Genetic Diversity of Skipjack Tuna in the Atlantic, Indian, and Pacific Oceans^{*1}

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Comparison of genetic data of serum esterase and transferrin systems of the skipjack tuna, *Katsuwonus pelamis* Linnaeus, collected from the Atlantic, Indian, and Pacific Oceans, together with the results reported earlier, (1) disclosed that fish from the Indian Ocean are distinguishable from those collected both in the Atlantic Ocean and the western Pacific Ocean and (2) suggested that the skipjack tuna, now inhabiting in the world's major oceans, first appeared in the Indian Ocean and then some of the members of the population emigrated to the other oceans, resulting in genetic diversification into the geographical populations, called the Atlantic Subpopulation, Indian Subpopulation, Western Pacific Subpopulation, and Central-eastern Pacific Subpopulation(s), after reproductive isolation.

Regarding the east-west difference of genetic compositions within the Pacific Ocean, analyses of our data on some 500 samples from more than 24,000 fish indicated the "step structure" with a gap between 160°E and 175°E more distinctly in the southern hemisphere. Apparent differences in allele frequencies of genetic systems, found recently in 6-phosphogluconate dehydrogenase and phosphoglucose isomerase, between the waters of Japan and Papua New Guinea suggested the necessity of further accumulation of the data before any conclusive statement on population structure in the regions.

In 1979, blood specimens of the skipjack tuna, *Katsuwonus pelamis* LINNAEUS, were collected for the first time from the Indian Ocean, since a series of genetic studies on population structure of the species was initiated at the United States National Marine Fisheries Service, Honolulu (the Former Bureau of Commercial Fisheries Biological Laboratory, Honolulu) some fifteen years ago. The study has been succeeded at the Kitasato University School of Fisheries Sciences, Sanriku, Japan under the cooperation from a number of domestic and/or overseas organizations in collecting research materials. The present paper summarizes all the published and unpublished genetic data, discusses a microevolutionary features of diversification of the skipjack tuna populations in the major oceans of the world, and update our view on population structures of the species in the Pacific Ocean by comparing our data with those collected by the other authors.

Materials and Methods

Skipjack Tuna Blood Samples

Blood specimen was taken from each fish,

preserved, and transported according to FUJINO.¹⁾ Fifty-five lots of blood samples were collected from some 1,200 skipjack tuna taken either by research vessel or commercial boats from the Indian and the Pacific Oceans in 1979 and 1980 (Table 1).

Electrophoresis

After being thawed, whole blood specimen was analysed by starch-gel electrophoresis for genetic variations in proteins and enzymes. Serum esterase and transferrin were analysed according to FUJINO *et al.*^{2,3)}. 6-Phosphogluconate dehydrogenase (6-Pgd) and phosphoglucose isomerase (Pgi) were analysed according to various authors with or without modifications as follows. For each enzyme, zymograms were compared between whole blood and hemolysate of red blood cells from a limited number of specimens to examine the origin of the enzyme.

6-Pgd 6-Pgd was analysed according to TANIGUCHI¹⁰⁾ as follows. (1) Stock buffer: A solution containing 0.1 M citric acid and 0.166 M N-(3-aminopropyl)-morpholine (pH 6.0). (2) Bridge buffer: 1:2.5 dilution of stock buffer; gel buffer: 1:20 dilution of stock buffer. (3) Stain-

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Table 1. Skipjack tuna blood samples collected from the Atlantic, Indian, and Pacific Oceans, 1965 through 1980

