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Genetic and Morphological Analysis of Geographic Differentiation in Japanese Common Freshwater Shrimp, *Paratya compressa* (Decapoda: Atyidae)

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Summary

Geographic differentiation of Japanese common freshwater shrimp, *Paratya compressa*, was examined by electrophoretic and morphological analysis. Fourty-one populations were classified into three geographic groups: northern, central, and southern Japan. The Nei's genetic distance (D) between the Northern and Central group is 0.2549. The D between the Southern group and the above two groups is 0.5419. All populations in the Southern group consisted of individuals having dorsal rostral spines on the carapace and small egg size, while all populations in the Northern group consisted of individuals having no spine on the carapace and large egg size. The Central group consisted of the populations of individuals having spines, populations of individuals having no spine and populations of both individuals. The egg size of Central populations was large, except the Biwa Lake population (middle size). From these morphological data, the Southern and Northern group are two typical subspecies, *P. c. compressa* and *P. c. improvisa*, respectively. This suggests that the morphological differentiation corresponds with genetic differentiation. The Central group, however, suggests that genetic differentiation is sometimes independent of the morphological differentiation.

The genetic distance between species is roughly correlated with their morphological divergence. If two populations are geographically isolated, the two populations tend to accumulate genetic differences. Such genetic differentiation should be roughly correlated the morphological difference. Morphological divergence among spatially separated populations is called geographic variation. Numerous biologists have descrived the subspecies in many organisms on the basis of geographic variation.

A previous paper (1) revealed that Nei's genetic distance (D) between the two *Paratya* subspecies (Decapoda: Atyidae) was 0.597, based on 18 enzyme loci by starch-gel electrophoresis. These subspecies were classified by the existence of dorsal rostral spines on the carapace. *P. c. compressa* has spines and is found in

southern Japan, while *P. c. improvisa* lacks spines and is found in northern Japan.

The aim of this study is to reveal the geographic differentiation among 41 populations of *P. compressa* collected from throughout Japan by electrophoretic and morphological analysis and to discuss the correlation of genetic differentiation with morphological differentiation.

Materials and Methods

Specimens of *Paratya compressa* were collected from 41 different locations in Japan, except Hokkaido, during the months of February-October in 1990-1994. The electrophoretic data have been obtained from the previously published papers (2, 3) and from additionally unpublished data (see Fig. 1 and Table 1). Allele frequencies were calculated at 19 enzymatic loci in 41 populations. Nei's genetic distance (D) (4) among populations was calculated from the allele frequency data. The dendrogram was drawn by the group-average linkage method.

As the morphological characters, number of dosal and ventral rostral spines (DRS and VRS), the number of dorsal rostral spines from the tip of cornea to the

