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Interspecific Genetic Divergence in Sciaenids from Japan and Its Adjacent Waters

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Abstract Genetic divergence and phylogenetic relationships among *Nibea mitsukurii*, *Nibea albiflora*, *Pennahia argentata*, *Argyrosomus japonicus*, *Atrobucca nibe* and *Larimichthys crocea* were investigated by examining the electrophoretic patterns of 14 enzymes. The allele frequencies of 21 loci were estimated to calculate the genetic distances (*D*). The average *D* value among the sciaenid species increased in proportion to the level of taxonomic category. Relationships estimated by genetic markers well accorded with those estimated by morphological characters. The 6 sciaenid species were clearly divided into two distinct groups at a *D* value of 1.41.

Electrophoretic analysis of protein (especially enzyme) variants has been widely used in the study of many aspects of intraspecific- and speices-level taxonomy. The reviews of Allendorf and Utter (1979), Avise (1975) and Ayala (1983) have shown that conspecific populations consistently demonstrate high levels of genetic (allozyme) similarity, as measured by Rogers (1972) or Nei's (1972) coefficients of genetic similarity, and that closely related species show much lower levels of genetic similarity. Related populations and species can thus be analysed for percentages of shared allozymes and these values used in making taxonomic decisions. Taniguchi et al. (1972, 1986) applied several biochemical markers detected by an electrophoretic method to the systematic study of fishes in the families Platycephalidae and Sparidae. These studies confirmed the principle that isozyme genes are convenient markers to estimate the phylogenetic relationships of fishes.

This study utilizes isozyme gene markers to determine the genetic divergence and phylogenetic relationships among 6 sciaenid species (Pisces, Sciaenidae).

Materials and methods

Species names, number of individuals of each species tested, and sampling areas are given in Table 1.

The specimens were placed on dry ice upon capture and kept frozen until tested. The skeletal muscle, drumming muscle, liver, heart and eye were dissected from each individual specimen. The cell-lysate obtained by freezing and thawing was directly subjected to electrophoresis for phenotypic analysis. Starch gel electrophoresis was carried out following the procedure described by

Table 1. Scientific names (Trewavas, 1977), sampling locations and number of samples examined.

Subfamily	Tribe	Species	Japanese name	No. of samples	Location
Otolithinae	Otolithini	*Pennahia argentata*	shiroguchi	30	Inland Sea, off Takamatsu
		Argyrosomus japonicus	ohnibe	6	Tosa Bay, off Kochi
		Atrobucca nibe	kuroguchi	40	East China sea, 32°15′N, 124°25′E
	Nibeini	*Nibea mitsukurii*	nibe	40	Tosa Bay, off Kochi
		Nibea albiflora	koichi	35	Inland Sea, off Takamatsu
	Collichthyini	*Larimichthys crocea*	fuhsei	7	East China sea 32°15′N, 123°25′E

Taniguchi and Numachi (1978), using a citric acid-aminopropylmorpholine (C-APM) buffer system of pH 6.0 (Taniguchi et al., 1978).

The list of enzymes, tissue specificity and loci are given in Table 2. A locus was considered polymorphic when the frequency of the most common allele was less than or equal to 0.99. When mutiple loci coded for an enzyme, the locus with the most anodal migration was designated one, the next two, and so on. Allelic variants were designated according to their relative mobility, the most common allele being designated 100 and other alleles being given numbers that indicated their mobility relative to that of the common allele. Cathodal systems were designated in a similar way but were given a negative sign. The identity or difference of alleles at the same locus was decided by the banding position of isozymes on the same gel, based on the assumption that the isozyme bands migrating to the same position were composed of the same aminoacid coded by the same gene. Genetic distance was calculated from the formula proposed by Nei (1972). The dendogram was drawn by the unweighted pair-group method (UPGMA) (Sneath and Sokal, 1973).

