Morphological and genetic characteristics of sea bass, *Lateolabrax japonicus*, from the Ariake Sea, Japan

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Abstract Sea bass, *Lateolabrax japonicus*, from the Ariake Sea, characterized by black dots on the lateral body region as in the Chinese sea bass, *L.* sp., were examined and compared morphologically and genetically with *L. japonicus* and *L.* sp. Some meristic characters of the Ariake form tended to fall midway between values for the two former species. Genetic features, evaluated by isozyme analyses, indicated that the Ariake form as represented a simple Mendelian population, there being no significant differences from a Hardy-Weinberg equilibrium according to chi-square tests. Although some extreme differences in allelic frequencies were found at some loci between *L. japonicus* and *L.* sp., the Ariake form possessed many heterozygotes at the *PROT-1** locus, in addition to allelic frequencies at some loci conforming to those of *L.* sp. Average allele numbers per locus, rate of polymorphic loci and average heterozygosity of the Ariake form were higher than for either *L. japonicus* or *L.* sp., indicating high genetic variation in the former. The results suggested that the Ariake population is genetically independent of other populations of *L. japonicus*, but might be genetically influenced by *L.* sp.

Key words. — Sea bass; *Lateolabrax*; Ariake Sea; morphology; genetics.

Based on morphological and genetic differences observed in Japanese and Chinese sea bass, Yokogawa and Seki (1995) concluded that the Chinese sea bass was specifically distinct from *Lateolabrax japonicus* (Cuvier), the former being referred to as *Lateolabrax* sp. Subsequently, Yokogawa and Tajima (1996) proposed the common English name "spotted sea bass" for *L.* sp. Further, Nakayama et al. (1996) recognized significant morphological differences in developing larvae of the two species.

L. sp. is characterized by many clear black dots on the lateral body region. Sea bass from the Ariake Sea, Japan are also known to have similar external features (Katayama, 1960a, b, 1965). Therefore in this study, morphological and genetic characteristics of sea bass from the Ariake Sea were examined.

Materials and Methods

Sea bass from the Ariake Sea (hereafter called Ariake form) used in this study were obtained offshore from Shimabara City, Nagasaki Prefecture, on 18th–26th, May, 1993. Forty specimens (345–535 mm TL, average 420.6 mm TL) caught by hook and line were used for the morphological and genetic analyses.

The specimens were preserved in a refrigerator at −30°C until electrophoretic analyses and thereafter fixed in 10% formalin for examination of morphological characters. All methods followed Yokogawa and Seki (1995).

Results

Morphological characters. — Average values and ranges of the proportions of length-measured characters of the Ariake form, together with the average values of Japanese and Chinese species examined previously (hereafter called *Lateolabrax japonicus* and *L.* sp., respectively) are shown in Table 1. Average values of the Ariake form were close to either *L. japonicus* or *L.* sp. in some characters, but distinctly different to both in others. Thus, no general tendency in these characters for the Ariake form was apparent. The average value of the pectoral scaly area length (PSAL) in the Ariake form was greater than in *L. japonicus* and *L.* sp.

Average values and ranges of meristic counts in the Ariake form, together with the average values for *L. japonicus* and *L.* sp. are shown in Table 2. Although the average values for the former tended to be close to those for *L. japonicus*, the range of some character counts was intermediate between *L. japonicus* and *L.* sp.

Figures 1–3 show frequency distributions of the number of pored lateral line scales (LLS), number of total gill rakers (GR) and number of vertebrae (VT), respectively, in the Ariake form, together with data for *L. japonicus* and *L.* sp.

The histogram of LLS in the Ariake form indicated a bimodal pattern, the concavity between

Table 1. Proportions of body characters in the Ariake form, *Lateolabrax japonicus* and *L.* sp.

