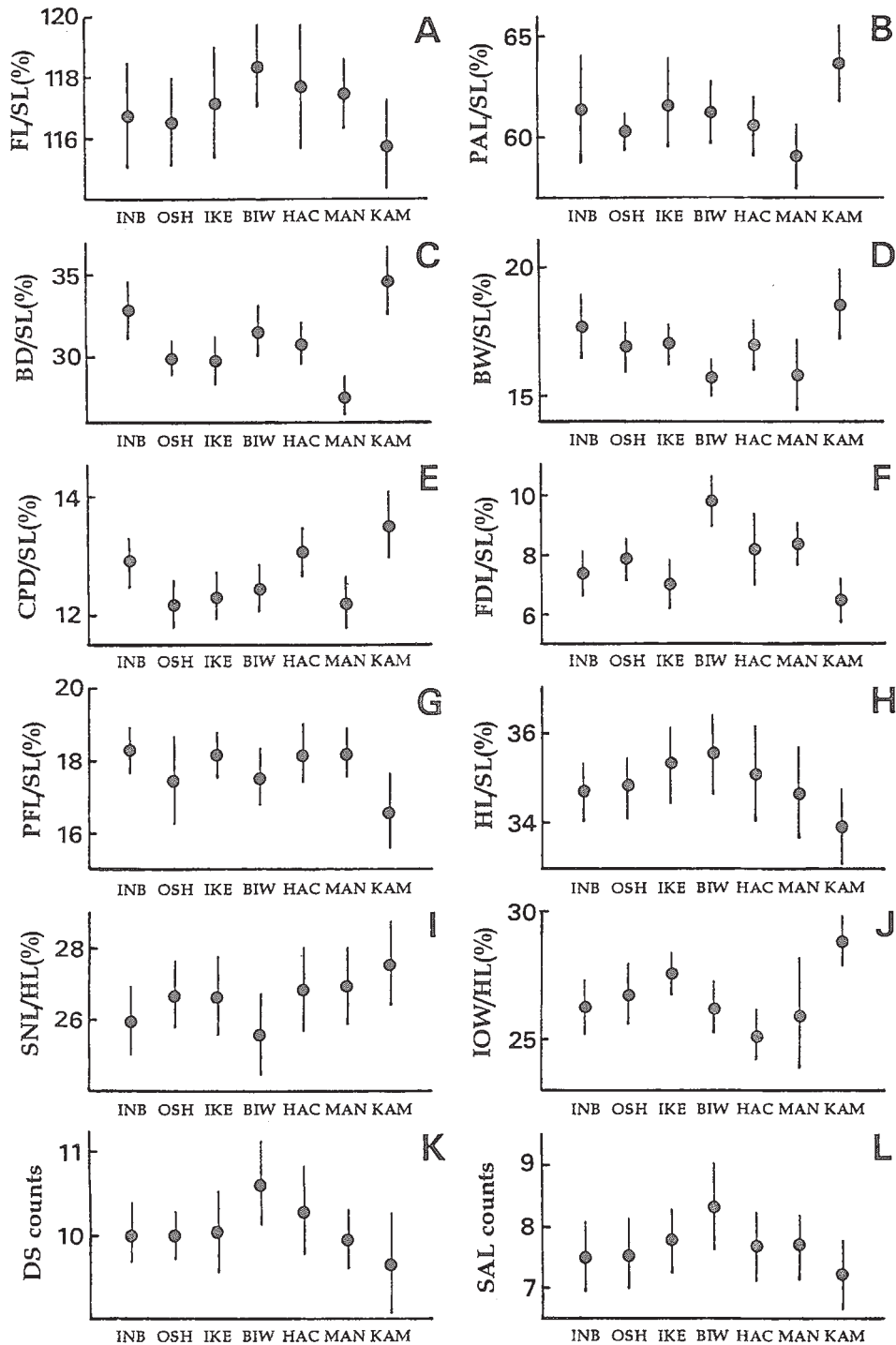
\* Average value of KAM population at extreme of range.

