Genetic Diversity and Population Structure of *Pseudobagrus fulvidraco* in the Nakdong River

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Enzyme electrophoresis was used to estimate genetic diversity and population genetic structure of *Pseudobagrus fulvidraco* in Korea. Nine of the 14 loci (64.3%) showed detectable polymorphism. Genetic diversity at the population and species levels were 0.286 and 0.277, respectively. Analysis of fixation indices, calculated for all polymorphic loci in each population, showed a substantial deficit of heterozygotes relative to Hardy-Weinberg expectations. This deficit is expected that it is due to a limited effective number of individuals per population. The average G_{ST} for polymorphic loci was 0.064, indicating that most (93.6%) of the genetic diversity occurred within populations. The indirect estimate of gene flow based on mean G_{ST} was 3.67. Given limited gene flow is expected to diverge genetically due to drift and reduced populations. Most populations in our study experience annual, severe demographic bottlenecks due to drought and floods.

Key words — Genetic diversity, Population structure, *Pseudobagrus fulvidraco*

Introduction

Gel electrophoresis coupled with histochemical staining of specific proteins was developed in the 1960s and became the most widely used method for measuring genetic variation in natural populations [13]. The technique is relatively inexpensive and provides a measure of many variable and non variable genes in individuals and populations. The gel phenotypes are easy to interpret and there are computer programmes available for data analyses. Most surveys of genetic diversity in marine species have used proteins, and diversity is measured as the average heterozygosity over many protein loci (heterozygosity is the proportion of individuals that are heterozygous at a single gene locus). This information has contributed greatly to an understanding of the evolutionary history of individual species and related group of species, and has provided insights into the relationships between allozyme diversity and life-history traits [5]. Despite the importance of knowledge on genetic variation for providing information for conservation purposes, detailed studies of genetic variation are not available for most taxa in Korea.

Population structure is a critical feature of a species because of its potential effect on rates of evolutionary change [27]. Exploring differences in population structure over a number of spatial scales can reveal how the causes of structure may change with scale [19]. Characterizing changes in population differentiation at different spatial scales can be done using a stratified sampling design and subsequent analysis of genetic data using Wright's [28] hierarchical F-statistics. One major advantage to this approach is the richness of the theoretical development as a guide for interpretation and summary of results.

Recent investigations of the spatial distribution of molecular markers such as allozyme or DNA within populations of animal species have indicated that individuals are not likely to be randomly distributed owing to the effects of factors such as limited gene flow and microhabitat selection [18].

Korean bullhead, *Pseudobagrus fulvidraco* (Richardson) is distributed in East Asia such as Korea, China and Japan (Fig. 1) [6]. Especially the species is mostly found in rocky and gravel rivers. The species has been used a good hot chowder, but, recently reduction of populations and individuals is serious. Populations that are reproductively isolated may gradually lose the effective population sizes. The rapid loss of new juveniles results in the permanent loss of gene pools with potential for species conservation. Although *P. fulvidraco* has been considered as an important species in ecology and aquaculture in Korea and studied feeding habits [6], culture [17], cytology [21], development [11], and histology [9], population structure of this species has not been studied.

The purposes of this paper are; 1) to estimate how much total genetic diversity is maintained in the species, 2) to describe how genetic variation is distributed within and

