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Genetic control of growth in the guppy (*Poecilia reticulata*)

Masamichi Nakajima*, Nobuhiko Taniguchi

Laboratory of Applied Population Genetics, Graduate School of Agricultural Science, Tohoku University, Sendai 981-8555, Japan

Abstract

It is important to consider the genetic control of growth in fish for fish breeding and aquaculture. In the guppy (*Poecilia reticulata*), the differences of growth were observed among strains, and between sexes, in the closed colonies maintained in the laboratory. The sire and dam variance components affecting the body length at different ages were estimated as a marker of growth by sib analysis. Furthermore, the effective number of loci contributing to the strain differences was estimated from the cross between a small (S) and large (F) strains, focusing on the standard length at 180 days old.

The estimated variance component and its change from the maternal and paternal halves were different between females and males. In females, the dam variance components have constantly indicated high values; however, the sire values were low. In males, the sire variance components have high values after reaching 120 days old. In contrast, the dam values, having high values before reaching 90 days old, decreased after reaching 120 days old.

The estimated number of loci contributing to the strain differences was 8.0 for females and 1.7 for males at 180 days old from the cross between females in the S strain and males in the F strain. These values were 3.5 for females and a negative value for males from the reciprocal cross. The negative value was due to a lower variance in the F_2 generation with respect to the F_1 generation.

From these results, it was estimated that a small number of genes was controlling the final body size of the guppy, and that some of them were probably located on the sex chromosome.

Keywords: Variance component; Guppy; Genetic control; Standard length; Effective number of loci; Growth; Heritability

* Corresponding author. Tel.: +81-22-717-8741; fax: +81-22-717-8743.
E-mail address: mnkjm@bios.tohoku.ac.jp (M. Nakajima).

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1. Introduction

It is important to consider the genetic control of growth in the fish for fish breeding and aquaculture. It is a well-known fact that the body size, body length, body weight, etc., in fish are extremely variable characters. A component of the additive genetic variation significantly greater than zero was demonstrated in the length at 63 days in the guppy (Ryman, 1972). The genetic control of growth was mainly examined as an estimation of heritability. Heritabilities have been estimated on growth in many fish species and these were summarized by Tave (1993). It is important for the fish breeding to elucidate the change in genetic control of growth at various ages in the same population. Nakajima and Fujio (1993) reported a change in the heritability with age using the strain comparison. The authors suggested the different genetic controls in three stages on the growth curve, namely, maternal genotypic effects on the body size at birth, growth genes in the growing stage, and an inhibitory gene influencing final body size of male. The authors also suggested that the genetic effect from the maternal half (dam) would be different from the effect in the paternal half (sire).

There are many strains of guppies that were mainly created based on body color, color pattern, fin shape, etc., in male. The genetic differences among strains were examined by isozyme analysis (Macaranas and Fujio, 1987; Barinova et al., 1997, 1998). The strain differences were also reported in four growth-related characteristics and four reproductive traits in the guppy (Macaranas and Fujio, 1988). These strain differences were caused by the genetic differences affecting each characteristic, and the genetic control of several quantitative traits were examined using these strain differences in the guppy, such as the body length (Nakajima and Fujio, 1993), seawater resistance (Nakajima et al., 1995), thermal resistance (Fujio et al., 1995), and vertebral number (Nakajima and Fujio, 1999).

The estimates of the number of genes contributing to the variance of the quantitative characteristics within and between populations are fundamental for the study of the mechanisms of heredity. A variety of statistical techniques have been proposed for estimating the effective number of genetic loci contributing to the difference in a metrical trait between two inbred lines grown in a common environment. The original method was devised by Wright (1952), and this method was introduced in several studies (Roderick and Schlager, 1968; Lande, 1981; Falconer, 1989). Falconer (1989) calculated the effective number of loci (n) using this method in abdominal bristles in Drosophila ($n = 98$), thorax length in Drosophila ($n = 50$), 6-week weight in mouse ($n = 32$) and litter size in mouse ($n = 2$), respectively. Yamanaka et al. (1995) reported that there are approximately nine loci affecting the male body size at 180 days old. This was determined using a cross experiment between Fancy (F) and Standard (S) strains, which have apparent differences in the body length for males at 180 days old.

