

Geographic Variation in the Molecular, Morphological and Reproductive Characters of the Ayu *Plecoglossus altivelis* (Plecoglossidae) in the Japan-Ryukyu Archipelago

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Abstract In an attempt to clarify geographic variation in the ayu *Plecoglossus altivelis*, the molecular, morphological and reproductive characters of populations from various localities in the Japan-Ryukyu Archipelago were examined. An electrophoretic analysis of enzymes encoded by 18–28 loci and univariate and multivariate analyses of 12 meristic and 17 morphometric characters indicated that there are two distinct groups of ayu in the archipelago: that of the Japan Islands and that of the Ryukyu Islands. Within the Japan Islands group, a landlocked population of Lake Biwa was found to diverge somewhat from other amphidromous populations genetically and morphologically. The Lake Biwa population was noted as being by far the most fecund, departing from a north-south cline of fecundity observed in amphidromous populations. Though no virtual divergence was observed among amphidromous populations in the Japan Islands in molecular data, divergence among these populations was considerable in morphological and fecundity data. Differences in geographic variation patterns are attributed to qualitative differences inherent in molecular and organismal characters: organismal characters are responsive to selection and also directly altered by environmental influences in part but molecular characters are hardly so. The evolution of different characters may have proceeded at different rates among geographic populations of ayu.

The problem of geographic variation in a species is both of theoretical and practical importance. Knowledge of the population structure of a species is essential not only for elucidating its nature and speciation but also for appropriate management of species stocks.

In the present research, a study was conducted on the geographic variation in the ayu *Plecoglossus altivelis*. Ayu are normally amphidromous and annual; that is, they spawn in the lower reaches of rivers in the autumn, the larvae flow into the sea where they spend the winter months and then migrate into rivers the following spring. They grow and mature in rivers and spawn the following autumn. This species is distributed throughout most of the Japan-Ryukyu Archipelago. *P. altivelis* is a very important fish for Japanese freshwater fisheries, and thus is given considerable attention. Some studies have been made regarding the geographic variation of this fish. A few authors have pointed out that a landlocked population in Lake Biwa differs from amphidromous populations in reproductive characters (Funasaka *et al.*, 1963; Azuma, 1973b). Ayu in the Ryukyu Islands is considered by some authors to differ from that of the Japan Islands in behavior (Kawa-

nabe, 1972) and certain meristic traits (Inoha and Sesoko, 1965; Shokita *et al.*, 1975). However, the overall picture of the geographic variation of this species is still not complete.

Previously, we examined biochemical-genetic variation in populations of ayu within the Japan Islands (Nishida and Takahashi, 1978), and between population from the Ryukyu Islands and selected populations from the Japan Islands (Nishida, 1985a). In the present study, the results of this examination and some new molecular data are summarized and analyzed along with data on the morphological and reproductive characters in geographic populations of ayu in the Japan-Ryukyu Archipelago. The objectives of the present study are: 1) assessment of the significance of the differences between landlocked population in Lake Biwa and amphidromous populations in the Japan Islands by comparing with the interpopulational variation in the latter, and 2) determination of divergence between ayu in the Japan and Ryukyu Islands. The use of a wide array of characters should provide a more complete understanding of the nature and significance of variation in this species.

Materials and methods

Samples. Population samples of *P. altivelis* were taken from 15 localities in the Japan-Ryukyu Archipelago (Fig. 1). The sample numbers, collection sites, developmental stages of fish (young and subadults-adults designated as Y and A respectively), and sample sizes (biochemical-genetic, meristic, morphometric and reproductive characters designated as N(bi), N(me), N(mo), and N(re), respectively) are as follows: 1) Mouth of Lagoon Hachiro, Y, N(bi)=32, N(me)=100; 2) Mouth of Oppa River, Y, N(bi)=60, N(me)=105; 3) Yoshida River, A, N(me)=43, N(mo)=43, N(re)=21; 4) Mouth of Yada River, Y, N(bi)=50, N(me)=100; 5A) Ado River, Lake Biwa system, A, N(me)=31, N(mo)=31; 5B) Ado River, Lake Biwa system, A, N(re)=11; 5C) Lake Biwa system, Y & A, N(bi)=598; 6) Otoko River, A, N(re)=10; 7) Mouth of Tenryu River, Y, N(bi)=57, N(me)=100; 8) Nita River, Tsushima Island, A, N(bi)=50, N(me)=30, N(mo)=30; 9) Shidaka River, Tsushima Island, A, N(re)=12; 10) Chunji River, Cheju Island, A, N(me)=14, N(mo)=14; 11) Mouth of Kuma River, Y, N(bi)=42, N(me)=100; 12A) Amori River, Y & A, N(bi)=101, N(me)=82; 12B) Amori River, A, N(me)=32, N(mo)=32; 13) Lake Ikeda, A, N(me)=42; 14A) Sumiyo River, Amami-oshima Island, A, N(me)=10; 14B) Sumiyo River, A, N(bi)=45, N(me)=25, N(mo)=25; 15A) Yona River, Okinawa Island, Y, N(me)=83; 15B) Yona River, Okinawa Island, A, N(me)=31, N(mo)=31. Ayu of Lake Biwa are released in many rivers throughout Japan. To avoid mixing with the Lake Biwa fish, all amphidromous fish samples, except sample 6, were taken from rivers into which Lake Biwa fish had not been released, or from among young fish migrating up to the mouth or lower reaches of rivers from the sea. Sample 6 fish were caught in coastal waters, marked as amphidromous fish and released into Otoko River along with Lake Biwa fish.

Electrophoresis. Horizontal starch-gel electrophoresis was used to analyze variation in biochemical-genetic characters of 8 populations of ayu. Nineteen enzyme loci were scored for all 8 samples; 27–28 loci were available for some individuals in 3 (5C, 12A, 14B) of the above 8 samples. The loci and electrophoretic conditions are described elsewhere (Nishida and Takahashi, 1978; Nishida, 1985a). Nei's (1972) genetic distance was calcu-

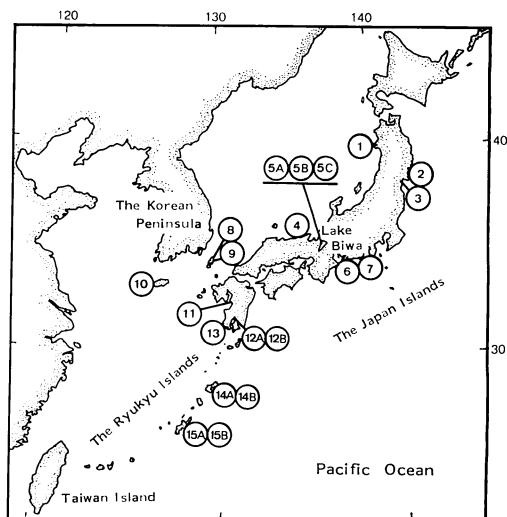


Fig. 1. Sample localities of *Plecoglossus altivelis* in the Japan and Ryukyu Islands. See text for locality data.

lated for each pairwise combination of populations. A dendrogram was constructed from the genetic distance matrix following the UPGMA procedure (Sneath and Sokal, 1973), so as to summarize the overall biochemical-genetic similarities of these populations.