	Ariake		*L. japonicus*[1]	*L.* sp.[1]
	Average	Range	Average	Average
Total length[2]	119.16	115.13–122.60	121.69	119.17
Fork length[2]	114.00	111.28–117.18	115.11	114.00
Pre-anus length[2]	65.41	62.18–73.00	66.04	66.76
Body depth[2]	23.09	21.01–27.58	24.24	26.28
Body width[2]	13.32	11.68–16.25	13.38	13.46
Caudal peduncle depth[2]	9.15	8.22–10.73	9.28	10.35
Caudal peduncle length[2]	22.36	20.49–24.36	21.61	22.09
Pre-dorsal length[2]	34.52	32.67–36.79	35.24	35.00
First dorsal fin length[2]	14.30	12.31–15.55	14.10	12.62
Second dorsal fin length[2]	10.69	8.07–13.50	11.82	12.57
Anal fin length[2]	11.69	9.61–13.72	12.49	14.33
Pectoral fin length[2]	16.10	14.66–19.47	17.05	16.08
Pelvic fin length[2]	16.84	15.00–19.01	17.57	18.33
Head length[2]	30.60	28.96–32.69	31.98	32.56
Snout length[3]	26.59	24.14–28.57	26.25	25.10
Orbital diameter[3]	16.59	14.49–19.01	17.70	24.83
Interorbital width[3]	22.30	20.33–23.87	21.20	21.64
Suborbital width[3]	10.39	8.55–12.17	11.26	10.72
Upper jaw length[3]	43.05	40.00–45.98	42.36	44.21
Lower jaw length[3]	46.99	43.10–49.95	46.43	46.82
Pectoral scaly area length[4]	29.00	19.96–41.26	26.73	19.43

[1]Data from Yokogawa and Seki(1995); [2]percentage of standard length; [3]percentage of head length; [4]percentage of pectoral fin length.

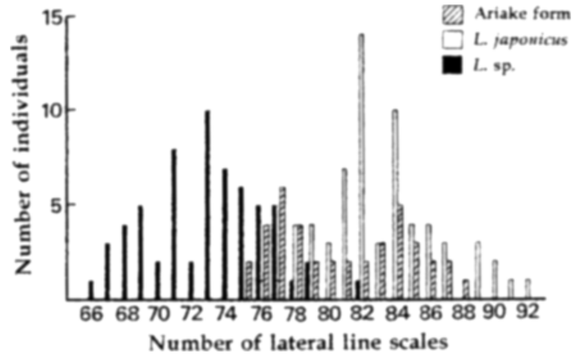

Fig. 1. Frequency distributions of lateral line scales (LLS) in the Ariake form, *Lateolabrax japonicus* and *L.* sp.

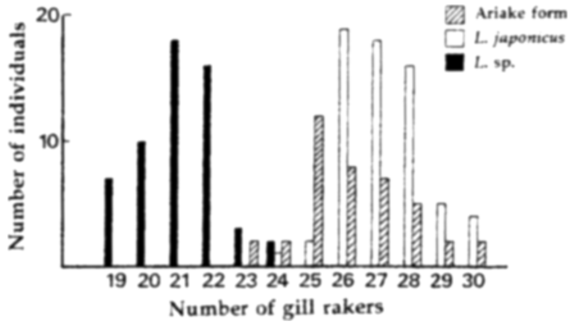

Fig. 2. Frequency distributions of total gill rakers (GR) in the Ariake form, *Lateolabrax japonicus* and *L.* sp.

the peaks corresponding closely to the border between *L. japonicus* and *L.* sp. The range of LLS was 75–88, intermediate between the two species (Fig. 1), although inclined somewhat towards *L. japonicus*.

The histogram of GR in the Ariake form (modal number 25) corresponded closely to that of *L. japonicus* (modal number 26) (Fig. 2). GR range in the Ariake form was 23–30, slightly overlapping that of *L.* sp.

The modes of vertebral (VT) frequencies in *L. japonicus* and *L.* sp. were explicitly separated, that is, 36 and 35, respectively. The histogram of the Ariake form indicated a mode of 36, which, however, was not as dominant as those for *L. japonicus* or *L.* sp., (40.0% of the total had fewer than 36 vertebrae, a characteristic of *L.* sp.). The range of VT in the Ariake form, 34–37, wholly included those of the two species (Fig. 3).

The lateral body dot numbers in the Ariake form, together with data for *L.* sp., are shown in Figure 4. In the Ariake form, 67.5% of the total possessed dots, the most dominant dot numbers

Table 2. Meristic counts in the Ariake form, *Lateolabrax japonicus* and *L.* sp.