Geographical areas	No. of blood samples		Months sampled	Years sampled* ¹
	in lot	in fish		
<i>Atlantic Ocean</i>				
Caribbean Sea	3	215	Feb-Apr, Nov	1966, 1967 ²⁾
Gulf of Guinea	13	599	Sep-Nov	1967 ²⁾ , 1968* ²
<i>Indian Ocean</i>				
	8	199	Jan, Feb, Jun	1979, 1980* ²
<i>Pacific Ocean</i>				
Japan coast	233	8,796	Jan-Dec	1966-1969 ^{3,4,5)} , 1973 ³⁾ , 1977 ³⁾ -1980* ²
Mariana Islands	4	65	Dec	1979
Palau Islands	22	1,627	Jan-Dec	1966, 1967 ^{3,4)} , 1977* ²
Papua New Guinea	25	597	Jan-Mar, Nov, Dec	1973, 1975 ³⁾ , 1976, 1979* ²
Solomon Islands	12	264	Jan, Feb, Dec	1971, 1972 ³⁾
New Hebrides	7	139	Jan-May	1971 ³⁾
New Caledonia	2	98	Jan, Feb	1971 ³⁾
Australia, east coast	7	141	Mar, Jun, Oct, Nov	1975 ³⁾
Tasmania	1	25	Mar, Apr	1971 ³⁾
New Zealand	9	280	Jan, Mar, Apr	1970, 1971, ^{7,8)} 1977* ²
American Samoa	7	238	Feb, Mar, Aug	1967, 1970 ⁷⁾
Marshall Islands	18	241	Aug-Nov	1977, 1978 ³⁾
Hawaiian Islands	124	8,820	Jan-Dec	1965-1967 ^{3,4,5)} , 1969 ³⁾ , 1979* ²
Line Islands	10	607	Sep	1967 ³⁾
Society Islands	16	677	Jan	1969 ³⁾
Areas between Soc. Is. and Baja California	5	388	Jan-Mar, Jul, Oct	1967, 1968 ³⁾
Baja California	9	501	Aug, Sep	1965 ^{3,4)} , 1967 ³⁾
Ecuador	14	687	Jul, Sep	1968 ³⁾
Total	549	25,204		

*¹ Citation number identifies the reference for the published data.*² Include unpublished data.

ing mixture: 100 ml of 0.1 M Tris-aminomethane-HCl (pH 8.0). To this add 50 mg of gluconate-6-phosphate (Na₃ salt), 10 mg of NBT*, 30 mg of NADP*, and 5 mg of PMS*. (4) Procedures: Electrophoresis was carried out with a constant current of 1.5 mA per cm width of gel for 16 h at 4°C. Gel was stained for 5 h at 37°C in dark.

Pgi Pgi was analysed according to WALL *et al.*¹¹⁾ as follows. (1) Bridge buffer: A solution containing 0.223 M Tris-aminomethane, and 0.082M citric acid (pH 5.8). Gel buffer: 1:20 dilution of bridge buffer. (2) Staining mixture: 10 ml of 0.05 M Tris-aminomethane-HCl (pH 8.0). To this add 40 mg of D-fructose-6-phosphate (barium salt), 16 mg of MTT*, 2 mg of NADP, 48 mg of MgCl₂, 10 units of glucose-6-phosphate dehydrogenase, and 2 mg of PMS. (3) Procedures: Electrophoresis was carried out with a constant voltage

of 5 V per linear cm of gel for 20 h at 4°C. Gel was stained for one h at 37°C in dark.

Genetic Data

Among many genetic systems studied³⁾, serum esterase system (E_{SD})³⁾ has been most extensively used for population study. Population data of serum transferrin system (T_{SD})⁴⁾ were obtained from smaller numbers of specimens. The published data include 8 lots (320 fish) from the Atlantic³⁾ and 490 lots (23,691 fish) from the Pacific Ocean.³⁻⁵⁾ The unpublished data include 8 lots (639 fish) taken from the Gulf of Guinea of the equatorial eastern Atlantic in 1968, 8 lots (199 fish) from the equatorial eastern Indian Ocean in 1979 and 1980, and 27 lots (500 fish) from the areas off the east coast of Japan in 1979 and 1980, Palau in 1977, Papua New Guinea in 1979, New Zealand

* NBT: Nitro blue tetrazolium, NADP: Nicotinamide-adenine dinucleotide phosphate, PMS: Phenazine methosulfate, MTT: 3-(4,5-dimethyl-2-thiazolyl)-2,5-diphenyl tetrazolium bromide.

Table 2. Serum esterase and transferrin allele frequencies of the samples from the Atlantic and Indian Oceans