Meristic characters. The following 12 meristic characters were counted: vertebrae (V, including the urostyle), dorsal fin rays (D), anal fin rays (A), pectoral fin rays (P_1), pelvic fin rays (P_2), caudal fin rays (C), pored scales in the lateral line (LLS), scales above the lateral line (SALL), scales below the lateral line (SBLL), comb-like teeth on upper jaw (CTU), comb-like teeth on lower jaw (CTL), and gillrakers (GR). The methods of counting followed Hubbs and Lagler (1958) basically. Vertebral number was counted on radiographs. Specimens with fused vertebrae were not used for vertebral counts. Each fin ray number was from principal rays. Fin rays and comb-like teeth were counted either from preserved specimens or fish stained slightly with alizarin red. Gillrakers on the first gill arch on the right side were counted after being removed and stained with alizarin red. Nearly all counts were made with a binocular dissecting microscope. V, D, A and P_1 were counted in nearly all samples; other meristic characters were counted for 7 selected population samples of subadults or adults collected from the river.

Morphometric characters. The following 24

morphometric characters were measured by a conventional method described by Hubbs and Lagler (1958) with slight modifications as noted below (see Nishida, 1985b, for illustrations): body length (BL), pre-anal length (PAL), predorsal length (PDL), interorbital width (IOW, the fleshy width), snout length (SL), length of upper jaw (LUJ), head length (HL, measured up to the edge of the opercular membrane), length of pectoral fin (LP_1F), length of pelvic fin (LP_2F), length of caudal peduncle (LCP), depth of caudal peduncle (DCP), body depth (BD), length of longest caudal ray (LLC), length of depressed dorsal (LDD), snout width (SW), length of 2nd dorsal ray (L2D), length of 3rd dorsal ray from the last (L3DL), length of dorsal base (LDB), length of longest anal ray (LLA), length of longest gillraker (LLGR), pre-ventral length (PVL), body depth at anus (BDA, length of an imaginary vertical line at the anus), length above the lateral line (LALL, perpendicular distance from the dorsal origin to the lateral line), and length below the lateral line (LBLL, perpendicular distance from the pelvic origin to the lateral line). In addition, the length of each principal ray of the dorsal fin was recorded for selected individuals. All measurements were taken with calipers and measured to the nearest 0.1 mm, with the exception of LLGR which was measured to the nearest 25 μ m with an ocular micrometer under a binocular dissecting microscope. These morphometric characters were measured for the same 7 samples of subadults or adults that were counted for the 12 meristic characters. Three 2-year old specimens in the sample from Okinawa Island (15B) were not used in the morphometric analyses because of their exceptionally large size and somewhat different body form from the other specimens in this sample.

Fecundity. Ayu normally spawn only one batch of eggs in a spawning season, though some females, especially those in Lake Biwa, spawn more than once in a spawning season (Nishida, 1978; Matsuyama and Matsuura, 1984, 1985). Thus, the number of the first batch eggs was used for the estimation of fecundity in the present study. Eggs of the first batch can be easily distinguished from others by their large size and accumulated yolk in the heavy ovary during the advanced stages of maturity. At these stages, the ovary constitutes more than 5% of the body weight. A subsample was taken from the central part of the left ovary,

and the number of eggs of the first batch in the subsample was counted under a binocular dissecting microscope. Fecundity was estimated by multiplying the number of eggs in the subsample with the ratio of total ovarian weight to subsample weight. Though Matsuyama and Matsuura (1983) observed eggs of the first batch to gradually decrease in number during maturation, variation introduced by differences in gonad development must have been minimal, since nearly all the specimens used in this study were at advanced stages of maturity with ovaries constituting more than 10% the body weight.

Statistical analyses. An analysis of variance (ANOVA) and a Duncan's multiple range test were made to determine significant differences among the sample means of each meristic character. Sexes were combined for analyses, since meristic characters in *P. altivelis* hardly showed any sexual dimorphism (Nishida, 1985b).

Morphometric characters were correlated to overall body size. Nearly all morphometric characters and GR in all samples showed significant ($P < 0.05$) correlation to body length, as shown below. An analysis of covariance (ANCOVA), with BL as an independent size variable, was conducted for determination of significant differences among the samples in these characters (Snedecor and Cockran, 1980). For interpopulational comparisons, GR and morphometric characters for a BL of 120 mm (near the average length) were estimated from the linear regression on BL for each sample.

Sexually immature subadult ayu showed no substantial sexual dimorphism in morphometric characters, but sexually mature adults exhibited significant differences between the two sexes in many morphometric characters due to the onset of sexual maturity in both males and females (Nishida, 1985b). Since some samples included partially mature specimens, five morphometric characters (LP_1F , LP_2F , LDD, LDB, and LLA) in more than half of the samples were found to be significantly different between sexes at a 1% level by ANCOVA. These characters were excluded from the analyses to avoid the effects of possible character change due to sexual maturity. The two sexes were combined for all further analyses to maximize sample size. L3DL was also omitted in further analyses since it seemed to undergo considerable change due to the influence of the

social status of the fish (Nishida, in prep.). Consequently, 17 morphometric characters and BL were used for further analyses.

The same procedure as that for morphometric characters was followed for fecundity data analyses in which fecundity and body length were log transformed.

The patterns of overall morphological variation among the 7 population samples were examined by cluster analysis and stepwise discriminant function analysis. The mean values for the 11 meristic characters and estimates for GR and the 17 morphometric characters for a BL of 120 mm were used in the cluster analysis. The characters were not standardized. A phenogram was derived by the UPGMA procedure (Sneath and Sokal, 1973). Squared Euclidian distances across all characters were used to measure dissimilarities between samples.

For the stepwise discriminant function analysis, the size factor was removed from GR and all morphometric characters in each individual. A linear regression was calculated for each log transformed variable, with log BL as the independent variable, for all individuals pooled into a single sample. This regression is regarded as representing the hypothetical, standard value of each variable for all observed sizes. Residual values of each individual from the regression can be used as size-independent measurements. The residual values for GR and the 17 morphometric characters were subjected to the stepwise discriminant function analysis along with raw values for the 11 meristic characters. Another size correcting method was used for the GR and morphometric characters: the measurements were divided by BL, and the resulting ratio values were used as size-independent variables. The overall conclusions from the use of the ratios were similar to those from the use of residual values. Some problems have been pointed out in the use of ratios for statistical analyses (Atchley *et al.*, 1976). In this paper, only the results from residual values are presented.

Basic linear regression analysis and ANCOVA were conducted using FORTRAN programs. Descriptive statistics, ANOVA, Duncan's multiple range test, cluster analysis, and stepwise discriminant function analysis were performed using SPSS programs (Nie *et al.*, 1975; Miyake and Yamamoto, 1976; Miyake *et al.*, 1977). All computations were made at the Kyoto University

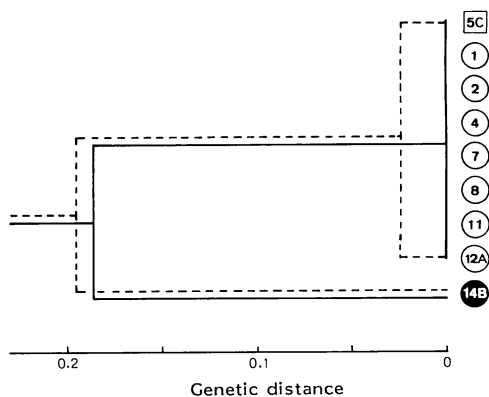


Fig. 2. UPGMA phenogram derived from Nei's genetic distances for geographic populations of *Plecoglossus altivelis*. Open square, Lake Biwa population; open circle, amphidromous populations in the Japan Islands; solid circle, amphidromous population in the Ryukyus. Solid lines, based on 18–19 loci; dotted lines, based on 27–28 loci.

Data Processing Center and the University of the Ryukyus Computation Center.