**Results**

*Morphological Characters*

Morphometric measurements of the popula-

tions examined and graphic comparisons of some significant characters are shown in Table 2 and Fig. 4, respectively. The average values of each character varied considerably by population, representing its unique characteristics.



**Fig. 4.** Graphic comparisons of morphological characters. Dark circles indicate average values of each population. Longitudinal bars indicate standard deviations (unbiased value). For locality abbreviations, see Table 1. A: Fork length (FL); B: Pre-anus length (PAL); C: Body depth (BD); D: Body width (BW); E: Caudal peduncle depth (CPD); F: First dorsal fin length (FDL); G: Pectoral fin length (PCFL); H: Head length (HL); I: Snout length (SNL); J: Interorbital width (IOW); K: Dorsal spine (DS) counts; L: Scales above lateral line (SAL) counts.

Among the examined populations, the Kamina-mazugoshi population showed the highest average values for pre-anus length, body depth, body width, caudal peduncle depth, pre-dorsal length, snout length and interorbital width, and the least average values for total length, fork length, first dorsal fin length, pectoral fin length, pelvic fin length, head length, orbital diameter, additionally, dorsal fin spine number and numbers of scales above and below the lateral line (Fig. 4, Table 2).

Altogether 17 (50%) of the total morphological and meristic characters examined in the Kamina-mazugoshi population represented one extreme or the other of the range of average values for the populations overall (Table 2), i.e. the former population showed a much higher degree of specialization than the others, although the latter were also characterised by some unique characteristics.

Variances (unbiased values) of the morphological characters are shown in Table 3. Regarding

**Table 3.** Unbiased variances of morphological characters of largemouth bass populations examined

Population <sup>1</sup>	INB	OSH	IKE	BIW	HAC	MAN	KAM
Total length <sup>2</sup>	3.663	3.249	3.340	2.523	4.829	7.501	2.057
Fork length <sup>2</sup>	2.980	2.163	3.357	1.906	4.202	1.391	2.192
Pre-anus length <sup>2</sup>	7.104	0.937	5.048	2.550	2.390	2.653	3.686
Body depth <sup>2</sup>	3.313	1.216	2.181	2.535	1.511	1.319	4.211
Body width <sup>2</sup>	1.576	1.078	0.654	0.547	0.970	1.864	1.954
Caudal peduncle depth <sup>2</sup>	0.190	0.179	0.181	0.175	0.182	0.188	0.303
Caudal peduncle length <sup>2</sup>	1.823	1.713	1.438	1.645	1.255	1.099	1.355
Pre-dorsal length <sup>2</sup>	1.466	0.769	2.482	1.214	1.577	1.566	1.318
First dorsal fin length <sup>2</sup>	0.577	0.528	0.694	0.732	1.503	0.518	0.569
Second dorsal fin length <sup>2</sup>	0.913	0.947	2.394	1.613	1.534	0.746	1.143
Anal fin length <sup>2</sup>	0.731	1.023	1.131	1.082	1.667	0.678	0.795
Pectoral fin length <sup>2</sup>	0.456	1.530	0.484	0.626	0.671	0.537	1.124
Pelvic fin length <sup>2</sup>	0.997	0.627	0.661	0.659	1.063	0.615	0.421
Head length <sup>2</sup>	0.432	0.455	0.768	0.824	1.159	1.005	0.740
Snout length <sup>3</sup>	0.970	0.903	1.297	1.314	1.432	1.208	1.517
Orbital diameter <sup>3</sup>	2.463	2.781	1.866	2.694	3.800	1.414	1.278
Interorbital width <sup>3</sup>	1.163	1.466	0.668	1.082	0.979	4.817	1.070
Sub-orbital width <sup>3</sup>	3.906	2.314	5.715	2.741	9.483	6.551	2.078
Upper jaw length <sup>3</sup>	3.984	2.179	6.060	1.292	4.212	6.031	2.139
Lower jaw length <sup>3</sup>	2.026	2.272	6.662	1.647	5.404	3.523	6.679
Dorsal fin spines	0.141	0.083	0.248	0.264	0.277	0.136	0.369
Dorsal fin soft rays	0.200	0.290	0.248	0.465	0.566	0.407	0.289
Anal fin spines	0.000	0.040	0.162	0.013	0.150	0.150	0.023
Anal fin soft rays	0.381	0.277	0.600	0.684	0.478	0.172	0.424
Pectoral fin soft rays	0.141	0.377	0.190	0.182	0.293	0.402	0.340
Pelvic fin spines	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pelvic fin soft rays	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pored scales on lateral line	3.301	5.823	4.462	6.306	4.863	4.342	2.924
Scales above lateral line	0.357	0.340	0.290	0.466	0.337	0.292	0.353
Scales below lateral line	5.307	1.007	0.929	0.910	1.136	1.291	0.754
Gill rakers (upper limb)	0.227	0.343	0.162	0.238	0.103	0.153	0.213
Gill rakers (lower limb)	0.355	0.660	0.100	0.553	0.378	0.340	0.249
Gill rakers (total)	0.790	0.833	0.362	0.892	0.378	0.539	0.581
Vertebrae	0.442	0.583	0.379	0.453	0.425	0.784	0.659
Average of length-measured characters	2.037	1.416	2.354	1.470	2.491	2.261	1.831
Average of meristic characters	0.832	0.761	0.681	0.816	0.670	0.644	0.513
Total average	1.540	1.147	1.624	1.190	1.741	1.595	1.288