Geographical areas	Lot no.	Number of fish examined	Month and year sampled	Locality		Freq. of alleles		Fork length in cm
				lat.	long.	E ¹ _{sj} *	T ² _{sj}	
<i>Atlantic Ocean</i>								
Caribbean Sea	1	92	Feb, Apr, 1966	12~19N	62~67W	0.761	0.710	46-64
	2	25	Nov, "	12N	61W	0.800	0.652	48-68
	3	98	Mar, 1967	12N	61W	0.719	0.727	50-65
Gulf of Guinea	4	21	Oct, "	4S	5~10E	0.714	0.559	46-53
	5	19	" "	8S	11E	0.711	0.647	49-65
	6	22	" "	7S	11E	0.773	0.614	42-52
	7	24	" "	8S	12E	0.750	0.792	45-56
	8	19	Nov, "	8S	11E	0.684	0.711	38-59
	9	77	Sep, 1968	7S	11E	0.760	0.617	41-62
	10	103	Oct, "	9S	12E	0.718	0.655	36-50
	11	14	" "	10~11S	12~13E	0.821	0.714	53-90
	12	100	" "	8S	12E	0.665	0.686	41-49
	13	26	Nov, "	10S	12E	0.712	0.712	45-50
<i>Indian Ocean</i>	14	100	" "	12S	12E	0.775	0.694	44-54
	15	35	" "	12S	13E	0.800	0.706	45-52
	16	39	" "	12S	12E	0.731	0.679	44-52
	1	25	Jun, 1979	0N	96E	0.840	0.720	35-42
	2	24	" "	0N	96E	0.833	0.688	34-40
	3	25	Jan, 1980	0N	96E	0.820	0.620	41-58
	4	25	" "	1N	95E	0.820	0.620	44-55
	5	25	" "	1N	95E	0.880	0.813	30-54
	6	25	" "	1N	95E	0.820	0.660	42-53
	7	25	" "	0N	96E	0.860	0.780	43-56
	8	25	Feb, "	0N	96E	0.920	0.783	42-57

* Calculated from these values were rejection limits for the distribution at 5 and 10% significance levels: 0.743 ± 0.086 and 0.743 ± 0.072 for the Atlantic population and 0.849 ± 0.071 and 0.849 ± 0.059 for the Indian population respectively.

in 1977, and Hawaii in 1979. These published and unpublished data amounted to 549 lots, consisting of 25,204 specimens from the Atlantic, Indian, and Pacific Oceans as summarized in Table 1. The data were used to analyse genetic diversity of populations within and/or between oceans. Genetic data of the systems, newly developed, were used to examine any possibility of subgrouping within each subpopulation identified by serum esterase and transferrin systems.

Results

Genetic Compositions of Populations from the Atlantic and Indian Oceans

Table 2 summarizes the frequencies of alleles of E_{sj}^1 and T_{sj}^2 at the serum esterase and transferrin loci for the 24 lots of samples from the Atlantic and Indian Oceans. No significant difference was seen in the frequency distributions of the two alleles between Caribbean Sea and Gulf of Guinea within the Atlantic Ocean, as reported before.²⁾

Fig. 1 compares the distributions of E_{sj}^1 frequency between the Atlantic and Indian Oceans as well as the Pacific Ocean. The difference between the Atlantic and Indian Oceans is significant. The populations in the two oceans were named as "the Atlantic Subpopulation" and "the Indian Subpopulation". Fig. 1 also indicates that most samples from Papua New Guinea can be distinguished clearly from those from the Indian Subpopulation but not from those from the western Pacific Subpopulation.

Heterogeneous Genetic Compositions within the Pacific Ocean

Comparisons of frequency distribution of serum esterase allele, E_{sj}^1 , obtained through a series of extensive collections have demonstrated a marked east-west difference in the Pacific Ocean, indicating a higher frequency in the western Pacific than that in the central-eastern Pacific Ocean. The observation led to recognition of at least two different subpopulations, named "the Western Paci-

Fig. 1. Rejection limits, at 5% significance level, of serum esterase allele frequency distributions for the populations from the Atlantic, Indian, and Pacific Oceans, calculated from the individual figures as indicated by small dots. The upper limits for the Atlantic Ocean and Papua New Guinea and the lower limit for the Indian Ocean at 10% significance level are also given.

Fig. 2. Frequency distribution of serum esterase allele E_{S1} against longitude in the Pacific Ocean. Small dots and open circles represent individual lots of samples taken from the northern and southern hemispheres respectively. The two rejection limits at the right represent those for the two known subpopulations as calculated before⁹⁾.

fic Subpopulation" and "the Central-eastern Pacific Subpopulation(s)".^{8,9-9)} Recently a question was raised, however, whether the eastwest difference is of a nature of "step" or "cline" by the Skipjack Programme of the South Pacific Commission after the statistical analyses on a limited number of samples.¹²⁾

Fig. 2 summarizes all our published and unpublished data of frequency of allele E_{S1} (refer Table 1) against longitude in the Pacific Ocean. It can be stated from this figure that 1) the rela-

tion of the low value in the eastern Pacific and the high value in the western Pacific is obvious, that 2) the eastwest difference is not of a clinal structure but of step, indicating a marked gap between 160°E and 175°E in the southern hemisphere, and that 3) both the two groups of fish with high values and those with low values of E_{S1} occurred in the region between 140°E and 175°E of the northern hemisphere. The fact, represented by the third statement can be understood by the observations of the occurrence of fish from the central-eastern