Results

Molecular characters. The biochemical-genetic variations among 9 population samples are summarized in Fig. 2, using the UPGMA clustering algorithm. This figure shows considerable genetic divergence of the Ryukyu population from other populations of the Japan Islands: the first major dichotomy separates the Amami-oshima population (14B) from all others to a great degree. The mean genetic distance between them was 0.19 based on 27–28 loci; approximately the same value, 0.20, was obtained based on 18–19 loci common to all samples. Populations within the Japan Islands were rather homogeneous, though the Lake Biwa population (5C) was found to differ somewhat from the amphidromous populations of this region when using the larger data set (28 loci). Though Tsushima Island and Amami-oshima Island are both far from the main islands of Japan, the former's population (8) hardly differed from the populations of the main islands of Japan in contrast to the large divergence of the latter's (14B).

Morphological characters.

Meristic characters. The data on 12 meristic

Table 1. Mean±SD and range of meristic characters and body length (mm) in geographic populations of *Plecoglossus altivelis*.

Character	3	5A	8	10	12B	14B	15B
(N)	(43)	(31)	(30)	(14)	(32)	(25)	(31)
V	61.4±0.58 ^a (60-63)	61.8±0.65 ^b (61-63)	61.7±0.54 ^c (61-63)	61.7±0.61 (61-63)	60.9±0.67 (60-62)	59.3±0.61 (58-60)	60.0±0.64 ^d (58-61)
D	10.3±0.44 (10-11)	10.0±0.45 (9-11)	10.4±0.49 (10-11)	10.4±0.51 (10-11)	10.1±0.46 (9-11)	10.6±0.50 (10-11)	10.5±0.51 (10-11)
A	15.0±0.80 (14-17)	14.9±0.46 ^c (14-16)	15.0±0.81 (14-17)	15.3±0.61 (14-16)	14.8±0.75 (13-17)	16.6±0.87 (14-18)	16.0±0.67 ^d (15-18)
P ₁	13.8±0.62 (13-15)	14.5±0.57 (13-15)	13.8±0.59 (13-15)	13.8±0.58 (12-14)	14.1±0.55 (13-15)	12.4±0.58 (11-13)	12.1±0.30 (12-13)
P ₂	8.0±0.27 (7-9)	8.0±0.00 (8-8)	8.0±0.00 (8-8)	8.1±0.27 (8-9)	8.0±0.00 (8-8)	8.0±0.00 (8-8)	8.0±0.00 (8-8)
C	19.0±0.15 (18-19)	19.0±0.00 ^d (19-19)	19.0±0.00 (19-19)	19.0±0.00 (19-19)	19.0±0.00 (19-19)	19.0±0.00 (19-19)	18.8±0.34 (18-19)
LLS	63.1±1.04 (61-65)	63.3±1.62 ^c (60-66)	63.9±0.94 (62-66)	63.5±0.76 (62-65)	62.8±1.09 (61-66)	60.8±1.12 (59-63)	60.7±1.08 (59-63)
SALL	18.3±0.80 (17-20)	21.9±1.03 (20-25)	17.8±1.01 (16-20)	18.9±1.56 (17-22)	20.0±1.23 (18-23)	14.4±0.49 (14-15)	16.1±0.57 (15-17)
SBLL	12.4±0.78 (11-14)	14.4±0.96 (13-17)	11.4±0.93 (10-13)	11.4±0.94 (10-14)	12.6±0.56 (12-14)	9.4±0.65 (8-10)	10.1±0.51 (9-11)
CTU	14.8±0.72 (13-16)	13.9±0.62 (13-15)	15.0±0.41 (14-16)	15.4±0.65 (14-16)	15.0±0.72 (14-17)	13.5±0.59 (13-15)	13.1±0.51 (12-14)
CTL	13.7±0.85 (12-16)	13.5±0.68 (12-15)	13.5±0.51 (13-14)	14.1±0.66 (13-15)	14.2±0.64 (13-16)	12.5±0.51 (12-13)	12.3±0.53 (11-13)
GR	39.6±2.43 ^a (35-45)	41.7±1.82 ^c (38-46)	41.9±1.75 (38-47)	41.7±1.98 (38-45)	41.4±1.48 (39-46)	35.2±1.88 (33-39)	34.9±1.75 (32-38)
BL	114.7±11.34 (96.3-148.2)	121.9±8.39 (97.4-134.5)	119.4±12.44 (97.2-147.5)	109.9±23.88 (77.5-151.7)	129.8±12.40 (106.9-151.5)	93.2±13.15 (75.5-113.2)	97.9±11.71 (75.1-113.2)

a, N=41; b, N=28; c, N=29; d, N=30; e, N=26.

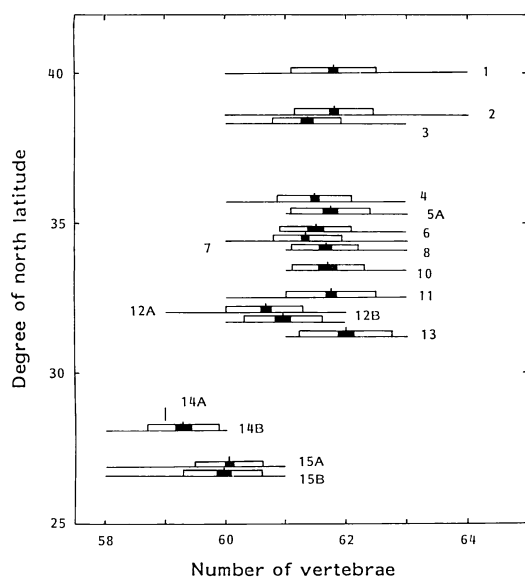


Fig. 3. Number of vertebrae in geographic populations of *Plecoglossus altivelis* in relation to the degree of north latitude of their localities. Horizontal lines, ranges; vertical lines on bars, means; solid bars, two standard errors of the means; open and solid bars together, two standard deviations of the means.

characters and body length for 7 samples are presented in Table 1. Three meristic characters for 16 samples plotted against latitude are shown in Figs. 3–5. Differences among samples were statistically significant ($P < 0.001$, ANOVA) for all characters other than P_2 and C, which were very stable at 8 and 19 rays, respectively. The samples were found to differ significantly ($P < 0.01$) from ANCOVA with respect to GR.

The difference between the populations in the Japan and Ryukyu Islands was the principal pattern of geographic variation in each character; no meristic character appeared to be clearly related to latitude. The Ryukyu populations had higher counts in dorsal and anal fin rays and lower counts in the other characters. Differences in V, A, P_1 , LLS, SALL, SBLL, CTL and GR were significant ($P < 0.05$, Duncan's multiple range test) between the Japan and Ryukyu Islands populations (Table 1, Figs. 3–7). Highest and lowest mean values of some characters (V, A, SALL and SBLL) were observed not in the Okinawa Island population but in that of the Amami-oshima Island. Significant differences in V, SALL, SBLL and CTU ($P <$

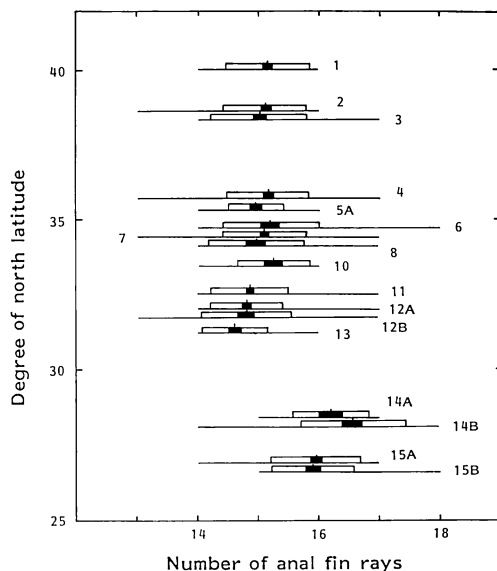


Fig. 4. Number of anal fin rays in geographic populations of *Plecoglossus altivelis* in relation to the degree of north latitude of their localities. Symbols are the same as in Fig. 3.