	Ariake		*L. japonicus*[1]	*L.* sp.[1]
	Average	Range	Average	Average
Dorsal fin spines	13.00	12–14	12.85	12.95
Dorsal fin soft rays	12.48	11–13	12.78	13.07
Anal fin spines	3.00	3–3	3.00	2.98
Anal fin soft rays	7.23	6–8	7.73	7.53
Pectoral fin soft rays	16.90	16–18	16.85	16.31
Pelvic fin spines	1.00	1–1	1.00	1.00
Pelvic fin soft rays	5.00	5–5	5.00	5.00
Pored scales on lateral line	80.75	75–88	83.08	72.86
Scales above lateral line	16.00	14–18	14.85	15.82
Scales below lateral line	19.40	16–22	19.37	19.18
Gill rakers (upper limb)	8.43	6–11	9.66	6.38
Gill rakers (lower limb)	17.80	15–21	17.52	14.70
Gill rakers (total)	26.23	23–30	27.19	21.07
Vertebrae	35.58	33–37	35.89	34.95

[1] Data from Yokogawa and Seki (1995).

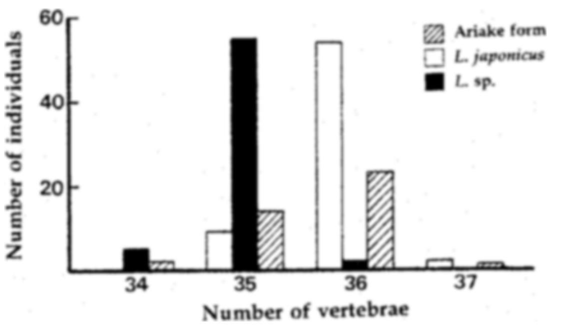

Fig. 3. Frequency distributions of vertebrae (VT) in the Ariake form, *Lateolabrax japonicus* and *L.* sp.

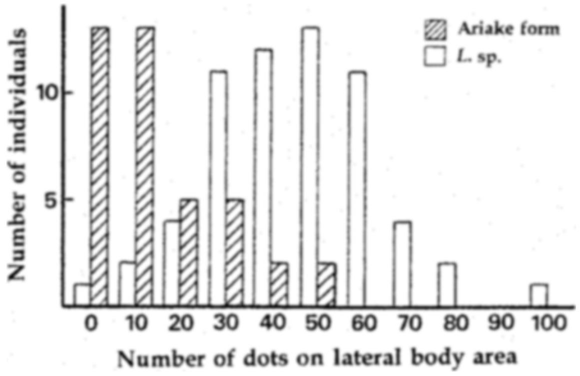

Fig. 4. Frequency distributions of number of dots on the lateral body area in the Ariake form and *Lateolabrax* sp.