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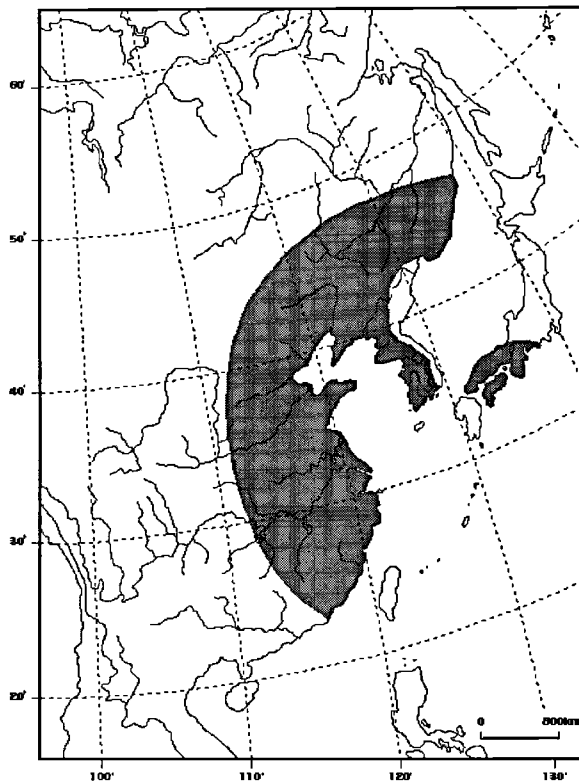E-mail : bklee@deu.ac.kr

Fig. 1. Geographic distribution of *Pseudobagrus fulvidraco*. among populations, and 3) to estimate the effective population number at equilibrium when gametes contribute to random mating events.

Materials and Methods

Sampling procedure and enzyme electrophoresis

P. fulvidraco was collected from six populations or areas in Korea during 2006 (Table 1). We collected samples from several localities per population because local densities at depths of 0.2 -3.0 m can not exceed $5/m^2$. Some samples were kindly supplied from commercial suppliers at the same localities. Eighteen to twenty-eight individuals were collected from each population and one caudal fin per each

Table 1. Collection localities for populations of *Pseudobagrus fulvidraco* as source for isozyme analysis

Code	Collecting sites	No. samples	Depth (m)
PSF-1	Cheondo-gun, the Dongchang-cheon	25	2.3
PSF-2	Namgi-up, the Nakdong River	28	1.6
PSF-3	Uiryeong-gun, Yangcheon River	23	2.0
PSF-4	Milyang-si, the Milyang River	26	1.2
PSF-5	Sancheong-gun, the Nam River	25	2.5
PSF-6	Sacheon-si, Deokcheon River	18	3.5

fish was used in this study.

Electrophoresis was performed using 12.0% starch gel. Buffer systems and enzyme staining procedures from Soltis et al. [23] were used to assay eight enzyme systems; alcohol dehydrogenase (ADH, EC 1.1.1.1), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), isocitrate dehydrogenase (IDH, EC 1.1.1.42), malate dehydrogenase (MDH, EC 1.1.1.37), esterase (EST, EC 3.1.1.2), 6-phosphogluconate dehydrogenase (PGD, EC 1.1.1.43), phosphoglucomutase (PGM, EC 5.4.2.2), and shikimate dehydrogenase (SKD, EC 1.1.1.25). The procedures for starch gel electrophoresis were as reported by Soltis et al. [23]. For enzymes which resolved more than one zone of activity, the most anodal isozyme is arbitrarily designated 1, with the others sequentially assigned higher numbers. Likewise, alleles were designated sequentially with the most anodally migrating allozyme designated 'a' and progressively slower forms 'b', 'c', and so on. The *P. fulvidraco* isozymes expressed phenotypes that were consistent in subunits structure and genetic interpretation with most isozyme studies, as documented by Weeden and Wendel [24].

Data analysis

Five standard genetic parameters were estimated using a computer program (LYNSPROG) developed by M.D. Loveless and A. Schnabel and POPGENE computer version 1.31 [29]; the percent of polymorphic loci (P), mean number of alleles per locus (A), the number of alleles per polymorphic locus (A_P), effective number of alleles per locus (A_E), and gene diversity (He) [7]. Subscripts refer to species (s) or population (p) level parameters. Observed heterozygotes (Ho) were compared to Hardy-Weinberg expected value using Wright's fixation index (F) or inbreeding coefficients [26]. These indices were tested for deviation from zero by x^2-statistics [10].

Nei's gene diversity formulae (H_T, H_S, D_M, and G_{ST}) were used to evaluate the distribution of genetic diversity within and among populations [15]. In addition, x^2-statistics were used to detect significant differences in allele frequencies among populations for each locus [25]. Nei's genetic identity (I) was calculated for each pairwise combination of populations [14].