<sup>1</sup> Refer to abbreviations in Table 1.

<sup>2</sup> Percentage of standard length.

<sup>3</sup> Percentage of head length.

the Kaminamazugoshi population, although character variances tended to be smaller in general, the average values of the length-measured characters and overall average were about midway for the populations considered. However, the average value for meristic characters in the Kaminamazugoshi population were significantly lower than in the other populations (Table 3).

#### Genetic Characters

Following electrophoresis, 10 enzymes and 1 non-enzymic protein were detected, and 20 loci were presumed (Table 4). Allelic frequencies and heterozygosities of the populations examined are shown in Table 5; genetic polymorphisms were found at only 4 loci (*AAT-1\**, *MDH-1\**, *MDH-2\**, *PGDH\**). Hardy-Weinberg fitness was examined by chi-square tests on the polymorphic loci. Although the chi-square values were apparently significant in some cases, they could not be so regarded because expected values of less than 5 were included<sup>31</sup>. However, the *AAT-1\** locus in the Hachiman population was a significant at 5% owing to an excess of heterozygotes, such being reflected in the Ho/He ratio of this population (Table 5).

Pie graphs of the allelic compositions of the 4 polymorphic loci are shown in Fig. 5. The

populations differed completely, sharing no similar allelic compositions (Fig. 5). For example, at the *AAT-1\** locus, the Inba population had a low frequency of the B allele, the Ikehara population a high frequency, the Hachiman population approximately 50%, and the remaining populations lacked the allele (Fig. 5, Table 5). Similar situations were reflected by the other polymorphic loci.

It should be noted that the frequency of the B allele at the *AAT-1\** locus in the Hachiman population was approximately 50%, compared with that at the *MDH-1\** and *MDH-2\** loci of the Manno population being both 25% (Fig. 5, Table 5) (see later discussion). It was also noteworthy that the Kaminamazugoshi population lacked genetic variability at all the loci, unlike the other populations (Fig. 5, Table 5).