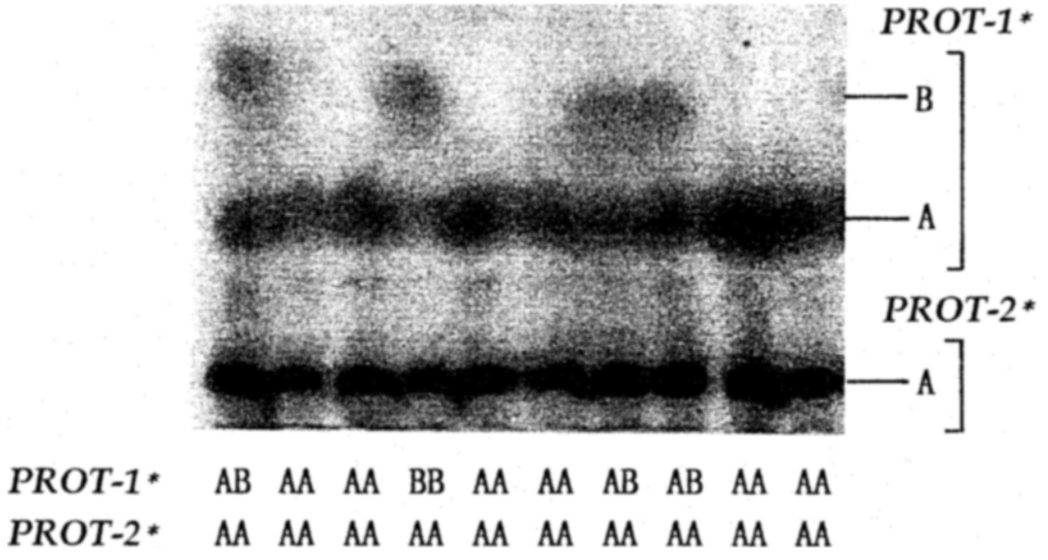

Fig. 5. Electrophoretogram of general proteins in the Ariake form. Upper case letters represent genotypes, at *PROT-1** locus; A: **100* allele, B: **170* allele, at *PROT-2** locus; A: **100* allele.

being 10–20 (ranging 0 to about 60). Although the presence of dots on the lateral body surface is a typical character of the Ariake form, the shape of the histogram differed somewhat from that for *L.* sp., which is also characterized by dots (Fig. 4).

Dorsal squamation on the head was examined, all of the Ariake specimens having well-developed scale rows from the interorbit to the internasal area. The rows subsequently extended anteriorly over the nostrils as in *L. japonicus*.

Genetic characters. — At the *PROT-1** locus, at which alleles are totally replaced between *L. japonicus* and *L.* sp. (Yokogawa and Seki, 1995), monomeric heterozygotes appeared frequently (Fig. 5). The fitness of the allelic frequencies at polymorphic loci, including *PROT-1**, according to Hardy-Weinberg equilibria was examined by chi-square tests (Table 3). Because no χ^2 values were significant at the 5% level, the Ariake form was regarded as having originated from a simple Mendelian population.

Average allele numbers per locus, rate of polymorphic loci and average heterozygosity (average rate of heterozygous loci per individual) of the Ariake form, together with values for

L. japonicus and *L.* sp. are shown in Table 4. Compared with *L. japonicus* and *L.* sp., the values of these genetic features in the Ariake form were somewhat higher. In addition, the Ho/He ratio in the Ariake form was greater than 1, indicating an excess of heterozygotes, unlike the situation in *L. japonicus* or *L.* sp. in which excesses of homozygotes were found (Table 4). This showed the Ariake form as having high genetic variation.

The frequency distribution of heterozygosity (rate of heterozygous loci in each individual) in the Ariake form is shown in Figure 6, being a plain binomial distribution. If F_1 hybrids existed in the population, a typical convexity should be recognizable in the high heterozygosity zone (Taniguchi et al., 1985; Macaranas et al., 1986; Yokogawa, 1996). In the present population, however, no evidence of this was apparent.

Allelic frequencies of dotted and non-dotted individuals from the Ariake Sea are shown in Table 5. Although differences in the allelic frequencies between them, following chi-square tests, were not significant because of the low

Table 3. Fitness for Hardy-Weinberg equilibrium by chi-square tests of polymorphic loci in the Ariake form

Locus	Alleles	d. f.[1]	χ^2	p[2]
*sAAT-1**	3	3	0.686	0.877
*ADH**	2	1	1.246	0.264
*GAPDH-1**	2	1	0.006	0.938
*GAPDH-2**	2	1	0.009	0.924
*GPI-1**	2	1	3.358	0.067
*GPI-2**	2	1	0.062	0.803
*sIDDH**	3	3	0.681	0.878
*IDHP**	2	1	0.027	0.870
*LDH**	2	1	0.001	0.975
*sMDH-1**	2	1	0.121	0.728
*sMEP**	3	3	0.111	0.991
*MPI-1**	2	1	1.183	0.277
*PGDH**	3	3	0.026	0.999
*PGM**	3	3	6.060	0.109
*PROT-1**	2	1	0.580	0.446
*sSOD**	2	1	0.006	0.938

[1]Degrees of freedom; [2]risk percentage of chi-square value.

Table 4. Genetic features of the Ariake form, *Lateolabrax japonicus* and *L.* sp.