A phenetic relationship was constructed by the neighbor-joining (NJ) method using the NEIGHBOR program in PHYLIP version 3.57 [4].

The genetic structure within and among populations

was also evaluated using Wright's [28] F-statistics F_{IT}, F_{IS}, and G_{ST}. The F_{IT} and F_{IS} coefficients measure excesses of homozygotes or heterozygotes relative to the panmictic expectations within the entire samples and within populations, respectively. The G_{ST} coefficient estimates relative population differentiation. Deviations of F_{IT} and F_{IS} from zero were tested using χ^2-statistics [10]. Two indirect estimates of gene flow were calculated. One estimate of Nm (the number of migrants per generation) was based on G_{ST} [27] and the other was based on the average frequency of "rare" alleles found in only one population [22].

Results

Genetic diversity

Fourteen loci encoding eight enzyme systems were screened. Nine of them (64.3%) showed detectable polymorphism in at least two populations (Table 2). The remaining five loci (Est-3, Idh-1, Mdh-2, Pgd-2, and Pgm-1) were monomorphic in all populations. An average of 55.5% polymorphism was found within populations, with individual population values ranging from 46.2% to 64.3%

Table 2. Allele frequencies at nine polymorphic loci in populations of *P. fulvidraco*

Locus	Allele	PSF-1	PSF-2	PSF-3	PSF-4	PSF-5	PSF-6
Adh	a	0.203	0.229	0.326	0.273	0.314	0.275
	b	0.750	0.743	0.674	0.727	0.686	0.725
	c	-	0.028	-	-	-	-
Est-1	a	-	0.145	0.180	-	0.111	0.060
	b	0.448	0.395	0.820	0.550	0.444	0.417
	c	0.345	0.263	-	0.317	0.267	0.357
	d	0.207	0.197	-	0.133	0.178	0.167
Est-2	a	1.000	0.740	0.867	0.800	0.815	1.000
	b	-	0.260	0.133	0.200	0.185	-
Gpi	a	0.283	0.432	0.650	-	-	-
	b	0.717	0.568	0.350	-	-	-
Idh-2	a	1.000	0.567	0.667	0.833	0.771	0.625
	b	-	0.267	0.333	0.167	0.229	0.219
	c	-	0.166	-	-	-	0.156
Mdh-1	a	0.145	0.086	0.136	0.180	0.172	0.122
	b	0.661	0.776	0.687	0.667	0.625	0.662
	c	0.194	0.138	0.167	0.153	0.203	0.216
Pgd-1	a	0.196	0.080	0.174	0.125	0.167	-
	b	0.804	0.720	0.826	0.875	0.750	0.750
	c	-	-	-	-	0.083	0.250
Pgm-2	a	0.275	0.261	-	0.309	0.204	0.278
	b	0.725	0.739	1.000	0.691	0.796	0.722
Skd	a	0.861	0.761	0.696	0.588	1.000	1.000
	b	0.139	0.239	0.304	0.412	-	-

(Table 3). The average number of alleles per locus (A) was 1.80 across populations, ranging from 1.64 for the population with the lowest number of alleles to 2.07 for the population with the highest number of alleles. The effective number of alleles per locus, or the number of alleles needed within a locus to maintain the current level of heterozygosity was similar at the species and the population level (Aes = 1.61; Aep = 1.57). The mean genetic diversity within populations was 0.277. The population PSF-2 (Namgi) had the highest expected diversity (0.336), while population PSF-3 (Uiryeong) had the lowest (0.224). Overall, mean observed heterozygosity at the population levels different to the expected value (Hop = 0.144; Hep = 0.277).

Genetic structure

Total genetic diversity values (H_T) varied from 0.234 (Est-2) to 0.657 (Est-1), giving an average 0.417 over all polymorphic loci (Table 4). The absolute measure of genetic differentiation among populations (D_M) was very low (0.030).

