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Degree of Intraspecific Genetic Divergence and Variability in Three Sciaenid Species

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Abstract Genetic variations in *Nibea mitsukurii, N. albiflora* and *Pennahia argentata* from different localities were assayed electrophoretically. The genetic variability in *N. mitsukurii* was relatively high. According to the chi-square values for heterogeneity between two localities and genetic distance (D) values, *N. albiflora* from the Ariake Sea and the Inland Sea or the East China Sea (D=0.0092 in average), and *N. misukurii*, from Tosa Bay vs. Atsumi Bay (D=0.0067) were considered to be independent subpopulations. The D value in *N. albiflora* from the Inland Sea vs. the East China Sea was quite small (D=0.0010). In *P. argentata* populations, the D values were also small. Further, the relationship between genetic and geographic distances observed in the three species were discussed. *P. argentata* showed a positive relationship between these two factors as compared to *N. mitsukurii* or *N. albiflora*. It seemed that the lower level of genetic divergence might be due to the frequent gene flow within the large-scale and wide distributional range of the population.

During the past decade the application of gel electrophoresis coupled with selective enzyme staining has shown that a large amount genetic variation exists in natural populations of many species (Allendorf and Utter, 1979). Phenotypes of allozyme can be scored during most stages of their life cycle and their genetics more easily interpreted than the proportional and meristic characters employed in fish taxonomy.

Genetic differences among populations within a defined body of water may conceivably decrease with time, due to gene flow by migration within subpopulations. Alternatively, genetic differentiation could become accentuated through time, perhaps because subpopulations become increasingly associated with discrete breeding areas (Felley and Avise, 1980).

The fishes of the family Sciaenidae contribute substantially to the fisheries of the warm and shallow seas and estuaries of the world. *Nibea mitsukurii* (Jordan et Snyder) commonly known as nibe croaker, extends along the coast of the Pacific Ocean from Sendai Bay in the north to Hyuga Basin (an open bay) in the south. *Nibea albiflora* (Richardson), commonly known as roncader, occurs in Hongkong, the East China Sea and northwards to Port Arthur and southern Japan. *Pennahia argentata* (Houttuyn), commonly known as white croaker, is widely distributed in Japanese, Korean and Chinese waters (Trewavas, 1977).

Most of the studies on sciaenid taxonomy of Japan and its adjacent regions have been based mainly on morphological characters. Comprehensive and phylogenetical studies of this particular group of fishes based on the anatomical characters and allozymes were performed (Taniguchi, 1969a, b, 1970; Menezes and Taniguchi, 1988). The present investigation utilizes the techniques of allozyme electrophoresis to estimate the levels of genetic variation within the populations of the three sciaenid species and to compare the genetic divergence between subpopulations of a species.

Material and methods

Fig. 1 gives the areas of collection of the three sciaenid species. The precise locality along with the length and weight range are shown in Table 1.

Fish collected were placed immediately on dry ice for transport to the laboratory, and were stored at −20°C for 1–7 days prior to processing. Skeletal muscles, drumming muscles, liver, heart, and eye were dissected from each specimen for electrophoretic analysis. The procedures used for preparation of enzyme and protein samples and horizontal starch gel electrophoresis were those described by Taniguchi and Numachi (1978). The buffer system used was citric acid–aminopropylmorpholine (C–

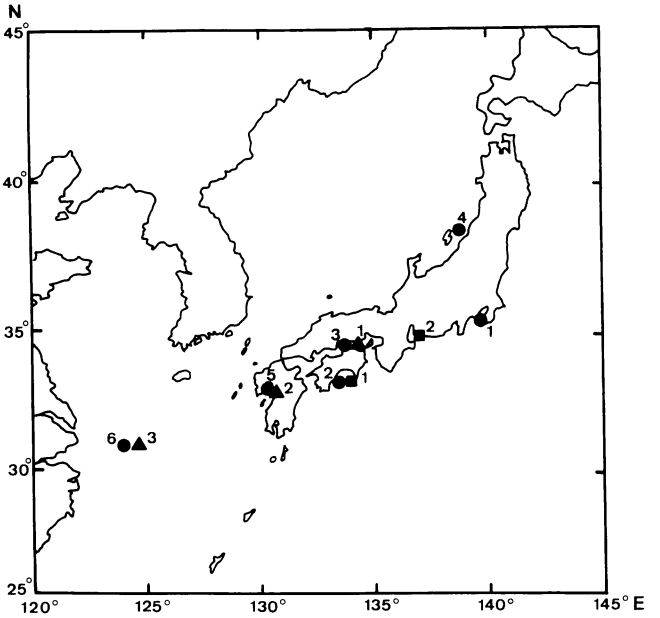

Fig. 1. Map of Japan showing the areas of sample collection.

