HERITABILITY FOR GROWTH RELATED TRAITS IN GIANT FRESHWATER PRAWN (*Macrobrachium rosenbergii*) AT VARIOUS DEVELOPMENTAL STAGES AND CULTURE CONDITIONS ESTIMATED BY INTRACLASS CORRELATION

Imron# and Rommy Suprapto

Research and Development Institute for Fish Breeding

(Received January 2nd, 2013; Accepted May 10th, 2013)

ABSTRACT

Heritability estimates of commercially important traits are of important in order to seek the best strategy of selective breeding program to be implemented. A study aimed at estimating the magnitude of this parameter for growth related traits, expressed in wet weight (WW), total length (TL), and standard length (SL), has been carried out in giant freshwater prawn (GFP). Particular emphasis was given to investigate the effect of ages and culture conditions on the magnitude of the heritability estimates. Nineteen full-sib families were established through individual pair mating. The families, namely groups of offsprings derived from each mating pair were raised through three stages of rearing activities: first-stage nursery (40 days), second-stage nursery (70 days), and grow-out rearing (130 days). Heritability for growth at each stage was estimated through the method of full-sib analysis or intraclass correlation. Components of variance used to produce the heritability estimates were obtained through the method of analysis of variance. Results showed that heritability estimates varied with both ages and culture conditions. The heritability estimates (± standard errors) at 40 days for WW (0.69±0.151), TL (0.64±0.148), and SL (0.70±0.144) were higher than those observed at 70 days (WW = 0.24±0.15; TL = 0.22±0.15; and SL = 0.20±0.14) and 130 days (WW = 0.24±0.058; TL = 0.22±0.05; and SL = 0.20±0.60). A similar pattern was found with respect to the culture conditions. The estimates found in grow-out at lower stocking density (5 individual/m^2) days (WW = 0.24±0.058; TL = 0.22±0.05; and SL = 0.20±0.60) were higher than those observed at grow out at higher stocking density (20 individuals/m^2) days (WW = 0.12±0.058; TL = 007±0.05; and SL = 0.14 ± 0.60). The possible causes of the observed patterns and implications that these findings may have on the breeding program of GFP are discussed.

KEYWORDS: heritability estimate, full-sib family, giant freshwater prawn, intra-class correlation

INTRODUCTION

Heritability is a measure of the proportion of phenotypic variance which is controlled by genetic variance and could be transmitted to the next generation. Information on heritability estimate of a trait may serve as good information with respect to the choice of the best strategy that should be used to improve it. Traits with a high heritability value for instance, could effectively be improved through individual selection; while those with lower values may use other selective breeding method such as family selection or marker assisted selection (Tave, 1995). Additionally, heritability value also possesses predictive role in estimating the response to selection in breeding program.

Due to these beneficial properties, many studies aiming at obtaining the heritability estimates of commercially important traits have been undertaken in aquatic animals (reviewed in Dunham *et al.*, 2001). In GFP

Corresponding author. Research Institute for Fish Breeding, Jl. Raya 2 Sukamandi, Subang 41256, West Java, Indonesia. Phone: +62 260 520500
E-mail: imronnawawi@yahoo.com

however, not many information with regard to this matter are available. An Early study trying to investigate the feasibility of obtaining the heritability estimate of growth at juvenile stage was carried out by Malecha *et al.* (1984). The latest information came from Kitcharoen *et al.* (2012) who studied the heritability estimates for body weight, carapace length, claw length, body length, total length, at two months and six months old. Apart from the limited number of published information, the heritability is not a general and static characteristic of a breeding population (Gjedrem, 2005). It is property not only of traits, but also of the way the phenotype is measured, of the population, and of the environmental conditions in which individuals are raised (Falconer & MacKay, 1996). Consequently, heritability estimates are strictly valid only for particular traits of particular populations which are raised under particular conditions. It may change when environmental conditions are changed and or if a population responds to selection. Due to these properties, some are sceptical and considered that heritability estimation as less useful. However, when data set used to generate the estimates are large and consist of many full-sib and half-sib families, and came from varying environmental conditions, the estimates seem to be useful. In fact, most breeding programs have used the estimates to initiate or to develop their breeding program.

