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Genetic parameters of growth in rainbow trout, *Oncorhynchus mykiss*, at early rearing stage

M. Yousefian

Yousefianeco@yahoo.com

Caspian Sea Ecology Research Center, P.O.Box: 961 Sari, Iran

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Abstract: The heritability response for growth of rainbow trout during early developmental stages was detected on the basis of full-sib and half-sib cross between the selected lines. The experiment was done in Shahid Bahonar Salmon Propagation Center, Kelardasht, Iran. Breeders were taken from the stocks maintained in this station. A bifactorial cross was done between two line using four randomly sire and four randomly chosen dams form each line

Analysis of variance revealed a significant difference at 300 days of age between half and full-sib ($P<0.026$). The effective difference in weight between half/full-sibs of juveniles was not statistically significant on 150 days ($P>0.817$) and 225 days ($P>0.081$). No significant difference between mean body weight of male and female half-sib group was found ($P>0.05$); neither were there significant differences between sireline ($P<0.324$) and dam line ($P<0.230$) at age of 300 days.

The heritability ranged from 0.093 to 0.223 in sire and 0.11 to 0.329 in dam groups. The average heritability in sire regardless of age was 0.16 and in dams 0.21. The heritability in total regardless of age and sex was estimated about 0.185.

Genetic parameters (h^2) were different between dams (0.15-0.27) and sires (0.13-0.19) for all ages of samplings and for age of 150 day old, was significant ($P<0.035$).

Keywords: Rainbow trout, Heritability, Full-sib, Half-sib

Introduction

Variation in growth rate, hatchability and survival rate of larvae are characteristic of all fish species. Variation is due to various environmental factors as well as genetics of fishes (Anthony *et al.*, 2001). The effects of environment can be established as early as during the period of oocyte development.

Growth is affected by many genes, since almost every change in the body structure or organ functions will affect food intake or assimilation in one way or another. Genetic studies are needed to design effective breeding programs aimed at improving production.

Previous genetic studies have revealed moderate levels of genetic variation for growth rate of salmonids, allowing its genetic improvement (Kinghorn, 1983; Gjerde, 1988; Gjerde & Schaeffer, 1989; Crandell & Gall, 1993; Winkelman & Peterson, 1994; Henryona *et al.*, 2005; Kause *et al.*, 2006).

Selection in animal breeding programs has been effective largely because of the preservation of relatively high additive genetic variance for morphological characters including those directly related to economic value (i.e. weight) (Mousseau & Roff, 1987; Roff, 1997). This is typically reflected by heritability (h^2) estimates for morphological (production) characters in agricultural species (Roff, 1997; Arango *et al.*, 2002; Splan *et al.*, 2002; Hassen *et al.*, 2003). Genetic variance for production characters in salmonid fish also tends to be high (h^2_a>0.4) (Gjerde & Gjedrem, 1984; Gjerde & Schaeffer, 1989; Wangila & Dick, 1996; Jonasson & Gjedrem, 1997; Fishback *et al.*, 2002; Vandeputte *et al.*, 2002).

There are few references on the genetic analysis of early development in salmonids. In rainbow trout, strain effects are found on hatching time (Fergusen *et al.*, 1985), which also seems to have an additive genetic component (h^2=0–0.23) depending on incubation (McIntyre & Blanc, 1973). In rainbow trout there is also a small maternal effect (m^2=0.02-0.04) and large dominance effect (Snoker, 1986). On early survival, maternal effects are always present in rainbow trout, but potentially sire effects may be significant (Blanc & Poisson, 1983) or not (Nagler *et al.*, 2000). In methods employed in fish breeding, more precise results are obtained by the complete bifactorial dispersion complex resulting from diallelic crosses of different degress of complexity.

The external fertilization of eggs in rainbow trout and the high fertility of female, facilitate the simultaneous conduction of a large number of crosses.

In this paper, in order to better define the setting up of the response to selection in rainbow trout, an experiment was designed to detect the heritability response on growth during early developmental stages on the basis of full-sib and half-sib cross between the selected lines.

Materials and methods

Rainbow trout breeders were taken from the stocks maintained at Shahid Bahonar Salmon Propagation Center, Kelardasht, Iran in 1999-2002. The 3-year-old mature rainbow trout were randomly selected from two lines A and B and artificially stripped. A bifactorial cross (2×2) was done between A and B lines using four random sire and four randomly chosen dams from each line (Fig. 1), thus in total 8 full-sib and 8 half-sib families were crossed and used in the present study. The number of eggs used as family size for each cross was 200 eggs. The 16 full-sib and half-sib families were randomly distributed in 32 incubators (each treatment was done in 2 replicates).