APM) of pH 6.0 (Clayton and Tretiak, 1972).

The list of enzymes and proteins analysed, E.C. number, tissue specificity, locus, and number of alleles are given in Table 2. A locus was considered polymorphic when the frequency of the commonest allele was less than or equal to 0.95. For an enzyme with multiple loci code, the locus with the most anodal migration was designated as "one", the next as "two", and so on.

Average heterozygosity was determined by totalling the observed number of heterozygotes for each locus, dividing this by the total number of individuals in the sample, and averaging over all loci. Genetic divergence between populations was expressed by

Table 1. Length and weight ranges of the three sciaenid species collected from different localities.

Species	Lot	Locality	Number of fish	Total length (cm)	Weight (g)
Nibea mitsukurii	#1	Tosa Bay, off Kochi	40	28.2–35.2	285.9–588.9
	#2	Atsumi Bay, off Miya	30	8.8–27.9	7.1–294.5
N. albiflora	#1	Inland Sea, off Takamatsu	35	26.0–39.2	168.9–595.1
	#2	Ariake Sea, off Kashima	40	19.2–34.5	66.3–521.3
	#3	East China Sea, off Nagasaki	31	11.7–34.2	28.4–467.4
Pennahia argentata	#1	Tokyo Bay, off Chiba	100	14.3–24.5	45.2–187.1
	#2	Tosa Bay, off Kochi	34	16.7–22.7	80.7–168.0
	#3	Inland Sea, off Takamatsu	30	15.1–20.5	41.5–140.7
	#4	Japan Sea, off Niigata	101	18.1–31.4	104.7–438.9
	#5	Ariake Sea, off Kashima	30	16.7–27.1	136.7–281.1
	#6	East China Sea, 31°40′ N, 124°10′ E	81	14.0–19.6	54.5–107.2

Nei's (1972) indices of genetic similarity (I) and genetic distance (D). Genetic distances reflect estimates of net codon differences between pairs of populations. Thus, a large value for I and a correspondingly small value for D ($D=-\log_e I$) between two populations would imply a close phenetic relationship. The phylogenetic divergence time was calculated from the genetic distance (Nei, 1975).

Results

Genetic variability. Twenty-three loci were detected based on the electrophoretic patterns of eleven enzymes, hemoglobin and sarcoplasmic proteins (Table 2). *N. mitsukurii* had five polymorphic loci in Tosa Bay and four in Atsumi Bay when the criterion for polymorphism was lower than 0.95 in major allele frequency. *N. albiflora* had four polymorphic loci in the Inland Sea, five in the Ariake Sea and two in the East China Sea, while *P. argentata* had two polymorphic loci in Tokyo Bay, two in Tosa Bay, two in the Inland Sea, three in the Japan Sea, two in the Ariake Sea and three in the East China Sea. The heterozygosity of *N. mitsukurii* was 0.094 in Tosa Bay and 0.059 in Atsumi Bay. The heterozygosity of *N. albiflora* was 0.047 in the Inland Sea, 0.054 in the Ariake Sea and 0.029 in the East China Sea, while that of *P. argentata* was 0.038 in Tokyo

Table 2. List of enzymes and other proteins examined, locus names and tissue specificity observed in *Nibea mitsukurii*, *N. albiflora* and *Pennahia argentata* from different localities. ADH, alcohol dehydrogenase (E.C. 1.1.1.1); a-GPD, a-glycerophosphate dehydrogenase (1.1.1.8); AAT, aspartate aminotransferase (2.6.1.1); FH, fumarate hydratase (4.2.1.2); GPI, glucose-phosphate isomerase (5.3.1.9); HEM, hemoglobin; IDH, isocitrate dehydrogenase (1.1.1.42); LDH, lactate dehydrogenase (1.1.1.27); MDH, malate dehydrogenase (1.1.1.37); ME, malic enzyme (1.1.1.40); MPI, mannosephosphate isomerase (5.3.1.8); PGM, phosphoglucomutase (2.7.5.1); 6-PGD, 6-phosphogluconate dehydrogenase (1.1.1.44); SOD, superoxide dismutase (1.15.1.1); SP, sarcoplasmic protein. P*, polymorphic (observed at less than or equal to 0.95 of maximum allele frequency); P, polymorphic ($P \leq 0.995$); M, monomorphic; #, lot number. E, eye; DM, drumming muscle; H, heart; L, liver; SM, skeletal muscle.

