Estimation of the Heritability for Growth Traits at 3 Months and 5 Months of Pacific White Shrimp, *Litopenaeus Vannamei*

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Abstract. To provide the necessary genetic parameters for Litopenaeus vannamei breeding program, the heritabilities were estimated in the breeding process. Heritabilities were estimated for the body weight (BW), total length (TL), the body length (BL), first abdominal segment depth (FASD), third abdominal segment depth (TASD), first abdominal segment width (FASW), partial carapace length (PCL) of L. vannamei were measured in 3-5 months old. The estimates were calculated from 7 body measurements on progeny resulting from a nested mating design. 17 half-sib families and 42 full-sib families of L. vannamei were obtained by artificial assistant fertilization of 2-5 females with a single male, and the measurements were obtained 3-5 months after metamorphism. Point estimate for heritabilities based on the sire component were moderate, and they were 0.452±0.029, 0.368±0.025, 0.387±0.026, 0.403±0.023, 0.415±0.033, 0.441±0.028, 0.422±0.027 for BW, TL, BL, FASD, TASD, FASW and PCL at 3 month, and 0.515±0.031, 0.394±0.028, 0.409±0.028, 0.412±0.028, 0.420±0.029, 0.429±0.029, 0.415±0.028 for BW, TL, BL, FASD, TASD, FASW and PCL at 5 month, respectively, all of which differ significantly from zero ($P<0.01$).

Introduction

Genetic improvement of breeding stocks becomes increasingly important in aquaculture, even slight improvement, body weight and size magnitude would result in surprised advance when the heritability is high. In breeding programs, body size is a common performance trait at a certain age. Heritability and genetic correlation are two important parameters that measure the relative magnitude of additive genetic variation and co-variation. Henderson’s (1973) pioneering work provided a technique that enabled the separation of genetic and environmental effects when predicting bull and cow breeding values. The technique has now dominated the analysis of data from livestock improvement schemes, both in the prediction of breeding values and the estimation of genetic parameters. Most early published estimates of genetic parameters in aquatic animal breeding have been calculated by methods of least squares or by regression of response on selection differentials (Hetzel et al, 2000; Gjedrem and Olesen, 2005; Neira et al, 2006; Maluwa and Gjerde, 2007; Rezk et al, 2009). Recently, aquatic animal breeding literature shows that the nested analysis of variance model are beginning to be used to estimate variance components in some species (Andriantahina et al, 2011; Ibarra et al, 2005; Nhan et al, 2009).

