Kasetsart J. (Nat. Sci.) 45 : 1047 - 1057 (2011)

Estimating Genetic Parameters for Weight and Body Size of Pacific White Shrimp (*Litopenaeus vannamei*) by Restricted Maximum Likelihood Method

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ABSTRACT

This study was designed to estimate genetic parameters for weight and body size at tagging (77 d post hatch) and at harvest (124 d post hatch) of *Litopenaeus vannamei*. At harvest, a total of 1,664 individuals from 12 full-sib families reared under three different pond conditions were measured, with mean ± SD of 18.70 ± 3.00 g for body weight (BW), 11.67 ± 1.14 cm for body length (BL), 8.72 ± 1.03 cm for abdominal length (AL), 2.9 ± 0.2 cm for carapace length (CL), 74.62 ± 1.85 for percent tail length, and 25.38 ± 1.85 for percent carapace length. Body ratio was 1.60 ± 0.15 g/cm for BW/BL. Sex, days post hatch and pond had significant effects on weight and size traits ($P < 0.05$). Variance components were estimated by a restricted maximum likelihood procedure with animal mixed linear models. At harvest, estimates of heritability ± SE were 0.37 ± 0.14 for BW, 0.34 ± 0.13 for BL, 0.35 ± 0.13 for AL, 0.13 ± 0.06 for CL, 0.05 ± 0.03 for percent tail length and percent carapace length, and 0.34 ± 0.13 for BW/BL. The results suggested that a high amount of genetic response would be obtained through selection for body weight and size traits as the estimates of heritability for these traits were relatively high. Furthermore, the high genetic correlations between body weight and size traits (BL, AL and BW/BL) imply that an improvement in body weight will cause simultaneous changes in abdominal length as well as the ratio of body weight to body length. The study demonstrated the application of a mixed linear model technique and restricted maximum likelihood procedure for estimating variance components in shrimp with a small set of experimental data.

Keywords: *Litopenaeus vannamei*, heritability, genetic correlation, restricted maximum likelihood, mixed model

INTRODUCTION

Culture of Pacific white shrimp (*Litopenaeus vannamei*) has become the most important sector of Thailand's aquaculture industry, representing 98% of total shrimp production in 2008 (FAO, 2008). The rapid expansion of white shrimp farming is due to the higher yields and lower production cost compared to those of tiger shrimp *Penaeus monodon* (Lebel *et al*., 2010). At present, Thailand is among the top five producers of farmed shrimp and the world's leading exporter

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Received date : 19/04/11 Accepted date : 11/07/11

of shrimp products. Shrimp production reached 507,500 t valued at USD 1.4 billion in 2008 (FAO, 2008). Thailand exports white shrimp in various formats, including fresh, chilled, frozen whole-shrimp and headless shrimp (Gillett, 2008). Body size traits (in particular abdominal (tail) length) are considered important characters by shrimp processors and consumers.

In 2002, *L. vannamei* broodstock were introduced to Thailand from Hawaii for post larval production by the Department of Fisheries (DoF). The success of white shrimp culture in the country has led to increased demand for imported broodstock. However, the sustainability of white shrimp farming is highly dependent upon the availability and genetic improvement of local stock. At present, a number of commercial producers have developed selective breeding programs using their own broodstock. Selective breeding of white shrimp in Thailand is at an early stage compared to the USA and Latin America.

Estimating genetic parameters for aquatic animals is traditionally based on the simple regression and analysis of variance (ANOVA) approaches and requires the use of 20–30 half-sib families (Falconer and Mackay, 1996). With balanced data, variance components are obtained by equating observed and expected mean squares from an analysis of variance and solving the resulting equations. Most data obtained from fish and shellfish, however, are unbalanced and influenced by fixed and random effects. For example, days post hatch, tank, as well as sex, are known to have significant fixed effects and need to be corrected to provide unbiased estimates of genetic parameters (Kolstad, 2005). The mixed model methods, which are routinely applied in livestock, are more efficient for unbalanced situations (Henderson, 1984). The models have been used for unbiased estimation of genetic parameters and breeding values under different culture environments in white shrimp (Gitterle *et al*., 2005). In previous studies, genetic parameters of shrimp were estimated by ANOVA and simple regression methods (Benzie *et al*., 1997; Pérez-Rostro *et al*., 1999; Argue *et al*., 2002; Uraiwan *et al*., 2002).