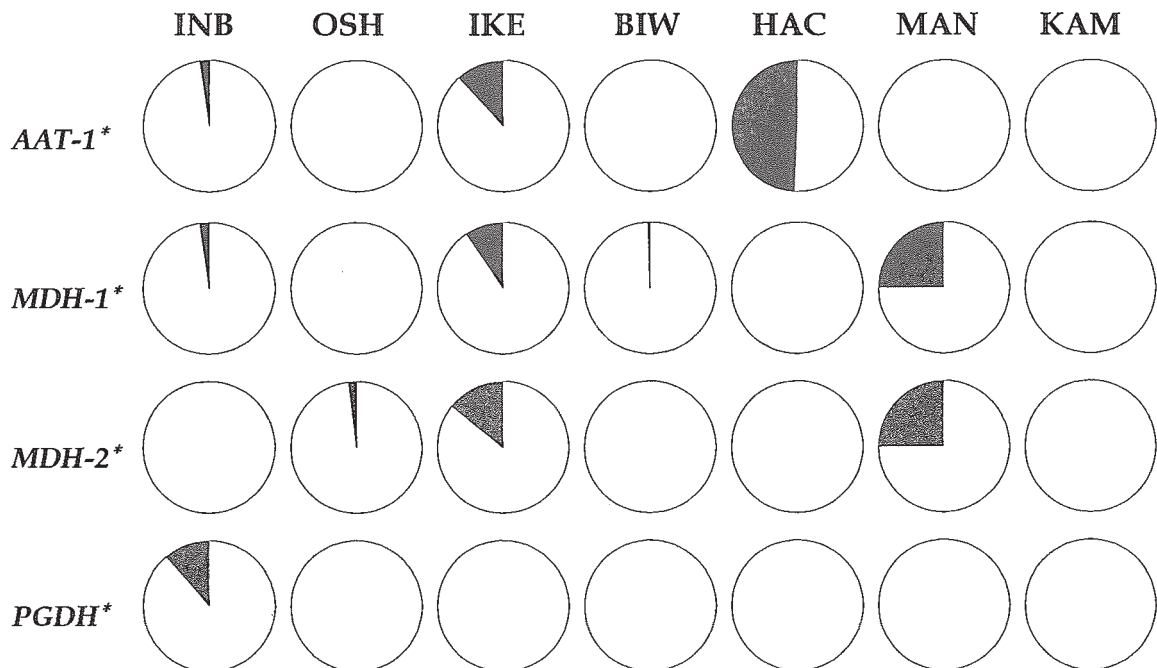
The average heterozygosity values ( $H_o$ ) differed considerably by population (Table 5), ranging from 0.0000 (KAM) to 0.0500 (MAN). The  $H_o/H_e$  ratio also varied by population, ranging from 0.7829 (INB) to 1.3333 (MAN). This showed that some populations were characterised by excess homozygotes whereas others had excess heterozygotes, suggesting that the genetic peculiarity of each population reflected the variations in heterozygosity (Table 5). The

**Table 4.** Enzymes, protein and tissues examined

Enzyme or protein name	Enzyme number	Locus	Tissue
Aspartate aminotransferase	2.6.1.1	<i>AAT-1*</i>	Liver
		<i>AAT-2*</i>	Liver
Alcohol dehydrogenase	1.1.1.1	<i>ADH*</i>	Liver
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	<i>GAPDH-1*</i>	Liver
		<i>GAPDH-2*</i>	Liver
		<i>GAPDH-3*</i>	Muscle
L-Iditol dehydrogenase	1.1.1.14	<i>IDDH*</i>	Liver
Isocitrate dehydrogenase (NADP <sup>+</sup> )	1.1.1.42	<i>IDHP-1*</i>	Liver
		<i>IDHP-2*</i>	Muscle
Lactate dehydrogenase	1.1.1.27	<i>LDH-1*</i>	Muscle
		<i>LDH-2*</i>	Muscle
Malate dehydrogenase	1.1.1.37	<i>MDH-1*</i>	Muscle
		<i>MDH-2*</i>	Muscle
		<i>MDH-3*</i>	Muscle
Phosphogluconate dehydrogenase	1.1.1.44	<i>PGDH*</i>	Liver
Phosphoglucomutase	5.4.2.2	<i>PGM*</i>	Muscle
General protein		<i>PROT-1*</i>	Muscle
		<i>PROT-2*</i>	Muscle
		<i>PROT-3*</i>	Muscle
Superoxide dismutase	1.15.1.1	<i>SOD*</i>	Liver