Pacific Subpopulation(s) in the waters off the east coast of Japan as reported before.⁹⁾ It might be interesting to note that there is an indication of some north-south difference in $E^{\frac{1}{2}}_{83}$ allele frequency within the central-eastern Pacific Ocean, particularly in the region east of Hawaiian waters, indicating the mean values 0.485 and 0.447 for the northern and southern hemispheres respectively. On the basis of the observations described above, genetic distances between the four known subpopulations were calculated by using serum esterase and transferrin allele frequencies according to Nei¹³⁾ as shown in Fig. 3. It can be stated from this figure that skipjack tuna, *Katsuwonus pelamis*, now inhabiting in the major oceans of the world first appeared in the Indian Ocean, then a part of members of the population emigrated to the westward, and the other parts to the eastward, resulting in the formation of the geographical populations or subpopulations noted above after genetic isolations.

Simultaneous Occurrence of Fish from Different Subpopulations

After a series of intensive collections of blood samples from the waters adjacent to Japan in 1977 and 1978, FUJINO⁶⁾ described that fish from the two known subpopulations distributed to the waters off the Pacific coast of Japan in late spring through fall and that the relative abundance of fish from the Western Pacific Subpopulation was approximately 40 to 50% in May and June and became to dominate gradually through October, averaging 65% for the whole season. The results from more recent collections in 1979 supported the statements (Table 3). The similar observations could be expected in the Tasman Sea and the adjacent regions, where the ranges of the different subpopulations overlap each other.

Table 3. Relative abundance of fish from the two subpopulations of skipjack tuna in the samples taken from waters off the east coast of Japan in different seasons, 1977 through 1979

Month	Western* ¹ Pacific Subpopula- tion, %	Cent.-east.* ¹ Pacific Subpopula- tion (s), %	Number of* ² lots examined
Apr.	100 (2)	0 (0)	2
May	50 (3)	50 (3)	6
Jun.	38 (11)	62 (18)	29
Jul.	64 (16)	36 (9)	25
Aug.	88 (7)	12 (1)	8
Sep.	76 (26)	24 (8)	34
Oct.	100 (6)	0 (0)	6
Total	65 (71)	35 (39)	110

*¹ Figures in parenthesis indicate numbers of lots identified.

*² In addition, unidentified were one lot in May, three in June, and two each in July, September, and October.

New Genetic Systems

1) 6-Phosphogluconate dehydrogenase (6-Pgd)

Activity of 6-Pgd was observed in an anodally migrating zone on the zymograms both of whole blood and hemolysate of red blood cells without any difference (Fig. 4). Among the ten phenotypes theoretically possible, determined by four alleles, four phenotypes, 1-2, 2, 2-3, and 2-4 have been observed in 594 specimens examined as shown in Table 4. The zymogram patterns of heterozygotes suggested a dimeric structure in the species. Among the four alleles, 6-Pgd² (wild type) dominated throughout the areas examined. Although in a very low frequency, a variant allele 6-Pgd⁴ occurred only in the Japanese waters (frequencies of allele 6-Pgd⁴=0.010 or phenotype 2-4=0.019), but missing in the neighbouring area, Papua New Guinea, within the western Pacific Ocean. More data must be collected to examine

Fig. 3. Genetic diversity of skipjack tuna in the Atlantic, Indian, and Pacific Oceans.

any possibility of subgrouping of fish within the Western Pacific Subpopulation.

2) Phosphoglucose isomerase (Pgi) Activity of Pgi was observed in an anodally migrating zone on the zymograms both of whole blood and hemolysate of red blood cells without any difference (Fig. 4). Among the forty-five phenotypes theoretically possible, determined by nine alleles, nine phenotypes, 1·6, 2·6, 3·6, 4·6, 5·6, 6, 6·7, 6·8, and 6·9, have been observed in 643 specimens examined as shown in Table 4. The zymogram patterns of heterozygotes suggested a dimeric structure in the species. Although being low fre-

quencies, some difference can be seen between the areas adjacent to Japan and Papua New Guinea within the western Pacific in the relative frequencies of two alleles Pgi^3/Pgi^6 , giving 2.00 ($=0.010/0.005$) and 0.36 ($=0.004/0.011$) respectively. Further accumulation of data from the two areas might prove a possible subdividing the Western Pacific Subpopulation.