Incubation went on at 8±0.5°C until hatching around 420 degree days (°D), and then until swim–up at 750 degree days (°D). After hatching the fish were transferred to nursery tanks, one tank for each full-sib family of 150 fry. The tanks were rectangular, of 2×0.5×0.2m, receiving about 12 $Lmin^{-1}$ of fully oxygenated water. Feeding was initiated when the fry showed signs of swimming. At 50 days of age, the fish were transferred to a set of 1.5×1.5×1m concrete pond, with a volume of 2000L receiving about 30 $Lmin^{-1}$ of fully oxygenated water. Feeding was provided by hand feeding at a rate of 1.5% body weight per day. Water temperature ranged from 8-12°C with an average 11±1.41°C.

Mean weight at the ages of 150, 225 and 300 days in fish from different treatments were measured, abnormal individuals were removed from the analysis. A total of 480 individuals were analyzed. The placing of full-sib and half-sib was randomized in rearing facilities.

The determination of heritability was done from the expansion of the variance of phenotypic variation using variance analysis. For this purpose, it was necessary to obtain a sufficient number of related offspring simultaneously. The offspring was obtained by diallelic crosses. Offspring produced by one female from different males are half-sibs with respect to each other, while the individuals within each given offspring group represent full-sibs (Fig. 1)

The variation components were calculated, using conventional techniques and methods of bifactorial variance analysis (Kirpichnikov, 1981). The sum of square deviations of variance "between females" and "between males" due to the interaction of females and males and random deviations i.e. "within the offspring" are then determined. The calculations are made using the following formula:

1) $SS_{♀♀} = nb\ \Sigma(\overline{X}_{♀♀} - \overline{X})^2$

2) $SS_{♂♂} = na\ \Sigma(\overline{X}_{♂♂} - \overline{X})^2$

3) $SS_{♀♀♂♂} = n\ \Sigma(\overline{X}_{♀♀♂♂} - \overline{X}_{♂♂} - \overline{X})^2$

4) $SS_w = n\ \Sigma(\overline{X} - \overline{X}_{♀♀♂♂})^2$

5) $SS_w = (X - \overline{X})^2$

Where $\overline{X}$ is a common mean for all fish, $\overline{X}_{♀♀}$ mean value for different offspring of female. $\overline{X}_{♂♂}$ mean value for different off spring of male.

$\overline{X}_{♀♀♂♂}$ mean value for different offspring of male and female. $\overline{X}$ is individual measurements. "n" is the number of individuals in a given offspring. "a", is the number of females. "b", is the number of males.

The so–called observed variance (MS or V) may then be calculated; they are obtained after the deviation of the sum of the squared values by the number of degrees of freedom: a-1 for $SS_{♀♀}$, (b-1) for $SS_{♂♂}$, (a-1)(b-1) for the deviation of the interaction, and abn-1 for SS_{ph}. The transition to true or causal variances δ^2 is accomplished using the following formulae

$\delta^2_D = (V_D - V_{D.S})/nb$ $\delta^2_S = (V_S - V_{D.S})/na$ $\delta^2_D = (V_{D.S} - V_W)/n$

The estimate variance components were done by Excel program based on the above equations and analysis of variance by SPSS, version 11.5.

Results

The mean weight of fingerlings in full/half-sib groups at 150, 225 and 300 days of rearing are presented in Table 1.

Table 1: Comparison of the half-sib (ANOVA) of rainbow trout at 150, 225, 300 days of growth

Variable	Half-sibs ± S.E.	Full-sibs ± S.E.
Growth at 150 days (g)	4.8 ± 0.13	4.7 ± 0.17
Growth at 225 days (g)	34.8 ± 0.04	31.8 ± 0.56
Growth at 300 days (g)	56.5 ± 1.1**	54.6 ± 0.93

(*) and (**) represent significant differences (P<0.05 and P<0.01)

Analysis of variance revealed a significant difference at 300 days of rearing between half and full-sib (P<0.026). The effective difference between half/full-sibs on the weight of juvenile was not significant at 150 days (P>0.817) and 225 days (P>0.081) weight gians of fishes. The difference between mean body weight for male and female half-sib group was not significant (P>0.05). The differences at 300 days old were not significant in sire (P<0.324), and dam line (P<0.230) too. The analysis of variance of weight heritability in rearing of rainbow trout in a diallelic cross of 2×2 type (complete bifactorial dispersion complex) are presented in Tables 2, 3 and 4 for different ages of sampling.