In this study, the variance components from the maternal half (dam) and paternal half (sire) were estimated by way of comparing the half-sib families at different stages of growth. The effective number of loci contributing to the strain difference of the body size at 180 days old were also estimated to investigate the genetic control of growth in the guppy.

2. Materials and methods

2.1. Fish specimens

Two guppy strains, F (Fancy) and S (Standard), were used and these were maintained as a closed colony in the laboratory for at least 60 generations. These were maintained in 60-l aquaria with a density of 300–500 individuals per aquarium. For the growth profiles, the litters obtained from single pair matings were reared in several 2.5-l aquaria and the density per aquarium was limited to a maximum of five individuals. The guppies were maintained at a temperature of 23 ± 2 °C and fed a ground carp diet twice a day, with dried *Daphnia* given as a supplement. The standard body length was measured as an index of growth at 30 days interval from birth until 180 days old. It was only possible to determine the sex after reaching 60 days old, so, the measured values before 60 days old were pooled for females and males. The differences of the standard length between S and F strains and between sexes were tested by ANOVA.

2.2. Sib analysis

The variance components at each age were calculated from the analysis of the half-sib families composed of the S strain. The offspring were obtained from five sets of half-sib families, each of which were composed of one male and two to four females. The offspring were separated to several 2.5-l aquaria and maintained at maximum density of five individuals per aquarium. The variance between the sire components, between dams within sire components, and within progeny component of the standard length was estimated by the analysis of the variance at each age. The LSML (Mixed Model Least Squares and Maximum Likelihood) computer program was used for the calculation of the variance at each component.

2.3. Estimation of effective number of loci

The estimation of the effective number of loci affecting the strain differences in the body length was conducted using the results of the cross experiment between the F and S strains (13 crosses) and its reciprocal cross (9 crosses). The F_1 generation obtained from the pair mating between S and F, and its reciprocal cross, were separated to several 2.5-l aquaria and were maintained with a maximum density of five individuals per aquarium. The F_2 generation was obtained by random mating in each of the family in the F_1 generation, and maintained at the same condition with the F_1 generation. The effective number of loci (n) was calculated from the following equation (Roderick and Schlager, 1968).

$$n = (m_1 - m_2)^2 / 8(V_{F_2} - V_{F_1})$$

where m_1 and m_2 are the means of the parental strains, and V_{F_1} and V_{F_2} are the computed variances of the F_1 and F_2 generations, respectively.

3. Results

3.1. Growth of parental strains

From 9 pairs of the F strain, 91 individuals were obtained, and from the 14 pairs of S the strain, 193 individuals were obtained for the experiment of growth in parental strains.

The growth curve of the standard length and change of variance of the standard length at each age of the S and F strains are presented in Fig. 1. The means of the standard length at 0 day old were 7.1 mm in the S strain and 6.9 mm in the F strain, respectively. The standard length of the S strain was significantly larger than that of the F strain at 0 day old. The sex and strain differences could be observed after the fish were 60 days old. The females were always larger than males in each strain after reaching 60 days old and the F strain was constantly larger than the S strain for females and males after reaching 30 days old. At 180 days old, the means of the standard length were 23.1 mm in the S strain and 25.8 mm in the F strain for females, and were 15.9 mm in the S strain and 19.0 mm in the F strain for males. After reaching 90 days old, the growth rate for males dramatically decreases and stabilizes, however, a continuous growth rate was observed among the females. This tendency could be observed in both the S and F strain.

The different patterns were also observed in the change of variance of the standard length between females and males. The variance of the standard length was 0.081 in the S stain and 0.070 in the F strain at 0 day old, and these values increased to 7.718 and 5.973 at 180 days old for females in both the S and F strains, respectively. On the other hand, the variance for males decreased from 3.298 and 2.569 at 60 days old, when the sex could not be detected, to 1.360 and 0.379 at 180 days old in the S and F strains, respectively. The variance in females continuously increased in growth, while, the males decreased until 120 days, then stabilized at a low value. In each of the family in each strain, the sex could be detected after reaching 60 days old. The male could be separated from the female by the existence of the gonopodium, which is the transformed anal fin in males, and the body color appeared after reaching 60 days old. The strain differences could not be observed in the period in which sex is determined and the color observed.