Results and discussion

The electropherograms of isozyme were compared among the sciaenid species. The patterns clearly showed similarities and differences among the genera in the positions of the homopolymeric band for each isozyme locus. The electrophoretic pattern of fourteen enzymes enabled the identification of 21 separate loci (Table 2). These isozymes, obtained stably and clearly in all 6 species, were used as genetic markers. Table 3 shows the alleles and allele frequencies at each of the 21 loci for the 6 sciaenid species. Two to ten alleles were detected for each locus, and many loci were monomorphic and fixed in an allele. When the allele frequencies are compared between every two species, more number of divergent loci were found in more distantly related species pair in morphological characters (Taniguchi, 1969a, b, 1970).

In order to estimate the degrees of genetic divergence among the 6 speices, the genetic distance (D) was calculated between every pair of species using the allele frequencies shown in Table 3. The D value will become zero when the allele frequencies of the two species compared are

Table 2. List of enzymes examined, loci identified and tissue assayed.

Enzyme	Locus	Tissue assayed
Alcohol dehydrogenase (ADH)	*Adh*	liver
Aspartate aminotransferase (AAT)	*Aat-1*	liver
	Aat-2	liver, drumming muscle
Isocitrate dehydrogenase (IDH)	*Idh-1*	liver
	Idh-2	heart, drumming muscle
Glucosephosphate isomerase (GPI)	*Gpi-1*	drumming muscle
	Gpi-2	drumming muscle
Lactate dehydrogenase (LDH)	*Ldh-1*	eye
	Ldh-2	heart
	Ldh-3	muscle
6-Phosphoglconate dehydrogenase (6-PGD)	*6-Pgd*	liver
Mannose phosphate isomerase (MPI)	*Mpi*	liver, heart
Esterase (EST)	*Est*	drumming muscle, eye, heart
Malate dehydrogenase (MDH)	*Mdh-1*	skeletal muscle, drumming muscle
	Mdh-2	heart
	Mdh-3	drumming muscle, skeletal muscle
Phosphoglucomutase (PGM)	*Pgm*	skeletal muscle
Super oxide dismutase (SOD)	*Sod*	liver
Fumarate hydratase (FM)	*Fm*	liver
Creatine kinase (CK)	*Ck*	drumming muscle
α-Glycerophosphate dehydrogenase (α-GPD)	*α-Gpd*	skeletal muscle

Table 3. Allele frequencies at 21 loci in six sciaenid species. The numerals in parentheses show numbers of samples examined. Nm, *Nibea mitsukurii*; Na, *Nibea albiflora*; Aj, *Argyrosomus japonicus*; Pa, *Pennahia argentata*; An, *Atrobucca nibe*; Lc, *Larimichthys crocea*.