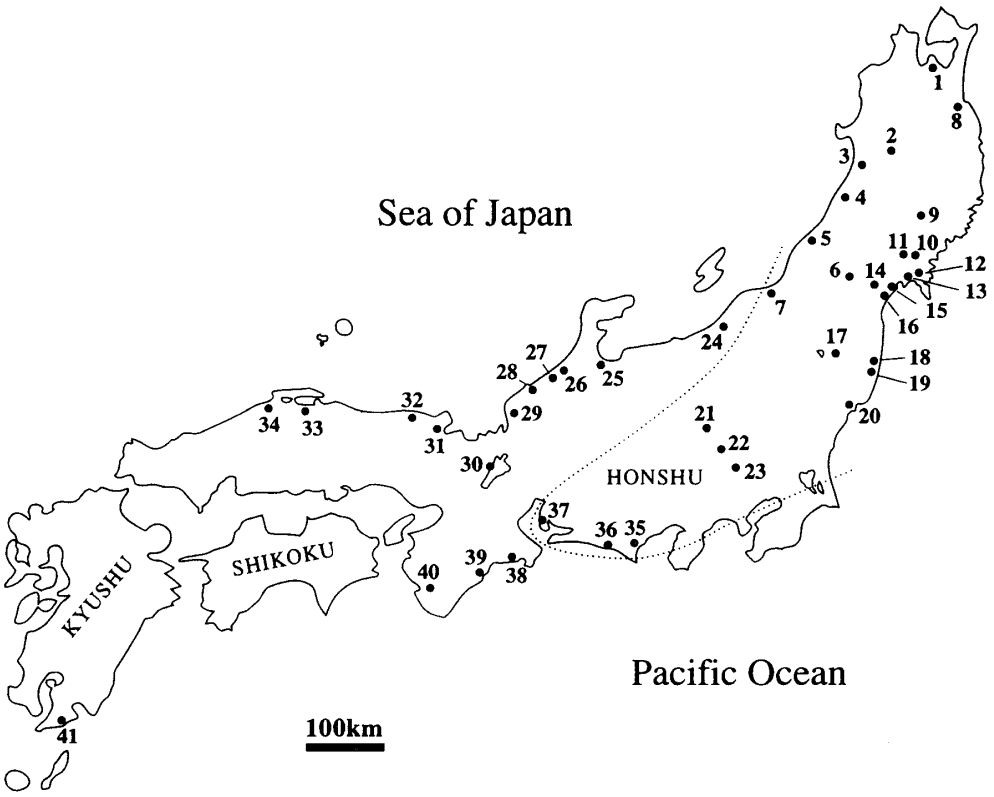

FIG. 1. Map showing collection site of *Paratya compressa*. Names of localities and sample size are shown in Table 1. A dotted line outlines the geographic ranges of *P. c. compressa* (left) and *P. c. improvisa* (right) proposed by Kamita (7) (Kamita's 'V'-shaped line)

TABLE 1. *Information of collection sites, sample sizes and references for 41 populations in Paratya compressa*

No. of locality	Collection sites	Sample size	References	No. of locality	Collection sites	Sample size	References
1	Shimizu River	31	Ikeda *et al.* [2]	21	Haruna Lake	27	Ikeda *et al.* [2]
2	Oh Marsh	50	ditto	22	Pond in Maebashi City	50	unpublished
3	Shirahata Pond	50	ditto	23	Pond in Ranzan Town	48	Ikeda *et al.* [2]
4	Oh Pond	50	ditto	24	Nagamine Pond	22	Ikeda *et al.* [3]
5	Kami Pond	50	ditto	25	Pond in Takaoka City	50	ditto
6	Dojo Marsh	36	ditto	26	Kahokugata Lake (A)	50	ditto
7	Miomote River	44	unpublished	27	Kahokugawa Lake (B)	52	ditto
8	Yamazaki Pond	50	Ikeda *et al.* [2]	28	Kobagata Lake	36	ditto
9	Yagisawa Pond	50	ditto	29	Hino River	44	ditto
10	Kamitomita Pond	50	ditto	30	Biwa Lake	32	ditto
11	Hinata Pond	57	ditto	31	Pond in Suki Town	40	ditto
12	Kitakami River	50	ditto	32	Yada River	31	ditto
13	Ushiami Pond	92	ditto	33	Hino River	50	ditto
14	Imosawa Pond	50	ditto	34	Pond in Sanraku Town	50	ditto
15	Kenmin-no-mori Pond	64	ditto	35	Ooi River	50	unpublished
16	Dainohara Pond	64	ditto	36	Tenryu River	48	ditto
17	Oguni Marsh	50	ditto	37	Sugitani Pond	26	ditto
18	Ukedo River	52	ditto	38	Iseji River	32	Ikeda *et al.* [3]
19	Takase River	96	ditto	39	Akaba River	50	ditto
20	Same River	50	ditto	40	Hiki River	32	ditto
				41	Kubota River	95	ditto

No. of locality is identical to Fig. 1.

orbital notch (the spines above the cornea or orbital notch were not counted) (DRSC), the number of dosal rostral spines on the carapace (including the spine above the orbital notch) (RSC) and egg volume were adopted. Ten eggs at the pre-eye stage of development were measured from each mother shrimp. The egg volume (V) was calculated from the formula $V=\pi LH^2/6$, where L and H are length and width of an egg, respectively.