The distribution of the standard length in the S and F strains at 180 days old are presented in Fig. 2. The distribution of the S strain in males clearly deviated from those of the F strain; however, the difference was less clear in females. The smallest individual in the S strain was 17.0 for females and 14.4 for males, and that in the F strain was 22.5 for females and 17.2 for males. The maximum body size in the S strain was 28.47 for females and 17.3 for males, and that in the F strain was 31.8 for females and 21.7 for males. The overlap in the distribution was extremely small for males. The body size of the males in the S strain was clearly smaller than that of the F strain. The significant differences of the standard length were observed at 0 day old and after reaching 60 days old between the S and F strains in each sex.

3.2. Sib analysis

From the five sets of the half-sib families, 7 to 20 offspring were obtained from each female, and a total of 193 offspring were obtained.

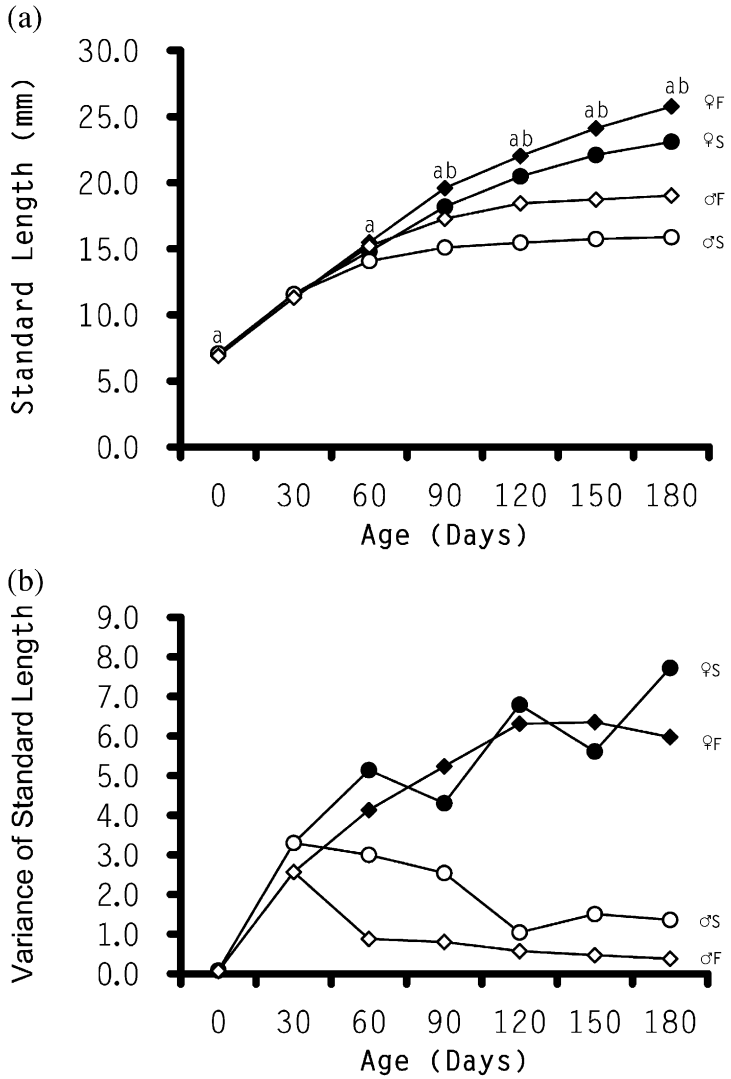

Fig. 1. Growth curve (upper) and change of its variance (lower) in S and F strain from 0 days old to 180 days old. The values at 0 and 30 days old, pooled data for females and males because sex could not be determined in these stages. ●: Female of S strain; ○: Male of S strain; ◆: Female of F strain; ◇: Male of F strain. (a) Significant differences ($P < 0.05$) between F and S strain in each sex. (b) Significant differences ($P < 0.05$) between female and male within each strain.