The applications of mixed model methodology have been demonstrated in white shrimp, with a large family dataset and complex pedigree information, that is, 12,658 individuals from 48 sires and 77 dams (Castillo-Juárez *et al*., 2007) and in a small experiment dataset of 124 individuals from 27 families (Pérez-Rostro and Ibarra, 2003b). Further, the application of the animal model analysis was demonstrated in freshwater prawn (*Macrobrachium rosenbergii*) with 19 families (Kitcharoen *et al*., 2011). In the present study, the heritabilities of body weight and size traits and genetic correlations between traits were estimated for white shrimp at age of tagging (77 d) and at harvest (124 d), using the restricted maximum likelihood (REML) algorithm. Phenotypic data and genetic information were obtained from 12 full-sib families of *L. vannamei* (1,664 individuals) reared under different environments.

MATERIALS AND METHODS

Production of full-sib families

The *L. vannamei* broodstock with known pedigree were an introduced strain from Hawaii obtained from a commercial hatchery in Chon Buri province. Twenty males and twenty females with mean ± SD weight of 45.0 ± 04.9 g and 57.6 ± 6.8 g respectively, were stocked in a 40,000 L concrete tank (bottom surface area of 5×8 m^2) for acclimation. Sea water in the maturation tank was changed 200% daily and was adjusted according to Wyban and Sweeney (1991), with the temperature maintained at 28 ± 0.5 °C, salinity at 33–35 ppt and dissolved oxygen of 4–5 $mg.L^{-1}$. Light was provided with a photoperiod of 13 hr of light and 11 hr of darkness. Broodstock were fed four times a day at 0830, 1100, 1300 and 1600

hours with squid and polycheates at 24–28% of their body weight. After 7 d of acclimation, the females were unilaterally eye-stalk ablated to induce maturation and spawning. A mature female with full ovarian development, containing eggs at stage IV (Primavera, 1985) was artificially inseminated by placing a sperm mass from a single spermatophore into the thelycum. The females were placed in individual spawning tanks (500 L) overnight. Twenty full-sib families were produced during January 21–24, 2009, of which, 12 were used in this experiment. Nauplii were obtained approximately 16 hr after spawning. Following four to five cycles of molting, nauplii from each family were sampled in a 5 L container and counted five times. The number of nauplii was used to estimate survival rates of PL10 (83.12 ± 11.44%).

Juvenile rearing and tagging

Approximately 40,000 nauplii were obtained for each family. They were kept separately in 500 L tanks at one family per tank and the temperature was maintained between 30 and 31 °C. Larvae were fed eight times a day with *Chaetoceros* at a density of 30,000–50,000 cells. mL^{-1} from the protozoean stage up to the early post larval stage. *Artemia* nauplii and an artificial diet with 40% protein were added from mysis up to PL10. The stocking density was reduced to 2 $PL.L^{-1}$. Juveniles with a mean body weight of 3.9 g (76–78 d post hatch) were individually injected with a visible implant elastomer tag to identify full-sib families. The tag was injected intramuscularly into the sixth left or right abdominal segments, using one of six fluorescent colors (yellow, green, pink, orange, blue and red). A total of 2,400 shrimp from 12 full-sib families were tagged and stocked in a 1,000 L tank for 2 d before being transferred to grow-out ponds. Prior to stocking, approximately 80 shrimp from each family were sampled and measured for body weight (BW) and body sizes, including body length (BL), tail length (AL) and carapace length (CL). Proportional traits, including percent tail length (%AL; AL × 100/BL), percent carapace length (%CL; CL × 100/BL) and ratio of body weight (BW/BL) were calculated for body length.