Results

Genetic Relationship and Geographic Distribution

A dendrogram was drawn, as shown in Fig. 2, to summarize the relationship

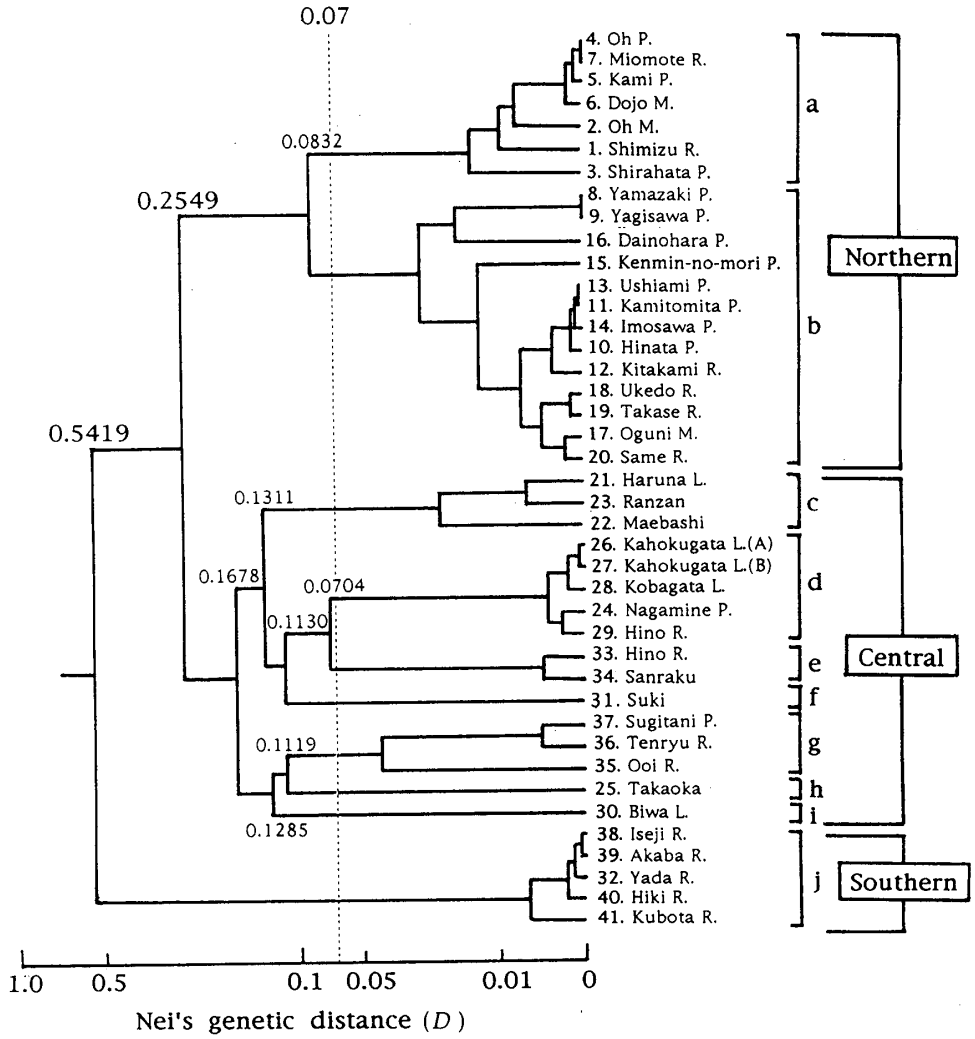

FIG. 2. Genetic relationship among 41 populations of *Paratya compressa* based on allozymic data. a: Japan Sea; b: Pacific Ocean; c: Kanto; d: Hokuriku; e: San-in; f: Suki; g: Tokai; h: Takaoka; i: Biwa Lake; j: Southern.

among 41 populations of *Paratya compressa*. The forty-one populations were classified into three geographic groups; northern, central and southern part in Japan. The genetic distance between the Northern and Central group is 0.2549. This value suggests level of subspecies. The genetic distance between the Southern group and above two groups was 0.5419. This value suggests level of species. Three geographic groups were characterized by predominant alleles at *Fdp-1* locus. All populations of the Northern group possesed $Fdp\text{-}1^{C}$. All populations of the Central group possesed $Fdp\text{-}1^{B}$, while all populations of the Southern group possesed $Fdp\text{-}1^{D}$.