In general, genotype frequencies do not conform to Hardy-Weinberg expectations. Chi-square tests indicated significant deviations from Hardy-Weinberg. As expected from the chi-square tests, F_{IS}, a measure of the deviation from random mating within six populations, was 0.497, range from 0.376 for Mdh-1 to 0.694 for Est-1 (Table 4). The observed high, significant, and positive F_{IS} value (0.497) indicates that there was a significantly deficit of heterozygotes in the populations.

On a per locus basis, the proportion of total genetic variation due to differences among populations (G_{ST}) ranged

Table 3. Percentage of polymorphic loci (P_P), mean number of alleles per polymorphic population (A_E), mean number of alleles per locus (A), effective number of alleles per locus (A_E), observed heterozygosity (Hop), Hardy-Weinberg expected heterozygosity or genetic diversity (Hep) for six populations of *P. fulvidraco*

Pop[a].	P_E	A	A_E	A_E	Hop (SD)	Hep (SD)
PSF-1	50.0	1.71	2.43	1.47	0.123 (0.019)	0.239 (0.063)
PSF-2	64.3	2.07	2.67	1.74	0.186 (0.021)	0.336 (0.067)
PSF-3	57.1	1.64	2.13	1.38	0.130 (0.020)	0.224 (0.055)
PSF-4	61.5	1.77	2.25	1.55	0.148 (0.020)	0.289 (0.063)
PSF-5	53.9	1.85	2.57	1.65	0.144 (0.019)	0.294 (0.070)
PSF-6	46.2	1.77	2.67	1.63	0.127 (0.016)	0.281 (0.074)
Mean	55.5	1.80	2.45	1.57	0.143 (0.008)	0.277 (0.027)
Species	66.3	2.07	2.67	1.61	-	0.286

a : Numerical codes as in Table 1.

Table 4. Total genetic diversity (H_T), genetic diversity within population (H_S), and the absolute measure of genetic differentiation among populations (D_M). The deviations of genotype frequencies from Hardy-Weinberg expectations over all populations (F_{IT}) and within individual populations (F_{IS}), and proportion of total genetic diversity partitioned among populations (G_{ST}) of *P. fulvidraco*

Locus	H_T	H_S	D_M	F_{IT}	F_{IS}	G_{ST}
Adh	0.412	0.408	0.004	0.422	0.427	0.008
Est-1	0.657	0.619	0.046	0.675	0.694	0.058
Est-2	0.234	0.213	0.025	0.424	0.474	0.088
Gpi	0.484	0.449	0.042	0.554	0.586	0.072
Idh-2	0.436	0.399	0.044	0.529	0.569	0.085
Mdh-1	0.487	0.483	0.005	0.372	0.376	0.008
Pgd-1	0.362	0.344	0.022	0.361	0.393	0.050
Pgm-2	0.348	0.329	0.023	0.450	0.480	0.054
Skd	0.332	0.282	0.060	0.383	0.476	0.151
Mean	0.417	0.392	0.030	0.463	0.497	0.064

from 0.008 for *Adh* and *Mdh-1* to 0.151 for *Skd* with a mean of 0.064, indicating that about 6.4% of the total allozyme variation was among populations (Table 4). Thus, the majority of genetic variance (93%) resided within populations. The estimated of gene flow based on G_{ST} was moderate ($Nm = 3.67$).

At the level of the sample as a whole, however, Wright's F coefficients showed that significant deficiencies of heterozygosites exist at all polymorphic loci. Analysis of fixation indices, calculated for all polymorphic loci in each population, showed a substantial deficiency of heterozygotes relative to Hardy-Weinberg expectations (Table 5). For example, 100% of fixation indices were positive (45/45), and 25 of them departed significant from zero (p < 0.05). The negative index which indicates as excess of