Experimental design and measurement of growth traits

Shrimp were transferred to grow-out ponds in two private shrimp farms located in Chon Buri and Rayong provinces. At the Chon Buri farm, shrimp were stocked at different densities in two 20,000 L concrete tanks (bottom surface area of 20 m^2). In tank #1, 1,000 shrimp were stocked at 50/m^2, including 80 tagged shrimp from each of 12 families and 40 untagged shrimp of similar size. In tank #2, 500 shrimp were stocked at 25 shrimp/m^2, including 40 tagged shrimp from each of 12 families and 20 untagged shrimp. At the Rayong farm, 20 tagged shrimp from each of 12 families and 60 untagged shrimp were stocked at a density of 100 shrimp/m^3 in a 3 m^3 net cage suspended in a shrimp pond (80 m^2), with a column of water of 1.8 m. The pond bottom was lined with PE plastic. A bio-floc system was used for water quality control (Crab *et al*., 2007), with temperature maintained at 30 ± 0.5 °C and DO at 4–5 $mg.L^{-1}$. Shrimp were fed to satiation five times a day at 0600, 1000, 1400, 1800 and 2200 hours with a commercial feed (40% protein). After 47 d of rearing (an average of 124 d post hatch), these shrimp were harvested and individually measured for the same traits as described for juveniles. Because the production of 20 families was completed in 4 d and measurement of the 12 families at harvest was made in 2 d, shrimp were grouped based on days post hatch (121–125 d). Sex was identified according to the presence or absence of the male's petasma between the first pleopods.

Statistical analyses and genetic parameters estimated

Analyses of variance was performed

using PROC GLM implemented in SAS computer software (SAS, 2003) to evaluate the fixed effects for body weight and size traits at tagging and harvest age and to estimate the least squares means for all traits. Results were tested for significance at the 95% level and highly significant results at the 99% level. Only the effect of days post hatch was tested at tagging age. At harvest, the fixed effects of sex, days post hatch and tank were evaluated. The (co)variance components were obtained by a restricted maximum likelihood (REML) procedure in ASREML software (Gilmour *et al*., 2002) using the animal model in Equation 1:

$$y = Xb + Za + e \quad (1)$$

where y is a vector of observations, b is a vector of fixed effects at tagging age (days post hatch) and at harvest (days post hatch, sex and pond), a is a vector of random animal additive genetic effects, e is a vector of random residual effects. X and Z are matrices relating observations to fixed effects (b) and animal genetic effects (a).

Assuming normality of the random effects (a and e) in Equation 2:

$$\begin{bmatrix} y \\ a \\ e \end{bmatrix} \sim N\left(\begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix} \begin{bmatrix} V & ZG & R \\ GZ' & G & 0 \\ R & 0 & R \end{bmatrix} \right) \quad (2)$$

where $V = \text{var}(y) = ZGZ' + R$, G is the genetic (co) variance matrix, $G = A\sigma_a^2$ and R is the residual (co)variance matrix, $R = I\sigma_e^2$, where A is the additive genetic relationship matrix among all shrimp in the pedigree file.

Heritability, genetic correlation and phenotypic correlation were estimated for body weight (BW), body length (BL), tail length (AL), carapace length (CL) percent tail length (%AL), percent carapace length (%CL), and body weight/ body length (BW/BL) based on (co)variance components estimated from the animal model. Heritability was estimated using Equation 3:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2} \quad (3)$$

Genetic correlation was estimated using Equation 4:

$$r_a = \frac{COV_{a(x,y)}}{\sqrt{(Var_{a(x)})(Var_{a(y)})}} \quad (4)$$

Phenotypic correlation was estimated by Equation 5:

$$r_p = \frac{COV_{p(x,y)}}{\sqrt{(Var_{p(x)})(Var_{p(y)})}} \quad (5)$$

RESULTS

Fixed effects of post-larval age, sex, and tank environment

The average days from hatching to tagging of the 12 families was 77 d. A total of 950 tagged shrimps were measured, with an average ± SD of 3.92 ± 0.96 g for BW, 6.90 ± 0.60 cm for BL, 5.12 ± 0.46 cm for AL, 74.09 ± 0.92 for %AL and 0.56 ± 0.09 g/cm for BW/BL. Least squares means and standard errors for size traits at tagging age among groups of juveniles, with different days post hatch are presented in Table 1. Highly significant differences in body weight and length were was observed among the three age groups, in which the 76 d and 77 d post hatch groups were heavier than the 78 d post hatch group. Body length was larger for the 77 d post hatch group than that of the 76 d and 78 d post hatch groups, with juveniles in the 78 d post hatch group being the smallest.