Several ways are available for the estimation of heritability, all of which are based on the degree of resemblance between relatives. The choice of the kinds of relatives to be used is dependent on several circumstances such as the level of precision to be obtained, the bias to be tolerated, and most importantly is the technical feasibility of providing the required data to be analysed. In most cases, it is the biological characteristics of species, particularly the reproductive aspects, which dictate the choice of kinds of relatives as well as the methods of heritability estimation. Several variants of offspring-parent regression and sib analyses are the most widely used methods for heritability estimation (Falconer & MacKay, 1996; Gjedrem, 2005).

Intraclass correlation coefficient (ICC) is a measure of the homogeneity of observations within the classes of a random factor relative to the variability of such observations between classes (Hays, 1988). In the context of breeding program in which several full-sib families exist, the ICC has been used to measure the degree of resemblance between related individuals which is the basis for estimating heritability. Specifically, the degree of resemblance is measured as either similarity of individuals within the same group or as difference between individuals in different groups. Since the total variance is the sum of between and within group variances, the degree of resemblance between related individuals, namely among individuals within the same family, could be expressed as the proportion of the between-group variance to the total variance (Falconer & MacKay, 1996).

This study was aimed mainly at estimating the heritability for growth-related traits in GFP. Specifically, it was designed to address how the estimates correlate with ages and culture conditions. These research questions were explored by the way of full-sib analysis or intraclass correlation.

MATERIALS AND METHODS

To address the two abovementioned research questions, the following study designs were applied. Firstly, comprehensive rearing experiments, which consisted of multiphase nursery and grow-out experiments, were conducted. This strategy was intended to answer the effect of ages on heritability estimates. The effect of culture condition on the magnitude of heritability estimates was approached by applying different management practices during grow-out stage, namely low and high stocking densities.

Establishment of Study Populations

GFP populations used for this study consisted of full-sib families, namely groups of individuals descended from a mating pair. Twenty full-sib families of similar ages were expected to be the test population. To achieve these requirements, 80 gravid females, indicated by yellowish ovary filling the majority of cephalothorax and 40 blue-claw males were collected from brooder holding pond. Three GFP brooders consisting of 2 females and 1 male were stocked into each mating compartment. The mating compartments were spaces of 1.5 m x 1 m x 0.6 m in size which were set in 20 m x 1.5 m x 0.6 m concrete tanks. A piece of net of 2 mm mesh size was vertically set to separate one compartment from another. The mating pairs were let in the mating

compartments until spawning. Daily inspection was carried out to ensure that the female broodstock mated and spawned their eggs into brood chamber for incubation. Once mating and spawning occurred, the males were taken out from mating compartments while females were let for another 2 weeks to incubate their fertilized eggs. When the egg mass are ready to hatch, characterized by greyish colour, they were transferred into 50 L conical hatching tanks. Only one female broodstock from each mating pair was selected. Hence, population of progenies derived from every female represents a full-sib family.

Once the eggs hatched, the broodstock was taken out from the tank while the larvae were left to continue a complete developmental stage and to metamorphose into post larvae which generally lasted for 20-35 days. Stocking density of larvae was standardized at 50 larvae/litre. During this period, standard operating procedures for larval rearing (New & Valenti, 2000) particularly with regard to the feeding practice and water quality management were applied. Ten to 12 days old post larva (PL-10—12) resulting from this stage were then harvested and were prepared for stocking for the next rearing stages (first stage juvenile, second stage juvenile, and grow-out stages).

Multi-Phase Nursery Rearing

In order to optimise survival and growth, two stage nursery rearing (New, 1990) was applied. First-stage nursery was lasted for one month starting from the newly metamorphosed PL. Each family was stocked in separated fine-mesh net cages of 1 m^2 in size suspended in an outdoor pond. At the beginning of the study, a homogenous family size and age was planned. However, asynchronous in mating and spawning as well as variation in egg fecundity among the brooders resulted in among-family variation, both in family size and age. With respect to the ages, the populations consisted of three different batches, the widest age differences of which was three weeks. Specifically, two weeks spanned between the first and the second batches, while one week differentiated between the second and the third batches. The issue of age differential was sorted by allowing each family to undergo the same rearing duration, namely one month. Therefore, depending on the date of stocking, the date of harvesting was adjusted accordingly. In contrast to family age, in which adjustment could be made on harvest date, no particular treatment was done to deal with variation in family size. Family sizes ranging from 400 to 1,000 individuals were stocked into 1 m^2 fine-mesh net cages. Instead, a statistical model was applied to correct for this fixed effect. For this purpose, stocking density (individual/cage) was assigned into three groups: 400-600; > 600-800; and > 800-1,000. During this stage, standard procedures for feeding and water quality management practices were applied. First-stage juveniles resulting from this stage were raised further to the second nursery stage.