Enzymes and proteins	Locus name	Tissue specificity	Genetic variability										
			N. mitsukurii		*N. albiflora*			*P. argentata*					
			#1	#2	#1	#2	#3	#1	#2	#3	#4	#5	#6
ADH	*Adh*	L	P*	P*	P*	P*	P*	P	P	P	P	P	P
a-GPD	*a-Gpd*	SM	P	P	P*	P*	M	P	M	M	M	P	P
AAT	*Aat-1*	L	P	M	P*	P	P	P	M	M	P	P	P*
	Aat-2	L, DM	P	M	M	P*	P	P	M	M	M	P	P
FH	*Fh*	L	M	M	M	P	M	P	P*	P*	P	M	P
GPI	*Gpi-1*	DM	P*	P	P	M	P	P*	P*	P*	P*	P*	P*
	Gpi-2	DM	P	P	P	M	P	P	P	P	M	P*	P
HEM	*Hem-1*	H	M	M	M	M	M	M	M	M	M	M	M
	Hem-2	H	M	M	M	M	M	M	M	M	M	M	M
IDH	*Idh-1*	L	M	P*	P	M	M	P	M	M	M	M	P
	Idh-2	H	P*	P	P	P*	M	M	M	M	M	M	M
LDH	*Ldh-1*	H	M	M	M	M	M	M	M	M	M	P	M
	Ldh-2	SM	M	M	M	M	M	P	M	M	M	M	P
MDH	*Mdh-1*	SM, DM	M	M	M	M	M	P	M	M	M	M	P
	Mdh-2	H	M	M	M	M	M	P	M	M	P	P	M
	Mdh-3	SM	M	M	M	M	M	M	M	M	M	M	M
PGM	*Pgm*	SM	P*	P*	P*	P*	P*	P	P	P	P*	M	P
6-PGD	*6-Pgd*	L	P*	P*	M	P	P	P	P	P	P	M	M
SOD	*Sod*	L	M	M	M	M	M	M	M	M	M	M	M
SP	*Sp-1*	SM	M	M	M	M	M	M	M	M	M	M	M
	Sp-2	SM	M	M	M	M	M	M	M	M	M	M	M
	Sp-3	SM	M	M	M	M	M	M	P	M	M	M	P
	Sp-4	SM	M	M	M	M	M	M	M	M	P*	M	P*

Bay, 0.043 in Tosa Bay, 0.041 in the Inland Sea, 0.044 in the Japan Sea, 0.054 in the Ariake Sea and 0.048 in the East China Sea (Table 3). *N. mitsukurii* had both the highest proportion of polymorphic loci and average heterozygosity. Levels of genetic variability are comparable to those reported in other vertebrates (Nevo, 1978).

Heterogeneity test. The differences in allele frequencies (Tables 4–6) between subpopulations were examined by the chi-square of heterogeneity test as shown in the value below the diagonal line in Table 7. Singnificant ($P<0.001$ and 0.01) heterogeneity was observed at four loci in *N. mitsukurii*, four loci in the Ariake Sea vs. the Inland Sea and the East China Sea of *N. albiflora*, one locus in the Inland Sea vs. the East China Sea, while the number of loci ranged from zero to four in *P. argentata*.

Genetic distance. The degree of differentiation among the different populations was measured by the genetic distance (D) which was calculated based on the allele frequencies of the various loci. Since biochemical genetic diversity and taxonomic separation are likely to be a function of evolutional time (Thorpe, 1983), the degree of genetic diversity may give a standard value for each level of taxonomic separation. The values of genetic distance (D) are shown above the diagonal line in Table 7. The D values among *P. argentata* populations of different locations ranged from 0.0006 to 0.0026. In *N. mitsukurii* for Tosa Bay vs. Atsumi Bay, the D value was 0.0067, while for *N. albiflora* from the Ariake Sea vs. the Inland Sea and the East China Sea, the values were $D=0.0093$ and $D=0.0091$ respectively. In *N. albiflora* from the Inland Sea vs. the East China Sea, the D value was quite small ($D=0.0010$). The D values of the three sciaenid species are somewhat smaller than the values of freshwater fishes, but more or less larger than the values of marine fishes except in a few cases, as seen in the published data (Table 8).

Genetic differentiation indicated by Gst. The Gst values of the three sciaenid species were 4.3% in *N. mitsukurii*, 9.0% in *N. albiflora*, and 2.1% in *P. argentata*. The Gst values of the three sciaenid species are generally smaller than the values of freshwater fishes, but somewhat larger than the values of marine fishes except in a few cases, as seen in the published data (Table 8).

Discussion

Genetic variability in *N. mitsukurii*. The proportion of polymorphic loci with average heterozygosity in *N. mitsukurii* is the highest of the three sciaenid species. Generally speaking, heterozygosity will decrease in a small population with inbreeding (Gall, 1987). The ratio of the proportion of polymorphic loci with the average heterozygosity is relatively low in the inbreeding population or simply mixed population (Fujio, 1981) and relatively high in the introgressive hybridized populations (Taniguchi et al., 1985) or large effective-size population. In the present study, we did not find any larger value in average heterozygosity, but the heterozygosities of *N. mitsukurii* were relatively higher than the other two species. *N. mitsukurii* is not a predominant species among the sciaenid species, it is difficult to think that *N. mitsukurii* has a large-sized population. There is a possibility that the level of variability of *N. mitsukurii* may be increased by introgressive hybridiza-

Table 3. Genetic variability observed in three sciaenid species. P*, polymorphic (observed at less than or equal to 0.95 of maximum allele frequency); P, polymorphic ($P\leqq0.995$); M, monomorphic; #, lot number.