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The estimates of heritabilities and genetic correlations for many aquatic species have been reported. The heritabilities and genetic correlations estimated from full-sib analysis of female progeny of crosses from three domestic rainbow trout stocks were moderately high (0.32–0.52) for each of post-spawning body weight, egg number, egg size, egg volume (Gall and Gross, 1978; Huang and Gall, 1990; Gall and Bakar, 1999). In addition, they reported that there were favorable and moderate to high genetic correlations between spawning body weight, egg volume, egg number and egg size. Norris and Cunningham (2004) reported that heritabilities of the body weight and flesh color of the Atlantic salmon were 0.6 ±0.3 and 0.2 ±0.1 and the genetic correlation was 0.4 ±0.5. Fishback et al (2002) reported that heritabilities of total length, weight and condition factor of rainbow trout ranged from 0.36 to 0.719, and the genetic correlation was 0.60 ±0.049. Ibarra et al (1999) reported that the realized heritability of total weight was higher (0.33 ±0.08 to 0.59 ±0.13) than that of shell width (0.10 ±0.07 to 0.18 ±0.08) in catarina scallop, Argopecten ventricosus; estimates of the genetic correlation between the two traits varied widely between experiments (1.25 ±-0.22 in experiment 1 and 0.33 ±0.31 in experiment 2). Jonasson et al (1999) reported that the heritability of 4-month cultured red abalone (Haliotis rufescens) in iceland was estimated to 0.11 (0.33 on the liability scale) and for shell length at the age of 8, 10, 18, and 24 months to 0.08, 0.06, 0.27, and 0.34, respectively. In coho salmon, the heritability of number of green (total) eggs was 0.42 ±0.08 and eyed (fertile) eggs 0.33 ±0.08 (Gall and Neira, 2004). Jonasson (1993) reported that the estimated heritabilities of broodstock of Atlantic salmon (Salmo salar) calculated based on sire components from the total material were 0.04 for survival, 0.16 for weight, and 0.10 for length when weight and length were adjusted to egg size and number of fish per tank. The heritability estimated for weight ranged from 0.380 to 0.600 in Oreochromis niloticus (Charo-Karisa et al, 2006) and from 0.120 to 0.560 reared in seven different test environments (Eknath et al, 2007). Toro (1990) reported that heritability for live weight and shell height in the European oyster Ostrea edulis ranged from 0.112 to 0.243 and the genetic correlations between the traits were found to be high at 0.963 and 0.995 for the first and second growing season, respectively. Hilbish (1993) reported that narrow sense heritability estimated for shell length was 0.58 ±0.10 for prodissoconch and 1.08 ±0.29 for 2-day old larvae and there was significant and positive genetic covariance between these two traits in Mercenaria mercenaria. Coman et al (2010) found moderate genetic correlation between shrimp weight at week 24 and week 32 (0.62 ±0.19). The moderate heritabilities for weight between week 24 and week 32 (0.23 to 0.39) were lower than that reported previously in P. monodon (Kenway et al, 2006; Macbeth et al, 2007) and L. vannamei (Argue et al, 2002); but consistent with values reported in several studies for other shrimp species (for instance, Hetzel et al, 2000; Perez-Rostro and Ibarra, 2003; Gitterle et al, 2005). To date, there have been rather limited literatures providing estimates of genetic parameters for the reproduction traits of penaeus species (Arcos et al, 2004, 2005; Ibarra et al, 2005). Perhaps other highly fecund aquaculture species follow the same evolutionary strategy with similar selection dynamics and heritabilities. Su et al (1997) reported that the estimated values of heritability were 0.65 for spawning date, 0.14 for spawning body weight, 0.60 for egg size, 0.55 for egg number, 0.52 for egg volume and 0.13 for fertility-hatchability. Spawning date had significant genetic correlations with spawning body weight, egg size and egg volume (0.51–0.73) as well as with egg number (0.25). Significant genetic correlations were also found for spawning body weight with egg size, egg number and egg volume (0.47–0.67), and for egg size with fertility-hatchability (0.35). Argue et al (2002) reported that the half-sib heritability estimated for growth was 0.84 ±0.43; the realized heritability for TSV resistance was 0.28±0.13. Benzie et al (1997) reported that the estimates for the heritability in size of juvenile P. monodon from half-sib mating were approximately 0.10 for both length and wet weight at 6 and 10 weeks. Nguyen Hong et al (2014)reported heritability for body colour and its genetic association with morphometric traits in Banana shrimp, and Kenway et al(2006) reported heritability and genetic correlations of growth and survival in black tiger prawn Penaeus monodon reared in tanks. Whatmore et al (2013) reported henetic parameters for economically important traits in yellowtail kingfish Seriola lalandi. Hung et al (2013) reported Quantitative genetic parameter estimates for body and carcass traits in a cultured stock of giant freshwater prawn.

Materials and Methods

Experimental Design

A classic nested mating design developed by Comstock and Robinson (1952) was employed to partition the phenotypic variation into its genetic and non-genetic causes. In this experiment each of 17 male *L. vannamei* was mated to an average of 3–5 females, thus generating 42 full-sib families and 17 half-sib families. Variance components for each trait were estimated using a single-trait animal model, while covariance components for pairs of traits were estimated using a two-trait animal model. The effects of males and females nested within males on growth were separated using nested analysis of variance (ANOVA).

Genetic Analysis

The covariance among full- and half-sibs provides the basis for the decomposition of phenotypic variance into genetic and environmental components of variance. The covariance among full- and half-sibs were calculated from the observed components of variance obtained from a three-level nested, ANOVA (Table 1) and the General Linear Models procedure of the Statistical Analysis System (SAS) (Kovac and Groeneveld, 2003).

The experiment was a three-level classic nested, unbalanced design. Therefore the number of offspring in dams and in sires and in dams within sires should revise. The Effective Means were computed using the equations:

Effective mean number of offspring in dams within sires: $K_1= [N-\Sigma(n_{ij}^2/dn_i)]/(D-S)$

Effective mean number of offspring in dams: $K_2=[\Sigma(n_{ij}^2/dn_i)-\Sigma(n_{ij}^2/N)]/(S-1)$

Effective mean number of offspring in sires: $K_3=(N -\Sigma dn_i^2/N)/(S-1)$ in which S=number of sires, D = number of dams, n_{ij} = number of offspring of the i-th sire and j-th dam, dn_1 = number of offspring of i-th sire, N = sum of number of offspring of all sires .