At harvest, a total of 1,664 shrimp were measured, with an average ± SD of 18.70 ± 3.00 g for BW, 11.67 ± 1.14 cm for BL, 8.72 ± 1.03 cm for AL, 74.62 ± 1.85 for %AL and 1.60 ± 0.15 g/ cm for BW/BL. Least squares means and standard errors for harvest size among groups (121–125 d post hatch) are shown in Table 2. The 122 d post hatch group was significantly larger than those in other groups. Proportional traits, however, were similar across age groups. Least squares means and standard errors for harvest size under

Table 1 Least squares means and standard errors for size traits at tagging age with different days post hatch.

Traits	Days post hatch		
	76	77	78
BW (g)	3.95±0.05^{b**}	4.06±0.04^{b}	2.92±0.10^{a}
BL (cm)	6.91±0.03^{b**}	7.02±0.03^{c}	6.18±0.06^{a}
AL (cm)	5.11±0.02^{b*}	5.21±0.02^{c}	4.57±0.05^{a}
CL (cm)	1.79±0.01^{b*}	1.81±0.01^{b}	1.61±0.02^{a}
%AL	74.01±0.05^{a*}	74.18±0.04^{b}	73.89±0.10^{a}
%CL	25.99±0.05^{b*}	25.82±0.04^{a}	26.11±0.10^{b}
BW/BL (g.cm^{-1})	0.56±0.01^{b*}	0.57±0.01^{b}	0.46±0.01^{a}

BW = body weight; BL = body length; AL = abdominal length; CL = carapace length; %AL= percent tail length; %CL = percent carapace length; BW/BL = ratio of body weight to body length.
Values in the same row with the same letters do not differ significantly.
Significance was tested at the 95% level (shown as * in the table) and at 99% for highly significant comparisons (shown as ** in the table).

Table 2 Least squares means and standard errors for size traits at harvest.

Traits	Days post hatch				
	121	122	123	124	125
BW (g)	19.45±0.27^{a}	20.52±0.20^{b}	19.77±0.14^{a}	19.56±0.09^{a}	19.72±0.13^{a}
BL (cm)	12.14±0.06^{ab}	12.40±0.04^{c}	12.24±0.03^{b}	12.17±0.02^{a}	12.23±0.03^{ab}
AL (cm)	9.19±0.05^{a}	9.38±0.04^{b}	9.23±0.02^{a}	9.19±0.02^{a}	9.24±0.02^{a}
CL (cm)	2.95±0.02^{a}	3.02±0.02^{b}	3.00±0.01^{b}	2.98±0.01^{a}	2.99±0.01^{ab}
%AL	75.53±0.15^{a}	75.39±0.11^{a}	75.26±0.08^{a}	75.32±0.05^{a}	75.32±0.07^{a}
%CL	24.47±0.15^{a}	24.61±0.11^{a}	24.74±0.08^{a}	24.68±0.05^{a}	24.68±0.07^{a}
BW/BL(g.cm^{-1})	1.59±0.02^{a}	1.64±0.01^{b}	1.61±0.01^{a}	1.60±0.01^{a}	1.61±0.01^{a}

BW = body weight; BL = body length; AL = abdominal length; CL = carapace length; %AL= percent tail length; %CL = percent carapace length; BW/BL = ratio of body weight to body length.
Values in the same row with the same letters do not differ significantly.
Significance was tested at the 95% level.

different culture environments and between sexes are presented in Table 3. Shrimp reared in the net cage were significantly larger than those stocked in the concrete tanks. For example, in the net cage, mean ± SD body weight and length were 23.25 ± 0.16 g and 14.16 ± 0.04 cm, respectively, while those in the concrete tanks were 17.97 ± 0.09 g and 11.27 ± 0.02 cm (at a density of 50/m^2), and 18.20 ± 0.12 g and 11.27 ± 0.03 cm (at a density of 25/m^2), respectively. Between sexes, females were significantly larger than males for all size traits, except percent tail length.

