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Genetic Divergence and Morphological Difference between the Spotted and Common Mackerel

Akihiro Kijima, Nobuhiko Taniguchi and Akira Ochiai

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Abstract Three types of mackerel, *Scomber* species, the typical spotted, non-spotted and their intermediate types collected from three locations in the adjacent waters of Japan were analyzed by starch gel electrophoresis and examined for some morphometric and meristic characters. Clear genetic differences between the typical spotted and non-spotted were observed at six loci, i.e. *αGpd-B*, *Idh-A*, *Ldh-A*, *Sod*, *Hem-1* and *Hem-2*, out of the 23 loci examined. The intermediate individuals genetically belong to either the spotted or non-spotted type and a genetical hybrid possessing both kinds of allele from the two typical types was not observed at all. These three types could be divided into two groups. Average genetic distances for intra- or inter groups were estimated as 0.006 and 0.414, respectively. Two morphological characters, the length of separated anal spine and the number of interneurai spines associated with the first dorsal fin spine, were found to be significant character separating the two groups. From the above results, the two groups of mackerel were clearly divided into two separate species, *Scomber australasicus* and *S. japonicus*.

It is well known that the two kinds of mackerel, common and spotted are captured around the waters of southern Japan and its adjacent areas. They are generally distinguished by the presence or absence of blackish spots on both lateral sides and the abdominal area. Though the occurrence of spotted mackerel ranges in more southern areas than that of common mackerel, both kinds are often captured at the same time and location in southern Japan. The number, size and distribution of the blackish spots, however, strongly varied within a kind obtained from the same area (Tamura and Ko, 1955; Murakami and Hayano, 1956). Tamura and Ko (1955) revealed that the number of gill rakers on the first gill arch were more numerous in common mackerel than in spotted mackerel, but their distribution overlapped to a high degree in the intermediate type. Murakami and Hayano (1956) indicated that the number of interneural spines associated with the first dorsal spine to the front of first ray of second dorsal fin was a useful characteristic for dividing two kinds. However, in the intermediate type, the number of interneural spines was observed to vary from one kind to the other. Moreover, many morphological and meristic characters also gave no clear distinction.

Fraser-Brunner (1950) identified the two kinds as variation within one species. Abe and Takashima (1958) also recognized them as one species involving two subspecies. On the other hand, Matsubara (1955) divided them into two separate species based on the number of first dorsal fin spines, scales on the lateral line and body shape. Matsui (1967) reviewed the differences between both kinds and recognized two species, *Scomber australasicus* and *S. japonicus*.

If the two kinds of mackerel are completely independent in reproduction, each should have different alleles as a result of long evolutional isolation. Several studies on allele distribution as detected by electrophoresis revealed genetic divergence among fish species. Johnson *et al.* (1972) surveyed muscle protein and six enzymatic systems of thirty-one species of scorpaenids belonging to three genera, and became first to analyze genetical relationships among them with alleles coded for isozymes. Examining the electrophoretically detectable alleles, Johnson (1975) clearly divided the atherinid fish genus *Menidia* into five species. Buth and Burr (1978) and Buth (1977, 1979, 1980) reported relationships between species in the genus *Campostoma*, *Moxostoma*, *Hypentelium* also based on comparisons of isozyme markers. In *Scomber scombrus* twenty enzymes and three non-enzymatic proteins were examined and 39 isozymic loci were detected (Smith and Jamieson, 1980). Isozymes have been considered as useful markers to estimate relationships among species and to determine taxonomic rank.

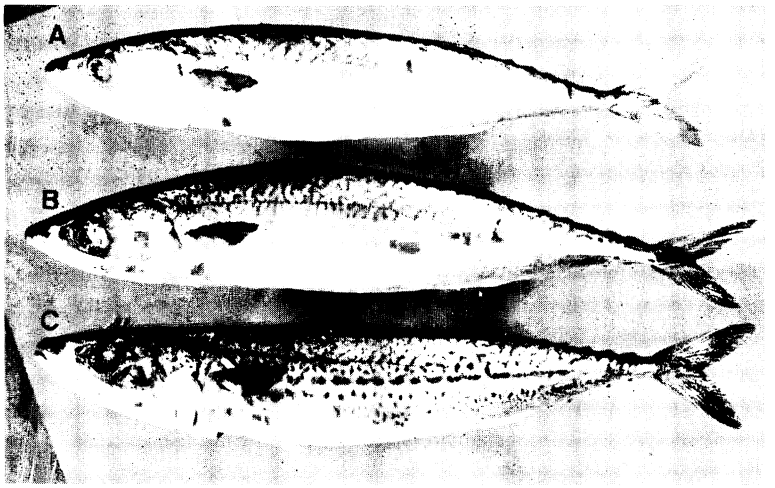

Fig. 1. Specimens of three types of mackerel examined. A, the typical non-spotted type collected from Tei; B, intermediate from Misaki; C, typical spotted type from Muroto.