Table 5. Wright's fixation indices for six populations of *P. fulvidraco*

Locus	PSF-1	PSF-2	PSF-3	PSF-4	PSF-5	PSF-6
Adh	0.376*	0.430**	0.516*	0.398*	0.477**	0.389
Est-1	0.787***	0.673***	0.336	0.604***	0.680***	0.753***
Est-2	-	0.287	0.442	0.597*	0.518**	-
Gpi	0.685**	0.547*	0.374			
Idh-2	-	0.322	1.000***	1.000***	0.423*	0.542***
Mdh-1	0.308	0.361	0.362*	0.392**	0.429***	0.413***
Pgd-1	0.324	0.460*	0.112	0.331	0.392	0.497*
Pgm-2	0.389	0.559	-	0.456	0.440	0.462
Skd	0.323	0.182	0.397	0.521*	-	-

Note: A dash indicates fixed loci. *, p<0.05; **, p<0.01; ***, p<0.001.

heterozygotes at those loci and in these populations was not found in any populations.

The values of genetic distance (D) for each pairwise combination of populations were below 0.55 in most populations (Table 6). Genetic identity values among pairs populations range from 0.947 to 0.990.

The similarity among *P. fulvidraco* populations can be seen in the NJ dendrogram, where total populations cluster at a below genetic distance 0.065 (Fig. 2). The NJ dendrogram provided a few insights into the genetic structuring of populations. In addition, the correlation between genetic distance and geographic distance was high ($r = 0.59$, p < 0.05), and indicated that about 65% $(1-r^2)$ of the variation in genetic distance was caused by unknown other factors than distance.

Discussion

P. fulvidraco maintains relatively high levels of allozyme variation compared to same species in Dong Ping Lake in China using microsatellite markers [12]. Nine of the 14 loci (64.3%) showed detectable polymorphism. Similar study of same species in Dong Ping Lake revealed a much higher

Table 6. Nei's unbiased genetic identity values of among *P. fulvidraco* (above diagonal) and genetic distances among populations (below diagonal)

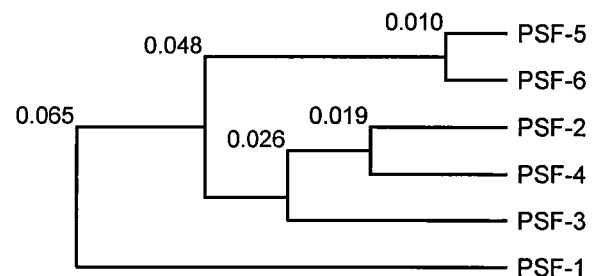| Pop.	PSF-1	PSF-2	PSF-3	PSF-4	PSF-5	PSF-6
PSF-1	-	0.977	0.947	0.981	0.990	0.986
PSF-2	0.024	-	0.966	0.981	0.988	0.988
PSF-3	0.055	0.035	-	0.978	0.975	0.958
PSF-4	0.020	0.019	0.022	-	0.980	0.971
PSF-5	0.010	0.012	0.025	0.021	-	0.990
PSF-6	0.015	0.012	0.043	0.030	0.010	-

Fig. 2. A dendrogram showing the phylogenic relationships among the six populations of *P. fulvidraco* based on data of genetic distance obtained by starch gel electrophoresis. Values are Nei's genetic identity. Codes of populations are given in Table 1.

level of polymorphism. Electrophoresis analysis showed that 19 pairs of primers reproducibly produced clear bands, and, of them 6 were polymorphic. There were totally 22 alleles of these microsatellite loci, and the number of alleles per locus ranged from 2 to 6. The average homozygosity, average polymorphism information content and average heterozygosity was 41.7%, 0.488, and 0.583, respectively [12]. The P, A, and Hep of Andros freshwater fish, *Gambusia hubbsi* by allozyme analysis was 14.3%, 1.30, and 0.042, respectively [20].

At a number of the studied loci significant deviation from Hardy-Weinberg proportions were found (Table 5). These were exclusively due to heterozygote deficiency, suggesting that some of the individuals might not be randomly interbreeding.