Heritability, genetic and phenotypic correlation

Estimates of heritabilities and standard errors of weight and body size at 77 and 124 d post hatch are presented in Table 4. Heritabilities estimated at 77 d were high for BW, BL, AL, CL, and BW/BL (0.50 ± 0.19 to 0.60 ± 0.20), and moderate for %AL and %CL (0.24 ± 0.11). Heritabilities of all traits decreased from 77 to 124 d, with moderate values for BW, BL, AL, and BW/BL (0.34 ± 0.13 to 0.37 ± 0.14), low for CL (0.13 ± 0.06), and very low for %AL and %CL

Table 3 Least squares means and standard errors for size traits at harvest between environments and sexes.

Traits	Environment			Sex	
	CT (50/m^2)	CT (25/m^2)	NC	Male	Female
BW (g)	17.97±0.09^{a*}	18.20±0.12^{a}	23.25±0.16^{b}	19.47±0.10^{a**}	20.14±0.10^{b}
BL (cm)	11.27±0.02^{a*}	11.27±0.03^{a}	14.16±0.04^{b}	12.18±0.02^{a*}	12.28±0.02^{b}
AL (cm)	8.35±0.02^{a*}	8.35±0.02^{a}	11.03±0.03^{b}	9.22±0.02^{a*}	9.27±0.02^{b}
CL (cm)	2.91±0.01^{a*}	2.92±0.01^{a}	3.13±0.01^{b}	2.96±0.01^{a*}	3.02±0.01^{b}
%AL	74.14±0.05^{a*}	74.07±0.07^{a}	77.88±0.09^{b}	75.50±0.06^{b**}	75.23±0.06^{a}
%CL	25.86±0.05^{b*}	25.93±0.07^{b}	22.12±0.09^{a}	24.50±0.06^{a*}	24.77±0.06^{b}
BW/BL(g.cm^{-1})	1.59±0.01^{a*}	1.60±0.01^{b}	1.64±0.01^{c}	1.59±0.01^{a**}	1.63±0.01^{b}

CT = concrete tank; NC = net cage; BW = body weight; BL = body length; AL = abdominal length; CL = carapace length; %AL= percent tail length; %CL = percent carapace length; BW/BL = ratio of body weight to body length.

Values in the same row for the three Environmental variables with the same letters do not differ significantly.

Values in the same row for the two Sex variables with the same letters do not differ significantly.

Significance was tested at the 95% level (shown as * in the table) and at 99% for highly significant comparisons (shown as ** in the table).

Table 4 Heritability estimates and standard errors for size traits at tagging age and at harvest.

Traits	Heritability	
	Tagging age (77 d)	Harvest (124 d)
BW (g)	0.60±0.20	0.37±0.14
BL (cm)	0.54±0.19	0.34±0.13
AL (cm)	0.50±0.19	0.35±0.13
CL (cm)	0.59±0.20	0.13±0.06
%AL	0.24±0.11	0.05±0.03
%CL	0.24±0.11	0.05±0.03
BW/BL (g.cm^{-1})	0.58±0.20	0.34±0.13

BW = body weight; BL = body length; AL = abdominal length; CL = carapace length; %AL= percent tail length; %CL = percent carapace length; BW/BL = ratio of body weight to body length.

(0.05 ± 0.03). Estimates of heritabilities at 77 d showed a greater magnitude of standard errors than those estimated at 124 d.

Genetic and phenotypic correlations and standard errors of size at tagging age (77 d) are shown in Table 5. Genetic correlations were high between BW and BL (correlation coefficient, r = 0.99 ± 0.01), BW and AL (r = 0.91 ± 0.01), BW and CL (r = 0.97 ± 0.02), and BW and BW/BL (r = 0.99 ± 0.01). In addition, high genetic correlations were obtained between BL and AL (r = 0.99 ± 0.01), BL and CL (r = 0.96 ± 0.02), BL and BW/BL (r = 0.98 ± 0.02). Negative and low genetic correlations with high SE were observed for BW with %AL (r = -0.14 ± 0.35) and %CL (r = 0.14 ± 0.35). Further, the lowest negative correlation was obtained between %AL and %CL (r = -0.99 ± 0.01). Body weight showed very high phenotypic correlations with BL (r = 0.95 ± 0.01), AL (r = 0.91 ± 0.01) and CL (r = 0.92 ± 0.01), but a moderate correlation with BW/BL (r = 0.31 ± 0.01). Negative to near zero correlations were obtained between BW and %CL (r = -0.07 ± 0.07), and BW and %AL (r =

0.07±0.07). Similar to genetic correlation, the lowest negative phenotypic correlation with low standard errors was obtained between %AL and %CL (r = -0.99 ± 0.01).