The fluctuation of the variance at separated components, between sires (σ_S^2), between dams within sires (σ_D^2), and within progeny (σ_W^2), are presented in Fig. 3. In females, the variance within the full-sib components and between dams within sire components increased with age. However, the variance between sire components indicated low values. The variance between dams within sire components decreased at once at 60 days

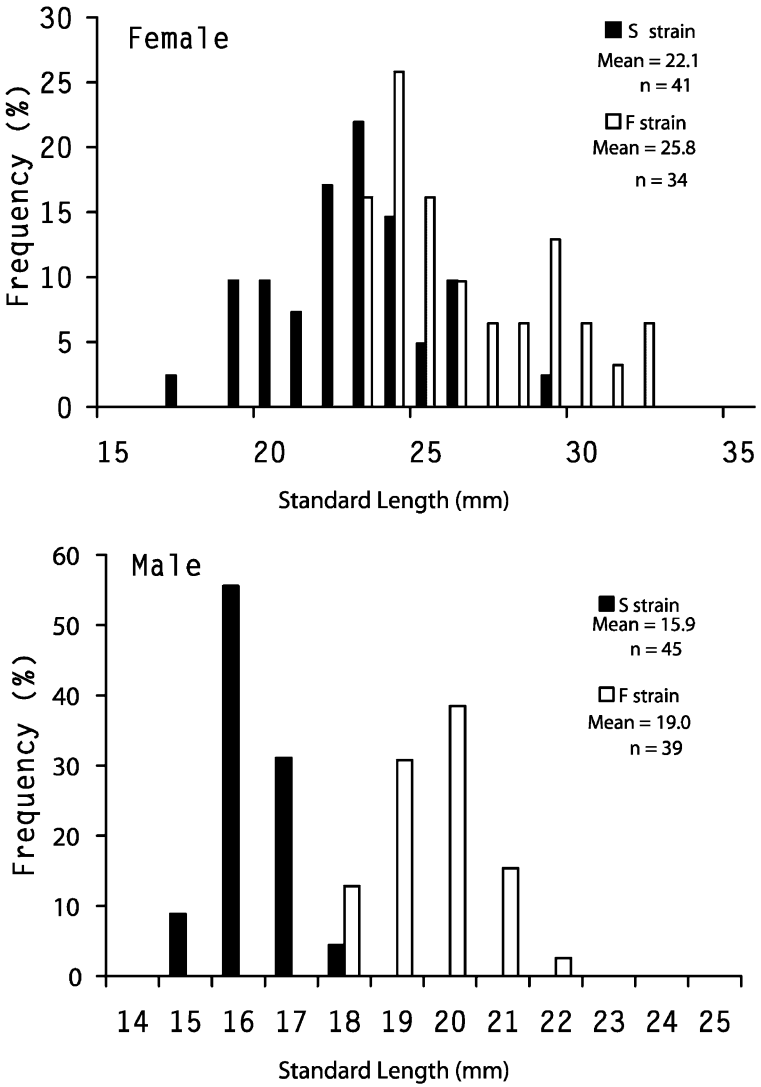

Fig. 2. Distribution of the standard length at 180 days old for females and males in F and S strain.

old. In males, the variance between sire components increased after reaching 90 days old, and the variance between dams within sire components decreased after reaching 60 days old. The progeny variance component for females was larger than that of males.

The fraction of each variance component to the total variance and its fluctuations according to age and sex are presented in Table 1 and Fig. 4. The different patterns of fluctuations between dam component (σ_D^2) and sire component (σ_S^2) variance were observed between females and males. High fractions of the dam component were observed at 0 day old. The fractions of the dam component in the females were