**Table 5.** Allelic frequencies and heterozygosities of largemouth bass populations examined

Locus	Allele	INB <sup>1</sup>	OSH <sup>1</sup>	IKE <sup>1</sup>	BIW <sup>1</sup>	HAC <sup>1</sup>	MAN <sup>1</sup>	KAM <sup>1</sup>
<i>AAT-1</i> *	*145 B	0.023	0.000	0.119	0.000	0.493	0.000	0.000
	*100 A	0.977	1.000	0.881	1.000	0.507	1.000	1.000
<i>AAT-2</i> *	*-100 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>ADH</i> *	*-100 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>GAPDH-1</i> *	*100 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>GAPDH-2</i> *	*100 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>GAPDH-3</i> *	*130 B	0.000	0.000	1.000	0.000	0.000	0.000	0.000
	*100 A	1.000	1.000	0.000	1.000	1.000	1.000	1.000
<i>IDDH</i> *	*-100 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>IDHP-1</i> *	*100 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>IDHP-2</i> *	*100 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>LDH-1</i> *	*100 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>LDH-2</i> *	*0 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>MDH-1</i> *	*140 B	0.023	0.000	0.095	0.005	0.000	0.250	0.000
	*100 A	0.977	1.000	0.905	0.995	1.000	0.750	1.000
<i>MDH-2</i> *	*150 B	0.000	0.020	0.143	0.000	0.000	0.250	0.000
	*100 A	1.000	0.980	0.857	1.000	1.000	0.750	1.000
<i>MDH-3</i> *	*-100 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>PGDH</i> *	*110 B	0.114	0.000	0.000	0.000	0.000	0.000	0.000
	*100 A	0.886	1.000	1.000	1.000	1.000	1.000	1.000
<i>PGM</i> *	*100 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>PROT-1</i> *	*100 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>PROT-2</i> *	*100 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>PROT-3</i> *	*0 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
<i>SOD</i> *	*100 A	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Average	Ho <sup>2</sup>	0.0114	0.0020	0.0310	0.0005	0.0313	0.0500	0.0000
Heterozygosity	He <sup>3</sup>	0.0145	0.0020	0.0313	0.0005	0.0250	0.0375	0.0000
	Ho/He	0.7829	1.0204	0.9873	1.0053	1.2502	1.3333	-

<sup>1</sup> Population abbreviations refer to Table 1.<sup>2</sup> Observed heterozygosity.<sup>3</sup> Expected heterozygosity by Hardy-Weinberg law.**Fig. 5.** Pie graph comparisons of allelic frequencies at polymorphic loci of the largemouth bass populations examined. Blank areas indicate major alleles (A), dark areas indicate minor alleles (B).



coefficient of gene differentiation ( $G_{ST}$ ) in the populations examined (after Nei<sup>32</sup>) was 0.080, indicating very little inter-population genetic variability.

### Discussion

Populations of largemouth bass in Japan differ morphologically one from the other (Fig. 2, Tables 2, 3), such differences being particularly prominent in the Biwa and Kaminamazugoshi populations (Table 3). It is known that most of the body proportions of largemouth bass change significantly from fingerling to adult with growth (increased or diminished), it happens even after the juvenile stage (Yokogawa, unpubl. data). Therefore, it can be expected that the Biwa population, which was represented wholly by fingerlings, differed morphologically from the other populations which comprised variously sized specimens (Table 1). However, the Kaminamazugoshi population, comprising variously sized individuals as in the remaining populations, has to be considered to be as morphologically specialized by comparison with the latter.

These observed morphological peculiarities basically reflect the genetic peculiarity of each population (Fig. 5, Table 5), although morphological characteristics can also be influenced by