Locus	Allele	Species					
		Nm(40)	Na(35)	Aj(6)	Pa(30)	An(40)	Lc(7)
Aat-1	136	0.000	0.000	0.000	0.000	0.975	0.000
	120	0.000	0.014	0.000	0.000	0.025	0.000
	112	0.000	0.000	0.000	1.000	0.000	0.000
	105	0.000	0.000	0.000	0.000	0.000	0.786
	100	0.987	0.929	0.000	0.000	0.000	0.000
	84	0.000	0.000	1.000	0.000	0.000	0.000
	76	0.013	0.000	0.000	0.000	0.000	0.000
	72	0.000	0.057	0.000	0.000	0.000	0.214
Aat-2	−50	0.038	0.000	0.000	0.000	0.000	0.000
	−83	0.000	0.000	0.000	0.000	0.000	1.000
	−100	0.962	1.000	1.000	1.000	1.000	0.000
Idh-1	119	0.000	0.014	0.000	0.000	0.000	0.000
	100	1.000	0.986	1.000	0.000	0.000	0.000
	92	0.000	0.000	0.000	0.000	1.000	0.000
	71	0.000	0.000	0.000	1.000	0.000	0.000
	56	0.000	0.000	0.000	0.000	0.000	1.000
Idh-2	212	0.000	0.029	0.000	0.000	0.000	0.000
	100	0.288	0.971	1.000	1.000	0.963	1.000
	25	0.712	0.000	0.000	0.000	0.038	0.000
Gpi-1	100	0.000	0.000	0.000	0.000	1.000	0.000
	93	0.000	0.000	0.000	0.897	0.000	0.929
	86	0.825	0.000	0.000	0.000	0.000	0.000
	83	0.000	0.000	1.000	0.000	0.000	0.000
	79	0.000	0.043	0.000	0.086	0.000	0.000
	66	0.175	0.000	0.000	0.000	0.000	0.000
	59	0.000	0.000	0.000	0.000	0.000	0.071
	55	0.000	0.957	0.000	0.017	0.000	0.000
Gpi-2	−50	0.013	0.000	0.000	0.000	0.000	0.000
	−100	0.986	0.986	1.000	0.983	0.863	1.000
	−127	0.000	0.014	0.000	0.000	0.138	0.000
	−130	0.000	0.000	0.000	0.017	0.000	0.000
Ldh-1	100	1.000	1.000	0.000	1.000	1.000	1.000
	50	0.000	0.000	1.000	0.000	0.000	0.000
Ldh-2	163	0.000	0.000	0.000	0.000	0.000	1.000
	100	1.000	1.000	1.000	1.000	1.000	0.000
Ldh-3	115	0.000	0.000	0.000	0.000	0.000	1.000
	106	0.000	0.000	1.000	0.000	1.000	0.000
	100	1.000	1.000	0.000	0.000	0.000	0.000
	97	0.000	0.000	0.000	1.000	0.000	0.000
Adh	−24	0.000	0.000	1.000	0.000	0.000	0.000
	−35	0.000	0.000	0.000	0.000	0.000	0.929
	−55	0.000	0.000	0.000	0.000	1.000	0.000
	−82	0.000	0.000	0.000	0.967	0.000	0.000
	−88	0.000	0.071	0.000	0.000	0.000	0.000
	−91	0.038	0.000	0.000	0.000	0.000	0.000
	−94	0.000	0.000	0.000	0.033	0.000	0.071
	−100	0.500	0.786	0.000	0.000	0.000	0.000
	−112	0.000	0.143	0.000	0.000	0.000	0.000
	−115	0.462	0.000	0.000	0.000	0.000	0.000

Table 3. Continued.

Locus	Allele	Species					
		Nm(40)	Na(35)	Aj(6)	Pa(30)	An(40)	Lc(7)
6-Pgd	112	0.000	0.000	1.000	0.000	0.000	0.000
	108	0.000	0.000	0.000	0.000	0.000	1.000
	100	0.787	1.000	0.000	0.000	0.000	0.000
	81	0.000	0.000	0.000	0.967	0.000	0.000
	77	0.213	0.000	0.000	0.000	0.986	0.000
	73	0.000	0.000	0.000	0.033	0.000	0.000
	58	0.000	0.000	0.000	0.000	0.014	0.000
Mpi	111	0.000	0.000	1.000	0.000	0.000	0.000
	108	0.000	0.000	0.000	0.000	0.225	1.000
	100	1.000	1.000	0.000	0.000	0.775	0.000
	96	0.000	0.000	0.000	0.183	0.000	0.000
	89	0.000	0.000	0.000	0.817	0.000	0.000
Est	112	0.000	0.000	0.000	0.000	1.000	0.000
	100	1.000	1.000	0.000	0.000	0.000	1.000
	97	0.000	0.000	1.000	0.000	0.000	0.000
	94	0.000	0.000	0.000	0.067	0.000	0.000
	88	0.000	0.000	0.000	0.933	0.000	0.000
Mdh-1	128	0.000	0.000	0.000	0.000	0.000	0.929
	117	0.000	0.000	0.000	1.000	0.000	0.000
	113	0.000	0.000	0.000	0.000	0.000	0.071
	100	1.000	1.000	0.000	0.000	0.013	0.000
	96	0.000	0.000	1.000	0.000	0.987	0.000
Mdh-2	100	1.000	1.000	0.000	1.000	0.000	0.000
	85	0.000	0.000	1.000	0.000	1.000	0.000
	60	0.000	0.000	0.000	0.000	0.000	1.000
Mdh-3	−56	0.000	0.000	0.000	1.000	0.000	0.000
	−100	1.000	1.000	0.000	0.000	0.000	0.000
	−122	0.000	0.000	0.000	0.000	1.000	1.000
	−178	0.000	0.000	1.000	0.000	0.000	0.000
Pgm	200	0.625	0.186	0.000	0.000	0.163	0.071
	100	0.375	0.814	1.000	0.967	0.837	0.929
	−33	0.000	0.000	0.000	0.033	0.000	0.000
Sod	114	0.000	0.000	1.000	0.000	0.000	0.000
	103	0.000	0.000	0.000	0.000	0.000	1.000
	100	1.000	1.000	0.000	0.000	0.000	0.000
	76	0.000	0.000	0.000	1.000	0.000	0.000
	73	0.000	0.000	0.000	0.000	0.987	0.000
	35	0.000	0.000	0.000	0.000	0.013	0.000
Fm	100	0.000	0.000	1.000	0.917	0.986	1.000
	80	1.000	1.000	0.000	0.000	0.000	0.000
	68	0.000	0.000	0.000	0.083	0.014	0.000
Ck	157	0.000	0.000	1.000	0.000	0.000	1.000
	100	1.000	1.000	0.000	1.000	1.000	0.000
α-Gpd	−33	0.000	0.000	0.000	0.000	0.987	0.000
	−100	0.975	0.943	0.000	0.000	0.000	0.000
	−115	0.000	0.000	0.000	0.000	0.000	1.000
	−117	0.000	0.000	0.000	1.000	0.000	0.000
	−150	0.000	0.000	0.000	0.000	0.013	0.000
	−183	0.000	0.000	1.000	0.000	0.000	0.000
	−233	0.025	0.057	0.000	0.000	0.000	0.000