Taniguchi (1974) did not observe a difference in electrophoretic pattern in the sarcoplasmic protein system of the two kinds of mackerel. The aims of the present study are: to clarify the relationship between the two kinds of mackerel and their intermediates, to estimate the degree of genetic divergence between them by using isozyme markers, and to reexamine morphological characters.

Materials and methods

Materials examined here were collected from Muroto and Tei, Kochi Prefecture, and Misaki, Kanagawa Prefecture, the Pacific coast of Japan, as shown in Table 1. These specimens were classified into three types by the blackish spots on lateral sides of the abdomen as follows: (A) the typical non-spotted type; (B) the intermediate type having no clear spots or small in size and/or having few spots; and (C) the typical spotted type having clear spots, as shown in Fig. 1. The *typical* non-spotted type was collected from off Misaki and Tei, whereas the other two types from off Muroto and Misaki in the same trap (Table 1). Samples were frozen immediately after catching and stored at less than −20°C until tested.

Table 1. Number and date of collection of the specimens analyzed.

Type	Collection localities		
	Tei	Muroto	Misaki
Date (1984)	13 June	18 June	13 Sep.
Typical non-spotted	50	0	2
Typical spotted	0	44	4
Spotted-intermediate	0	6	8

For the phenotypic analysis, the cell-lysate obtained by freezing and thawing were directly subjected to electrophoresis. Starch gel electrophoresis was carried out by the procedures reported by Taniguchi and Numachi (1978) and Sumantadinata and Taniguchi (1982). Eleven enzymes and two non-enzymatic proteins; alcohol dehydrogenase (ADH), alpha-glycerophosphate dehydrogenase (αGPD), aspartate aminotransferase (AAT), glucosephosphate isomerase (GPI), isocitrate dehydrogenase (IDH), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), malic enzyme (ME), phosphoglucomutase (PGM), sorbitol dehydrogenase (SDH), superoxide dismutase (SOD), sarcoplasmic protein (SP) and haemoglobin (HEM), were detected in muscle, liver, heart and eye as shown in Table 2.

Morphometric characters were measured before formalin fixation. Different proportions to its standard length (SL), such as: head length (HL/SL); body depth (BD/SL); body width (BW/SL); snout length (LS/SL); distance from the tip of the snout to first dorsal fin (1D/SL); to second dosal fin (2D/SL), to pectoral fin (PF/SL), to pelvic fin (PL/SL), to anal fin (AF/SL); length of first dorsal fin base (1DB/SL), second dorsal fin base (2DB/SL), pectoral fin base (PFB/SL), pelvic fin base (PLB/SL), anal fin base (AFB/SL), caudal fin base

(CB/SL); length of spine in anal fin (SA/SL); and eye diameter (ED/SL), were compared. Meristic characters, such as the number of dorsal spines (DS), dorsal rays (DR), pectoral rays (PR), pelvic spine (PLS), pelvic rays (PLR), and anal spines (AS), anal rays (AR), fin-lets (FL), gill rakers on the first gill arch (GR), interneural spines (IS) associated from the first dorsal fin spines to the anterior of second dorsal ray, and vertebrae (VT) were examined after fixing in 10% formalin solution. The number of gill rakers, interneural spines and vertebrae were counted after staining with about 0.01% alizarin red S solution.

Allelic frequencies were directly calculated from phenotypes. Chi-square tests were performed for the distribution of phenotypes with a Hardy-Weinberg equilibrium. Genetic distance was calculated by the formula proposed by Nei (1972) for estimating a degree of genetic divergence. Alleles were numbered consecutively as *A*, *B*, *C*, . . . from the most anodal to the most cathodal.

Results

Genetic characters. Results of the starch gel electrophoresis examined in the typical spotted and the typical non-spotted types of mackerel for eleven enzymes and two non-enzymatic proteins are summarized in Table 2.

The ADH activity appeared in liver and one band migrating to the cathode was observed at high frequency in both types, suggesting a common allele in *Adh* locus.

There were two zones of αGPD activity of which one is distributed in muscle and the other in liver. Two loci, *αGpd-A* and *αGpd-B*, were assumed for these two isozymes. In muscle, a band migrating at the same location to the cathode was observed in both types, suggesting these two have a

Table 2. Enzyme systems and tissues analyzed, electrophoretic buffer used, genetic loci coding to each enzyme systems and their genetic differentiation. C-AEA and C-APM represent citrate-aminopropyl diethanol amine buffer (pH 7.0) and citrate-aminopropyl morpholine buffer (pH 6.0), respectively. ND and D represent non-divergent locus and divergent locus, respectively.