Furthermore, a imaginary vertical line was drawn across the dendrogram as an attempt to delimit a group having a distance of about 0.07. Using this vertical line, the 41 populations are divided into ten subgroups. Twenty populations in the Northern group were divided into two subgroups, Japan Sea (a) and Pacific Ocean (b). Sixteen populations in the Central group were divided into seven subgroups; Kanto (c), Hokuriku (d), San-in (e), Suki (f), Tokai (g), Takaoka (h) and Biwa Lake (i). Five populations in the Southern group could not be divided. It indicates that the population structure of the freshwater shrimp, *P. compressa* has a tendency to split into a number of subgroups with localization.

Morphological Differentiation

To elucidate the relation of local subgroups with the number of dorsal rostral spines on the carapace (DRS), the mean and range of DRS was examined in 41 populations. As shown in Table 2, clear geographic differences were observed in this character and all populations were divided three categories by the existence of spines. All individuals in 20 populations of the Northern group had no spine (category I), while all individuals in five populations of the Southern group had spines (category II). However, the 16 populations of the Central group showed the two categories and category III consited of individuals having spines and no spines. All three populations of c subgroup showed category I, but the other subgroups consisted of only category III (e, f, h and i subgroups), I and III (g) or II and III (d) populations.

One population selected as the representative from each of the ten local subgroups, and number of dorsal rostral spines (DRS), the number of ventral rostral spines (VRS), number of dorsal rostral spines from the tip of cornea to the orbital notch (DRSC), and egg volume were examined. These characters were not significant difference among shrimps with varying body and age in both sex in a population. DRS varied from 10.04 to 21.74, VRS from 1.51 to 3.31, DRSC from 0.61 to 8.69, and egg volume from 0.014 to 0.100 in the mean value. The mean value and range in four characters of ten subgroups is shown in Fig. 3. In the three characters except for VRS, clear classification could be done. In DRS and

TABLE 2. *Mean and range of the number ofdorsal rostral spines on the carapace (RSC) of 41 populations in Paratya compressa*

Group	Subgroup	No. of locality	Mean (Renge)	Category	Group	Subgroup	No. of locality	Mean (Range)	Category
Northern	a	1	0(−)	I	Central	c	21	0(−)	I
		2	0(−)	I			22	0(−)	I
		3	0(−)	I			23	0(−)	I
		4	0(−)	I		d	24	1.23(1-2)	II
		5	0(−)	I			26	1.42(1-2)	II
		6	0(−)	I			27	1.39(1-2)	II
		7	0(−)	I			28	1.22(0-2)	III
	b	8	0(−)	I			29	0.96(0-2)	III
		9	0(−)	I		e	33	0.90(0-2)	III
		10	0(−)	I			34	0.28(0-1)	III
		11	0(−)	I		f	31	1.05(0-2)	III
		12	0(−)	I		g	35	0(−)	I
		13	0(−)	I			36	0(−)	I
		14	0(−)	I			37	0.35(0-2)	III
		15	0(−)	I		h	25	0.90(0-2)	III
		16	0(−)	I		i	30	1.19(0-2)	III
		17	0(−)	I	Southern	j	32	2.07(2-3)	II
		18	0(−)	I			38	2.28(2-3)	II
		19	0(−)	I			40	2.47(2-4)	II
		20	0(−)	I			41	2.32(2-3)	II

No. of locality is identical to Fig. 1 and Table 1.