Although F_{IS} is a direct parameter of inbreeding, Wright's fixation indices (100% positive) as well as the observed high, significant, and positive F_{IS} value (0.497) indicate that homozygotes were significantly in excess. In general, this high level of inbreeding can result from a variety of causes; null alleles, positive assortive mating (i.e., preferential mating among similar genotypes), selection for homozygotes, family structure within a restricted neighborhood causing mating among relatives, and the Wahlund affect caused by the artificial grouping of individuals from different breeding populations [3,8].

Null or silent alleles seem an unlikely explanation for the observed heterozygote deficiency, since it was observed at more than three loci and null alleles are not encountered this frequently. It is also possible that natural selection is acting on the loci. The time needed for selection to produce substantial allele frequency differences depends on how strong the selection is and if selection is strong enough to dominate gene flow and drift [1]. In this case, differentiation will appear more rapidly than at neutral loci [2]. This seems unlikely, since it would act against heterozygotes, which makes the polymorphisms unstable, and also because of constant fluctuations in the effective population size of *P. fulvidraco* in different localities.

From the data it is impossible to determine which is the main cause of heterozygote deficiency, but there is an indication that the significant deviations found in our populations are due to outcross-fertilization and to a minor degree to genetic drift. Inbreeding reduce genetic variability. Since *P. fulvidraco* is able to sexual-fertilize, one might speculate that it is able to live in environments that are often hostile, where the populations repeatedly go through bottlenecks (winter season), thus reducing genetic variation. Most populations in our study experience annual, severe demographic bottlenecks due to drought and floods. In addition, reduce of populations are expected to diverge genetically due to drift, the random loss of alleles having individuals due to sporadically fishing.

The population PSF-2 (Namgi) had the highest expected diversity (0.336), while population PSF-3 (Uiryeong) had the lowest (0.224) (Table 3). This has resulted in substructuring of *P. fulvidraco* populations into multiple genetically differentiated populations within as well as among populations of the several small incoming rivers into the Nakdong River. The population PSF-2 is located on lower part of the Nakdong River. Thus the population PSF-2 is less prone to effects of drought in winter and considered as potential avenues of intermittent migration during floods and passive migration.

Nei et al. [16] have shown that the reduction in average heterozygosity per locus depends not only on the size of the population bottleneck, but also on the subsequent rate of population growth. If population growth is rapid, reduction in average heterozygosity is small, even given a small number of founder. Most population sizes in Korea have a tendency to decrease gradually because Korean rivers have low depth and width.

Interestingly, the demographic and genetic approaches both suggested the occurrence of migration in at least two examples: in population PSF-2, between population PSF-3 and population PSF-4, in population PSF-3, between population PSF-5 and population PSF-6. The larger percentage of reassigned individuals observed in populations collected after the dry season indicates that genetic drift and migration between close populations occur mainly during the dry season and that long-distance migration may predominate during the rainy season. Indeed, this result is explained by both larger percentages of individuals reassigned to the same population and to other populations during the dry season. The fact that the results are only marginally significant may be due to a lack of statistical power.

Acknowledgment

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초록 : 낙동강에 분포하는 동자개 집단의 유전적 다양성과 집단구조

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전분 젤 전기영동을 사용하여 한국내 분포하는 동자개 여섯 집단에서 유전적 다양성과 집단구조를 평가하였다. 14개 대립유전자좌위에서 9좌위가 다형현상을 나타내었다(64.3%). 종수준과 집단수준에서 유전적 다양성은 각각 0.286과 0.277이였다. Wright의 고정지수에서 Hardy-Weinberg 평형에 비해 전반적인 이형접합체 결핍이 나타났다. 이 결핍은 집단내 유효한 개체수의 부족을 시사한다. 집단간 유전적 분화 정도는 0.064로 대부분의 유전적 변이(93.6%)가 집단내에 있음을 의미한다. 간접적으로 평가된 집단간 이주하는 개체수는 3.67로 나타났다. 제한된 유전자 유동과 유효집단의 감소는 유전적 부동을 유발하고, 주기적인 포획으로 인한 개체수의 감소는 유전자 상실로 이어지고 있다. 대부분의 집단이 겨울철 가뭄과 여름철 홍수로 심한 병목을 겪고 있었다.