Enzyme	Isozyme	Tissue	Buffer-system	Locus	Note
ADH	ADH	liver	C-AEA	*Adh*	ND
αGPD	αGPD-A	muscle	C-APM	*αGpd-A*	ND
	αGPD-B	liver	C-AEA	*αGpd-B*	D
AAT	AAT-A	liver	C-AEA	*Aat-A*	ND
	AAT-B	liver	C-AEA	*Aat-B*	ND*
GPI	GPI-A	heart	C-AEA	*Gpi-A*	ND
	GPI-B	heart	C-AEA	*Gpi-B*	ND
IDH	IDH-A	muscle	C-AEA	*Idh-A*	D
	IDH-B	liver	C-AEA	*Idh-B*	ND
LDH	LDH-A	eye	C-AEA	*Ldh-A*	D
	LDH-B	eye	C-AEA	*Ldh-B*	ND
	LDH-E	eye	C-AEA	*Ldh-E*	ND
MDH	MDH-A	muscle	C-APM	*Mdh-A*	ND
	MDH-B	heart	C-AEA	*Mdh-B*	ND
	mMDH	muscle	C-APM	*mMdh*	ND
ME	ME-A	muscle	C-AEA	*Me-A*	ND
	ME-B	muscle	C-AEA	?	?
PGM	PGM	liver	C-AEA	*Pgm*	ND*
SDH	SDH	liver	C-AEA	*Sdh*	ND
SOD	SOD	liver	C-AEA	*Sod*	D
SP	SP-1	muscle	C-APM	*Sp-1*	ND
	SP-2	muscle	C-APM	?	?
	SP-3	muscle	C-APM	?	?
	SP-4	muscle	C-APM	*Sp-4*	ND
HEM	HEM-1	heart	C-AEA	*Hem-1*	D
	HEM-2	heart	C-AEA	*Hem-2*	D

* Reversible frequency of allele in the locus.

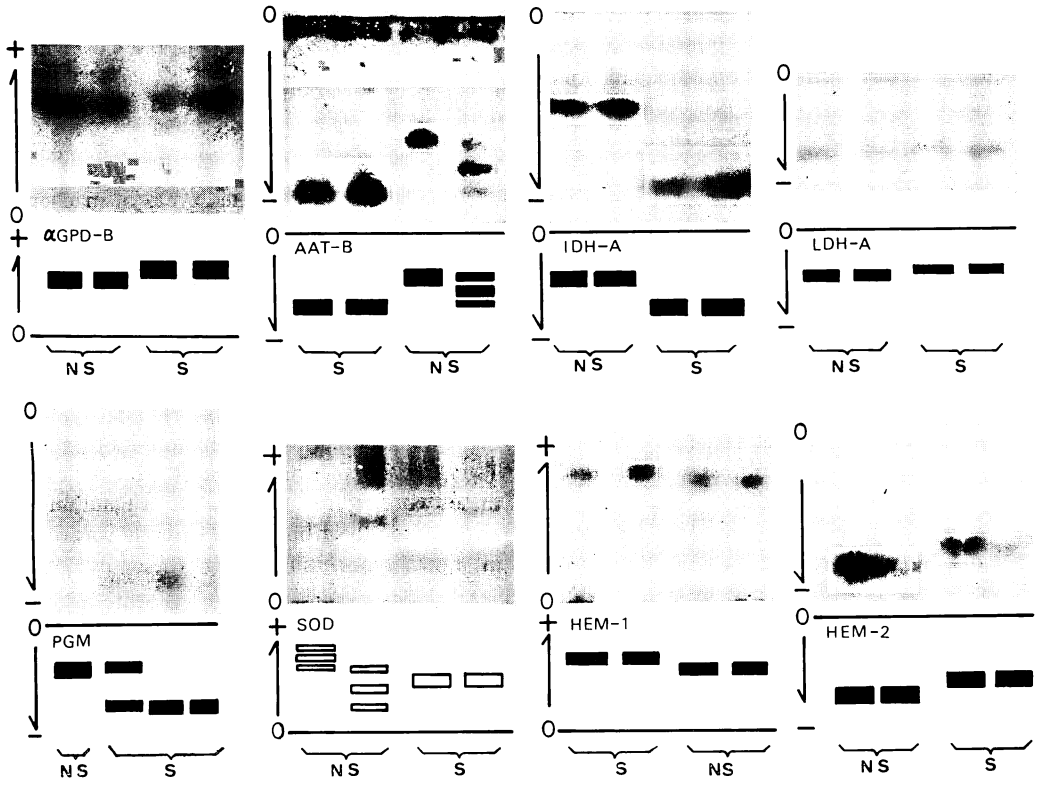

Fig. 2. Electrophoretic patterns of the typical spotted and non-spotted types of mackerel. NS, typical non-spotted; S, typical spotted.

common allele at the *αGpd-A* locus. The other isozyme found in liver was apparently different in the electrophoretic mobilities between the two types, migrating faster in spotted type than in non-spotted type. No heterozygote between them was observed, suggesting hybrids of these two types have not yet been observed so far (Fig. 2).