	Genetic variability										
	Nibea mitsukurii		*N. albiflora*			*Pennahia argentata*					
	#1	#2	#1	#2	#3	#1	#2	#3	#4	#5	#6
No. of loci	23	23	23	23	23	23	23	23	23	23	23
No. of P	9	8	8	8	7	13	7	6	8	8	13
No. of P*	5	4	4	5	2	2	2	2	3	2	3
Proportion of P	0.391	0.348	0.348	0.348	0.304	0.565	0.304	0.261	0.348	0.348	0.565
Proportion of P*	0.217	0.174	0.174	0.217	0.087	0.087	0.087	0.087	0.130	0.087	0.130
No. of alleles	33	31	33	31	30	38	33	31	33	32	38
Mean no. of alleles	1.435	1.348	1.435	1.348	1.304	1.652	1.435	1.348	1.435	1.391	1.652
Av. heterozygosity	0.094	0.059	0.047	0.054	0.029	0.042	0.041	0.043	0.048	0.049	0.051

Table 4. Allele frequencies of local populations for isozyme and sarcoplasmic protein loci of *Nibea mitsukurii*.

Lot no.	*Adh*			*a-Gpd*		*Aat-1*		*Aat-2*		*Gpi-1*		*Gpi-2*		*Idh-1*		*Idh-2*		*6-Pgd*		*Pgm*	
	A	*B*	*C*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*
#1	0.038	0.500	0.463	0.975	0.025	0.987	0.013	0.038	0.962	0.825	0.175	0.987	0.013	0	1	0.288	0.712	0.787	0.213	0.625	0.375
#2	0	0.569	0.431	0.967	0.033	1	0	0	1	0.967	0.033	0.983	0.017	0.077	0.923	0.034	0.966	0.867	0.133	0.833	0.167

Table 5. Allele frequencies of local populations for isozyme and sarcoplasmic protein loci of *Nibea albiflora*.

Lot no.	*Adh*			*a-Gpd*		*Aat-1*			*Aat-2*		*Fh*		*Gpi-1*		*Gpi-2*		*Idh-1*		*Idh-2*			*6-Pgd*		*Pgm*	
	A	*B*	*C*	*A*	*B*	*A*	*B*	*C*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*C*	*A*	*B*	*A*	*B*
#1	0.071	0.786	0.143	0.943	0.057	0.014	0.929	0.057	0	1	1	0	0.957	0.043	0.986	0.014	0.986	0.014	0.029	0.971	0	1	0	0.186	0.814
#2	0	0.950	0.050	0.938	0.063	0	0.988	0.013	0.088	0.913	0.988	0.013	1	0	1	0	1	0	0	0.825	0.175	0.974	0.026	0.563	0.438
#3	0	0.919	0.081	1	0	0	0.983	0.017	0.033	0.967	1	0	0.984	0.016	0.952	0.048	1	0	0	1	0	0.984	0.016	0.161	0.839

Table 6. Allele frequencies of local populations for isozyme and sarcoplasmic protein loci of *Pennahia argentata*. * Five alleles could not be identified because of poor resolution of the GPI isozyme bands in the previous paper (Menezes and Taniguchi, 1988).

Lot no.	*Adh*			*a-Gpd*		*Aat-1*		*Aat-2*		*Fh*		*Gpi-1**					*Gpi-2*		
	A	*B*	*C*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*C*	*D*	*E*	*A*	*B*	*C*
#1	0	0.923	0.077	0.990	0.010	0.995	0.005	0.031	0.969	0.990	0.010	0.423	0	0.500	0.077	0	0	0.995	0.005
#2	0.015	0.985	0	1	0	1	0	0	1	0.941	0.059	0.379	0.015	0.515	0.091	0	0.015	0.956	0.029
#3	0	0.967	0.033	1	0	1	0	0	1	0.917	0.083	0.482	0	0.393	0.071	0.054	0	0.983	0.017
#4	0	0.960	0.040	1	0	0.995	0.005	0	1	0.965	0.035	0.474	0	0.510	0.016	0	0	1	0
#5	0	0.967	0.033	0.967	0.033	0.983	0.017	0.017	0.983	1	0	0.460	0	0.420	0.120	0	0	0.883	0.117
#6	0	0.981	0.019	0.987	0.013	0.919	0.081	0.006	0.994	0.988	0.012	0.398	0	0.544	0.058	0	0	0.994	0.006