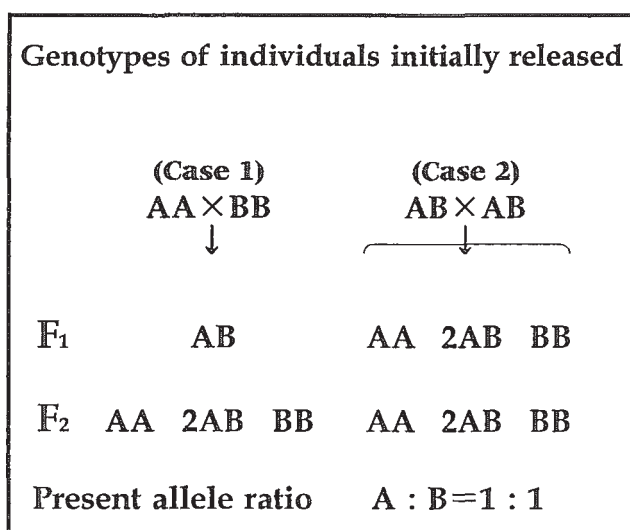
some environmental factors. Although the populations were genetically distinct one from the other (Fig. 5, Table 5), the small  $G_{ST}$  value suggested that inter-population genetic variability was very low. However, this could have resulted from the uniformity shown by the many monomorphic loci (Table 5).

Nishihara<sup>33</sup> compared the meristic characteristics of largemouth bass from Ashi Lake with those from the United States and France, and found some significant differences between the populations. It may also result from genetic differentiation (see later discussion).

One explanation for the Japanese largemouth bass populations having different genetic features is genetic drift (bottle neck effect), caused by an initial release of a small number of parents. Since most of the release of largemouth bass in Japan were non-systematic, by anglers<sup>14,15,19,20,22,23,28</sup>, it is likely that the numbers of the initially-released individuals were small in many cases, resulting in genetic drift and the resulting unique genetic peculiarities in many populations.

Although the fitness tests for Hardy-Weinberg law showed significance on very few cases because of the low genetic variability and the small sample numbers, the *AAT-1\** locus of the Hachiman population was clearly significant

#### *AAT-1\** locus : Hachiman population



#### *MDH-1\** and *MDH-2\** loci : Manno population

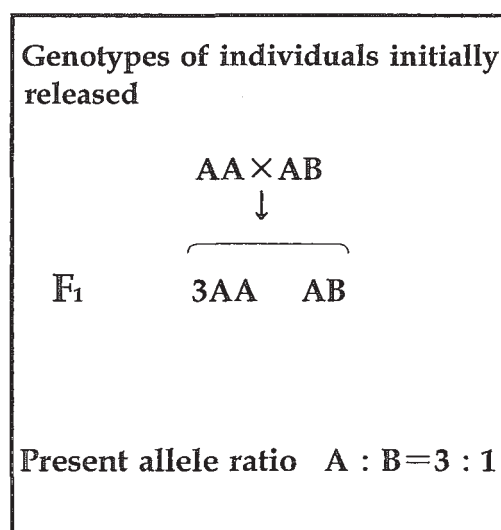


Fig. 6. Simple genetic models demonstrating the establishment of the present allelic compositions of selected populations.

evidence of the genetic drift. This may also account for the phenomenon that some populations showed an excess of homozygotes while others showed an excess of heterozygotes (Table 5).

Some simple models explaining the derivation of the present allelic compositions are illustrated in Fig. 6. The B allele frequency of the *AAT-1*\* locus of the Hachiman population was approximately 50% (Fig. 5, Table 5). Two cases ( $AA \times BB$ ,  $AB \times AB$ ) can be considered as shown in Fig. 6, both resulting in a frequency of 50% for the B allele. Although the models assume a single pair of parents, the same situation would result also from multiples of the same genotype coupling.

Although a significant excess of heterozygotes characterised in the *AAT-1*\* locus of the Hachiman population, this phenomenon could not occur theoretically in Case 2 ( $AB \times AB$ ) in Fig. 6. However, if, in Case 1 ( $AA \times BB$ ), the  $F_2$  generation completely replaced the  $F_1$  generation and the present population was generated only from  $F_2$  parents, the final result would be the same as that resulting from Case 2.