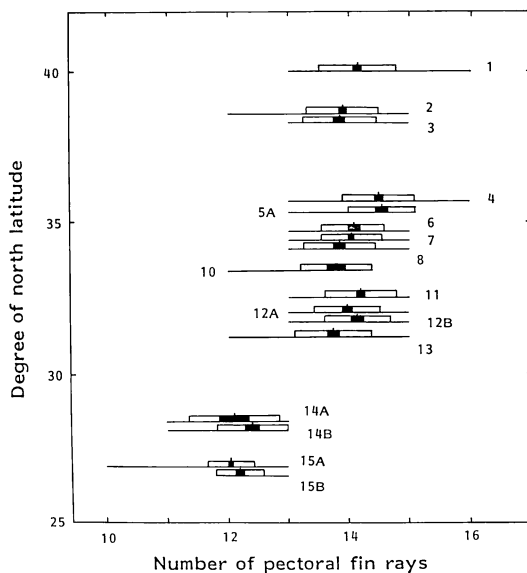


Fig. 5. Number of pectoral fin rays in geographic populations of *Plecoglossus altivelis* in relation to the degree of north latitude of their localities. Symbols are the same as in Fig. 3.

0.05, Duncan's multiple range test) were observed in both island populations in the Ryukyus.

Although significant differences within the Japa-

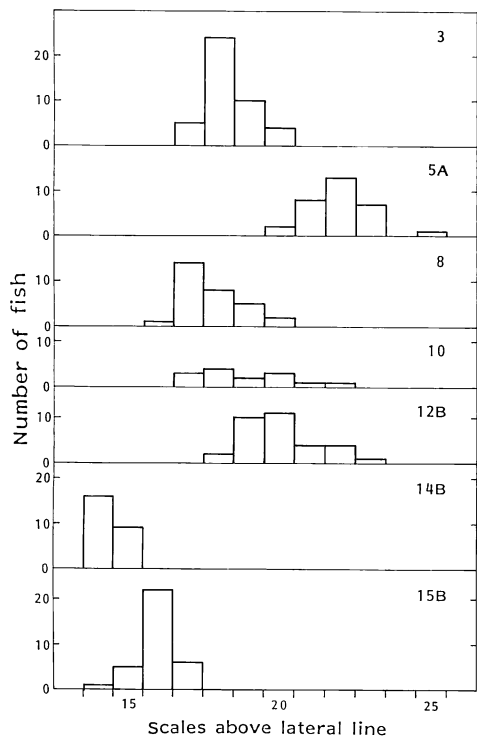


Fig. 6. Distribution of number of scales above the lateral line in geographic populations of *Plecoglossus altivelis*.

nese populations were occasionally observed in some characters, it was notable that specimens in the Lake Biwa population had more scales above and below the lateral line than those in other populations ($P < 0.05$, Duncan's multiple range test). SALL counts in the Lake Biwa population were 20 to 25 (mode 22), and 16 to 23 (modes 17 to 20) in the other populations of the Japan Islands (Table 1, Fig. 6). SBL counts in the lake population were 13 to 17 (mode 14), but only 10 to 14 (modes 11 to 13) in the other Japanese populations (Table 1, Fig. 7).

Morphometric characters. The estimated values for the 17 morphometric characters and GR for a BL of 120 mm are summarized in Table 2. All these characters showed significant correlation to BL in each sample ($P < 0.05$) with only an exception for LLGR in sample 12B. The results of ANCOVA indicated all characters to significantly ($P < 0.01$) differ among the samples.

Three general patterns of variation were observed among the populations, though variation among individual samples was considerable in many

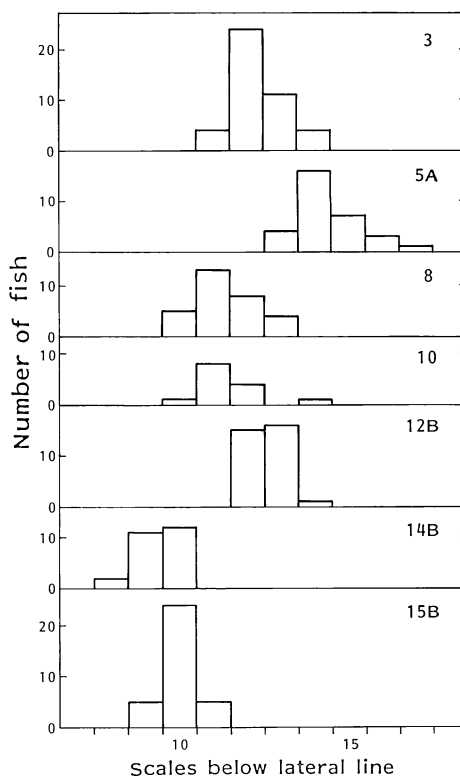


Fig. 7. Distribution of number of scales below the lateral line in geographic populations of *Plecoglossus altivelis*.

characters. The first geographic pattern was represented by IOW, DCP, SW, L2D, BDA, and LALL (Fig. 8a-f), for which there appeared large differences between the populations of the Japan and Ryukyu Islands. The Ryukyu populations showed higher values for these characters, the highest being observed exclusively in the Okinawa Island population. The second geographic pattern was that shown by HL and LLGR (Fig. 8g-h) whose values in Lake Biwa population were highest. The third pattern was that of random variation without the geographic regularities found in the other morphometric characters.

Differences in dorsal fin morphology were also found in ayu in the Japan and Ryukyu Islands. The dorsal fin of ayu elongates in relation to the social status of the fish (Nishida, in prep.). Each principal ray length of the dorsal fin was measured for both male and female specimens with the most elongated dorsal fins and also for those with the shortest dorsal fins in each population. The results

Table 2. Estimate \pm SE (mm) of morphometric characters and number of gillrakers for a body length of 120 mm from their regressions on body length in geographic populations of *Plecoglossus altivelis*. All regressions were significant ($P<0.05$) unless designated otherwise.