The heritability ranged from 0.093 to 0.223 in sire and 0.11 to 0.329 in dam groups. The average heritability in sire regardless of age was 0.16 and in dams 0.21. The heritability in total regardless of age and sex was estimated about 0.185.

Genetic parameters (h^2) were different between dams and sires for all ages of samplings and for age of 150 day old it was significant (P<0.035). The data of sire, dam and total heritability estimates for weight gain at different age are presented in Table 5.

Table 2: The analysis of variance of weight heritability, in 150 days of rearing for rainbow trout in a diallelic cross of 2×2 type

Rep.		*SS*	*df*	*MS*	*Var*	h^2
1	Déviation of female	0.123	1.000	0.123	0.101	0.329
	Déviation of male	0.079	1.000	0.079	0.065	0.212
	Déviation interaction	0.070	1.000	0.070	0.057	
	Random déviation	42.570	8.000	5.321	3.989	
	Total déviation	43.859	11.000	3.987		0.271
2		*SS*	*df*	*MS*	*Var*	h^2
	Déviation of female	0.045	1.000	0.045	0.051	0.232
	Déviation of male	0.038	1.000	0.038	0.043	0.196
	Déviation interaction	0.004	1.000	0.004	0.005	
	Random déviation	28.711	8.000	3.589	3.841	
	Total déviation	29.199	11.000	2.654		0.214
3		*SS*	*df*	*MS*	*Var*	h^2
	Déviation of female	0.105	1.000	0.105	0.090	0.309
	Déviation of male	0.065	1.000	0.065	0.056	0.191
	Déviation interaction	0.001	1.000	0.001	0.001	
	Random déviation	36.306	8.000	4.538	4.224	
	Total déviation	38.102	11.000	3.464		0.250
4		*SS*	*df*	*MS*	*Var*	h^2
	Déviation of female	0.045	1.000	0.045	0.049	0.218
	Déviation of male	0.038	1.000	0.038	0.042	0.184
	Déviation interaction	0.004	1.000	0.004	0.005	
	Random déviation	28.711	8.000	3.589	3.841	
	Total déviation	29.199	11.000	2.654		0.201

Table 3: The analysis of variance of weight heritability, in 225 days of rearing of rainbow trout in a diallelic cross of 2×2 type

Rep.		*SS*	*df*	*MS*	*Var*	h^2
1	Déviation of female	36.331	1.000	36.331	1.275	0.179
	Déviation of male	23.019	1.000	23.019	0.808	0.113
	Déviation interaction	58.080	1.000	58.080	2.038	
	Random déviation	1697.92	8.000	212.24	9.137	
	Total déviation	2079.13	11.000	189.01		0.146
2		*SS*	*df*	*MS*	*Var*	h^2
	Déviation of female	45.513	1.000	45.513	1.724	0.261
	Déviation of male	38.772	1.000	38.772	1.469	0.223
	Déviation interaction	24.112	1.000	24.112	0.914	
	Random déviation	1697.92	8.000	212.24	9.137	
	Total déviation	2079.13	11.000	189.01		0.242
3		*SS*	*df*	*MS*	*Var*	h^2
	Déviation of female	67.1187	1.000	67.118	1.86	0.206
	Déviation of male	37.5948	1.000	37.594	1.042	0.115
	Déviation interaction	0.2523	1.000	0.2523	0.007	
	Random déviation	1697.92	8.000	212.24	9.137	
	Total déviation	2079.13	11.000	189.01		0.161
4		*SS*	*df*	*MS*	*Var*	h^2
	Déviation of female	30.528	1.000	30.528	1.187	0.185
	Déviation of male	23.185	1.000	23.185	0.901	0.140
	Déviation interaction	8.367	1.000	8.367	0.325	
	Random déviation	1697.92	8.000	212.24	9.137	
	Total déviation	2079.13	11.000	189.01		0.162

Table 4: The analysis of variance of weight heritability, in 300 days of rearing for rainbow trout in a diallelic cross of 2×2 type