Genetic and phenotypic correlations and standard errors of body weight and size at harvest (124 d) are presented in Table 6. The values of genetic correlations were similar to those obtained at tagging age, with BW highly correlated with BL (r = 0.98 ± 0.01), AL (r = 0.97 ± 0.02), CL (r = 0.94 ± 0.05), and BW/BL (r = 0.99 ± 0.01). Higher genetic correlations were obtained between BW/BL and AL (r = 0.95 ± 0.04) and between BW/BL and CL (r = 0.93 ± 0.06). Percent tail (%AL) showed moderate correlations and high standard errors with BW (r = 0.36 ± 0.32), BL (r = 0.43 ± 0.31), AL (r = 0.53 ± 0.27), and BW/BL (r = 0.35 ± 0.32). The high values of the standard errors were likely due to the effects of small sample size and high levels of variation between correlations of the traits. Percent carapace (%CL), however, displayed negative correlations with body weight and all size traits. Overall, phenotypic correlations of BW and other size traits (BL, AL, CL, and BW/BL) were lower (r = 0.59 ± 0.02 to 0.96 ± 0.01) than genetic correlations of BW with the same traits (r = 0.94 ± 0.05 to 0.99 ± 0.01).

DISCUSSION

Post larval age (days post hatch), sex and culture environments are always treated as

Table 5 Genetic (above the diagonal) and phenotypic (under the diagonal) correlations and standard errors between size traits at tagging age.

	BW	BL	AL	CL	%AL	%BL	BWBL
BW		0.99±0.01	0.91±0.01	0.97±0.02	-0.14±0.35	0.14±0.35	0.99±0.01
BL	0.95±0.01		0.99±0.01	0.96±0.02	-0.07±0.36	0.07±0.36	0.98±0.02
AL	0.91±0.01	0.99±0.01		0.94±0.04	0.03±0.36	-0.03±0.36	0.84±0.01
CL	0.92±0.01	0.92±0.01	0.85±0.02		-0.32±0.32	0.32±0.32	0.86±0.01
%AL	0.07±0.07	0.20±0.07	0.33±0.07	-0.21±0.07		-0.99±0.01	-0.17±0.35
%CL	-0.07±0.07	-0.20±0.07	-0.33±0.07	0.21±0.07	-0.99±0.01		0.17±0.35
BW/BL	0.31±0.01	0.91±0.01	0.84±0.01	0.86±0.01	0.01±0.07	-0.01±0.07	

BW = body weight, BL = body length, AL = abdominal length, CL = carapace length, %AL= percent tail length, %CL = percent carapace length, and BW/BL = ratio of body weight to body length.

Table 6 Genetic (above the diagonal) and phenotypic (below the diagonal) correlations and standard errors between size traits at harvest.

	BW	BL	AL	CL	%AL	%CL	BWBL
CL	0.92±0.01	0.92±0.01	0.85±0.02		-0.32±0.32	0.32±0.32	0.86±0.01
BW		0.98±0.01	0.97±0.02	0.94±0.05	0.36±0.32	-0.36±0.32	0.99±0.01
BL	0.92±0.01		0.99±0.01	0.92±0.06	0.43±0.31	-0.43±0.31	0.97±0.02
AL	0.89±0.01	0.94±0.01		0.86±0.10	0.53±0.27	-0.53±0.27	0.95±0.04
CL	0.59±0.02	0.69±0.02	0.40±0.03		0.02±0.38	-0.03±0.38	0.93±0.06
%AL	0.07±0.03	-0.00±0.03	0.34±0.03	-0.72±0.02		-0.99±0.01	0.35±0.32
%CL	-0.07±0.03	0.00±0.03	-0.34±0.03	0.72±0.02	-0.99±0.01		-0.35±0.32
BW/BL	0.96±0.01	0.82±0.02	0.80±0.02	0.49±0.03	0.12±0.03	-0.12±0.03	