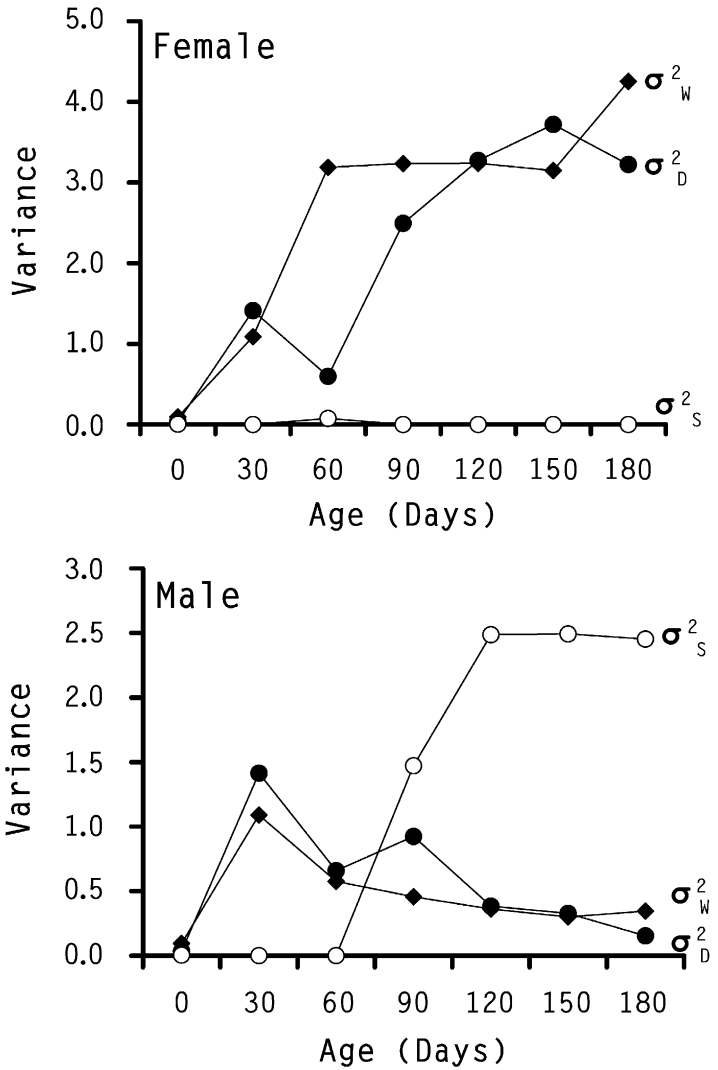

Fig. 3. Fluctuations of variance at three divided components, between sires (σ_S^2), between dams within sires (σ_D^2) and within progeny (σ_W^2).

constantly high, except at 60 days old, but those of the sire components had extremely low values. The males demonstrated a very different pattern of fluctuation in fraction in each of the variance pattern. The fraction of the dam components indicated a maximum value of 0.565 at 30 days old, and this decreased to 0.052 at 180 days old. In contrast, the fractions from the sire component increased from 0 at 60 days old to 0.831 with a maximum value at 180 days old. The sire variance component increased after reaching 60 days old, which is the beginning of the maturation stage for male individuals. These

Table 1
Fractions of variance component to total variance of maternal (dam) and paternal half (sire)

Age (Days)	Male		Female	
	Paternal	Maternal	Paternal	Maternal
0	0.028	0.254	0.028	0.258
30	0.000	0.565	0.000	0.565
60	0.000	0.534	0.020	0.155
90	0.516	0.324	0.000	0.435
120	0.770	0.119	0.000	0.503
150	0.799	0.105	0.000	0.542
180	0.831	0.052	0.000	0.444

Fraction of variance components were calculated by following formula; Maternal = $\sigma_D^2/(\sigma_D^2+\sigma_S^2+\sigma_W^2)$; Paternal = $\sigma_S^2/(\sigma_D^2+\sigma_S^2+\sigma_W^2)$.

results suggest that the body size of a mature male is strongly influenced by the genetic factors from the paternal half, while the genetic factors from the dam were separated to two stages, one before reaching 30 days old and one after reaching 90 days old.