The AAT activity was found only in liver and appeared in two zones, one migrating to anode and the other to cathode. These were assumed under the two distinct loci, *Aat-A* and *Aat-B*. In *Aat-A*, both types were fixed with an identical gene. Frequencies of *B* allele at the *Aat-B* were significantly higher in the spotted than in the non-spotted, though they had the same allele at low frequency as shown in Fig. 2 and Table 3.

In heart, GPI activity appeared also in two zones, of which one band migrated to anode and the other to cathode, being coded by *Gpi-A* and *Gpi-B* loci, respectively. Genetic differences have not been observed on these loci.

Appearence of IDH activity was also in two zones, one in muscle coded by *Idh-A* and the other in liver coded by *Idh-B*. Of the *Idh-A*, a fixed allele was supposed to be found in the spotted type, and this should be different from the fixed allele in the non-spotted type, as shown in Fig. 2. On the other hand, a common allele was observed at *Idh-B* which appeared only in liver.

The LDH activity in eye appeared in three zones. The two migrated to the anode (loci *Ldh-B* and *Ldh-E*) and the other to the cathode (locus *Ldh-A*). The *Ldh-B* and *Ldh-E* were fixed with a common allele in both types. In *Ldh-A*, an allele that appeared in the spotted was different from an allele in the non-spotted, as shown in Fig. 2.

The MDH activity appeared in three zones in muscle (loci *Mdh-A* and *mMdh*) and heart (loci *Mdh-B*). Genetic divergence and variation were not observed.

There were two zones in ME activity, assumed to be under two loci, *Me-A* and *Me-B*. The faster migrating band coded by *Me-B* was not so

Table 3. Allele frequencies at 23 loci in six lots of the three types of mackerel.

Locus	Allele	Group I				Group II	
		Typical non-spotted		Intermediate		Typical spotted	
		Tei	Misaki	Muroto	Misaki	Muroto	Misaki
Adh	*A*	0.020	0.000	0.000	0.000	0.045	0.375
	B	0.980	1.000	1.000	1.000	0.955	0.500
	C	0.000	0.000	0.000	0.000	0.000	0.125
αGpd-A	*A*	1.000	1.000	1.000	1.000	1.000	1.000
αGpd-B	*A*	0.000	0.000	0.083	0.000	0.000	0.000
	B	0.000	0.000	0.000	1.000	1.000	1.000
	C	1.000	1.000	0.917	0.000	0.000	0.000
Aat-A	*A*	1.000	1.000	1.000	1.000	1.000	1.000
Aat-B	*A*	0.760	0.750	0.750	0.063	0.000	0.125
	B	0.240	0.250	0.250	0.937	0.989	0.875
	C	0.000	0.000	0.000	0.000	0.011	0.000
Gpi-A	*A*	0.030	0.000	0.083	0.000	0.000	0.000
	B	0.000	0.000	0.000	0.063	0.023	0.000
	C	0.970	1.000	0.917	0.937	0.966	1.000
	D	0.000	0.000	0.000	0.000	0.011	0.000
Gpi-B	*A*	0.770	0.750	0.583	1.000	0.989	1.000
	B	0.000	0.000	0.000	0.000	0.011	0.000
	C	0.230	0.250	0.417	0.000	0.000	0.000
Idh-A	*A*	1.000	1.000	1.000	0.000	0.000	0.000
	B	0.000	0.000	0.000	1.000	1.000	1.000
Idh-B	*A*	0.000	0.000	0.000	0.000	0.011	0.000
	B	1.000	1.000	1.000	1.000	0.989	1.000
Ldh-A	*A*	0.000	0.000	0.000	1.000	1.000	1.000
	B	1.000	1.000	1.000	0.000	0.000	0.000
Ldh-B	*A*	1.000	1.000	1.000	1.000	1.000	1.000
Ldh-E	*A*	1.000	1.000	1.000	1.000	1.000	1.000
Mdh-A	*A*	1.000	1.000	1.000	1.000	1.000	1.000
Mdh-B	*A*	1.000	1.000	1.000	1.000	1.000	1.000
mMdh	*A*	1.000	1.000	1.000	1.000	1.000	1.000
Me-A	*A*	0.000	0.000	0.000	0.000	0.011	0.000
	B	0.990	1.000	1.000	1.000	0.989	1.000
	C	0.010	0.000	0.000	0.000	0.000	0.000
Pgm	*A*	1.000	1.000	1.000	0.000	0.011	0.000
	B	0.000	0.000	0.000	1.000	0.989	1.000
Sdh	*A*	0.000	0.000	0.000	0.063	0.000	0.000
	B	0.010	0.000	0.000	0.187	0.125	0.375
	C	0.010	0.000	0.083	0.000	0.011	0.000
	D	0.980	1.000	0.917	0.750	0.864	0.625
Sod	*A*	0.050	0.250	0.083	0.000	0.000	0.000
	B	0.400	0.500	0.167	0.000	0.000	0.000
	C	0.000	0.000	0.000	1.000	1.000	1.000
	D	0.010	0.000	0.000	0.000	0.000	0.000
	E	0.540	0.250	0.750	0.000	0.000	0.000
Sp-1	*A*	1.000	1.000	1.000	1.000	1.000	1.000
Sp-2	*A*	1.000	1.000	1.000	1.000	1.000	1.000
Hem-1	*A*	0.000	0.000	0.000	1.000	1.000	1.000
	B	1.000	1.000	1.000	0.000	0.000	0.000
Hem-2	*A*	0.000	0.000	0.000	1.000	1.000	1.000
	B	1.000	1.000	1.000	0.000	0.000	0.000