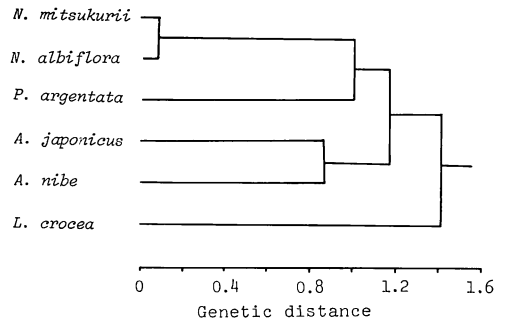

Fig. 1. Dendrogram showing the relationship among the 6 sciaenid species based on values of genetic distance.

completely identical, and will become infinite when the allele frequencies of the two species compared are completely divergent; namely, they do not share common alleles (Nei, 1972). Table 4 gives the list of genetic distances for each pair of species, and Table 5 shows the average genetic distance of each pair of subpopulations or species for various levels of taxa. The average D value among species (*N. mitsukurii* and *N. albiflora*) belonging to the same genus was found to be 0.092, while that among genera belonging to the same subfamily was 1.212, ranging from 0.861 to 1.668.

To estimate the relationships between the 6 species, a dendrogram was drawn based on the genetic distances (Fig. 1). From this dendrogram, the six species were clearly divided into two major groups at a distance of 1.41. One group included *N. mitsukurii*, *N. albiflora*, *P. argentata*, *A. japonicus* and *A. nibe* while the other group consisted solely of *L. crocea*. The first group was further divisible into two groups at a distance of 1.2, one group consisting of *N. mitsukurii*, *N. albiflora* and *P. argentata*, and the other of *A. japonicus* and *A. nibe*. It was possible to further divide this first group into two subgroups at a distance of 1.0, one subgroup consisting of *N. mitsukurii* and *N. albiflora*, and the other of *P. argentata*.

Table 4. Estimates of genetic similarity and distance between 6 sciaenid species. Values above diagonal are estimates of genetic distance, those below are estimates of genetic similarity. * The bias caused by small number of individuals was not corrected because the D values were larger than 0.15 (Nei, 1978).

Species	1	2	3	4	5	6
1. *Nibea mitsukurii*		0.092	1.460	1.080	1.085	1.668
2. *Nibea albiflora*	0.912		1.267	0.946	1.004	1.441
3. *Argyrosomus japonicus**	0.232	0.282		1.251	0.861	1.428
4. *Pennahia argentata*	0.339	0.388	0.286		0.975	1.271
5. *Atrobucca nibe*	0.338	0.366	0.423	0.377		1.234
6. *Larimichthys crocea**	0.189	0.237	0.240	0.281	0.291	

Table 5. Average and range of genetic distance in sciaenid species.