The variance and covariance of characters among different groups were calculated in Table 1.

Table 1. Analysis of variance and covariance for components of phenotypic variation

Source of variance	Degree of freedom (df)	Sum of squares (SS)	Mean square (MS)	Expected mean square E(MS)
Dams	$S \times D-1$	SS_D	MS_D	
Sires	$S-1$	SS_S	MS_S	$\sigma^2 + k_2\sigma_D^2 + k_3\sigma^2_S$
Dams/sires	$S \times (D-1)$	$SS_{D(S)}$	$MS_{D(S)}$	$\sigma^2 + k_1\sigma^2_D$
Offspring (error)	$S \times D \times (n-1)$	SS	MS	σ^2
Total	$N-1$	SS_T		

The key elements in Table 1 were calculated as follows:

$$SS_S = \sum_{i=1}^{S} \frac{x_{i\cdot\cdot}^2}{n_{i\cdot}} - \frac{x_{\cdots}^2}{n_{\cdot\cdot}} \tag{1}$$

$$SS_{D/S} = \sum_{i=1}^{S} \sum_{j=1}^{D_i} \frac{x_{ij\cdot}^2}{n_{ij}} - \sum_{i=1}^{S} \frac{x_{i\cdot}^2}{n_{i\cdot}} \tag{2}$$

$$SS_e = \sum_{i=1}^{S} \sum_{j=1}^{D_i} \sum_{k=1}^{n_{ij}} x_{ijk}^2 - \sum_{i=1}^{S} \sum_{j=1}^{D_i} \frac{x_{ij\cdot}^2}{n_{ij}} \tag{3}$$

Sires heritability was estimated as $h^2_F = 4\sigma^2_F/(\sigma^2_F + \sigma^2_D + \sigma^2_e)$, dams(dam) heritability was estimated as $h^2_D = 4\sigma^2_D/(\sigma^2_F + \sigma^2_D + \sigma^2_e)$, pooled (sire and dam) heritability was estimated as $h^2_{F+D} = 2(\sigma^2_F + \sigma^2_D)/(\sigma^2_F + \sigma^2_D + \sigma^2_e)$.

The phenotypic variance (V_P) was decomposed into the additive genetic variance (V_A), non-additive genetic variance (V_N) and environmental variance (V_E), and the environmental variance (V_E) was decomposed into the common environmental variance (V_{EC}) and the specific environmental variance (V_{ES}) using the standard decomposition of variance components (Falconer, 1989). The causal components of variance were estimated from the full- and half-sib covariance using the relationships in Table 2.

Table 2. Relationships between the covariance of full and half-sibs and causal components of phenotypic variance

Component of variance	Covariance components	Causal components	Calculation of component of variance
σ^2_S	COV_{HS}	$1/4\ V_A$	$\{MS- [(MS_{M(S)}-MS_E)/k_1] \times k_2 - MS_E\}/k_3$
σ^2_D	$COV_{FS} - COV_{HS}$	$1/4V_A + 1/4V_{NA} + V_{EC}$	$(MS_{D(S)}-MS_E)/k_1$
σ^2_E	$V_P - COV_{FS}$	$1/2\ V_A + 3/4V_D + V_{ES}$	MS_E
$\sigma^2_T = \sigma^2_S + \sigma^2_D + \sigma^2$	V_P	$V_A + V_{NA} + V_{EC} + V_{ES}$	
$\sigma^2_S + \sigma^2_D$	COV_{FS}	$1/2\ V_A + 1/4V_D + V_{EC}$	

Heritabilities were computed using the relationships: $h^2 = V_A/[V_A + V_{NA} + V_E]$. Thus heritabilites in the narrow sense of paternal half-sib and maternal half-sib and full-sib were computed using the respective relationships: $h^2_{HS(D)} = 4 \times \sigma^2_D/(\sigma^2_S + \sigma^2_D + \sigma^2)$.

The standard errors of heritabilities and genetic correlations were estimated as follows:

$$\sigma_{h^2_{S,M}} = 2\sqrt{\frac{2(1-r_{FS})^2[1+(k_1-1)r_{FS}]^2}{k_1(k_1-1)(M-1)}} \quad (4)$$

Results

The goal of the sampling procedure was to obtain 60 progeny for each of the 42 dams and averaged 148 progeny for each of the 17 sires and 2520 progeny for the sampling period.

The Accumulation Growth of Body Weight and The Body Size at 3 and 5 Months

The means, standard deviation and coefficients of variation (%) for the accumulation growth of body weight and the characters of body size at 3 and 5 months were calculated in Table 3.