In fact, both  $F_1$  and  $F_2$  individuals comprised the reproductive population, owing to largemouth bass generally requiring at least 3 years to reach maturity, thereafter breeding for the next 5-7 years<sup>7,9,18,34-37</sup>, the propagative period of the  $F_1$  and the  $F_2$  can overlapping. Since the  $F_1$  population comprises only heterozygotes (Fig. 6), the overall reproductive population would include excessive heterozygotes, a situation that would continue over successive generations. Therefore, for the Hachiman population, Case 1 appears to be a reasonable model.

The *MDH-1*\* and *MDH-2*\* loci in the Manno population, being both 25% (Fig. 5, Table 5), can be explained by the model illustrated in Fig. 6, the same situation resulting also from multiples of the same genotype coupling. These examples suggest that the Japanese largemouth bass populations have grown from an initial release of a small number of individuals in many cases.

While the morphological characteristics of the Kaminamazugoshi population were characterised

by extremes (Fig. 4, Table 2), no genetic variability was evident (Fig. 5, Table 5). On the basis of phenotypic variance ( $V_P$ ) in fishes being the sum of genetic variance ( $V_G$ ) and environmental variance ( $V_E$ )<sup>38-40</sup>, if the degree of  $V_E$  of each largemouth bass population was similar,  $V_P$  would be influenced by  $V_G$ . Therefore, a reduction in the  $V_G$  in the Kaminamazugoshi population should lower its  $V_P$ .

Although individual variances of the morphological characters of the Kaminamazugoshi population tended to be low, the average value overall was not the lowest of the populations examined (Table 3). Because the body proportions of largemouth bass change significantly with growth (Yokogawa, unpubl. data), examination of specimens of various size should result in greater variances.

In fact, the average values of the length-measured characters of the Biwa and Oshio populations, which comprised similarly sized specimens (Table 1), were rather less than the others (Table 4). In addition, the fact that these populations had very little genetic variability (Fig. 5, Table 5) may have directly influenced (thus reducing) on their morphological variability.

As for the Kaminamazugoshi population which comprised variously sized specimens (Table 1), the lower overall variance of morphological characters than found in the similarly size-structured populations at Inba, Ikehara, Hachiman and Manno (Table 4), may be evidence of reduced  $V_P$  in the former.

While meristic counts in fishes are believed to remain constant after the juvenile stage, they may well reflect  $V_P$ . In fact, the average variance of the meristic characters of the Kaminamazugoshi population was the lowest of all the populations (Table 3), clearly indicating reduced  $V_P$  in the former population. In the case of a clonal fish population, a prominent reduction in  $V_P$  because of lacking in  $V_G$  have been reported for ayu, *Plecoglossus altivelis*<sup>41-44</sup>. This is a similar phenomenon to that of the Kaminamazugoshi population in this study.

In conclusion, the Kaminamazugoshi population exhibits reduced morphological variability resulting from reduced genetic variability, and

very specialized morphological characteristics, which might have been almost completely fixed genetically to particular alleles, as the result of an initial release of a very small number of individuals.

To confirm this, examination of mitochondrial DNA, inherited only from the maternal parent is important. In such an analysis, the number of original female parents could be determined from the number of haplotypes in the population. This method would also confirm the likely situation of the haplotype variability in Japanese largemouth bass populations being much less than in the other naturally-occurring aquatic species. Such a status should be reconsidered including ecological impact of the transplanted exotic species like the largemouth bass to the Japanese native fauna.

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## 日本の淡水域におけるオオクチバスの 形態変異とその遺伝的特徴

横川浩治

特殊な形態を示す上鯨越池のオオクチバスと他の湖沼の集団との形態的、遺伝的比較を行なった。上鯨越池の集団は多くの形態形質において他の集団と差が認められ、各形質の分散が小さい傾向が認められた。遺伝形質では、各集団ごとに独特な遺伝子組成を示し、その母体となった親魚数が少なかつたことに起因する遺伝的浮動による影響の可能性が示唆された。特に、上鯨越池の集団はアイソザイム系遺伝子座において遺伝的変異が全くなかつたことから極めて少数の親魚から派生した集団であるものと推定され、たまたま形態的に特殊な数少ない親魚が放流されたことによりこのような集団が形成された可能性が考えられた。