Character	3	5A	8	10	12B	14B	15B
(N)	(43)	(31)	(30)	(14)	(32)	(25)	(31)
PAL	87.6 \pm 0.32	88.4 \pm 0.31	87.2 \pm 0.32 ^a	87.5 \pm 0.58	90.0 \pm 0.33	87.2 \pm 0.31	88.2 \pm 0.33
PDL	59.4 \pm 0.21	59.5 \pm 0.24	58.4 \pm 0.21 ^a	58.9 \pm 0.21	58.2 \pm 0.21	58.1 \pm 0.27	60.3 \pm 0.30
IOW	8.7 \pm 0.05	9.5 \pm 0.05	8.6 \pm 0.06	9.4 \pm 0.12	9.3 \pm 0.07	10.0 \pm 0.08	10.2 \pm 0.08
SL	9.8 \pm 0.07	11.1 \pm 0.12	10.4 \pm 0.11	10.3 \pm 0.20	9.9 \pm 0.11	11.0 \pm 0.16	10.6 \pm 0.15
LUJ	14.5 \pm 0.12	15.9 \pm 0.07	17.5 \pm 0.14	16.5 \pm 0.21	15.5 \pm 0.14	15.9 \pm 0.10	16.3 \pm 0.15
HL	28.6 \pm 0.12	31.0 \pm 0.11	28.9 \pm 0.20	29.9 \pm 0.27	29.6 \pm 0.19	30.0 \pm 0.17	30.0 \pm 0.23
LCP	16.5 \pm 0.14	16.0 \pm 0.18	16.0 \pm 0.15	16.7 \pm 0.11	16.4 \pm 0.14	16.4 \pm 0.24	15.9 \pm 0.24
DCP	10.4 \pm 0.09	10.6 \pm 0.06	10.5 \pm 0.07	10.9 \pm 0.12	10.4 \pm 0.07	11.3 \pm 0.10	12.2 \pm 0.10
BD	27.5 \pm 0.20	25.6 \pm 0.30	26.8 \pm 0.27	26.3 \pm 0.55	24.9 \pm 0.19	25.5 \pm 0.45	29.2 \pm 0.21
LLC	24.5 \pm 0.19 ^b	24.8 \pm 0.20	26.0 \pm 0.22	28.1 \pm 0.40	24.8 \pm 0.22	27.9 \pm 0.47	28.4 \pm 0.34
SW	5.2 \pm 0.05 ^b	5.6 \pm 0.07 ^c	4.7 \pm 0.07 ^d	5.0 \pm 0.15	5.0 \pm 0.09	6.0 \pm 0.11	6.5 \pm 0.10 ^e
L2D	19.6 \pm 0.19	20.5 \pm 0.20 ^e	19.3 \pm 0.14	21.6 \pm 0.27 ^e	18.7 \pm 0.19	23.8 \pm 0.62 ^f	27.9 \pm 0.60 ^e
PVL	60.8 \pm 0.22	62.2 \pm 0.37	58.8 \pm 0.25	60.3 \pm 0.40	61.7 \pm 0.27	60.4 \pm 0.24	60.8 \pm 0.31
BDA	19.3 \pm 0.13	19.0 \pm 0.16	19.2 \pm 0.11	19.9 \pm 0.32	18.4 \pm 0.15	20.5 \pm 0.37	23.7 \pm 0.15
LALL	14.9 \pm 0.12	15.4 \pm 0.17	15.1 \pm 0.14	16.2 \pm 0.29	14.6 \pm 0.13	16.4 \pm 0.34	19.4 \pm 0.16
LBL	15.7 \pm 0.19	12.9 \pm 0.21	12.9 \pm 0.18	12.9 \pm 0.22	13.3 \pm 0.20	11.7 \pm 0.26	12.7 \pm 0.15
LLGR	1.55 \pm 0.02	2.09 \pm 0.03	1.69 \pm 0.02	1.79 \pm 0.04	1.72 \pm 0.03*	1.49 \pm 0.04	1.75 \pm 0.03
GR	40.4 \pm 0.35 ^g	41.4 \pm 0.28 ^a	42.0 \pm 0.28	42.2 \pm 0.48	41.0 \pm 0.32	38.0 \pm 0.62	36.8 \pm 0.56

a, N=29; b, N=42; c, N=30; d, N=28; e, N=13; f, N=24; g, N=41.

* Regression not significant ($P>0.05$).

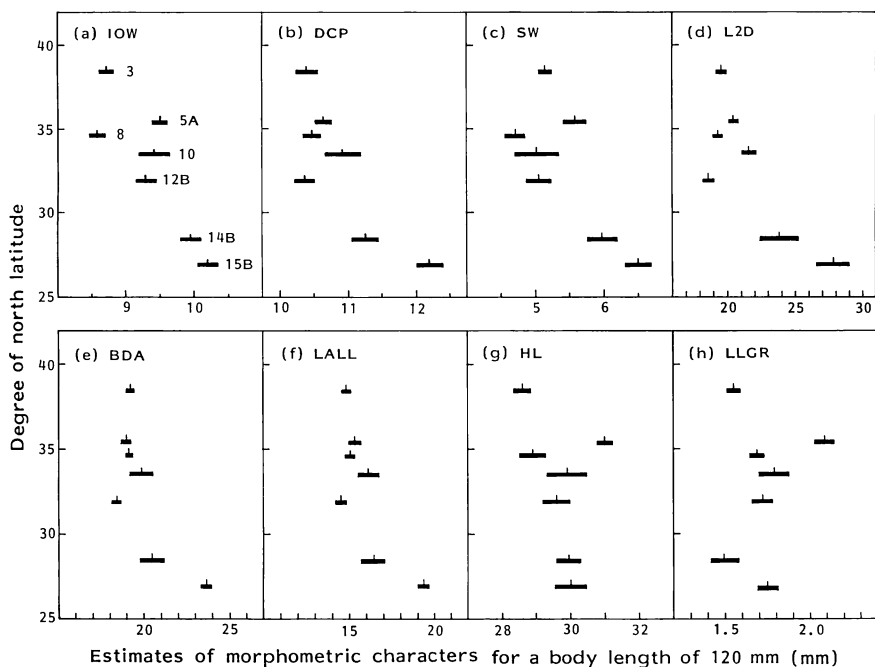


Fig. 8. Estimate of eight morphometric characters for a body length of 120 mm in geographic populations of *Plecoglossus altivelis* in relation to the degree of north latitude of their localities. Horizontal solid bars, 95% confidence limits; vertical lines on bars, estimates from regression lines on body length.

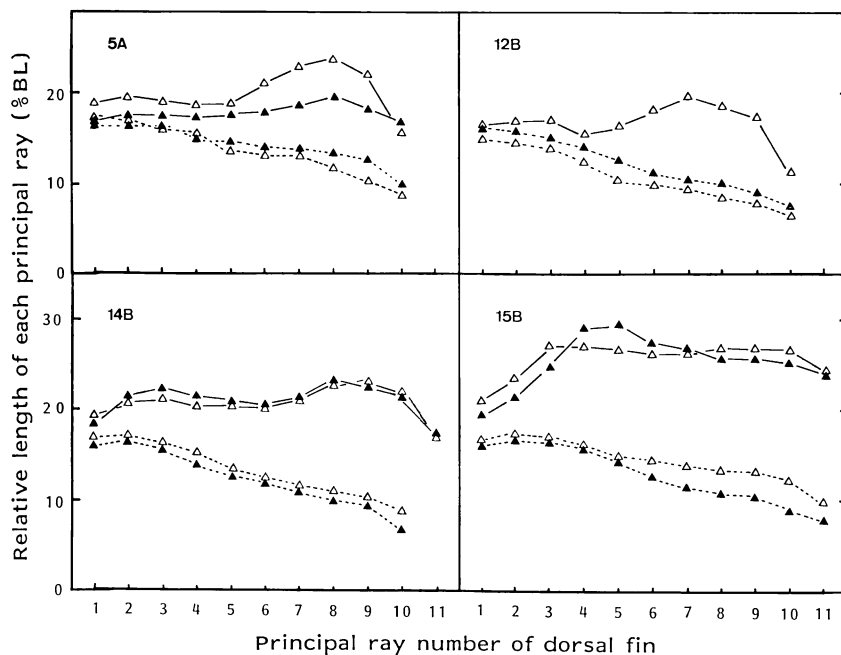


Fig. 9. Relative length of each principal dorsal ray of selected individuals in geographic populations of *Plecoglossus altivelis*. Solid lines, individuals with elongated dorsal fins; dotted lines, individuals with non-elongated dorsal fins. Solid triangles, males; open triangles, females.