Table 3. Mean and Standard deviation of the accumulation growth

Month	Trait	BW/g	TL/cm	BL/cm	FASD/ cm	TASD/cm	FASW/cm	PCL/cm
3	Mean	4.325	8.890	7.537	0.961	0.989	0.900	2.100
	Standard deviation	0.394	0.620	0.550	0.084	0.083	0.075	0.152
	CV (%)	10.98%	14.34%	13.70%	11.44%	11.92%	12.00%	13.82%
5	Mean	14.95	12.11	10.36	1.48	1.48	1.32	2.93
	Standard deviation	2.73	0.79	0.70	0.11	0.12	0.10	0.21
	CV (%)	18.26%	6.52%	6.76%	7.43%	8.11%	7.58%	7.17%

The coefficients of variations varied considerably among the various traits. The rank order of the variations was body weight (10.98%) that were higher; the body size (ranged from 11.44% to 14.34%) that were slightly lower at 3 month. The rank order of the variations was body weight (18.26%) that were higher; the body size (ranged from 6.52% to 8.11%) that were lower at 5 month.

Analysis of Variance of Body Weight and Body Size

Analysis of variance demonstrated great differences in wet weight and diameter of juveniles from different females mated with the same male and between males at both 3 and 5 months of age (Table 4).

Effective mean number of offspring for sires and dams was computed as follows:

Effective mean number of offspring in dams within sires: $K_1 = [N - \Sigma(n_{ij}^2/dn_i)]/(D-S) = 60$

Effective mean number of offspring in dams: $K_2 = [\Sigma(n_{ij}^2/dn_i) - \Sigma(n_{ij}^2/N)]/(S-1) = 60$

Effective mean number of offspring in sires: $K_3 = (N - \Sigma dn_i^2/N)/(S-1) = 148$

Table 4. Analysis of variance for components of phenotypic variation of Litopenaeus vannamei at 3 and 5 months of age.

		Body weight (BW)		Total length (TL)		
Source of variance	Degrees of freedom (df)	Mean square (MS)	F-value	Mean square (MS)	F-value	Expected mean square E (MS)
3 months						
Dam	41	1071.26	14.27**	9.08	9.87**	
Sire	16	2048.56	27.29**	17.21	18.71**	$\sigma^2+k_2\sigma^2_D+k_3\sigma^2_S$
Dams/sires	25	719.43	9.58 **	6.89	7.49**	$\sigma^2+k_1\sigma^2_D$
Full-sibs/dams	2478	75.07		0.92		σ^2
Total	2519					
5 months						
Dams	41	9438	19.14**	80.53	15.85**	
Sire	16	18759	38.05**	151.33	29.79**	$\sigma^2+k_2\sigma^2_D+k_3\sigma^2_S$
Dams/sires	25	5625	11.41**	61.56	12.12**	$\sigma^2+k_1\sigma^2_D$
Full-sibs/dams	2478	493		5.08		σ^2
Total	2519					

Table 4. Analysis of variance for components of phenotypic variation of Litopenaeus vannamei at 3 and 5 months of age (Continue 1).

		Body length (BL)		First abdominal segment depth (FASD)		
Source of variance	Degrees of freedom (df)	Mean square (MS)	F-value	Mean square (MS)	F-value	Expected mean square E (MS)
3 months						
Dam	41	4083	5.62**	6.01	6.75**	
Sire	16	7266	9.99**	10.71	12.03**	$\sigma^2+k_2\sigma^2_D+k_3\sigma^2_S$
Dams/sires	25	5567	7.66**	6.97	7.83**	$\sigma^2+k_1\sigma^2_D$
Full-sibs/dams	2478	727		0.89		σ^2
Total	2519					
5 months						
Dams	41	7997	7.58**	69.16	8.57**	
Sire	16	13172	12.48**	108.29	13.42**	$\sigma^2+k_2\sigma^2_M+k_3\sigma^2_S$
Dams/sires	25	5343	5.06**	65.16	8.06**	$\sigma^2+k_1\sigma^2_D$
Full-sibs/dams	2478	635		8.07		σ^2
Total	2519					

Table 4. Analysis of variance for components of phenotypic variation of Litopenaeus vannamei at 3 and 5 months of age (Continue 2).