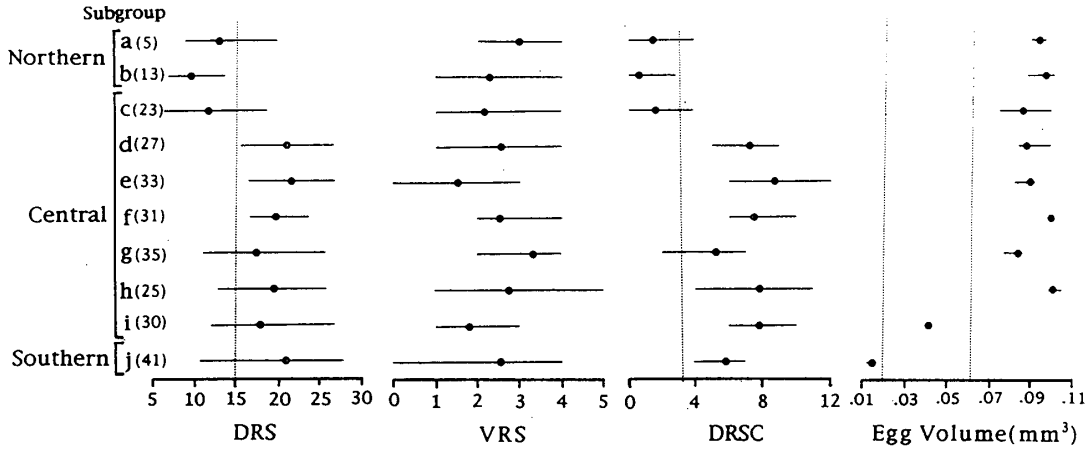

FIG. 3. Mean and range of four morphological characters in ten subgroups of *Paratya compressa*. Solid circles and horizontal bars indicate mean values and ranges, respectively. DRS: the number of dorsal rostral spines; VRS: the number of ventral rostral spines; DRSC: the number of dorsal rostral spines from the tip of cornea to the orbital notch. No. of locality is in each parenthesis (see Fig. 1 and Table 1).

DRSC, the a, b and c subgroup showed less clearly than other subgroups. In the egg volume, a, b, c, d, e, f, g and h showed large egg, but j subgroup (Southern group) showed small egg. While the i subgroup (Biwa Lake population) had middle size of egg. From these results, clear morphological differentiation was observed between the Northern and Southern group, but was not in the Central group.

Discussion

The result of the dendrogram showed 41 populations were classified into three geographic group; northern, central, and southern part in Japan. The dendrogram also showed that the population structure of *Paratya compressa* has a remarkable tendency to split into a number of subgroups with localization. The marked genetic differentiation should be caused by the geographic isolation.

Geographic isolation is usually thought to be almost invariably necessary for speciation to occur (5). The occurence of differences among spatially separated populations of the species is based on geographic variation of the morphology. According to morphological reports, *P. compressa* is classified into two subspecies by the existence of dorsal rostral spine on the carapace (6). *P. c. compressa* with spines live in the southern part, and *P. c. improvisa* without spine live in the northern part of Japan. Our morphological data on the Northern and Southern groups corresponds with the above two subspecies. It suggests that the morphological differentiation corresponds with genetic differentiation.

Kamita (7) detected two types (A and B) for egg size in *P. c. compressa*.

A-type (large egg) is very similar to *P. c. improvisa* in size of eggs, and some individuals of A-type have no dosal rostral spine on the carapace. Nishino (8) suggested that the large egg group (Kamita's A-type) of *P. c. compressa* is more closely related to *P. c. improvisa*, rather than the small egg group (B-type) of *P. c. compressa*. In our results, the Southern group indicates small egg and Northern group indicates large egg. These results showed two typical subspecies, *P. c. compressa* and *P. c. improvisa*. The population structure of the Central group is complex. Sixteen populations in the Central group consisted of three categories of populations by the existence of dorsal rostral spine on the carapace as shown in Fig. 4. This suggests that genetic differentiation is sometimes independent on the morphological differentiation in the Central group.