As for the first-stage nursery, the family rearing at the second-stage nursery was also carried out in separated net cages. Each family was stocked into a net cage of 9 m^2 in size, but with larger mesh size (0.2 mm), which were set in the outdoor ponds. Stocking density during the second stage was reduced to and standardised at 300 juveniles/cages (comparable to 33 individuals/m^2). The duration for the second-stage rearing was one month. Harvest dates, similar to that applied at the first-stage nursery, were adjusted that each family underwent the same rearing duration (1 month). Following the completion of second phase nursery, the product called second-stage juvenile, were individually tagged and raised further for growing to reach marketable size.

Grow-Out Rearing

To address the questions proposed in this study, namely the profile of heritability estimates in relation to varying ages and culture conditions, two strategies of grow-out rearing were applied. To study the heritability pattern among different ages, a grow-out rearing at low stocking density (5 individuals/m^2) was applied. This was intended to allow the individuals to express their genetic potentials. To address the second question, an additional grow-out experiment which differed from the first was implemented. This was carried out by implementing a grow-out rearing at higher stocking density (20 individuals/m^2). Different from nursery stage, in which families were raised in separate hapas, individuals belonging to different families were reared communally in a grow-out pond. Each individual was tagged with floy tag containing a unique number combination

which made the identification of family groups and other related information was possible. Grow-out rearing was carried out in 50 m^2 concrete ponds for 2 months. Total harvesting was done for all population in one time. Due to age differential of juveniles by the time of stocking as previously described, actually there were among individuals age variation within the harvested population. For the sake of simplicity, however, harvest population was assigned with 130 days. This was based on the fact that this batch comprised the majority of the populations.

Parameters Measurement

Three putatively growth related traits, namely wet weight, total length, and standard length were measured at the end of each rearing stage. At the nursery stages, a sample consisting of twenty individuals from each family were measured on the abovementioned traits. The wet weight was measured by weighing the whole body of individual sample using analytical balance to the nearest milligram. The total length is a body measure started from the tip of the rostrum to the tip of the telson while standard length is a body measure started from the base of rostrum to the tip of the telson. Both traits were measured using a plain ruler to the nearest millimetre. The same three parameters were also measured at the end of grow-out stage. Different from nursery stages however, the number of sample measured at the end of grow-out stage was not limited to a certain number. Instead, all individuals retaining readable tags were measured at the end of grow-out rearing.

Data analysis

Heritability estimates and their standard errors were calculated based on intraclass correlation coeffecient, which is the variance component within mating pairs. To obtain the estimates of variance components which was less confounded by factors other than mating pair, a statitical mix model equation (MME) as described by Kolstad (2005) was applied:

$$Y = Xb + Za + e$$

where:

- y = vector of observations with dimesion of nx1; n= numberof records
- b = vector of unknown fixed effects with dimension of px1; p=number of level for fixed effect;
- a = vector of unknown random animal effects with dimension of qx1; q= number of level for random effects
- e = vector of unknown random residual effects corresponding to the elements of y with dimension of nx1
- X = a known design matrix of order n x p, which relates the elements of y to those of b
- Z = a known design matrix of order n x q, which relates the elements of y to those of a

This model was applied to partition the phenotypic variance observed within population into its major causes, both fixed and random effects. With respect to the current study, the random effect was variance within mating pairs. The variance between mating pairs represented the fixed effect occurred within all rearing stages. The additional fixed effects were varied across rearing stages. At the age of 40 days differences in stocking density among hapas represented the additional fixed effect. At the age of 70 days, no additional fixed effect was considered as each family underwent relatively similar conditions. At the grow-out stage, the additional fixed effects were age (batches) and sexual differences among individuals. The variance components according to that statistical design were estimated using analysis of variance method implemented in SPSS software. The values of these components were then used to estimate the heritability and its standard error using the the formula of Becker (1985) as follow:

$$h^2 = 2t$$

$$t = (\sigma^2 S)/(\sigma^2 S + \sigma^2 W)$$

$$SE_{h^2} = 2\sqrt{((2(1-t)^2[1+k-1)t]^2/k(k-1)(s-1)}$$

where:

- h^2 = heritability
- SE_{h^2} = standard error heritability
- $\sigma^2 S$ = variance of mating pair
- $\sigma^2 W$ = variance within mating pairs
- k = number of progeny per mating pair
- s = number of mating pair
- t = intraclass correlation

RESULTS AND DISCUSSION

Following one month of breeding period, nineteen full-sib families were finally successfully produced out of 80 female brooders attempted to be spawned. This number was comparable to 25% spawning

success. Rearing condition during multiphase nursery and grow out period was normal as indicated by the profile of survival and growth at the respective stage (data not shown). Statistical and genetic parameters extracted from these populations therefore, could be considered as representing a normal population.

Partition of Phenotypic Variation

Partition of variance components of growth related trait in GFP at the age of 40, 70, and 130 days is presented in Table 1, while the corresponding heritability estimates are presented in Figure 1 and Figure 2.

Phenotypic variance within the test populations could be partitioned into several causal sources including differences due to sex, age, stocking density, mating pair, and within progenies. The last two variance components are of particular interest for heritability estimation. Their magnitudes however, are influenced by other sources of variance.

The effect of broodstock or mating pair on phenotypic variation of progeny was reflected by between-mating variance. Table 1 shows that the contribution of variance of mating pair to the phenotypic variation varied with both ages and culture conditions. With respect to ages, mating pair showed signifi-

Table 1. Partition of variance components for wet weight, total length, and standard length in GFP at varying ages and culture conditions. DF, n, and # indicate the degree of freedom, the number of sample, and the number of family, respectively while the double asterisks (**) indicate statistical significance at α=0.01

Source	DF	Mean Square	Variance component	% variance component	F-Ratio
40 days (n=360. 3Family=19)					
Wet weight					
Stocking density	2	0.013	0.0004	4.03	0.06
Between matings	16	0.064	0.0031	33.43	0.53
Within progenies	333	0.006	0.01	62.54	
Total length					
Stocking density	2	6.34	-0.24	0.00	0.00
Between matings	16	120.23	6.78	32.09	0.47
Within progenies	327	17.35	14.35	67.91	
Standard length					
Stocking density	2	1.50	-0.26	0.00	0.00
Between matings	16	69.74	3.49	35.24	0.54
Within progenies	326	6.42	6.42	64.76	
70 days (n=380. #Family=19)					
Wet weight					
Between matings	18	8.36	0.30	11.8	0.12
Within progenies	361	2.39	2.39	88.92	
Total length					
Between matings	18	394.12	14.01	10.94	0.12
Within progenies	361	114.01	114.01	89.06	
Standard length					
Between matings	18	136.43	7.53	14.76	0.17
Within progenies	361	46.40	43.47	85.24	

Source	DF	Mean Square	Variance component	% variance component	F-Ratio
130 days (A) (n=140. #Family=19)					
Wet weight					
Batch	2	301.07	34.65	0.27	0.53
Sex	1	2020.67	12922.94	99.16	197.19**
Between matings	17	42.48	8.88	0.07	0.14
Within progenies	109	44.49	65.54	0.50	
Total length					
Batch	2	3.12	0.18	0.09	0.10
Sex	1	30.33	205.26	98.92	111.60**
Between matings	17	3.34	0.23	0.11	0.12
Within progenies	113	1.84	1.84	0.89	
Standard length					
Batch	3	2.59	0.24	0.21	0.30
Sex	1	16.22	112.97	99.00	139.41**
Between matings	17	1.44	0.09	0.08	0.00
Within progenies	119	0.81	0.81	0.71	
130 days (A) (n=378. #Family=19)					
Wet weight					
Batch	2	87.10	0.00	2.09	0.00
Sex	2	1409.26	0.96	60.60	0.02
Between matings	16	88.59	2.48	2.18	0.06
Within progenies	358	39.95	39.95	35.13	
Total length					
Batch	2	1.34	0.00	0.00	0.00
Sex	2	18.15	0.96	36.28	0.59
Between matings	16	2.72	0.06	2.22	0.04
Within progenies	339	1.62	1.62	0.61	
Standard length					
Batch	2	1.38	0.04	0.03	0.05
Sex	2	8.83	118.18	99.35	172.18**
Between matings	16	1.68	0.05	0.04	0.07
Within progenies	358	0.69	0.69	0.69	