		Third abdominal segment depth (TASD)		First abdominal segment width (FASW)		
Source of variance	Degrees of freedom (df)	Mean square (MS)	F-value	Mean square (MS)	F-value	Expected mean square E (MS)
3 months						
Dam	41	1168.64	13.14**	18.88	9.91**	
Sire	16	2145.37	24.13**	25.42	18.79**	$\sigma^2+k_2\sigma^2_D+k_3\sigma^2_S$
Dams/sires	25	766.43	8.62 **	16.09	6.21**	$\sigma^2+k_1\sigma^2_D$
Full-sibs/dams	2478	88.92		1.86		σ^2
Total	2519					
5 months						
Dams	41	926.02	36.51**	183.26	25.28**	
Sire	16	563.48	22.22**	156.38	21.57**	$\sigma^2+k_2\sigma^2_D+k_3\sigma^2_S$
Dams/sires	25	220.52	8.62**	63.62	8.78**	$\sigma^2+k_1\sigma^2_D$
Full-sibs/dams	2478	25.36		7.25		σ^2
Total	2519					

Table 4. Analysis of variance for components of phenotypic variation of Litopenaeus vannamei at 3 and 5 months of age (Continue 3).

		Partial carapace length (PCL)		
Source of variance	Degrees of freedom (df)	Mean square (MS)	F-value	Expected mean square E (MS)
3 months				
Dam	41	1529.64	18.37**	
Sire	16	2145.28	25.76**	$\sigma^2+k_2\sigma^2_D+k_3\sigma^2_S$
Dams/sires	25	738.25	8.86 **	$\sigma^2+k_1\sigma^2_D$
Full-sibs/dams	2478	83.54		σ^2
Total	2519			
5 months				
Dams	41	2345.88	24.36**	
Sire	16	2567.16	26.66**	$\sigma^2+k_2\sigma^2_D+k_3\sigma^2_S$
Dams/sires	25	841.22	8.74**	$\sigma^2+k_1\sigma^2_D$
Full-sibs/dams	2478	96.29		σ^2
Total	2519			

Estimations of Heritability and Test of Significance

Heritabilities were calculated on the result of component of variance and covariance and test of significance ($t=h^2/\sigma_h^2$) of heritability were shown as Table 5.

All of the heritabilities were significantly different from zero (t-test, $p<0.01$).

Table 5. Heritabilities (h2) and their standard error (σh2)

Month	Trait	BW/g	TL/cm	BL/cm	FASD/cm	TASD/cm	FASW/cm	PCL/cm
3	Heritability(h^2)	0.452**	0.368**	0.387**	0.403**	0.415**	0.441**	0.422**
	Standard errors of heritability (σ_h^2)	0.029	0.026	0.0258	0.027	0.031	0.026	0.032
	Test of significance (t-test)	15.586	14.154	15.000	14.926	13.387	16.962	13.188
5	Heritability(h^2)	0.515**	0.394**	0.409**	0.412**	0.420**	0.429**	0.415**
	Standard errors of heritability (σ_h^2)	0.031	0.028	0.028	0.028	0.029	0.029	0.028
	Test of significance (t-test)	16.595	14.161	14.476	14.538	14.703	14.888	14.600

Notes: t0.05=1.960, t0.01=2.576. The symbol** denotes very significant.

Discussion

An animal model that includes a random effect for the additive genetic effect of each individual and incorporates a complete set of additive genetic relationships among all the individuals, allows an unbiased estimations of variance components, even for the data involving selection and non-random mating (Maluwa and Gjerde, 2006; Gao et al, 2008). In the present investigation full-sib family was taken as a random effect in an animal model to account for the covariance among full-sibs caused by common environmental, maternal and non-additive genetic effects, as well as half-sib family to account for covariance among half-sibs caused by common environmental, maternal, paternal and non-additive genetic effects. The results from the analyses indicated that this model was expected to be unbiased estimates of genetic parameters for the base population.

The estimated heritabilities indicate significant additive genetic variation for body weight and the characters of body size at 3 and 5 months. Sire heritabilties for the different variables were lower than dam heritabilities in many cases, however, all of the heritabilities were significant different from zero (t-test, p<0.01). These results show that it is possible to increase the body weight when selection is applied.

Although dam effects are omnipresent in the study, they were strongly reduced from the data of S. intermedius reported by Liu et al. (2005). However, the fact that they are still present after the juvenile phase may indicate that the quality of yolk reserves plays a role in early development. Dam effects may persist after the onset of exogenous feeding. Crandell and Gall (1993) reported that dam effects persist up to 2 years in rainbow trout and up to 18-month-old Arctic char (Nilsson, 1994).

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