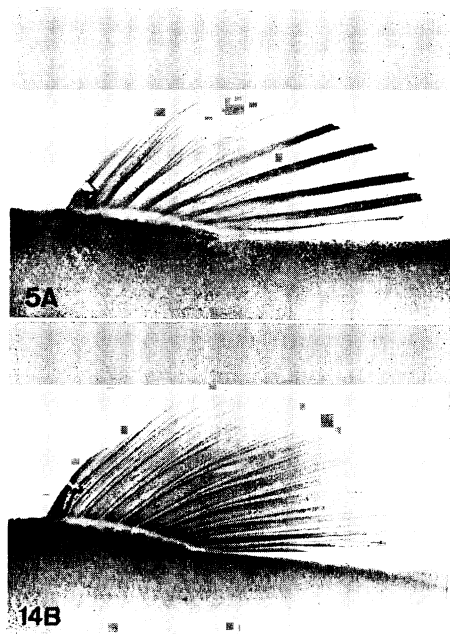


Fig. 10. Lateral view of the elongated dorsal fin of *Plecoglossus altivelis* in each of the Japan and Ryukyu Islands. Above, BL=117.3 mm, LDB=15.7 mm; below, BL=110.6 mm, LDB=15.6 mm.

from 4 selected populations are shown in Fig. 9. Dorsal fin form of specimens with the shortest fin in each sample was quite similar among the geographic populations (Fig. 9). However, the form of elongated dorsal fins considerably differed in the two regions: the anterior and posterior rays of dorsal fins were elongated in the Ryukyu Islands populations, but only the posterior rays of the fins were elongated in the Japan Islands populations (Figs. 9, 10). Membrane color of elongated dorsal fins was pale brown in the former populations but very black in the latter (Fig. 10). No differences could be observed in dorsal fin morphology between immature males and females in each sample.

Multivariate analyses. Two multivariate analyses, cluster analysis and stepwise discriminant function analysis, were performed to summarize all the morphological data and compare them with the results from molecular data analysis. Figure 11 shows the results of the UPGMA cluster analysis carried out on 12 meristic and 17 morphometric characters. Two major groups, identical to those from the analysis of molecular char-

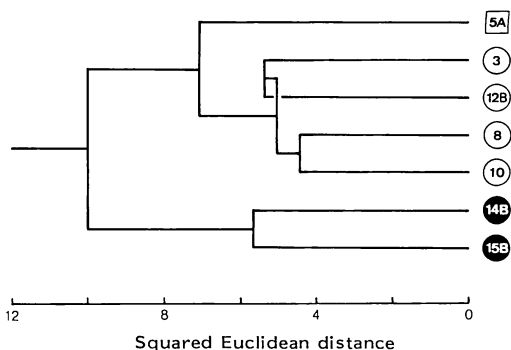


Fig. 11. UPGMA phenogram derived from squared Euclidean distances based on 29 morphological characters for geographic populations of *Plecoglossus altivelis*. Symbols for the population samples are the same as in Fig. 2.

acters, were evident: the populations in the Japan Islands comprised one group while those in the Ryukyu Islands made up the other, though there were considerable differences among the populations in each region. Within the Japan group, the first dichotomy separated the Lake Biwa population from the others.

The results of the stepwise discriminant function analysis were basically in agreement with those of the cluster analysis. Six significant canonical discriminant functions were formed in this analysis, but the first two canonical discriminant functions accounted for 68% of the total dispersion among populations (first function, 45%; second, 23%). The standardized discriminant coefficients for the first two functions are given in Table 3. When the sign is ignored, the size of the coefficient represents the relative contribution of that character to function. The first function was loaded mainly for such meristic characters as SALL, SBLL, A, and P_1 . The second function was loaded heavily for such morphometric characters as LUJ, PVL, and HL. The first two functions clearly separated the populations of the Ryukyus from those of the Japan Islands (Fig. 12). Though some divergence was found within the populations in the Japan Islands, an intermediate area between specimens of extremes, 5A and 8, was occupied by specimens of the other populations.

Fecundity. The regressions of log fecundity on log BL are summarized in Table 4. Regression slopes did not significantly differ among the populations ($P > 0.05$, ANCOVA), but differences in

Table 3. Standardized coefficients for the first two canonical discriminant functions from analysis of morphological characters of geographic populations of *Plecoglossus altivelis*.

Character	Function 1	Function 2
V	0.2299	-0.0379
D	-0.1622	-0.1972
A	-0.3315	0.3047
P ₁	0.2724	-0.1612
P ₂	-0.0506	0.1842
C	0.0677	0.0294
SALL	0.6695	-0.0379
SBLL	0.3667	0.2509
CTU	0.1826	-0.2389
CTL	-0.0127	-0.1709
GR	0.1535	-0.0493
PAL	-0.0595	-0.2640
PDL	-0.0058	0.0476
IOW	0.0326	0.3034
SL	-0.0636	0.0606
LUJ	-0.2653	-0.9863
HL	0.1969	0.5180
LCP	-0.1128	0.1703
BD	-0.1843	-0.2219
LLC	-0.2188	-0.3832
SW	-0.0608	0.2256
L2D	0.1517	0.4459
PVL	0.2004	0.5918
BDA	-0.0699	-0.3447
LALL	-0.1393	0.4118
LBLL	0.2771	0.2491
LLGR	-0.0805	0.2290
% of variance	45.35%	22.95%
Cumulative %	45.35%	68.30%

elevation were highly significant ($P < 0.01$, ANCOVA). Figure 13 shows the fecundity of populations for a BL of 120 mm plotted against the latitude of their localities. The Lake Biwa population (5B) was the most fecund (28.2×10^3 eggs at 120 mm BL), having about twice the number of eggs as the amphidromous populations from localities of similar latitude. Within the amphidromous populations, the southern populations tended to have fewer eggs (Fig. 13). Fecundity of the most southern population from Okinawa Island was 8.3×10^3 eggs, less than half that of the most northern population from the Tohoku district (20.0×10^3 eggs). Interpopulational variation in fecundity in *P. altivelis* was more than 3 fold, based on the extremes in all populations examined.

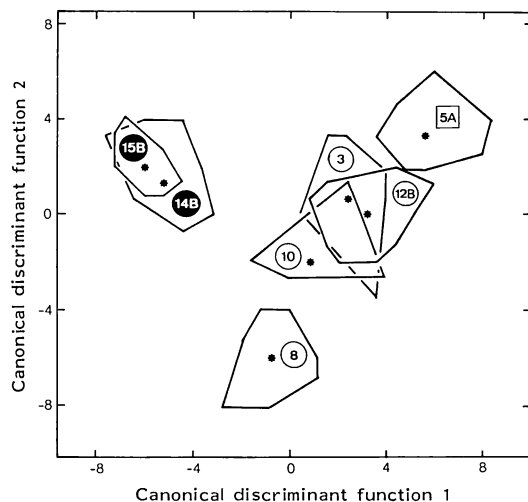


Fig. 12. Two-dimensional representation of discriminant function analysis of morphological characters for geographic populations of *Plecoglossus altivelis*. Lines connect the most dispersed values for the population centroid (asterisks). Symbols for the population samples are the same as in Fig. 2.

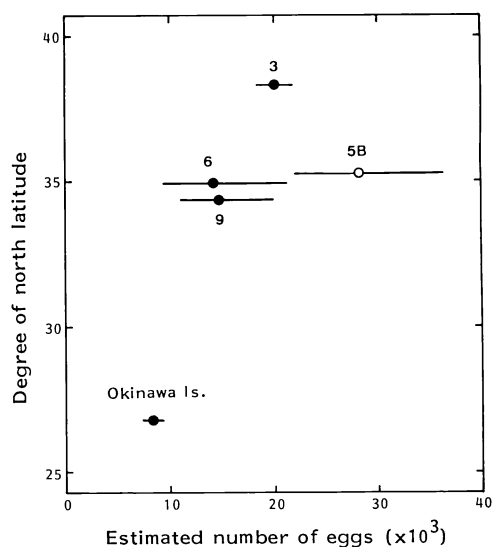


Fig. 13. Estimated fecundity for a body length of 120 mm for geographic populations of *Plecoglossus altivelis* in relation to the degree of north latitude of their localities. Solid circles denote amphidromous populations; open circle, Lake Biwa population. Bars indicate 95% confidential limits.