cant contribution to the phenotypic variation at the age of 40 days (33%-35%). The figures decreased at later ages, becoming 10%-15% and around 1% at the ages of 70 and 130 days, respectively. The extremely low contribution of mating pair variance at the age of 130 days seemed to associate with sexual effect. This effect explained almost all the phenotypic variation in the population (99%). With respect to culture conditions, a comparable profile was observed between low and high stocking density. In both conditions, mating pairs and batch differences contributed only small portion to the phenotypic variation (less 1%). The highest proportion was contributed by the sex effect (99%). Inclusion of sex effect to

the partition of phenotypic variation therefore, is appropriate.

Heritability Estimates among Growth-Related Traits

With a few exceptions, comparison of the magnitude of heritability estimates among WW, TL, and SL within particular ages were relatively comparable. Simplified into one decimal point, the heritability estimates at the age of 40, 70, and 130 days, were within the range of 0.6-0.7, 0.2-0.3, and 0.2, respectively (Figure 1). This feature, namely a slight difference in heritability estimates among the traits, is actually expected as the the three traits have often been used to express individual growth in fishes. With respect to GFP population, Imron & Suprapto (2009) have shown that positive correlation was observed between SL and WW. For the reason of consistency and measurement accuracy, they even recommended to use the SL as selection parameter to be used for breeding program of GFP targeting on improving growth rate (Imron & Suprapto, 2009). Due to these considerations, namely comparability of the estimates and the presence of tight correlation between SL and WW, then from this point onward the term growth related traits is referred to WW and SL. The TL was provided for complementary information.

Heritability Estimates at Varying Ages

In line with the profile of variance component (Table 1), heritability estimates for wet weight, total length, and standard length also varied with ages (Figure 1). Specifically, the magnitudes at 40 day old were higher than those of both at 70 days and at 130 days. The heritability magnitude in the first stage was more than double compared to those of the later stages. Conversely, the heritability estimates at the second-stage nursery and grow-out rearing were comparable. This profile suggests that at the early stage around 70% of the total phenotypic variance was contributed by genotypic variances. The effect of genotypic variances on the phenotypic variance however declined with ages, becoming 19% to 25% at the age of 70 days and 15% to 23% at the age of 130 days. It is of interest to note that a drastic reduction occurred in the heritability estimates between the age 40 days and later ages. Based on the characteristics of heritability estimates as discussed below, the maternal effect seems to be the most plausible explanation.

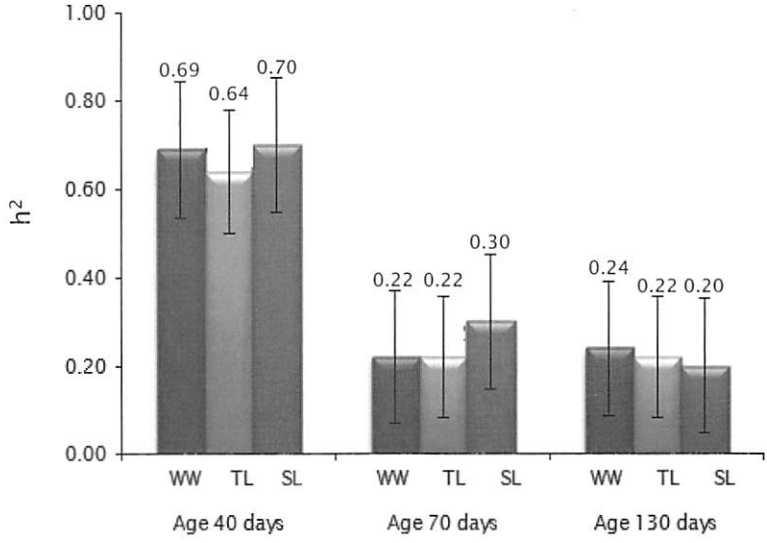

Figure 1. Heritability estimates for growth-related traits at the first nursery stage (40 days), second nursery stage (70 days), and grow-out stage (130 days) of GFP. The vertical bars indicated standard errors, while WW, TL, and SL stand for wet weight, total length, and standard length, respectively

Heritability estimate is a ratio between genotypic and phenotypic variances (VG/VP). The phenotypic variance (VP) itself is the sum of three components: genetic variance (VG), environmental variance (VE), and genetic-environmental interaction variance (VG-E) (Tave, 1995). Therefore, the ratio may change if any changes occur in VG, VE, or VG-E. With respect to the current study, it is obvious that no changes occurred with the VG as the same population was used for heritability estimation at all stages. Since the VG-E was not explored within this study, then the most probable component responsible for the changes in heritability estimates is the VE. The type of the environmental variances which has correlation with age is maternal effect.