Furthermore, a part of the Central group (d, e, f, and h subgroups) having large egg and some or no spines on the carapace correspond to Kamita's A-type in

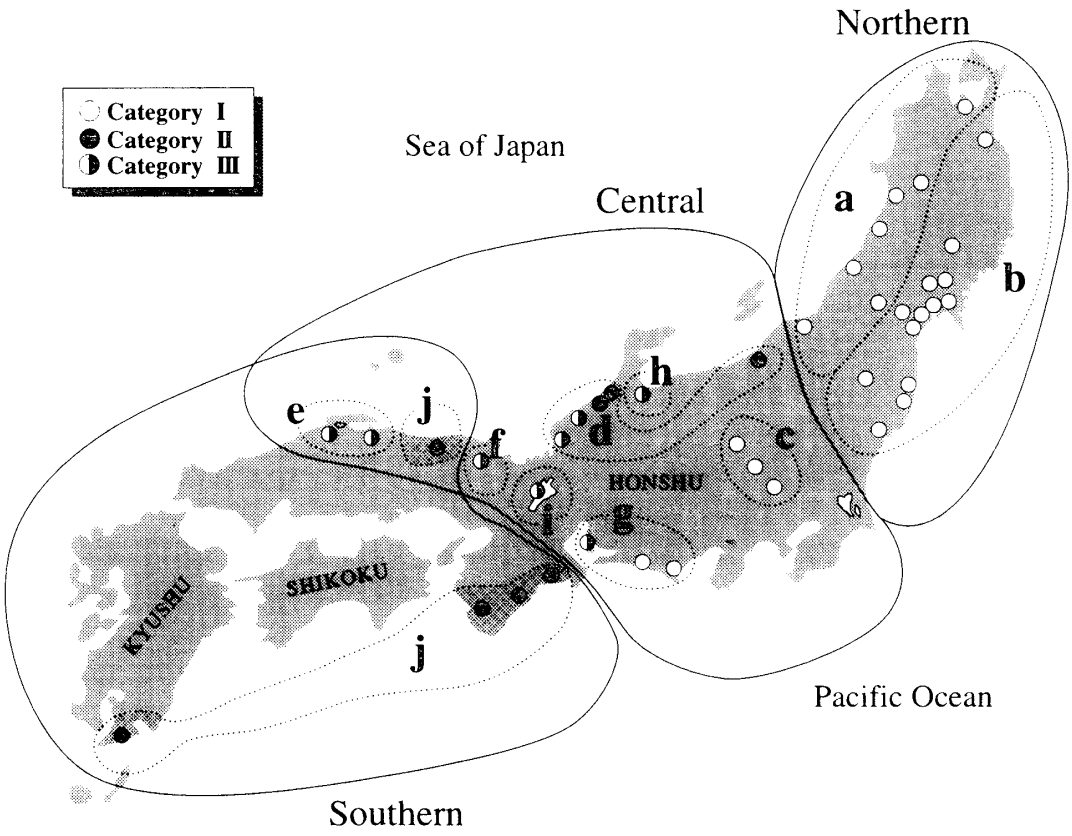

FIG. 4. Distributions of geographic groups, subgroups and populations as three categories (I, II and III) classified by the existence of dorsal rostral spine on the carapace in *Paratya compressa*. a : Japan Sea ; b : Pacific Ocean ; c : Kanto ; d : Hokuriku ; e : San-in ; f : Suki ; g : Tokai ; h : Takaoka ; i : Biwa Lake ; j : Southern. Category I : all individuals have no spine ; Category II : all individuals have spines ; Category III : the complex of individuals having spines and no spine.

P. c. compressa and the c and g groups correspond to *P. c. improvisa*. The dendrogram indicated that the Central group is more closely related to the Northern group, rather than the Southern group. This result supports Nishino's (8) suggestion.

The population in Biwa Lake (i subgroup) had smaller eggs than the other subgroups of the Central group. Nishino (8) also observed that eggs of Biwa Lake and the adjacent populations were smaller than A-type. Furthermore, we have detected different expression in MDH (malate dehydrogenase; E.C.1.1.1.37) isozymes between Biwa Lake and the other populations (3, 9). Further study is necessary for revealing the causes of these particularity in Biwa Lake population.

Acknowledgements

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