Discussions and Future Works

As discussed in the foregoing paragraphs of the present paper, it is evident that at least four

Table 4. Phenotype and allele frequencies at the 6-Pgd and Pgi loci in the skipjack tuna from the Indian and Pacific Oceans

6-Phosphogluconate dehydrogenase (6-Pgd)

Locality and lot number	Phenotype				No. of fish examined	Alleles			
	1·2	2	2·3	2·4		6-Pgd ¹	6-Pgd ²	6-Pgd ³	6-Pgd ⁴
<i>Indian Ocean</i>									
3	0	25	0	0	25	0.000	1.000	0.000	0.000
4	0	24	1	0	25	0.000	0.980	0.020	0.000
5	0	25	0	0	25	0.000	1.000	0.000	0.000
6	0	25	0	0	25	0.000	1.000	0.000	0.000
	0	99	1	0	100	0.000	0.995	0.005	0.000
<i>Pacific Ocean</i>									
Papua New Guinea									
18	0	24	0	0	24	0.000	1.000	0.000	0.000
19	0	25	0	0	25	0.000	1.000	0.000	0.000
20	0	25	0	0	25	0.000	1.000	0.000	0.000
21	1	23	0	0	24	0.021	0.979	0.000	0.000
22	0	24	0	0	24	0.000	1.000	0.000	0.000
23	0	25	0	0	25	0.000	1.000	0.000	0.000
24	0	25	0	0	25	0.000	1.000	0.000	0.000
25	0	25	0	0	25	0.000	1.000	0.000	0.000
26	0	24	0	0	24	0.000	1.000	0.000	0.000
	1	220	0	0	221	0.002	0.998	0.000	0.000
Japan, southwest*									
229	0	20	0	0	20	0.000	1.000	0.000	0.000
230	0	19	0	1	20	0.000	0.975	0.000	0.025
232	0	20	0	0	20	0.000	1.000	0.000	0.000
233	0	20	0	0	20	0.000	1.000	0.000	0.000
Japan, east*									
207	1	18	0	1	20	0.025	0.950	0.000	0.025
208	0	19	0	1	20	0.000	0.975	0.000	0.025
209	0	20	0	0	20	0.000	1.000	0.000	0.000
185	0	15	0	0	15	0.000	1.000	0.000	0.000
	1	151	0	3	155	0.003	0.987	0.000	0.010
Hawaii									
121	0	29	0	0	29	0.000	1.000	0.000	0.000
122	0	30	0	0	30	0.000	1.000	0.000	0.000
123	0	29	0	0	29	0.000	1.000	0.000	0.000
124	0	30	0	0	30	0.000	1.000	0.000	0.000
	0	118	0	0	118	0.000	1.000	0.000	0.000

* Samples identified as fish from the Western Pacific Subpopulation only.

Table 4. (cont.)

Phosphoglucose isomerase (Pgi)