		Ariake	*L. japonicus*[1]	*L.* sp.[1]
Alleles/Locus		2.100	1.826	1.850
P*		0.500	0.478	0.350
P		0.300	0.130	0.250
P+P*		0.800	0.609	0.600
Average	Ho	0.170	0.113	0.105
Heterozygosity	He	0.158	0.136	0.125
	Ho/He	1.074	0.829	0.840

[1]Data based on Yokogawa and Seki (1995). P*: polymorphism less than 0.95%; P: polymorphism over 0.95%; Ho: observed heterozygosity; He: expected heterozygosity.

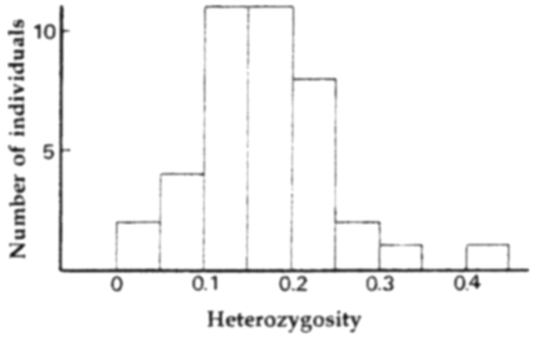

Fig. 6. Frequency distribution of heterozygosity (rate of heterozygous loci in each individual) in the Ariake form.

sample numbers, differences were recognized at the *GPI-1**, *LDH**, and *PROT-1** loci, at which great differentiation has been detected between *L. japonicus* and *L.* sp. (Yokogawa and Seki, 1995). The allelic compositions of these loci in the dotted type had shifted towards those in *L.* sp.

Regarding the pooled allelic frequencies of the Ariake form, at the *PROT-1** locus the frequency of the **170* allele, which occupies the locus in *L.* sp., was 0.213. Although the frequency was therefore closer to that of *L. japonicus*, the value nevertheless fell between those for *L. japonicus* and *L.* sp. Similarly, the pooled allelic frequencies at the *sAAT-1**, *ADH**, *GPI-1**, *sIDDH** and *LDH** loci of the Ariake form fell between those of the two species.

Discussion

Regarding morphological characters, although the Ariake form showed a range between *Lateolabrax japonicus* and *L.* sp. in some of the meristic counts, no general tendency in body proportions was apparent. Because some sea bass proportions are known to change with growth (for example, orbital diameter decreases with growth—Yokogawa and Seki [1995]), exact comparisons of proportions should be made on similarly-sized specimens. At this stage, because morphological characters, including PSAL and head scale development, may also change with growth, further comments on morphological characters cannot be made.

On the other hand, the meristic counts are considered to be generally stable with growth. Therefore, the LLS and GR counts in the Ariake form, which showed intermediate ranges between *L. japonicus* and *L.* sp., can be considered to reflect the former's genetic properties.

As for the genetic characters, pie graphs of allelic frequencies reported in some sea bass populations, including *L.* sp., are shown in Figure 7. Loci included are *ADH**, *GPI-1**, *LDH** and *PROT-1**, in which considerable differences have been recognized between *L. japonicus* and *L.* sp. Although the allelic compositions tended to vary by population in *L. japonicus*, it was clear that the allelic frequencies of the Ariake form differed from the other *L. japonicus* populations.

Although the allelic composition of the Ariake form was generally closer to *L. japonicus* rather than to *L.* sp., it shifted towards that of *L.* sp. at the loci noted above (Fig. 7), suggesting that the Ariake form has been genetically influenced by *L.* sp. However, such has not occurred recently, since there was no evidence of F_1 hybrids (Fig. 6).

L. sp. influence was also apparent in the LLS and GR characters. The occurrence of dots, which is a specific character of *L.* sp., can also be genetically affected, apparently by the same mechanism as operating in *L. japonicus* populations (Yokogawa, 1995).