Rep.		*SS*	*df*	*MS*	*Var*	h^2
1	Déviation of female	69.4083	1	69.4083	1.729	0.172
	Déviation of male	54.1875	1	54.1875	1.35	0.134
	Déviation interaction	11.7612	1	11.7612	0.293	
	Random déviation	2728.57	8	341.072	8.393	
	Total déviation	3304.79	11	300.436		0.153
2		*SS*	*df*	*MS*	*Var*	h^2
	Déviation of female	59.675	1.000	59.675	1.619	0.176
	Déviation of male	57.553	1.000	57.553	1.562	0.170
	Déviation interaction	17.424	1.000	17.424	0.473	
	Random déviation	2728.57	8.000	341.072	8.393	
	Total déviation	3304.79	11.00	300.436		0.173
3		*SS*	*df*	*MS*	*Var*	h^2
	Déviation of female	67.4028	1	67.4028	-1.629	0.158
	Déviation of male	39.9675	1	39.9675	-0.966	0.093
	Déviation interaction	257.242	1	257.243	-6.219	
	Random déviation	2728.57	8	341.072	8.393	
	Total déviation	3304.79	11	300.436		0.125
4		*SS*	*df*	*MS*	*Var*	h^2
	Déviation of female	42.639	1.000	42.639	1.106	0.115
	Déviation of male	55.470	1.000	55.470	1.439	0.149
	Déviation interaction	8.979	1.000	8.979	0.233	
	Random déviation	2728.57	8.000	341.072	8.393	
	Total déviation	3304.79	11.00	300.436		0.132

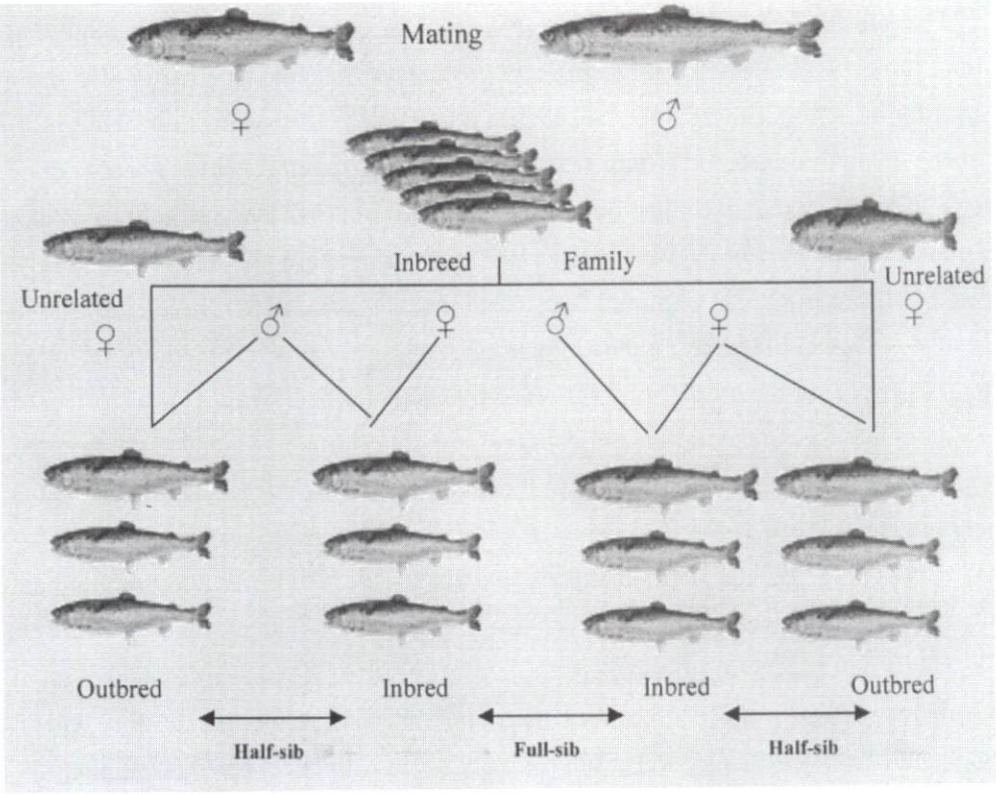

Figure 1: Crossing model producing full and half-sibs

Table 5: Comparison of survival and growth at 150, 225 and 300 days of the Half-sib (ANOVA) rainbow trout

Variable	$h^2_{♀♀}$±S.E	$h^2_{♂♂}$±S.E	$h^2_{♀♀♂♂}$±S.E
Weight at 150 days (g)	0.27±0.05	0.19±0.02	0.23±0.032
Weight at 225 days (g)	0.20±0.037	0.14±0.05	0.17±0.043
Weight at 300 days (g)	0.15±0.028	0.13±0.032	0.0.14±0.0.21

Four hundreds eighty offspring were studied from a 4 sire ×4 dams full fractional mating.