Table 4. Regression of log fecundity on log body length and estimated fecundity for a body length of 120 mm for geographic populations of *Plecoglossus altivelis*.

Statistic	3	5B	6B	9	Okinawa I.*
No. of individuals	21	11	10	12	10
Slope	2.510	3.612	4.140	2.634	1.932
Intercept	-0.920	-3.055	-4.457	-1.306	-0.097
Correlation coefficient	0.797	0.931	0.887	0.698	0.964
Fecundity at 120 mm BL ($\times 10^3$)	20.0	28.2	14.1	14.8	8.3
standard error (\times / \div)	1.05	1.12	1.20	1.15	1.05

* Data from Shokita *et al.* (1975) (corrected).

Discussion

Contrast in molecular and organismal variation.

Some differences in the patterns of geographic variation were evident in the molecular, morphological, and reproductive characters in *P. altivelis*. Whereas divergence among these populations was considerable in morphological and fecundity data, no virtual divergence was observed among amphidromous populations in the Japan Islands in allozyme data. Recently, thirteen amphidromous populations of this species in the southwestern part of the Japan Islands were analyzed electrophoretically by Seki and Taniguchi (1985). Their results also showed only very little divergence in allele frequency among them. These and the present molecular data indicate the amphidromous populations within the Japan Islands to be nearly homogeneous with respect to structural genes. This is probably due to gene flow among these populations. Genetic exchange by larval dispersion may possibly occur in coastal waters between adjacent populations and consequently, be stepwise among populations along the Japan Islands.

The picture of the genetic structure of amphidromous populations in the Japan Islands inferred from the present organismal data differs somewhat from that based on the molecular data. Some organismal differences among the populations may be environmentally induced in part. However, they cannot be attributed solely to ecophenotypic effects. Some differences are likely to arise from genetic divergence among the populations. Functional and ecological significance (Gatz, 1979) may possibly account for the morphological variations. Fecundity is a very important character directly related to fitness. Environmental conditions vary among localities in the Japan

Islands. Thus, it is reasonable to conclude that some organismal differences among amphidromous populations in the Japan Islands are due to differential selection according to place and consequently genetic. There is actually evidence that differences in morphological and reproductive characters of ayu are at least partially genetic (Nishida, in prep.).

Contradiction in variation patterns can be explained by qualitative differences inherent in molecular and organismal data. Organismal characters are responsive to selection but molecular characters are hardly so toward environmental conditions. Thus molecular data should be interpreted as a measure of gene flow and representative of a time scale of divergence among populations (Wilson *et al.*, 1977; Clayton, 1981). Selection maintaining geographic differences in morphological and reproductive characters in ayu must be sufficiently strong to suppress the integration effects of gene flow that may result in homogeneity in enzyme gene frequency in the Japan Islands. Evolution in different characters may have proceeded at different rates among populations of *P. altivelis*.

Such an apparent contradiction between molecular and organismal variation is not necessarily unusual in other animals in conspecific (Larson, 1980; Shaffer, 1983) as well as hetero-specific populations (Turner, 1973; Maxson and Wilson, 1975; Shaklee and Tamaru, 1981). This and the present results emphasize that use of both molecular and organismal data is necessary for a proper understanding of a species and their evolution.

Variation pattern in fecundity. It should be noted that there seems to be a north-south cline of fecundity in amphidromous populations and that the fecundity of the Lake Biwa population is by far the highest, departing from the cline. This is

in agreement with a suggestion by Azuma (1973a) that the Lake Biwa population may have higher fecundity. There is evidence that higher fecundity of the Lake Biwa ayu is genetic (Nishida, in prep.). Egg number is inversely related to egg size if the amount of reproductive effort is fixed. It, therefore, means that amphidromous populations in the north have more eggs of smaller size and the Lake Biwa population has the highest number of eggs of the smallest size. Natural selection should force females to make a compromise between egg number and egg size to maximize the number of offspring surviving under particular environmental circumstances.

Comparable data on fecundity (egg size) variation in the Japan-Ryukyu Archipelago are available for freshwater shrimps and prawns. Shokita (1979) has found amphidromous populations of several species of *Caridina* and *Macrobrachium* in the Ryukyus to have larger eggs than those in the Japan Islands. Their life cycles are similar to those of ayu. There may be a common selective mechanism to account for similar trends in fecundity variation among the amphidromous populations of ayu, shrimps and prawns. Nishino (1980) showed a Lake Biwa population of a shrimp *Palaemon paucidens* to have the smallest eggs (the highest fecundity) among geographic populations of this species throughout the Japan Islands. A north-south cline of egg size has also been found in the geographic populations of this species, but the reverse of that of ayu and other shrimps and prawns. Thus, the explanations of Nishino for this variation do not apply to ayu. Unlike those of ayu and *Caridina* and *Macrobrachium* species, most of the geographic populations of *Palaemon paucidens* examined by Nishino (1980) were from lakes and ponds.

The influence of environmental stability and heterogeneity (Cody, 1966, primarily for birds) may possibly be a clue to fecundity variation in *P. altivelis*. Stronger predation pressure and more competitive conditions for larvae in a more biologically diverse environment are likely to be of particular importance, since, generally, larger offspring from larger eggs should have greater ability to avoid predators and be better competitors than smaller ones. The larvae of ayu pass the winter in marine coastal waters (for amphidromous populations) or offshore waters of Lake Biwa (for the Lake Biwa population). It is highly probable

that species diversity is lower in the more northern coastal waters and least in the offshore waters of Lake Biwa. This trend of species diversity is consistent with the variation pattern of fecundity in ayu.

The geographic pattern of fecundity variation among amphidromous populations is also in agreement with a prediction based on the hypothesis of Itô (1978), that the low procurability of food by the young is a major factor affecting low fecundity (large egg size)/parental protection strategy. Food availability for larvae is likely to decrease in more southern localities where the amount of plankton is less (Raymont, 1963).

A compromise between egg number and size can also be influenced by other factors such as the food size of larvae. No information is presently available on this, however. Although both the above hypotheses may explain the variation pattern of fecundity in *P. altivelis*, information on their larval life is too limited to conclude which explanation is the more applicable.

There is also a north-south cline (the northern populations spawning earlier) found in the spawning season of ayu. The Lake Biwa population spawns earliest, departing from the cline (Shiraishi and Suzuki, 1962). There is a genetic basis for variation (Funasaka *et al.*, 1963; Nishida, in prep.), and the geographical variation in spawning season is considered to be also due to adaptation (Nishida, in prep.). Apparently, ayu has considerable genetic variations in reproductive and life history traits which arise from adaptation to each local environmental condition.

Characteristics of the Lake Biwa population. Within the populations in the Japan Islands, that of Lake Biwa differs considerably from the others. Morphologically, ayu of Lake Biwa have higher numbers of scales above and below the lateral line, and have longer heads and gillrakers. These characteristics may be useful for identifying Lake Biwa ayu. A higher number of longitudinal scales along the lateral line was suggested for Lake Biwa ayu by Azuma (1981). The longer head in the Lake Biwa population is in agreement with a suggestion by Azuma (1981) and Komada (1977). Komada (1985 and references therein) found some differences in mouth part morphology and dentition between Lake Biwa and sea-run forms during early development but none in adults. Various developmental differences not found in the present

comparison of adult specimens may possibly exist in morphology between the two forms.