Figure 8 shows a dendrogram of genetic distances (D values), after Nei (1972), made by the UPGMA method utilizing the sea bass populations shown in Figure 7. Although a criticism, that the numbers of loci based on the D values between the populations were not uniform, might be valid, the dendrogram shape could not have changed very much, even if unexamined allelic frequency data were added, because the allelic compositions of *L. japonicus* populations examined by Tsuda (1989) were similar to those found by Yokogawa and Seki (1995). According to the figure, *L. japonicus* populations, except the Ariake form, formed close clusters, the Ari-

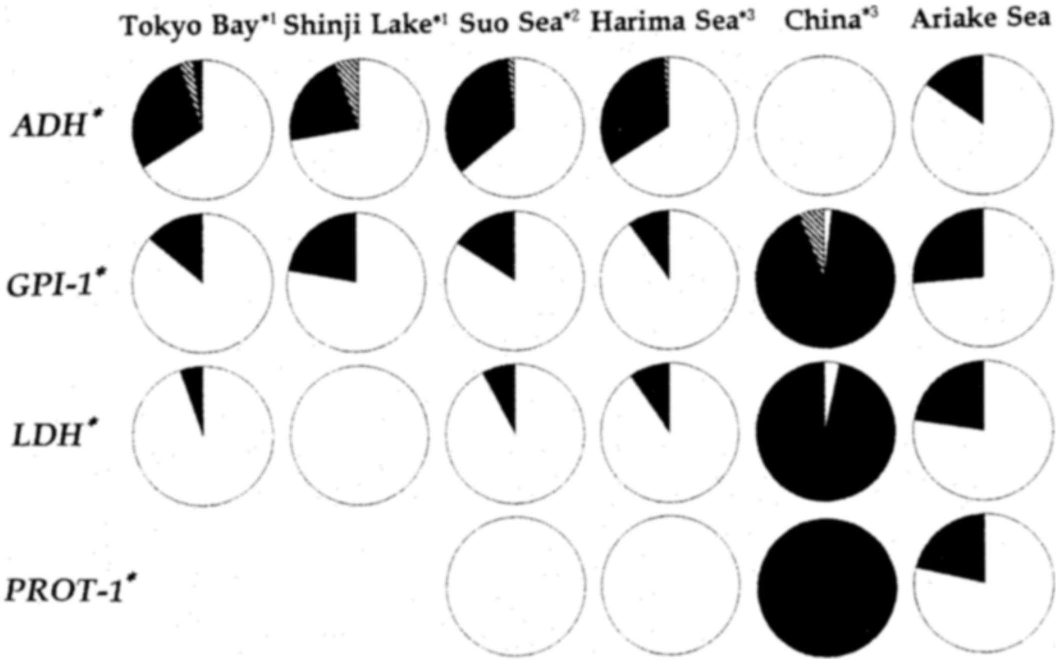

Fig. 7. Pie graph comparisons of allelic frequencies at significant loci in selected sea bass populations. Allelic frequencies given in Table 4. From *1Tsuda (1989); *2Yokogawa unpublished; *3Yokogawa and Seki (1995).