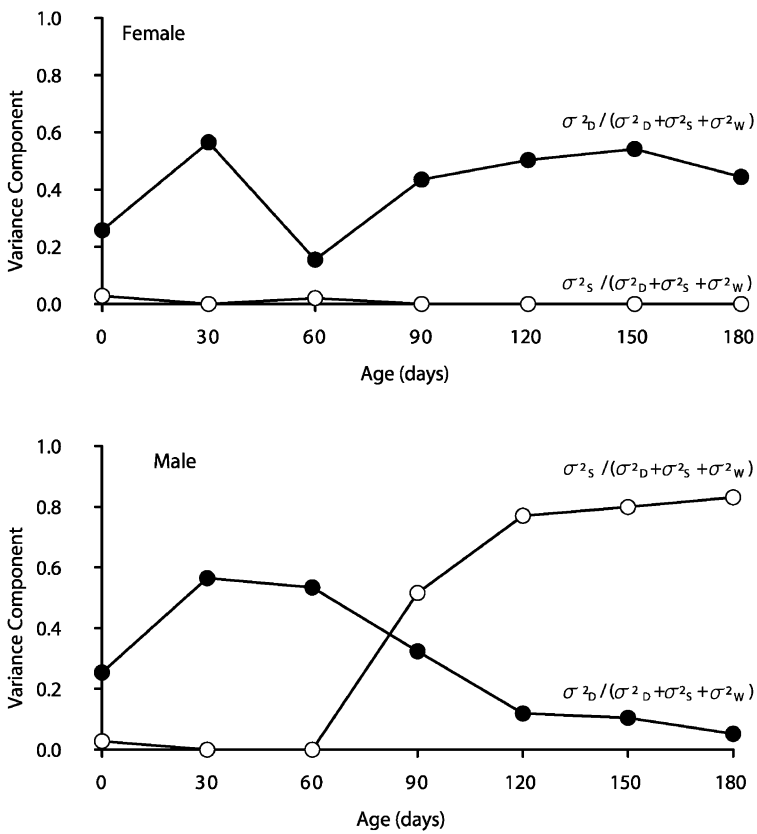

Fig. 4. Fluctuations of fractions of variance component to total variance from dam component (●) and sire component (○), from 0 to 180 days old.

Table 2
Estimate of effective number of loci which contribute to the strain differences for standard length between S and F strain at 180 days old

Cross ♀ × ♂	Sex	Mean standard length (SL) (mm)				Variance of SL		Estimated effective number of loci
		S	F	F_1	F_2	F_1	F_2	
S × F	Female	22.9	–	27.9	27.2	5.7	6.5	8.0
	Male	–	19.0	18.0	17.9	0.4	1.2	1.7
F × S	Female	–	29.6	27.4	28.2	3.1	4.7	3.5
	Male	15.6	–	18.4	17.8	0.8	0.6	–

3.3. The effective number of loci contributing to the strain differences on standard length between S and F

From the nine crosses of females in the S strain and males in the F strain (S × F), 80 offspring were obtained, and 193 offspring were obtained from the 14 crosses of the F × S, as the F_1 generations. On the other hand, 201 offspring were obtained from the S × F and 186 offspring were obtained from the F × S, as the F_2 generations. The standard length, its variance, and estimated effective number of loci are presented in Table 2. The standard length in F_1 and F_2 generations is distributed between the standard length of the parental strains.

The effective number of the loci affecting the strain differences on the standard length between the S and F strains were calculated at 180 days old, because the strain differences were clearly observed at 180 days old in each sex. The calculated numbers were 8.0 for females and 1.7 for males from the cross between the females in the S strain and males in the F strain (Table 2), and 3.5 for females and a negative value for males from the cross between the females in the F strain and the males in the S strain. The negative value is due to the lower variance of the standard length in the F_2 generation than that of the F_1 generation. If the segregation of alleles affecting the strain differences occurred, the variance observed in the F_2 generation was expected to be larger than the F_1 generation. The low variation in the F_2 generation from the cross between the F and S strains suggests that the strong genetic effect of the male in S, which is a small size strain.

4. Discussion

The high variance components were estimated at several stages, and the patterns of fluctuation of the dam and sire components were different between females and males. When these values are converted into heritability estimates, assuming autosomal inheritance, high values of more than 1.0 are obtained, however, heritabilities have to range from 0 to 1.0 theoretically. If the genes of interest are located on the autosomes, both variance components from the maternal and paternal halves should have the same pattern of fluctuation. In the case of the X-linked inheritance, the paternal parent is not a factor of variance because there are no X chromosomes from the paternal half in the male offspring, and the female offspring have the same X chromosome from the paternal

parent. In the case of the Y-linked inheritance, the factor of variance is only the Y chromosome in the male offspring. The low variance components from the paternal half and the high variance components from the maternal half in female offspring suggest the X-linked determination, and high variance components from the paternal half in the male offspring suggest the Y-linked determination of the growth in the guppy. In this case, the fraction of the maternal and paternal halves to the total variance indicates the minimum heritability estimates.