Environmental parameters and the community structure of the lake differ considerably from those of marine coastal waters. Some organismal characteristics of the Lake Biwa form of ayu are likely due to adaptations to particular environmental conditions of the lake. As discussed above, the extremely high fecundity of the Lake Biwa form may possibly be due to adaptation to specific environmental conditions. Longer gillrakers characteristic of this form may also be related to the mode of life of the fish. Some Lake Biwa ayu depend on zooplanktons as their main source of food throughout life (Azuma, 1973a) and longer gillrakers would facilitate the acquisition of such food. It is plausible that the longer gillrakers indicate adaptation to the particular conditions of the lake.

Such adaptations likely required a fairly long period during the course of evolution. Ayu are rather easily landlocked. A well-known landlocked population other than that in Lake Biwa lives in Lake Ikeda and seems to have started doing so in the last hundred years or so (Shimazu, 1950). This landlocked population has neither long gillrakers nor high fecundity (Nishida, in prep.), indicating the characteristics of the Lake Biwa form have not resulted merely from landlocking. Kawanabe (1975, 1976) hypothesized that the Lake Biwa population may have invaded the lake during the later inter-glacial ages and survived at least up through the latest glacial age. The genetic distance value between the Lake Biwa and sea-run forms was found to correspond to a divergence time of about 1×10^5 years (Nishida, 1985a), supporting the hypothesis. Fairly long subsistence of the Lake Biwa form of ayu in a specific environment of the lake would explain its most organismal characteristics.

During the present age, the lake had contact with the sea through the Yodo River until a dam was constructed at the upper part of the river in 1904. Furthermore, ayu of Lake Biwa have been transplanted to various rivers over the Japan Islands for several decades. The molecular data, however, indicate that opportunity for gene exchange between the Lake Biwa and sea-run forms has been too small to cancel out genetic differences.

If many differences between the two forms of ayu are the result of adaptation as discussed above,

the adaptive differences, especially those in reproductive characters, may be a major factor preventing extensive gene exchange between them. As shown above, eggs of the Lake Biwa ayu are by far the smallest. Even when the Lake Biwa form of ayu are transplanted to rivers flowing into the sea and spawn successfully, their smallest larvae must cope with stronger predation pressure and more competitive conditions in marine coastal waters than in the lake. Survival rate of the offspring of the lake form may be extremely low in biologically diverse environments of marine coastal waters. Earlier maturation of Lake Biwa ayu may also be disadvantageous in waters other than the lake system, since the spawning season appears to be optimal in each locality. Besides, earlier maturation may be a factor that reduces mating between the two forms, as suggested by Seki and Taniguchi (1985).

Divergence of Ryukyu populations. Both molecular and morphological data clearly indicate that there are two distinct groups of *P. altivelis* in the Japan-Ryukyu Archipelago, that of the Japan Islands and that of the Ryukyu Islands. Although molecular data could not be obtained for ayu in Okinawa Island, results of morphological analyses indicate that the ayu in this island may be closely related to those in Amami-oshima Island.

The large divergence of the Ryukyu populations from the other populations may be due in part to the influence of stochastic processes associated with limited population size on the smaller islands isolated by the open sea. Nevertheless, the large divergence of the Ryukyu populations cannot be accounted for only on the basis of isolation today. The Tsushima Island population does not differ very much from those of the main islands of Japan in molecular and morphological characters in contrast to the Amami-oshima Island population, even though Tsushima Island is isolated by the open sea just as is Amami-oshima Island. Furthermore, the morphology of the population of Cheju Island, also an isolated island, does not particularly differ from that of the Japanese populations.

The discrepancy can be resolved by paleogeographic considerations. Geological studies suggest that the lowering of the sea level in the last glacial age caused the Japan Islands to be basically connected to the Korean Peninsula (Kizaki and Oshiro, 1977). This would make possible the

free gene exchange among populations of Cheju and Tsushima Islands and the main islands of Japan, resulting in genetic continuity. In contrast, the Tokara Channel, which separates Amami-oshima Island from the main islands of Japan, has been there since the middle Pleistocene period. Islands in the Ryukyus have been connected to each other at certain times since the middle Pleistocene period by upheavals and sea level drops (Kizaki and Oshiro, 1977). This geological history would explain the close relationship of amphidromous populations both in the waters of the Japan and adjacent islands and the Ryukyus, and also the large divergence of populations of the Ryukyus and Japan Islands.

Morphologically, the Ryukyu populations are characterized by low numbers of scales above and below the lateral line, pectoral fin rays and vertebrae, a high number of anal fin rays, and several morphometric features. One very interesting and distinct feature of these populations is their distinctive morphology of elongated dorsal fin being higher at the anterior part and paler in color. Elongated dorsal fins of *P. altivelis* may function to convey some social meaning, since only the dorsal fins of territorial individuals elongate and become colorful (Nishida, in prep.). Kawanabe (1972) found the territorial behavior of ayu in the Ryukyus to differ from that in the Japan Islands. In the Ryukyus, the chasing of invaders by residents is fitful and interspecific. Differences in dorsal fin morphology between ayu in the Japan and Ryukyu Islands may be related to differences in their territorial behavior.

The distinctiveness of Ryukyu population morphology as well as that of allozymes supports the previous suggestion that ayu in the Ryukyus should be given a taxonomic status as a subspecies (Nishida, 1985a). Available information suggests that distribution of this type of ayu is limited only to the Ryukyu Islands. The morphological and electrophoretic similarities of ayu in Tsushima and Cheju Islands with those in the main islands of Japan suggests that ayu in the Korean Peninsula may also be similar to those in the Japan Islands, since both Tsushima and Cheju Islands are geographically closer to the Korean Peninsula than to the main islands of Japan. From figure 9 of Jordan and Evermann (1903), ayu in Taiwan Island seem similar to those in the Japan Islands but not to those in the Ryukyus, having many

small scales above and below the lateral line. Because Taiwan Island was connected to the Chinese Continent during the last glacial age, it may be reasonable to consider that the ayu in the Chinese Continent may share more similarities with those in the Japan Islands than with those in the Ryukyus. The hypothesis regarding the range of the Ryukyu type ayu is now being tested by examining *P. altivelis* populations in the Korean Peninsula, the Chinese Continent and Taiwan Island.

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- 日本・琉球列島におけるアユの分子、形態および繁殖形質の地理的変異
- 西田 睦
- アユにはいくつかの変異の存在が示唆されているが、地理的変異の全体像はまだ明らかでない。そこで、日本・琉球列島各地から得た集団の分子、形態および繁殖形質を調査した。18-28 遺伝子座が支配する酸素分子の電気泳動分析および 29 の形態的形質の分析結果より、この地域のアユ集団は、これらの形質において明瞭に異なる日本列島グループと琉球列島グループに大別されることが明らかになった。びわ湖の陸封アユ集団と日本列島産両側回遊型集団との分化程度は、上のそれに比べると小さいものの、びわ湖アユはいくつの特異性を有していた。とくに、両側回遊型集団に見られた北方ほど卵数が多いという傾向からはずれ、その卵数は著しく多かった。このようなびわ湖集団の特異性は、びわ湖に特殊な環境への適応の結果と思われる。日本列島の両側回遊型集団間において、分子形質はほとんど均質であったが、形態形質や卵数にはかなりの変異が認められた。形質間に見られるこうした地理的変異パターンの差異の一部は、分子レベルと表現型レベルで進化様式が異なることを反映したものと考えられる。
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