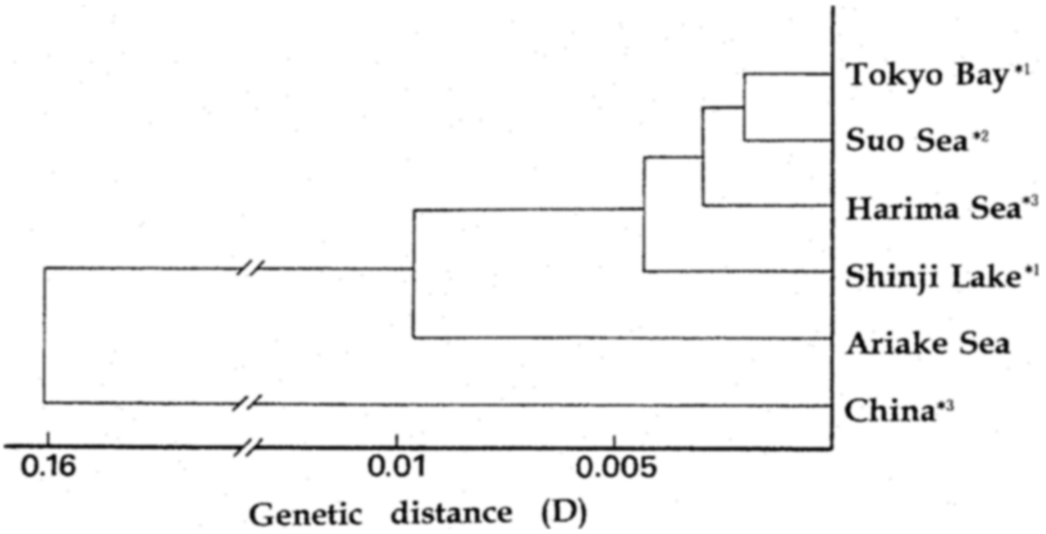

Fig. 8. Genetic distance dendrogram for selected sea bass populations. From *1Tsuda (1989); *2Yokogawa unpublished; *3Yokogawa and Seki (1995). Allelic frequencies at 20 loci, examined by Yokogawa and Seki (1995) and Yokogawa (unpubl.), and 13 loci, not including *PROT-1** examined by Tsuda (1989) were used for the calculation of D values.

ake form being separated from the former by a genetic distance of nearly 0.01 (subspecific level according to Menezes et al. [1990]).

Kinoshita et al. (1995) examined the morphometrics of larval *L. japonicus* from various localities around the Japanese archipelago, finding that the larval Ariake form was significantly different from other *L. japonicus* populations. They considered that the Ariake form was a relict population from the Asian continent, such an opinion being given some support by the present genetic evidence.

In any case, it can be concluded that the Ariake form is independent of other *L. japonicus* populations. Several hypotheses regarding its origin are considered as follows:

Hypothesis 1: *L.* sp. has been introduced into the Ariake Sea artificially, resulting in introgressive hybridization.

Hypothesis 2: During the divergence of *L. japonicus* and *L.* sp. from a common ancestor, an intermediate form has been isolated in the Ariake Sea.

Hypothesis 3: Following the divergence of *L. japonicus* and *L.* sp., the latter secondarily entered the Ariake Sea on single or some occasions, resulting in introgressive hybridization.

Hypothesis 4: After the specific divergence of *L. japonicus* and *L.* sp., population mixing occurred by diastrophism, resulting in introgressive hybridization over a wide area. Thereafter, a hybridized population has been isolated in the Ariake Sea.

Although the relative merits of the hypotheses are difficult to determine, hypotheses 3 and 4 may be the most reasonable.

The Ariake Sea is considered to be a specialized region, including some peculiar animal species and an overall faunal affinity with the Asian continent (Sugano, 1981; Washio et al., 1996). Menezes et al. (1990) examined genetic divergence in some sciaenid fishes, including specimens from the Ariake Sea, finding that the Ariake Sea population of *Nibea albiflora* was distinct from the other populations of that species. The genetic divergence of the Ariake Sea population of *N. albiflora* was supported by significant differences in morphological characters (Takita, 1974), not unlike the situation for the Ariake form of *L. japonicus* found in this study.

Furthermore, it is known that the populations of bluespotted mud hopper, *Boleophthalmus pectinirostris*, and constricted tagelus, *Sinonovacula constricta*, which are typical faunal components of the Ariake Sea, are genetically divergent from populations on the continent (Furukawa et al., 1996; Y. Natsukari, pers. comm.). Such genetic divergences are also supported by significant differences in morphological characters (Koga, 1993; Yoshimoto, 1994).

Such evidence suggests that the faunal population in the Ariake Sea has been isolated for a considerable time; that is, that the Ariake Sea itself has been isolated from other water bodies.

In the case of the sea bass, it appears reasonable to propose that *L. japonicus* and *L.* sp. populations became mixed at some time, the resulting introgressively-hybridized population being subsequently isolated in the Ariake Sea. This possibility is supported by the considerable genetic variation in the Ariake form (Table 4).

It may be significant that theoretical hybridization of *L.* sp. with *L. japonicus* with a rate of 0.213 (the **170* allele frequency at the *PROT-1** locus in the Ariake form [Table 5]), results in expected allelic frequencies at loci for the markers shown in Figure 7, being fairly close to those found in the Ariake form.