BW = body weight, BL = body length, AL = abdominal length, CL = carapace length, %AL= percent tail length, %CL = percent carapace length, and BW/BL = ratio of body weight to body length.

fixed effects for estimating quantitative genetic parameters in crustaceans (Argue *et al*., 2002; Pérez-Rostro and Ibarra, 2003a; Kenway *et al*., 2006; Castillo-Juárez *et al*., 2007). Argue *et al*. (2002) found that age effects were correlated with the harvest weight and weight gain in white shrimp. Similarly, significant fixed effects of post larval age on weight and body length were observed at tagging age (76–78 d) and harvest (121–125 d) in the present study. For white shrimp, it is difficult to obtain a large number of families on the same day. Castillo-Juárez *et al*. (2007) reported in their study that it took 23 d to produce 101 full-sib families. In the present experiment, the production of 20 families was completed in 4 d.

Pond and tank environments, including density, pond type, culture site and system, were found to have significant effects on shrimp growth. The results in the present study suggested that weight and body size at harvest significantly differed between the grow-out sites and rearing conditions. Despite a higher density (100 /m^2), the shrimp reared in a net cage in Rayong province had a larger size at harvest than those reared at the lower densities (50 and 25 shrimp/m^2) in the concrete tanks in Chon Buri province. There was no genotype-environment interaction among tanks and the net cage according to similar rankings of families between the environments (data not shown). Significant differences in body weight were likely due to the effects of the bio-floc system used in the pond. Microbial flocs might provide additional food source for shrimp in the net cage. When compared between different culture systems, Argue *et al*. (2002) observed higher growth rates and survival of shrimp reared in a raceway tank than those in a round pond. In addition to different pond type, high and low stocking densities were found to have significant effects on the estimates of heritability for adult body weight (Ibarra and Famula, 2008). Significant environmental effects and density on growth and survival of white shrimp were further demonstrated by Gitterle *et al*. (2005) and Castillo-Juárez *et al*. (2007).

Female white shrimp are typically larger than males of the same age. Chow and Sandifer (1991) reported that sexual dimorphism was observed at an average weight of 13–15 g. Similar to the report by Pérez-Rostro *et al*. (1999), the females (18.09 g) were larger than males (16.96 g) at day 160 and at harvest, the females were 4.5% heavier than males (Gitterle *et al*., 2005). In the present study, females were highly significantly heavier than males (20.14 and 19.47 g) and displayed a greater weight and body length ratio (1.63 and 1.59 g/cm) that was also highly significant. Males, however, had a greater percent tail length (75.5 and 75.23%) that was highly significant, which was consistent with the report by Argue *et al*. (2002). Moss and Moss (2006) suggested that sexual growth dimorphism in white shrimp may be attributed to a physiological advantage of the females, including higher feed conversion efficiency and better food utilization.

Heritability estimates of weight and body size at a specific age in white shrimp varied from high to low (more than 1.0 to 0.15), depending on the experimental designs, the estimation methods used and the population size. In the study by Pérez-Rostro *et al*. (1999), the estimates of heritability using the REML procedure were lower than those estimated by ANOVA. For example, the REML estimates of heritability were 0.6 ± 0.20 for BW and 0.54 ± 0.19 for BL at 68 d (3.9 g), whereas the ANOVA estimates were very high, with 0.84 ± 0.17 for body weight and 0.86 ± 0.18 for length at 58 d (4.2 g). The large heritability estimates were likely due to the effects of separate rearing of post larvae prior to tagging and the varied stocking density among families caused by the early mortality (Pérez-Rostro *et al*., 1999). These effects increased the variation between families. As a result, an upwardly biased estimation of heritabilities was obtained for the traits. When using the REML method, the estimates of heritability from the 27 full-sib

families were low for body weight (0.2 ± 0.17) and length (0.15 ± 0.16) at 17 wk (average body weight of 2.7 g; Pérez-Rostro and Ibarra, 2003b). The use of covariate analysis in their study to correct for early different densities decreased variation between families, resulting in low heritability estimates. In contrast, failure to adjust for different rearing densities among full-sib families and the effects of separate cage rearing resulted in large estimates of heritability for weight (0.84 ± 0.17) and body length (0.86 ± 0.18; Pérez-Rostro *et al*., 1999).