Table 4. Genetic distance between every pair of six lots of three types under the diagonal and its mean values of lots within and between groups above the diagonal.

	Group lot	Group I			Group II		
		Typical non-spotted		Intermediate		Typical spotted	
		Tei	Misaki	Muroto	Misaki	Muroto	Misaki
I	Tei						
	Misaki	0.000		0.005		0.414	
	Muroto	0.003	0.011				
II	Misaki	0.405	0.402	0.415			
	Muroto	0.405	0.402	0.415	0.001		0.008
	Misaki	0.425	0.424	0.437	0.011	0.011	

stable that the locus was not counted the alternative calculation, while the slower band coded by *Me-A* was stable. Genetic difference at *Me-A* was not observed.

Typical monomeric patterns were demonstrated in PGM activity in liver which were coded by two alleles at *Pgm* locus. All individuals of the non-spotted had *A* allele, while all of the spotted had *B* allele except for one in the spotted from Muroto which exhibited a heterozygote of *A*/*B* as shown in Fig. 2.

The SDH activity appeared as typical tetrameric patterns in liver, expressing the presence of four alleles at *Sdh* locus. Genetic divergence was not observed between the two kinds.

The SOD activity in liver appeared in the typical dimeric pattern, expressing the presence of five alleles (*A*, *B*, *C*, *D*, *E*) at *Sod* locus. Of the five alleles the *C* allele was observed and fixed in spotted alone, whereas the other four alleles were in non-spotted type, as shown in Fig. 2. This indicated a genetic divergence between the two kinds.

The SP activity in muscle appeared in four zones migrating to cathode, being coded by four loci, *Sp-1*, *Sp-2*, *Sp-3* and *Sp-4*. The *Sp-1* and *Sp-4* were monomorphic and a genetic divergence was not observed. The *Sp-2* and *Sp-3* were omitted from the scoring because these were not stable.

Two zones of HEM bands were observed in blood. The anodal and cathodal bands were supposed to be coded by the *Hem-1* locus and the *Hem-2* locus. A genetic divergence was observed in both loci (Fig. 2).

Phenotype frequencies of the two lot samples, one sample of the typical spotted type from Muroto and another of the typical non-spotted type from Tei (Table 1), were in fair agreement with the Hardy-Weinberg equilibrium in all of the polymorphic systems analyzed. The proportion of polymorphic loci at less than 0.99 in maximum allele frequency was 0.348 and at less than 0.95 was 0.043 in the typical spotted from Muroto, whereas in the typical non-spotted from Tei the values were 0.304 and 0.130, respectively. The average heterozygosities observed (H^{obs}) and expected (H^{exp}) were 0.022 and 0.022 in the spotted from Muroto, while in the non-spotted from Tei, these were 0.057 and 0.062, respectively. The non-spotted was more variable than the spotted.