However, the theoretical allelic frequencies at some other loci, such as *IDHP** and *PGM**, do not correspond with those of the Ariake form. To explain this conflict, some possibilities were considered. It is unknown at this time when introgressive hybridization occurred. Should the allelic frequencies at some loci of either or both species at that time have differed from those of the modern forms, the hybridized allelic frequencies would also have differed from the theoretical values given here.

On the other hand, some genetically-independent populations of *L.* sp. may also exist, with a population distinct from the specimens examined by Yokogawa and Seki (1995) hybridizing with *L. japonicus*. In fact, Yokogawa and Tajima (1996) reported that the Taiwanese form of *L.* sp. was somewhat divergent both morphologically and genetically from the Chinese form, supporting the above suggestion. However, more information, not only supporting hybridization but also clarifying its process exactly is necessary.

Table 5. Allelic frequencies of the Ariake form (dotted and non-dotted types), *Lateolabrax japonicus* and *L.* sp.

Locus	Allele	Frequency				
		Ariake			*L. japonicus*[1]	*L.* sp.[1]
		Dotted	Non-dotted	Pooled		
sAAT-1*	*100	0.865	0.917	0.882	0.792	0.981
	*85	0.135	0.042	0.105	0.208	0.019
	*65	0.000	0.042	0.013	0.000	0.000
sAAT-2*	*−100	1.000	1.000	1.000	1.000	1.000
ADH*	*−50	0.000	0.000	0.000	0.011	0.000
	*−100	0.833	0.885	0.850	0.659	1.000
	*−150	0.167	0.115	0.150	0.330	0.000
GAPDH-1*	*100	0.981	1.000	0.988	1.000	1.000
	*85	0.019	0.000	0.013	0.000	0.000
GAPDH-2*	*100	0.972	1.000	0.982	0.986	1.000
	*−200	0.028	0.000	0.018	0.014	0.000
GPI-1*	*130	0.000	0.000	0.000	0.000	0.060
	*110	0.278	0.231	0.263	0.100	0.922
	*100	0.722	0.769	0.737	0.900	0.018
GPI-2*	*−100	0.942	1.000	0.962	0.937	0.940
	*−250	0.058	0.000	0.038	0.063	0.060
sIDDH*	*165	0.096	0.154	0.115	0.037	0.200
	*100	0.885	0.846	0.872	0.963	0.800
	*−50	0.019	0.000	0.013	0.000	0.000
IDHP*	*120	0.019	0.038	0.026	0.000	0.000
	*100	0.981	0.962	0.974	0.912	0.588
	*70	0.000	0.000	0.000	0.088	0.412
LDH*	*100	0.259	0.154	0.225	0.097	0.966
	*−100	0.741	0.846	0.775	0.903	0.034
sMDH-1*	*100	0.960	0.917	0.946	0.986	1.000
	*70	0.040	0.083	0.054	0.014	0.000
sMDH-2*	*−100	1.000	1.000	1.000	1.000	1.000
sMEP*	*150	0.037	0.038	0.038	0.079	0.050
	*100	0.944	0.962	0.949	0.886	0.900
	*50	0.019	0.000	0.013	0.035	0.050
MPI-1*	*125	0.357	0.444	0.383	0.306	0.363
	*100	0.643	0.556	0.617	0.694	0.638
MPI-2*	*100	1.000	1.000	1.000	1.000	0.987
	*75	0.000	0.000	0.000	0.000	0.013
PGDH*	*120	0.000	0.038	0.013	0.000	0.011
	*100	0.981	0.962	0.974	1.000	0.989
	*55	0.019	0.000	0.013	0.000	0.000
PGM*	*115	0.000	0.000	0.000	0.021	0.060
	*100	0.370	0.346	0.363	0.465	0.500
	*75	0.611	0.654	0.624	0.507	0.431
	*55	0.019	0.000	0.013	0.007	0.009
PROT-1*	*170	0.259	0.115	0.213	0.000	1.000
	*100	0.741	0.885	0.787	1.000	0.000
PROT-2*	*100	1.000	1.000	1.000	1.000	1.000
sSOD*	*145	0.000	0.038	0.013	0.000	0.000
	*100	1.000	0.962	0.987	1.000	0.964
	*20	0.000	0.000	0.000	0.000	0.036

[1] Data from Yokogawa and Seki (1995).

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