Lot no.	*Idh-1*			*Ldh-1*		*Ldh-2*		*Mdh-1*		*Mdh-2*		*6-Pgd*			*Pgm*			*Sp-3*		*Sp-4*	
	A	*B*	*C*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*A*	*B*
#1	0.020	0.975	0.005	1	0	0.995	0.005	0.990	0.010	0.995	0.005	0.005	0.995	0	0	0.979	0.021	1	0	1	0
#2	0	1	0	1	0	1	0	1	0	1	0	0.015	0.985	0	0.044	0.956	0	0.985	0.015	1	0
#3	0	1	0	1	0	1	0	1	0	1	0	0	0.967	0.033	0	0.967	0.033	1	0	1	0
#4	0	1	0	1	0	1	0	1	0	0.965	0.035	0.015	0.985	0	0.036	0.877	0.087	1	0	0.940	0.060
#5	0	1	0	0.983	0.017	1	0	1	0	0.967	0.033	0	1	0	0	1	0	1	0	1	0
#6	0	0.981	0.019	1	0	0.994	0.006	0.994	0.006	1	0	0	1	0	0.012	0.982	0.006	0.995	0.005	0.840	0.160

tion with *N. albiflora* in the water area around the Kii Channel where the *N. mitsukurii* populations are faced with the *N. albiflora* populations, although these two species are considered to be sibling species principally having allopatric distributions. This hypothesis is supported by findings of individuals with intermediate body color pattern between the two species, although this hypothesis has a difficulty in explaining the allele substitution at *Gpi-1* locus between these two species. Further study should be continued to resolve this problem.

Isolation of the Ariake Sea subpopulation of *N. albiflora*. The *D* and Gst values will be reflected to the level of differentiation among subpopulations. The *D* and Gst values of the three sciaenid species seemed to accord with the level of marine demersal fishes. Particularly, the values of *N. mitsukurii* and *N. albiflora* are larger than that of *P. argentata*. This result suggests that *N. mitsukurii* and *N. albiflora* may have ecological characteristics which make them sensitive to the geographical barrier.

The Ariake Sea subpopulation of *N. albiflora* seemed to be well isolated from the other subpopulations such as those of the East China Sea and the Inland Sea. The genetic distance of the Ariake Sea subpopulation vs. the other subpopulations is much larger than that of the East China Sea vs. the Inland Sea subpopulations of *N. albiflora* (Fig. 2). The mean genetic distance (D=0.0092) is almost equal to the value of 0.01 that is indicative of a local race (Nei, 1972). Furthermore, the highly significant heterogeneity in allelic frequencies at two loci (*Idh-2* and *Pgm*) suggests that these two groups represent ge-netically distinct subpopulations and that each locality would have its own breeding population. The differentiation of the Ariake Sea subpopulation of *N. albiflora* from the other subpopulations may be accelerated by the closed nature of the sea for more than six thousand years (Minato et al., 1965). But the geologic time does not accord well with the evolutional time calculated roughly as 47 thousand years based on the *D* values between the Ariake Sea and the other localities. The genetic differentiation of the Ariake Sea subpopulation is supported by the significant difference in morphological characters (Takita, 1974).

Genetic differentiation between southern and northern subpopulations of *N. mitsukurii*. The genetic relationships between these subpopulations are shown by a dendrogram in Fig. 2. In the *N. mitsukurii* population, the genetical discontinuity between Tosa Bay and Atsumi Bay suggests a barrier

Table 7. Genetic distances (above the diagonal) and number of loci being significant in the chi-square of heterogeneity test (below the diagonal) between populations of 3 sciaenid species. Divergence time (year) is given in parenthesis.

1. *Pennahia argentata*

	Tokyo Bay	Tosa Bay	Inland Sea	Japan Sea	Ariake Sea	China Sea
Tokyo Bay		0.0006 (3000)	0.0009 (4500)	0.0009 (4500)	0.0009 (4500)	0.0017 (8500)
Tosa Bay	2		0.0008 (4000)	0.0010 (5000)	0.0011 (5500)	0.0018 (9000)
Inland Sea	1	0		0.0011 (5500)	0.0011 (5500)	0.0026 (13000)
Japan Sea	4	2	1		0.0018 (9000)	0.0015 (7500)
Ariake Sea	1	0	2	3		0.0025 (12500)
China Sea	3	3	4	4	3	

2. *Nibea albiflora*

	Inland Sea	Ariake Sea	China Sea
Inland Sea		0.0093 (46500)	0.0010 (5000)
Ariake Sea	4		0.0091 (45500)
China Sea	1	4	

3. *N. mitsukurii*

	Tosa Bay	Atsumi Bay
Tosa Bay		0.0067 (33500)
Atsumi Bay	4	

Table 8. Summary of genetic distance and Gst value within fish species. Gst in some paper was calculated by the allele frequencies shown in each one.