The fluctuation of the heritabilities with growth were reported by Kinghorn (1983) in the salmonid fish. Nakajima and Fujio (1993) also reported the fluctuation of the heritability according to the growth, and the authors suggested that the fluctuations of the heritability are due to three different genetic controls occurring during growth. These are the maternal genotypic effects on the body size at birth, genes responsible for the growth in the growing stage, and an inhibitory gene influencing the final body size for males. High genetic influence from the maternal half was also observed at day 0 in this study, supporting the assumption of the presence of a maternal effect at the beginning of growth. Maternal effect was also reported for seawater resistance (Shikano et al., 1997). These results suggest a strong genetic effect from the female parent on the early stage of growth, which may be caused by the condition of the female parent since a guppy is an ovoviviparous fish. There is a possibility that the maternal factors influence their offspring either through the egg quality, and/or by the environmental influences before birth. It was often reported that the egg quality influences the viability of larva (Marteinsdottir and Steinarsson, 1998), and growth and survival (Utting and Millican, 1997) in other species.

The fluctuation of the variance components for females were different from the patterns observed in males, suggesting different genetic controls of growth in both females and males. The growth rate of male guppies falls suddenly after reaching 90 days old and almost stops, but females continue to grow. In this study, the variance from the sire components for females are extremely low, in contrast to that of the dam components, which indicated very high values. These results also suggest large maternal influences on their offspring. Since the yolk is already absorbed in this stage and the growing conditions were equal among each litter, it is not thought that there are maternal effects. On the other hand, high values of variance from the sire components were observed after 90 days for males. The standard length of a matured male is more strongly influenced by the male parent. These results suggest that the gene(s), which influence the final body size of the male, is/are located on the sex-chromosome and especially that the gene(s) which influence the final body size of the male may be located on the Y-chromosome. Houde (1992) suggested the Y-linked inheritance of the relative extent of the orange-pigmented spots in the male guppy from the large sire components of variance and the small dam components of variance. In the guppy, several genes have been detected on the sex chromosome. Fujio et al. (1990) reported the low temperature resistant gene on the sex chromosome, and the crossing over between the X and Y chromosome. Nakajima et al. (1998) also reported the crossing over between the X and Y chromosome using the cobra gene, which is usually located on the Y chromosome. The guppy is the first animal in which a Y-linked inheritance was demonstrated (Winge, 1923; Winge and Ditlevsen, 1938, 1948). The genes detected

on the Y chromosome are genes which mainly affect color pattern, such as red spots (Winge, 1923), and cobra patterns (Nakajima et al., 1998; Phang et al., 1999). Nakajima and Fujio (1993) suggested that there are genes that inhibit the growth after reaching 60 days old, and these genes influence the final body size of the guppy.

The number of loci which affect the strain differences between the S and F strains at 180 days old were small, and ranged between 3.5 and 8.0 for females and up to 1.7 for males. The small number of loci estimated was similar to the value, of 9.0, estimated by Yamanaka et al. (1995). This calculation is valid on three conditions: (1) all favourable alleles have been fixed at both strains; (2) all the genes have equal effects; and (3) all genes have initial frequencies of 0.5 (Falconer, 1989). Failure of condition (1) or (2) leads to the estimation of the number of locus to be too low, and the failure of condition (3) leads to the overestimation of the number of loci. In this study, a negative value was obtained for the cross between the female in the F strain and the male in the S strain. It was caused by a smaller variance in the F_2 the generation than in the F_1 generation. In theory, larger variances have to be observed in the F_2 generation over that of the F_1 generation, which is caused by the segregation of the fixed genes at both strains. The loss of segregation in the F_2 generation suggests that the existence of the major gene(s) which lead the small size of the S strain, probably located on the sex chromosome. The number of loci may have been underestimated due to the possibility of the linkage between genes located on the sex chromosome. In the sib analysis, the Y-linked inheritance was suggested in matured male body size. These results suggested that the small number of loci affects the matured male body size, and some of them are probably located on the Y-chromosome.

Recently, the location of the locus affecting the quantitative traits were detected by linkage analysis using the molecular genetic markers (Lander and Botstein, 1989; Berrettini et al., 1994; De Sanctis et al., 1995; Mole et al., 1996; Mousseau et al., 1998). These methods are important to apply for further consideration of the genetic control of the growth in fish.

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