Locality and lot number	Phenotypes									No. of fish examin.	Alleles								
	1·6	2·6	3·6	4·6	5·6	6	6·7	6·8	6·9		Pgi ¹	Pgi ²	Pgi ³	Pgi ⁴	Pg ⁵	Pgi ⁶	Pgi ⁷	Pgi ⁸	Pgi ⁹
<i>Indian Ocean</i>																			
3	0	0	0	0	0	24	0	0	1	25	0.000	0.000	0.000	0.000	0.000	0.980	0.000	0.000	0.020
4	0	0	0	0	0	25	0	0	0	25	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000
5	1	0	1	0	0	22	1	0	0	25	0.020	0.000	0.020	0.000	0.000	0.940	0.020	0.000	0.000
6	0	0	0	0	0	23	0	0	2	25	0.000	0.000	0.000	0.000	0.000	0.960	0.000	0.000	0.040
	1	0	1	0	0	94	1	0	3	100	0.005	0.000	0.005	0.000	0.000	0.970	0.005	0.000	0.015
<i>Pacific Ocean</i>																			
Papua New Guinea*																			
18	0	0	0	0	0	24	0	0	1	25	0.000	0.000	0.000	0.000	0.000	0.980	0.000	0.000	0.020
19	0	0	0	0	0	24	0	0	1	25	0.000	0.000	0.000	0.000	0.000	0.980	0.000	0.000	0.020
20	0	0	1	0	0	24	0	0	0	25	0.000	0.000	0.020	0.000	0.000	0.980	0.000	0.000	0.000
21	0	0	0	0	0	25	0	0	0	25	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000
22	0	0	0	0	0	22	0	1	1	24	0.000	0.000	0.000	0.000	0.000	0.960	0.000	0.020	0.020
23	0	0	0	0	0	24	0	0	1	25	0.000	0.000	0.000	0.000	0.000	0.980	0.000	0.000	0.020
24	0	0	0	0	0	24	0	1	0	25	0.000	0.000	0.000	0.000	0.000	0.980	0.000	0.020	0.000
25	0	0	1	0	0	23	0	0	1	25	0.000	0.000	0.020	0.000	0.000	0.960	0.000	0.000	0.020
26	0	0	1	1	1	22	0	0	0	25	0.000	0.000	0.020	0.020	0.020	0.940	0.000	0.000	0.000
	0	0	3	1	1	212	0	2	5	224	0.000	0.000	0.007	0.002	0.002	0.974	0.000	0.004	0.011
Japan, south west*																			
229	0	1	0	0	0	19	0	0	0	20	0.000	0.025	0.000	0.000	0.000	0.975	0.000	0.000	0.000
230	0	0	0	0	0	20	0	0	0	20	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000
231	0	0	1	0	0	18	0	1	0	20	0.000	0.000	0.025	0.000	0.000	0.950	0.000	0.025	0.000
232	0	0	0	0	0	19	0	1	0	20	0.000	0.000	0.000	0.000	0.000	0.975	0.000	0.025	0.000
Japan, east*																			
194	0	1	0	0	0	19	0	0	0	20	0.000	0.025	0.000	0.000	0.000	0.975	0.000	0.000	0.000
196	0	0	0	0	0	18	0	0	1	19	0.000	0.000	0.000	0.000	0.000	0.974	0.000	0.000	0.026
209	0	0	1	0	0	18	1	0	0	20	0.000	0.000	0.025	0.000	0.000	0.950	0.025	0.000	0.000
210	0	0	0	0	0	18	0	2	0	20	0.000	0.000	0.000	0.000	0.000	0.950	0.000	0.050	0.000
212	0	0	0	0	0	20	0	0	0	20	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000
213	0	0	0	0	0	19	0	0	1	20	0.000	0.000	0.000	0.000	0.000	0.975	0.000	0.000	0.025
	0	2	2	0	0	188	1	4	2	199	0.000	0.005	0.005	0.000	0.000	0.972	0.003	0.010	0.005
<i>Hawaii</i>																			
121	0	0	0	0	0	29	0	0	1	30	0.000	0.000	0.000	0.000	0.000	0.983	0.000	0.000	0.017
122	0	0	1	0	0	29	0	0	0	30	0.000	0.000	0.017	0.000	0.000	0.983	0.000	0.000	0.000
123	0	0	0	0	0	30	0	0	0	30	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000
124	0	1	0	0	0	29	0	0	0	30	0.000	0.017	0.000	0.000	0.000	0.983	0.000	0.000	0.000
	0	1	1	0	0	117	0	0	1	120	0.000	0.004	0.004	0.000	0.000	0.988	0.000	0.000	0.004

* Samples identified by serum esterase allele frequency as fish from the western Pacific Subpopulation only.

Fig. 4. Zymograms of 6-phosphogluconate dehydrogenase (upper) and phosphoglucose isomerase (lower) of the skipjack tuna.

subpopulations, genetically distinguishable from each other, distribute in the major oceans of the world. They were named the Atlantic, Indian, Western Pacific, and Central-eastern Pacific Subpopulations. Insufficient data from the Atlantic and Indian Oceans, however, suggested a necessity of further efforts on population studies with additional genetic systems to examine any possibility of subgrouping within each subpopulation identified.

Regarding the east-west difference in E^1_{8J} allele frequencies within the Pacific Ocean, our analyses of the data over 500 lots, conducted in response to the question raised by the South Pacific Commission's Skipjack Survey and Assessment Programme, exhibited "step structure", supporting our earlier results, that led to recognition of at least two subpopulations in the Pacific Ocean. Some apparent difference in E^1_{8J} allele frequencies between the northern and southern hemispheres in the central-eastern Pacific Ocean and in 6-Pgd and Pgi allele frequencies between Papua New Guinea and Japanese waters suggested a necessity of further efforts on population study with more genetic systems.

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