The intermediate individuals collected from Misaki and Muroto as well as the two typical types were analyzed by electrophoresis. The allele frequencies of the six lots of three types are summarized in Table 3. As shown in Table 3, the intermediate individuals from Muroto had identical alleles and showed similar allelic frequency pattern to the typical non-spoted at all loci. On the other hand, the intermediate individuals from Misaki were similar to the typical spotted at all loci. A genetical hybrid which had both kinds of allele of the two typical types at the genetically divergent loci was not observed at all in the present study. The intermediate individuals could be classified into either typical spotted or non-spotted type. This indicated that the six lots of the three types tested were clearly divided into two groups, one was the typical spotted and intermediate from Misaki (Group I), and the other was the typical non-spotted and intermediate from Muroto (Group II).

To estimate the degree of genetic divergence among locations of the three types of the two

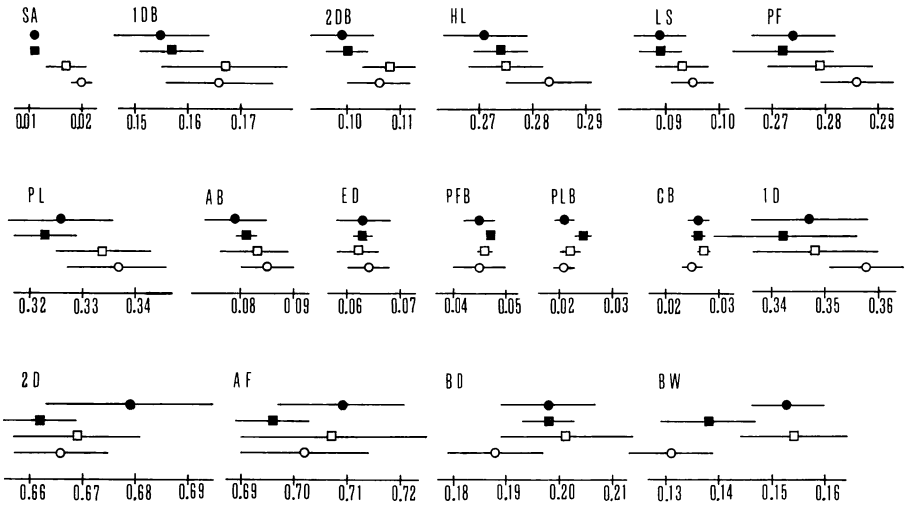

Fig. 3. Morphometric characters in the typical non-spotted from Tei (○), typical spotted (●), and intermediate from Muroto (□) and Misaki (■). (○) and (□) belong to Group I, (●) and (■) to Group II. The spotted-intermediate individuals from Muroto were captured at the same time with the typical spotted.

groups, genetic distance was calculated. Genetic distance ranged from 0.001 to 0.011 (0.008 average) in Group I, and from 0.000 to 0.011 (0.005 average) in Group II. On the other hand, genetic distance between lots of two groups ranged from 0.402 to 0.437 (0.414 average) as shown in Table 4. Genetic distance was considerably higher between groups than within a group. The above results strongly indicate that the two kinds of mackerel are clearly divided into two species and the intermediate types belong to either spotted or non-spotted mackerel.

Morphological characters. Eighteen morphometric and twelve meristic characters were measured or counted for each individual in the typical spotted from Muroto and intermediate types from Misaki belonging to Group I, and in the typical non-spotted from Tei and intermediate from Muroto belonging to Group II. These characters were compared between groups as shown in Figs. 3 and 4.

Morphometric characters. The length of separated anal spine of the typical spotted was significantly shorter than that of the typical non-spotted. The length of the first dorsal fin base (1DB), second dorsal fin base (2DB), head length (HL), snout length (LS), snout to pectoral fin (PF), snout to pelvic fin (PL), snout to first dorsal fin (1D), and anal fin base (AB) tended to be smaller in the typical spotted than in the typical non-spotted, though no significant differences were observed between them. The length of snout to second dorsal fin (2D) and to anal fin (AF), body depth (BD) and body width (BW) deviated in a broad range and tended to be larger in the typical spotted than in the typical non-spotted. Eye diameter (ED), length of pectoral fin base (PFB), pelvic fin base (PLB) and caudal fin base (CB) deviated in a narrow range in both types and no tendency of one being larger or smaller than the others was observed.

In the intermediate individuals from Misaki (Group I) and Muroto (Group II), SA, 1DB and 2DB values were similar to those in each typical type, respectively. HL, LS, PF, PL, AB, 1D, 2D, AF, BD, and BW showed values found between the two typical types or nearer to another group rather than its own group. The ED, PFB, PLB and CB deviated in a narrow range and showed similar values for all types.