Species	No. of locations	Genetic distance (Average±SD)	Gst (%)	References used for calculating Gst
〈Marine fish〉				
Nibe croker	2	0.0067	4.3	present study
Roncador	3	0.0065±0.0047	9.0	present study
(except Ariake)	2	(0.0010)	(1.3)	
White croker	6	0.0014±0.0006	2.1	present study
Atlantic herring	3	0.002±0.001	1.4	Anderson et al. (1981)
Atlantic herring	6	0.0010±0.0004	1.25	Grant (1984)
(North Ameria vs. Europe)		0.0011±0.0005	0.26	
Pacific herring	21	0.039±0.021	15.9	Grant and Utter (1984)
(Asia-Bering Sea)		(0.0026±0.0017)	(0.9)	
Pacific Halibat		0.0002±0.0007		Grant et al. (1984)
(Gulf of Alaska vs. Bering Sea)	2		0.4	
(Gulf of Alaska and Bering Sea vs. Japan)	3		0.9	
Atlantic cod	2	0.022	8.0	Grant and Stahl (1988)
Pacific cod	11	0.025	22.0	Grant et al. (1987)
(North America vs. Asia)	11		18.9	
(North America)	9	0.0007±0.0006	0.2–1.7	
(Asia)	2	0.0041±0.0026		
African hake				Grant et al. (1988)
(Genus *Merluccius*)				
M. capensis	13	0.0007	1.7	
M. paradoxus	10	0.0006	1.3	
Red seabream		0.0015	0.7	Unpublished data
Damselfish	6	—	0.9	Shaklee (1984)
Hypsoblennius jenkinsi	3	—	15.7	Present (1987)
〈Anadromous and amphidromous fishes〉				
Salmonids				Ryman (1983)
Atlantic salmon	32	—	21.4	
Brown trout	35	—	36.7	
Rainbow trout (North America)	38	—	15.0	
Sockeye salmon	18	—	5.8	
Chum salmon		—	0.5	Okazaki (1982)
North America:	14	0.00207±0.00188	2.5	
(Western Alaska)	2	0.00060	0.27	
(Central Alaska)	3	0.00018±0.00007	1.94	
(Alaska, total)	5	0.00102±0.00093	2.22	
(Fraser River)	3	0.00023±0.00007	0.60	
(British Columbia)	6	0.00072±0.00061	0.81	
Japan:	43	—	1.0	
(Hokkaido)	14	0.00059±0.00039	1.12	
(Honshu, Pacific coast)	13	0.00094±0.00073	2.70	
(Honshu, Japan Sea coast)	16	0.00255±0.00208	5.17	
Ayu				Seki et al. (1988)
(Amphidromous)	9	0.0012	0.0	
(Amphidromous vs. landlocked)	12	0.0197	13.7	
〈Freshwater fish〉				
Catostomus plebeius	4	0.001–0.254	8.3–88.4	Ferris et al. (1982)
Genus *Hypentelium*				Buth (1980)
H. etowanum	2	0.005	8.9	
H. nigricans	3	0.021±0.016	55.1	
H. roanokense	2	0.027	40.0	

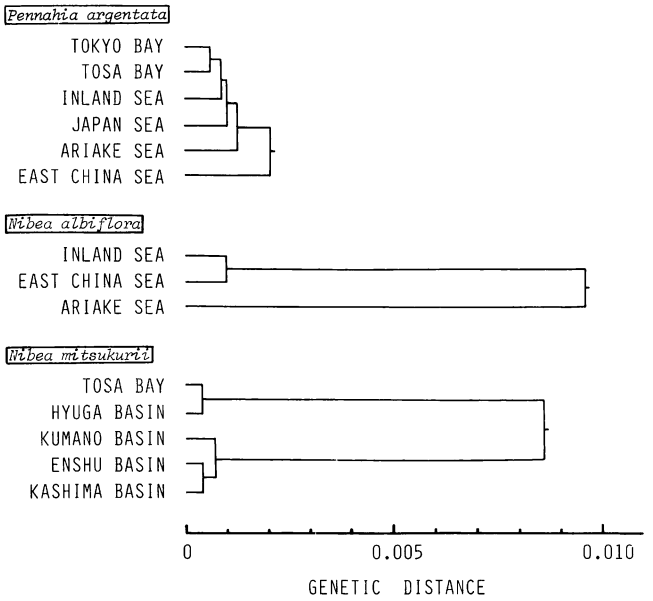

Fig. 2. Dendrogram showing the relationship between *Pennahia argentata*, *Nibea albiflora*, and *N. mitsukurii* populations. The previous data (Taniguchi, 1980) is applied in *N. mitsukurii*.

preventing gene flow between these two localities. This result agrees with the previous report (Taniguchi, 1980) which suggested that the cold water mass occurring in the area off Cape Shiono Misaki and the deep sea off the Kii Channel may be a functional barrier against the gene flow between Tosa Bay and Kumano Basin subpopulations. This phenomenon may be specific in *N. mitsukurii* because it is not observed in the population of *P. argentata*.