Discussion

The genetic management of breeding stocks in aquaculture becomes more and more important to ensure long-term sustainable development, especially in rainbow trout for which rearing systems are highly intensive. In this species, growth rate is one of the major traits to be improved (Vandeputte *et al.*, 2002), which can be done to a variable extent through the choice of appropriate strains (Kinghorn, 1983; Refstie, 1990; Sylven & Elvingston, 1992), crossbreeding for heterosis (Gjerde, 1988), chromosome set manipulations (Chourrout *et al.*, 1986; Quillet, 1994) and finally, selective breeding (Vandeputte *et al.*, 2002). For this last method, selection in fish breeding schemes has been effective and farmers would often prefer it because of the preservation of relatively high additive genetic variance for morphological characters including those directly related to economic value (Mousseau & Roff, 1987; Roff, 1997; Guy *et al.*, 2005). In this respect, heritability as a valuable genetic component is widely used to estimate morphological characters in fish species.

There are several published articles on the heritability of different characteristics of rainbow trout, but there are very few references on the genetic analysis of early rearing stages. Guy *et al.* (2005) estimated genetic variance for body weight (UTT), condition factors (BW) and resistance to acute thermal shock (Kf) in a three-generational rainbow trout (*Oncorhynchus mykiss*). Heritability was high for all three traits ($h^2_{UTT} = 0.041 \pm 0.07$; $h^2_{BW} = 0.46 \pm 0.04$; $h^2_{Kf} = 0.52 \pm 0.04$) in an extended animal model including terms for strain origin and hybrid effects. McKay and his coworkers (1986) studied on the relative magnitude of additive genetic effects, for size and growth at sexual maturity in rainbow trout at 2.5 and 4 years of age using a factorial mating system. Heritability estimates for length and weight ranged from 0.13±0.17 to 0.38±0.22. (McKay *et al.*, 1986).

In the present study, we estimated the additive genetic component (h^2=0.14-0.23) depending on rearing stages from 150 to 300 days of rainbow trout rearing. The dam component of variance was consistently larger than the sire component ($h^2_{♀♀} = 0.23 > h^2_{♂♂} = 0.17$). A similar experiment was reported by Gall and Huang (1988), which showed that with the exception of nursery weight, the estimated

heritability of body weight at all ages were 0.20±0.11 when based on half-sib variance components. The estimated heritability of nursery weight was high (0.52 ±0.15) but in their work the dam component of variance was smaller than the sire component, which is in contrast to those estimated in the present work. They suggested some type of confounding of rearing method and distribution of families within the rearing system (Gall & Huang, 1988).

Actually, in some study on heritability of rainbow trout, as stated before by Crandell and Gall (1993), sex had a significant ($P<0.05$) effect on body weight at all ages. Heritability estimates obtained without consideration of sex ranged from 0.12 to 0.57 when all records were included and from 0.11 to 0.54 for records of sexed fish (Crandell & Gall, 1993).

In the present study, there was a remarkable difference of heritability between different ages as well as the dam effects, therefore it seems that the estimation of heritability of rainbow trout is depending on many parameters such as; the origin of breeders, situation of offspring, order of genes, age and sex of fish, intensity of selection of breeders, and mostly the experimental condition.

The heritability estimates obtained from restricted maximum likelihood were higher than expected, ranging from 0.36 to 0.71 for the growth traits, total length, weight and condition factor (Anthony *et al.*, 2001)

The heritability of the weight and body length in fishes is generally not as high as we obtained in the present study and its determination depends to some extent on, as stated before, the conditions of the experiments. The eggs of different females may be of very different qualities, which are in part determined by the genotype but to even greater extent by external environment. The variance analysis as a method of heritability calculation for fish along with its advantages has a number of serious draw backs, that should be considered. The extent of genetic variation of females and males used in diallelic crosses may be very different. In such cases, heritability calculation suffers from a much lower precision (Nikoro & Vasilyeva, 1976).

Based on the result of the present study, the heritability in male and female was different but not significant ($P>0.05$), therefore the results seems to be precise.

Other difficulties in estimation of heritibilaty by variance analysis are the technical complexities associated with crossing and the cultivation of the offspring. It is particularly difficult to achieve joint cultivation of fishes from different broods. Usually one has to divide these into three or four batches and to place them in different ponds. In the present study we could manage the eggs of different treatments (crosses) in separate incubators and rearing them in trough and ponds separately. The higher estimation of heritability at early stage of rearing (nursery stages) compared to juvenile stages, may be considered as higher environmental effect at later stage of rearing.

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