Meristic characters. Seven out of eleven meristic characters, such as, the number of dorsal rays (12), pelvic spine and rays (I+5), anal spine and rays (I, I+11), finlets (5+5) and vertebrae (14+17) were stable and observed to be same in both types. The number of pectoral rays in the typical spotted was slightly fewer than in the typical non-spotted, but greatly overlapped at 20. The num-

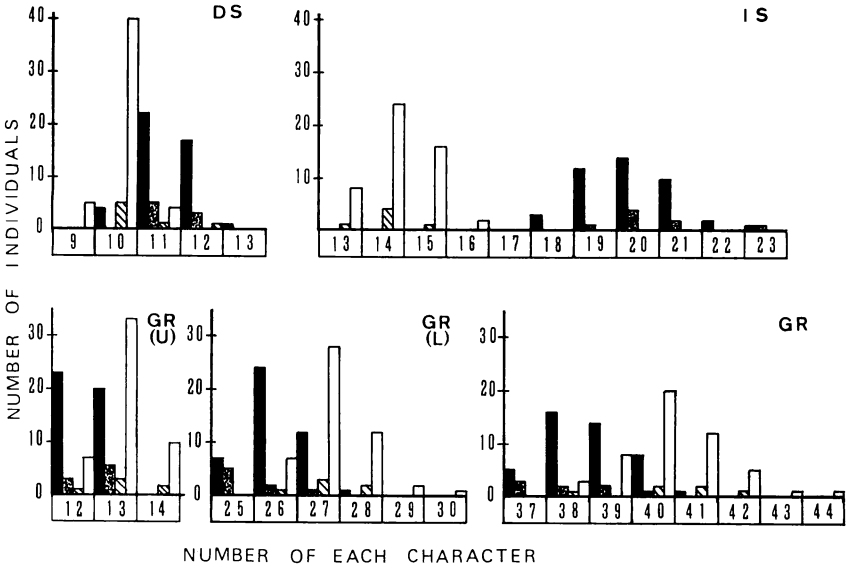

Fig. 4. The distribution of meristic characters of the number of dorsal spines (DS), interneural spines (IS) and gill rakers (GR) (U, upper; L, lower branch). □ and ▨ represent typical non-spotted from Tei and spotted-intermediate from Muroto belonging to Group I. ■ and ▩ represent typical spotted from Muroto and intermediate from Misaki belonging to Group II.

ber of dorsal spines in the typical spotted ranged from 10 to 13 whereas in the typical non-spotted from 9 to 12 as shown in Fig. 4. The number of interneural spines (IS) in the typical spotted was more than 18, whereas in the typical non-spotted less than 16, indicating a clear morphological divergence. The number of gill rakers on the first upper branch in the typical spotted was slightly fewer in number than in the typical non-spotted, although an overlap was observed.

In the intermediate, the number of DR, PLS, PLR, AS, AR, FL and VT were also stable and identical in number for all types. In other meristic characters such as DS, IS, PR and GR, the intermediate individuals showed similar distribution to its own Group (I or II) as shown in Fig. 4.

Discussion

Differences in morphological characters between the common and spotted mackerel were found in the length of anal spine, in the number of first dorsal fin spines, the number of interneural spines associated with the first dorsal spines and gill rakers by several authors (Table 5). The length of anal spine of common mackerel was significantly conspicuous compared with spotted mackerel, as shown by Matsui (1967). This character could be a good external taxonomic character. The number of the first dorsal fin spines showed a clear tendency to be lower in common than in spotted mackerel, though the frequency of the character overlapped at the range of 10 to 12. The number of the first dorsal fin spines in the intermediate individuals were not always observed to be in between the two kinds. The tendency to have greater number of gill rakers by the common as compared to spotted mackerel was in accordance with the present study, though the distribution was wide. There was no tendency to have larger or smaller number of gill rakers in the intermediate individuals. The number of interneural spines was much more numerous in spotted than in common mackerel in all previous reports as well as in the present study. Murakami and Hayano (1956) observed the two peaks in the intermediate individuals.

Although considerable morphological differences between the two kinds of mackerel were observed, there are two interpretations in taxonomic rank for them; 1) two separate species (Matsubara, 1955; Matsui, 1967) or 2) two subspecies in one species (Fraser-Brunner, 1950; Abe

Table 5. Differences in meristic characters between two kinds of mackerel.