Maternal effect is defined as environmental influences on the phenotypes of offspring attributed by the condition of the female (Falconer & MacKay, 1996). It is most notable in mammals since embryonic development occurs inside the female body (in the uterine environment). In aquatic organism in which fertilization and embryonic development occurs generally outside of the female body, maternal effect is mediated by reproductive capacity of the female or the features of eggs. Study with Pacific white shrimp, *Penaeus vannamei* (Perez-Rostro *et al.*, 1999) found that heritability for early larval length which measured in families produced 15 days after ablation were larger that those estimated in families produced at 45 and 75 days after ablation. The lower estimate in the second and the third groups were assumed to correlate with maternal effect, namely lower reproductive quality of females used to produce the families. Morley *et al.* (1999) who investigated the mechanism of maternal effect in herring, *Clupea harengus*, found that reduction in the yolk volume was followed by reduction in the size of hatchlings. Summarizing results of several studies, Dunham (2004) explained that mechanisms by which the female broodstocks influence their offsprings are associated with egg quality, specifically egg size. Larger broodstocks tend to produce larger eggs and tend to produce larger larvae, which also seems to show faster growth. This association however lasted for only on the early stage of life cycle and the effect gradually decreases with age. Besides, the duration of maternal effect also varied from species to species.

Study in the same taxon by Kitcharoen (2012) found that heritability at 2 months for carapace length (0.35±0.15) and body weight (0.26±0.13) were higher than those estimated at 5 months which were, (0.12±0.75 and (0.18±0.12), respectively. Study in other crustacean taxa, *Penaeus monodon*, Jarayabhand *et al.* (1998) found a similar trend. Heritability estimates of growth expressed in total length declined by 50% from 0.153±0.060 at the age of 25 days to 0.073±0.037 at the age of 65 days. When expressed in total weight, the estimate was even lower (0.053±0.029). A comparable results on the same taxon were also obtained by Benzie (1995). He found that heritability for growth estimated from dam component reduced by 30% from 0.56 at three weeks of age to 0.39 at six weeks of age. In Pacific abalone, *Haliotis discus*, maternal effect in metamorphosis and larval size were detected at day six and became insignificant at days 10 and 20 (Deng *et al.*, 2005). Study by Heath *et al.* (1999) suggest that positive correlation between egg size and juvenile growth ended at the age of 45 days. With respect to the data obtained within this study, the decreased of maternal effect seemed to have observed at the age of 70 days. The actual time when the maternal effect started to occur may come earlier. The phenomena observed within this study confirmed with those of previous results.

Heritability Estimates at Different Stocking Density

Influence of environmental variance on phenotypic variance which eventually affects the heritability estimates was also observed in this study. As shown in Figure 2, heritability estimates of low density group ranging from 0.2-0.24 were higher than those of high density group (range: 0.07-0.14). These figures suggest that in lower stocking density genetic control was more pronounced than in high stocking density. It also suggested that genes associated are differently expressed in different environmental conditions. In lower stocking density condition, genetic potentials seemed to be better expressed. From genetic point of view, these data show the presence of genotype by environment interaction.

Several studies have documented the effect of culture condition on heritability estimates of various traits. Busack & Gall (1983)