Item		Source of the data
Between conspecific subpopulation	D=0.0017 (0.00087–0.00220) (in *Pennahia argentata* from 4 locations based on 28 loci)	Menezes and Taniguchi (unpublished)
	D=0.0390 (in *Nibea albiflora* from 2 locations based on 29 loci)	
	D=0.0074 (in *Nibea mitsukurii* from 2 locations based on 29 loci)	
Between congeneric species	D=0.0920 (in genus *Nibea* on 29 loci)	present study
	D=0.3530	Fitzsimons et al. (1985)
Between consubfamilial genera	D=1.2120	present study

Genetic divergence between congeneric species has been observed in many fishes using biochemical markers. An average genetic distance between species has been reported as being 0.627 in 10 species of the genus *Lepomis* (Avise 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), 0.243 in 3 species of *Hypentelium* (Buth, 1980) and 0.353 in 3 species of the sciaenid genus *Cynoscion* (Fitzsimons et al., 1985). In the family Pleuronectidae, the average genetic distance was reported as being 0.01 between populations, 0.13 between subspecies, 0.62 between species and 1.11 between genera (Ward and Gelleguillos, 1983). In the family Carangidae, Kijima et al. (1986) indicated the average genetic distance as being 0.880 between species, 2.046 between genera and 2.290 between subfamilies, while in sparid fish Taniguchi et al. (1986) reported the average genetic distance as being 0.002 between conspecific subpopulations, 0.115 between congeneric species, 0.842 between consubfamilial genera and 1.273 between subfamilies. The average value found between consubfamilial genera in the sparid fish was almost identical to that found at the species level in carangid fish (Taniguchi et al., 1986). In fishes, as in other organisms (Ayala, 1983) the average genetic distance tends to be larger in higher taxa. This was reflected in the present study, where the *D* value between consubfamilial genera was larger than the *D* value between congeneric species, and that between congeneric species was larger than that between conspecific populations. The two species of *Nibea* (*N. mitsukurii* and *N. albiflora*) were, however, less diversified than the species level of the other genus, *Cynoscion* (Fitzsimons et al., 1985). The genetic distance was more or less equal to the subspecies level in published data (Taniguchi et al. 1986).

Taniguchi (1969a, b, 1970) studied the systematic relationships among the sciaenid species of the Japan and China Seas based on the osteology of the neurocranium, vertebrae, premaxillary and dentary. The present data support the classification based on the neurocranium. The sciaenid species in the present study were clearly divisible by the biochemical genetic markers into two distinct groups. One of the group included only *L. crocea*, while the other group, consisting of the remaining 5 species, could be further divided at lower *D* levels into the *Nibea*-form (*N. mitsukurii* and *N. albiflora*), the *Pennahia*-form (*P. argentata*) and the *Argyrosomus*-form (*Argyrosomus* and *Atrobucca*). The *Pennahia*-form was found to be closer to the *Nibea*-form, while the *Argyrosomus*-form was intermediate between the *Pennahia*-form and *Pseudosciaena*-form (*Larimichthys*-form). Evidence obtained from the biochemical genetic study suggests that the *Pseudosciaena*-form evolved independently, and supports the result obtained from morphological studies.

The genetic distances thus give supplemental but important evidence pertaining to taxonomic problems on the recognition of species or subspecies which cannot be solved by conventional methods. It may be concluded that isozymes are useful markers to estimate relationships among species and to determine their taxonomic rank, as reported in earlier studies.

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日本およびその近海産ニベ科魚類の遺伝的分化

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日本産ニベ科魚類，ニベ，コイチ，シログチ，オオニベ，クログチおよびフーセイの 6 種について，14 種類のアイソザイムの電気泳動像を検出し，それらの間の遺伝的分化と系統関係を調べた．21 遺伝子座の対立遺伝子頻度を推定し，各魚種間の遺伝的距離 (*D*) を求めた．*D* 値は比較する 2 種間の分類学的位置関係が遠くなるほど大きくなった．遺伝標識にもとづいて推定された類縁関係は内部および外部形態にもとづく結果とよく一致した．ニベ科魚類は *D* 値が 1.41 のところで，大きく 2 群に分けられた．

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