Character	Spotted	Common	Note	Reference
The length of anal spine	not as conspicuous as common	conspicuous		Matsui (1968)
Number of first dorsal spines	11–12	9–10		Matsubara (1955)
	10–13	9–11	9–12 in intermediate	Tamura and Ko (1955)
	12<	10>	overlapped at 11	Abe and Takashima (1958)
	10–13	9–10		Matsui (1968)
				Collette and Nauen (1983)
Number of gill rakers (lower branch)	24–26	27<	the probavility for error: 3–8%	Tamura and Ko (1958)
Number of interneural spines	17–23	12–16	two peaks in intermediate	Murakami and Hayano (1956)
	17–22	13–17		Abe and Takashima (1958)
	15–20	12–15		Matsui (1968)*

* Matsui (1968) explained that the difference of the number in the above reports was due to usage of different methods of counting.

and Takashima, 1958). One of the factors confusing taxonomic rank of the two mackerels may be caused by the existence of many intermediate individuals concerned with color pattern.

A species is defined as "groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr, 1969). In addition, due to isolation for a long evolutional generation a group would become independent of the other group genetically, different alleles would be acclimated and then become a different genetic composition. The genetic compositions can be easily revealed by electrophoretically detectable isozyme markers and genetic divergences between populations or species can also be calculated based on these marker genes (Nei, 1972).

Several studies on genetic divergence for freshwater fishes based on Nei's genetic distance calculated from electrophoretic data have been conducted. Average genetic distance between species was reported as 0.627 in 10 species of genus *Lepomis* (Avice and Smith, 1974a, b), 0.421 in 5 species of *Menidia* (Johnson, 1975), 0.214 in 2 species of *Moxostoma* (Buth, 1977), 0.229 in 3 species of *Campostoma* (Buth and Burr, 1978), 0.251 in 7 species of *Notropis* (Buth, 1979), and 0.243 in 3 species of *Hypentelium* (Buth, 1980), based on more than 14 isozymic loci. Average genetic distances between populations in the species were also reported as 0.004 in *Moxostoma*, 0.020 in *Campostoma*, 0.010 in *Notropis*, and 0.019 in *Hypentelium*. A completely genetic divergence was observed in at least one locus between species. In the present study the genetic distance between groups ranged from 0.402 to 0.425, and within groups from 0.000 to 0.011. This indicates that the value between the two kinds is considered as the species level.

There is one problem on whether the individuals showing intermediate morphological characters are hybrids between two kinds of mackerel. Generally, natural hybridization and introgression between species shows high average heterozygosity in the hybrid individuals (Fujio, 1977; Taniguchi *et al.*, 1985). The clear division of the two groups in the morphological intermediate from Misaki and Muroto was observed but higher average heterozygosity was not observed. Moreover, complete genetic divergence was observed at 6 loci between the two groups. These facts strongly indicate that the intermediate individuals in morphological characters were not genetic hybrids, and genetic introgression has not yet occurred between the two kinds. We conclude that the two kinds are the two distinct species, *Scomber australasicus* and *S. japonicus*.

The differences between the intermediate and typical spotted from Muroto captured at the same time were species-specific morphological characters. The lengths of SA, 1DB and 2DB of the intermediate from Muroto were about the

same as those of the typical non-spotted from Tei. Therefore these characters were considered as species-specific characters. On the other hand, HL, LS, PF, PL, 1D, AB, 2D, AF, BD and BW were considered as characters fluctuated by living environments depending on the fact that values for the intermediate from Muroto were between the typical non-spotted from Tei and typical spotted from Muroto and/or nearer to the typical spotted.

There are many problems on species-relationship between populations, subspecies or species like the present study. Electrophoretically detectable isozymic allele are not only useful markers to investigate these problem, but also to estimate the considerarable morphological character for taxonomy.

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(Department of Cultural Fisheries, Faculty of Agricul-

ture, Kochi University, Nankoku, Kochi 783, Japan)

マサバとゴマサバの遺伝的分化と形態的差異

木島明博・谷口順彦・落合　明

多くの形態形質値の分布が重なり，体側腹部の小黒斑の性状に種々の中間型がみられるマサバとゴマサバについて，アイソザイム遺伝子を標識にして遺伝的分化の程度を調べた．その結果，遺伝子座のうち，*αGpd-B*, *Idh-A*, *Ldh-A*, *Sod*, *Hem-1* 及び *Hem-2* の6遺伝子座において完全な遺伝的分岐が認められた．これらの遺伝子座において，中間型はマサバまたはゴマサバの何れかと同じ組成を示した．さらに遺伝的距離は中間型を含めてグループ内で平均 0.006，グループ間では 0.414 となった．以上のことから，マサバとゴマサバはそれぞれ独立種とするのが妥当であると結論された．遺伝的に分けた2種の形態形質を比較したところ，種的な形質と環境によって変化する形質とに分けられた．したがって，分類形質の検討にもアイソザイムマーカーが極めて有効であると考えられた．

(783 南国市物部乙 200 高知大学農学部水族生態学講座)