Generally, common environmental effects on heritability estimation can be reduced by stocking tagged animals in the same ponds or tanks. Results showed that the heritabilities of all traits decreased from age at tagging (an average of 77 d) to age at harvest (an average of 124 d), when shrimp were stocked in the same tanks. Estimates of heritability for size at harvest were moderate for BW, BL, AL and BW/BL, with values ranging from 0.34 ± 0.13 to 0.37 ± 0.17, and were similar to those obtained for 29 wk old shrimp (14.57 g), with values of 0.34 ± 0.18 for BW and 0.28 ± 0.18 for BL (Pérez-Rostro and Ibarra, 2003b). The heritability estimates obtained in the study by Pérez-Rostro and Ibarra (2003b) were also were comparable to those reported for *P. monodon* (0.32 ± 0.13) at a similar age of 32 wk (Coman *et al*., 2010), but were lower than the REML estimates (0.55 ± 0.07) for the body weight of tiger prawn at 30 wk (Kenway *et al*., 2006). The heritability estimates from the present study, however, were larger than those obtained under standard commercial conditions, with a large number of full- and half-sib families. Gitterle *et al.* (2005) reported that the REML estimates of heritability for the harvest size of two selected lines of white shrimp were 0.17 ± 0.04 and 0.24 ± 0.05. The use of 430 full-sib families (with 204 paternal half-sib families) and the application of the animal model resulted in the highly accurate estimates of heritability reported in their study.

Heritability is a property of the population, which can change with selection and age. It is not valid to use the heritabilities estimated in wild populations or commercial selected lines for making selection decisions in different populations (Gitterle *et al.,* 2005). Furthermore, the heritability estimates at an early developmental stage should not be used for selection at an adult age. In the present study, estimates of heritability at tagging size were higher with large standard errors than those at harvest size. The decision as to which traits to choose for improvement should be based on the more reliable heritability estimates. In the present study, there were four traits that had similar heritability and standard errors—namely, BW, BL, AL and BW/BL.

Genetic correlation is particularly important in a breeding program, which provides a more accurate prediction of breeding values (Kolstad, 2005). Correlations were high between body weight and size traits, including BL, AL and CL at tagging age and harvest, ranging from 0.91 ± 0.01 to 0.95 ± 0.01 for phenotypic correlation, and from 0.91 ± 0.01 to 0.99 ± 0.01 for genetic correlation. However, the phenotypic correlation between BW and BW/BL was low (0.31 ± 0.01) at tagging age, but was high (0.96 ± 0.01) at harvest. Correlations obtained in the present study were consistent with those reported in other studies (for example, Pérez-Rostro *et al*., 1999; Pérez-Rostro and Ibarra, 2003b). High correlations between body weight and size traits at harvest suggested that genetic improvement of BW would cause improvement of these size traits simultaneously. For instance, improved tail length, which is considered an important trait for shrimp processors, can be achieved through selection for increased body weight.

CONCLUSION

The present study demonstrated that

unbiased estimates of genetic parameters could be obtained using a small experimental dataset (12 full-sib families), with complete pedigree records. The genetic parameters estimated for size at harvest by mixed-model techniques in this study were comparable to those reported for larger commercial experiments (150 to 400 families). The accuracy of the heritability estimates increased at harvest (124 d) where individuals were tagged to allow mixing of families, thus minimizing the influence of environmental effects. The overestimation of heritability at tagging age (77 d) with a greater magnitude of standard error was due to the common environmental effect of full-sib families. The observations of moderate heritabilities for weight, body length and body ratios indicated selection potential for these traits. Moreover, strong positive genetic correlations between these traits suggested that selection for increased body weight would be an efficient way to improve tail length in the white shrimp population in this study.

ACKNOWLEDGEMENTS

The authors would like to thank the shrimp hatchery in Chon Buri province for providing the white shrimp broodstock and facilities. Comments from anonymous reviewers are also acknowledged.

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