Correlation between genetic distance and geographic distance in *P. argentata*. The correlation between genetic distance and geographic distance was observed in the *P. argentata* population. This phenomenon is different from those of *N. mitsukurii* or *N. albiflora*. This phenomenon may suggest more frequent migration between subpopulations in the early developmental (planktonic) stage. This is supported by the facts that this species has its habitat and spawning ground more offshore than the other two, and that it has a wide distribution (Takita, 1974; Taniguchi, 1982).

The cause of differences in genetic differentiation by species. Pronouced genetic differentiation between subpopulations has usually been interpreted as resulting from physical or ecological barriers or geographical distance. When subpopulations become isolated, they adapt to local environments where evolutionary forces (mutation, genetic drift, founder effect and selection) permit differential changes to occur within the population (Ahmed, 1975; Avise, 1976). Consequently, the gene pools of these isolated subpopulations exhibit a greater genetic distance as time passes. In addition, due to isolation for a long evolutional generation a group would become independent of the other group genetically, different alleles would be substituted and then become a different genetic composition.

On the other hand, the migration between subpopulations may prevent the genetic differentiation. The efficiency of migration will be determined by the ecological characteristics.

These differences in the degrees of genetic divergence and variability observed in the three sciaenid species may be caused by the ecological specificities related to the location of spawning ground, range of migration in the egg, larva and adult stages, etc. Comparative studies of ecological characters for these sciaenid species should be tried in relation to the isolation between subpopulations.

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Literature cited

Allendorf, F. W. and F. M. Utter. 1979. Population genetics. Pages 407–454 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 8. Academic Press, New York.

Ahmed, M. 1975. Speciation in living oysters. Adv. Mar. Biol., 13: 357–397.

Anderson, L., N. Ryman, R. Rosenberg and G. Stahl. 1981. Genetic variability in Atlantic herring (*Clupea harengus*): description of protein loci and population data. Hereditas, 95: 69–78.

Avise, J. C. 1976. Genetic differentiation during speciation. Pages 106–122 *in* F. J. Ayala, ed. Molecular evolution. Sinaeur Associates, Inc., Sunderland.

Buth, D. G. 1980. Evolutionary genetics and systematic relationships in the catostomid genus *Hypentelium*. Copeia, 1980(2): 280–290.

Clayton, J. W. and D. N. Tretiak. 1972. Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Bd. Canada, 29: 1169–1172.

Felley, J. D. and J. C. Avise. 1980. Genetic and morphological variation in bluegill populations in Florida lakes. Trans. Amer. Fish. Soc., 109: 108–115.

Ferris, S. D., D. G. Buth and G. S. Whitt. 1982. Substantial genetic differentiation among populations of *Catostomus plebeius*. Copeia, 1982(2): 444–449.

Fujio, Y. 1981. Gyorui syudan no seikagakuteki keishitsu no hen' isei. Mar. Sci. Monthly, 13(1): 35–41. (In Japanese.)

Gall, G. A. E. 1987. Inbreeding. Pages 47–48 *in* N. Ryman and F. Utter, eds. Population genetics and fishery management. Univ. of Washington Press.

Grant, W. S. 1984. Biochemical population genetics of Atlantic herring, *Clupea harengus*. Copeia, 1984(2): 357–364.

Grant, W. S. and G. Stahl. 1988. Description of electrophoretic loci in Atlantic cod, *Gadus morhua*, and comparison with Pacific cod, *Gadus macrocephalus*. Hereditas, 108: 27–36.

Grant, W. S. and F. M. Utter. 1984. Biochemical population genetics of Pacific herring (*Clupea pallasi*). Can. J. Fish. Aqu. Sci., 41: 856–864.

Grant, W. S., D. J. Teel and T. Kobayashi. 1984. Biochemical population genetics of Pacific halibat (*Hippoglossus stenolepis*) and comparison with Atlantic halibat (*H. hippoglossus*). Can. J. Fish. Aqu. Sci., 41: 1083–1088.

Grant, W. S., C. I. Zhang, T. Kobayashi and G. Stahl. 1987. Lack of genetic stock discretion in Pacific cod (*Gadus macrocephalus*). Can. J. Fish. Aqu. Sci., 44: 490–498.

Grant, W. S., I. I. Becker and R. W. Leslie. 1988. Evolutionary divergence between sympatric species of southern African hake, *Merluccius capensis* and *M. paradoxus*. I. Electrophoretic analysis of proteins. Heredity, 61: 13–20.