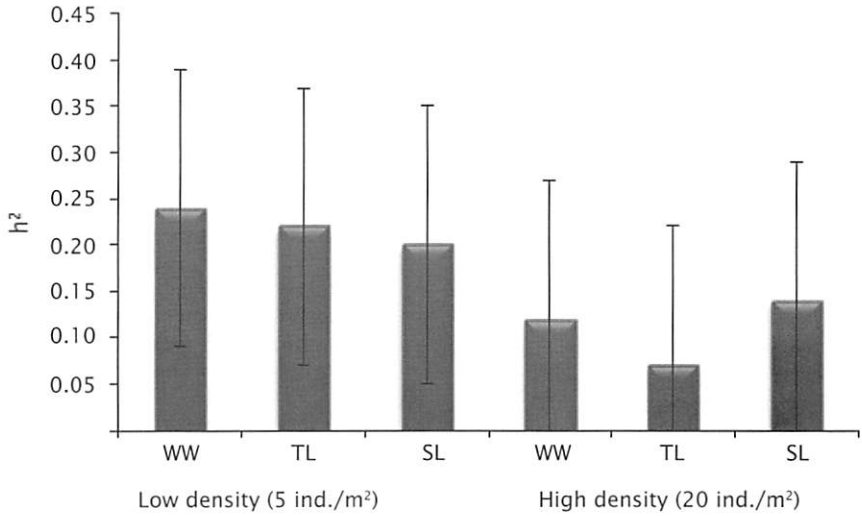

Figure 2. Heritability estimates for growth-related traits at different culture conditions; low (5 individuals/m²) and high (20 individuals/m²) stocking density. The Vertical bars indicate standard errors, while WW, TL, and SL stand for wet weight, total length, and standard length, respectively

reported the presence of genotype-environment interaction in the heritability of age at maturity in male. He noted that maturation of the first male to mature in a tank appeared to be under much weaker genetic control. In other study, Bentsen *et al.* (2012) found that heritability estimate for growth at harvest in generation 4 of nile tilapia was higher for the population raised in cages than those raised in ponds. The heritability in pond treated with standard fertilization and supplemental feed was 0.29±0.09 while under cage environment the magnitude was 0.68±0.16.

Implications for Breeding Program

One of the uses of heritability estimates in breeding program is to make prediction on selection response. An accurate prediction of selection response will be obtained if appropriate heritability estimates are used. Failure to apply this principle may lead to inaccurate prediction of selection response. To give an example, we will use the estimates obtained from the present study used for illustration. Based on the results obtained from the present study, heritability estimates varied with both ages (developmental stages) and culture conditions (stocking density). With respect to the ages for instance, the estimates were variable. They were of high magnitude in the early stage (age of 40 days), but reduced substantially at the later stages (age of 70 and 130 days). To use heritability estimates for growth at 40 days to predict selection response at 70 or 130 days for instance, would result in highly inaccurate prediction. If this is applied, then the realized selection response would be much lower than those predicted. A similar principle also holds for other environmental factors such as culture condition. Based on the data obtained from this study, it would not be inappropriate to use heritability estimate for growth from the population raised in lower stocking density to make prediction on selection response for the population raised in higher stocking density. In summary, due to the characteristics of heritability estimates, which are specific for population, trait, and environment, their use for predicting selection response could not be generalized. Instead, breeders should choose the estimates that have high similarity in those respective aspects to their case. Additionally, as far as available, breeders should use narrow sense rather than broader sense heritability estimates.

It is of our concern that heritability estimates obtained by full-sib analysis or intraclass correlation is confounded by maternal effect as previously described. Besides, they are also confounded by the presence of dominance and epistasis genetic effect that could not respond to selection. While the bias in heritability estimates resulting from maternal effect can be sorted out by comparing the estimates between the early and later stages, the experimental method applied in the present study did not allowed to sort dominance and epistasis effects from that of additive genetic effect. Due to the presence of these confounding effects the estimates therefore are categorized as broad sense heritability. For the purpose of breeding program, the interest is actually in the narrow sense heritability, namely the phenotypic variance contributed by additive genetic effect. This is so because it is the additive genetic effect that responds to selection. However, in the absence of published narrow sense heritability estimates, the broad sense heritability estimates could still be useful. At least they may provide the upper limit of narrow sense heritability, given that theoretically, narrow sense heritability estimates will not be higher than broad sense heritability estimates.

CONCLUSION

The magnitude of heritability estimates for growth in GFP was influenced by developmental stages and culture condition. Among different developmental stages, the heritability estimates at early stages were significantly higher than those at later stages. At the same age, the heritability estimates at lower stocking density were higher than those at higher stoking density. These specific characteristics should be seriously taken into account when breeders would like to make prediction on selection response by using heritability estimates generated from other studies.

ACKNOWLEDGEMENTS

The authors would like to thank the members of Giant Fresh Water Research group at the Research Institute for Fish Breeding for all the assistance during the course of the study. This study was jointly funded by the Ministry of Marine and Fisheries and grant from the Ministry of Research and Technology to the first author.

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