Menezes, M. R. and N. Taniguchi, 1988. Interspecific genetic divergence in sciaenids from Japan and its adjacent waters. Japan. J. Ichthyol., 35(1): 40–46.

Minato, M., M. Gokase and M. Hunahashi. 1965. The geologic development of the Japanese Inlands. Tsukiji Syokan, Tokyo, 442pp.

Nei, M. 1972. Genetic distance between populations. Amer. Nat., 106: 283–292.

Nei, M. 1975. Molecular population genetics and evolution. North-Holland, Amsterdam, 288 pp.

Nevo, E. 1978. Genetic variation in natural populations: patterns and theory. Theor. Pop. Biol., 13: 121–177.

Okazaki, T. 1982. Genetic study on population structure in chum salmon (*Oncorhynchus keta*). Bull. Far Seas Fish. Res. Lab., 19: 25–116.

Present, T. M. C. 1987. Genetic differentiation of disjunct Gulf of California and Pacific outer coast populations of *Hypsoblennius jenkinsi*. Copeia, 1987(4): 1010–1024.

Ryman, N. 1983. Patterns of distribution of biochemical genetic variation in salmonid: differences between species. Aquaculture, 33: 1–21.

Seki, S., N. Taniguchi and S. Jeon. 1988. Genetic divergence among natural populations of ayu from Japan and Korea. Nippon Suisan Gakkaishi, 54(4): 559–568. (In Japanese.)

Shaklee, J. B. 1984. Genetic variation and population structure in the damselfish, *Stegastes fasciolatus*, throughout the Hawaiian Archipelago. Copeia, 1984(3): 629–640.

Takita, T. 1974. Study on the early life history of *Nibea albiflora* (Richardson) in Ariake sound. Bull. Fac. Fish. Nagasaki Univ., 38: 1–55. (In Japanese.)

Taniguchi, N. 1969a. Comparative osteology of the sciaenid fishes from Japan and its adjacent waters. 1. Neurocranium. Japan. J. Ichthyol., 16(2): 55–67.

Taniguchi, N. 1969b. Comparative osteology of the sciaenid fishes from Japan and its adjacent waters. II. Vertebrae. Japan. J. Ichthyol., 16(4): 153–156.

Taniguchi, N. 1970. Comparative osteology of the sciaenid fishes from Japan and its adjacent waters. III. Premaxillary and dentary. Japan. J. Ichthyol., 17(4): 135–140.

Taniguchi, N. 1980. Nanseikaiiki ni okeru nibe no shuzoku bunka to kakuriyouin. Bull. Japan. Soc. Fish. Oceanogr., 36: 53–57. (In Japanese.)

Taniguchi, N. 1982. Nibe no seibutsugaku V. Shoki hatsuiku dankai. Aquabiology, 20(3/4): 210–215. (In Japanese.)

Taniguchi, N. and K. Numachi. 1978. Genetic variation of 6-phosphogluconate dehydrogenase, isocitrate dehydrogenase and glutamic-oxaloacetic transaminase in the liver of Japanese eel. Nippon Suisan Gakkaishi, 44(12): 1351–1355.

Taniguchi, N., J. M. Macaranas and R. S. V. Pullin. 1985. Introgressive hybridization in cultured tilapia stocks in the Philippines. Nippon Suisan Gakkaishi, 51(8): 1219–1224.

Thorpe, J. P. 1983. Enzyme variation, genetic distance and evolutionary divergence in relation to levels of taxonomic separation. Pages 131–152 *in* G. S. Oxford and D. Rollinson, eds. Protein polymorphism. Academic Press, London.

Trewavas, E. 1977. The sciaenid fishes (croakers and drums) of the Indo-West Pacific. Trans. Zool. Soc. Lond., 33: 253–541, pls. 1–15.

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ニベ科魚類3種の種内集団間の遺伝的分化と変異性

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日本産ニベ科魚類，ニベ (*Nibea mitsukurii*)，コイチ (*N. albiflora*)，およびシログチ (*Pennahia argentata*) の3種の種内集団間の遺伝的分化と変異性について調べた．遺伝的変異性はニベで比較的高かった．有明海と瀬戸内海・東シナ海のコイチ間および土佐湾と渥美湾のニベ間の遺伝的距離 (*D*) はそれぞれ 0.0092, 0.0067 であり，それらは独立した集団と考えられた．瀬戸内海と東シナ海のコイチ間 (D=0.0010) およびシログチ集団内の遺伝的分化は小さかった．遺伝的距離と地理的距離の関係は，シログチにおいて正の相関が認められた．種内の地方集団間の遺伝的分化の程度の差が魚種によって異なることについて，生態的特性における魚種間差に関連づけて考察した．

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