

Heritability for body weight at harvest size in the Pacific white shrimp, *Penaeus (Litopenaeus) vannamei*, from a multi-environment experiment using univariate and multivariate animal models

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Abstract

To estimate family BLUP breeding values and the heritability of body weight at harvest size (BW) in the Pacific white shrimp, *Penaeus (Litopenaeus) vannamei*, an experiment was conducted using information from two farm units of a Mexican hatchery and two shrimp population densities at each location. Data consisted of 12,658 shrimps that were siblings from 48 sires and 77 dams with a nested dam–sire structure. Shrimps were individually weighed at an average age of 130 days post-hatching. BW phenotypic mean (S.D.) was 18.2 (2.4) g, with values ranging from 8.4 to 30.0 g. Data were analyzed using univariate and multivariate models that considered BW within location by density pond environment as a different trait and included or not a common full-sib effect (*c*). The multivariate animal model included fixed effects of days from hatching and sex. For univariate models that included *c* effects, BW heritability (S.E.) estimates ranged from 0.24 (0.14) to 0.35 (0.18) across environments (heritability was zero in one environment). For multivariate models (excluding the environment with zero heritability) the heritabilities increased and ranged from 0.37 (0.06) to 0.45 (0.09). Standard errors of heritabilities and *c* effects were both drastically reduced in the multivariate analysis. Pairwise genetic correlations between environments were from 0.80 (0.08) to 0.86 (0.04). These differences may be indicative of genotype–environment interaction for BW at 130 days post-hatching. Statistical problems found to separate *c* from additive genetic effects both in univariate models were reduced using multivariate models. Correlation between family raw phenotypic means and family BV means from the multivariate analysis was 0.93 indicating a rather low risk of miss selecting superior families if BLUP solutions were neglected using replicated environment data. It is also concluded that use of incorrect statistical models or unreplicated data may lead to biased or inaccurate estimates of genetic parameters in shrimp breeding programs.

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Keywords: Shrimp breeding; Pacific white shrimp; *Penaeus (Litopenaeus) vannamei*; BLUP; Family selection; REML; Multivariate animal models

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1. Introduction

The development and application of selective breeding programs is becoming an increasingly important strategy for increasing the economic efficiency of farmed shrimp (Argue et al., 2002; Pérez-Rostro and Ibarra, 2003b; Gitterle et al., 2005a,b). Until recently, most breeding programs in the aquaculture industry were based on ad-hoc methodologies based on mixtures of individual and family raw data, mainly because individual identification was not feasible and mixing families in performance tests was not possible. However, methods for tagging individuals are now available (e.g., Arce et al., 2003) permitting mixed model techniques, commonly used for years in farm animals, to be applied in fish and shrimp breeding programs (Bolívar and Newkirk, 2002; Gall and Bakar, 2002; Gitterle et al., 2005a,b). Mixed models are very flexible and can be used for unbiased estimation of genetic parameters and breeding values under a range of different situations. Most of the published genetic parameters and mean family breeding values in shrimp farms have been estimated using simple regression (Hetzl et al., 2000) and ANOVA procedures (Benzie et al., 1997; Argue et al., 2002). Mixed model analysis has also been recently used; one with a large data set coming from commercial conditions (Gitterle et al., 2005a) and another using a smaller data set from experimental conditions (Pérez-Rostro and Ibarra, 2003a).

Using mass and family selection techniques in aquaculture have proven to be effective and some results show an increase of body weight from 9 to 14% in selected shrimp populations compared to wild shrimp in only three generations (Preston et al., 2004). Another study showed that a line selected for growth was 21% larger than the unselected control line after only one generation (Argue et al., 2002).

We conducted a multi-environment experiment with the following objectives: a) to estimate the heritability of body weight at harvest size (BW) in the Pacific white shrimp, *Penaeus (Litopenaeus) vannamei*, using univariate and multivariate animal models; b) to estimate genetic correlations between environments and c) to estimate correlations of full-sib family best linear unbiased predicted (BLUP) breeding values means for BW with BW family raw phenotypic means.

2. Materials and methods

2.1. Broodstock selection

The study was carried out in two shrimp farm units from a Mexican hatchery, one located in Pozos, Sinaloa, and the other in Guasave, Sinaloa, both in the northwest of Mexico. A large

number of the procedures were performed according to the commercial hatchery management practices. By the end of October 2003 the broodstock were selected from two Pozos ponds that had been stocked with post-larvae coming from the 2002 family selection program. These families originally came from a mass selection program that started in 1998 in which wild shrimp from Sinaloa, Mexico, and domesticated shrimp from Venezuela, Colombia, Florida and Ecuador had been incorporated.

Using body weight as the criterion, the top 30% of the females and top 15% of the males were selected. Selected shrimp were individually tagged using numbered rings placed on one ocular peduncle. The broodstock were stocked into maturation tanks at a density of eight shrimp/m², with males and females placed in separate tanks. Maturation tank dimensions were 12 × 3 m with a water column of 0.35 m, kept at 28–29 °C, with a salinity of 34 ppt and a daily water exchange rate of 400%. They were fed with commercial pellets containing 35 to 40% protein. After 14 to 21 days to let the shrimp adapt to this new environment, and in order to accelerate the gonad maturation process, unilateral ocular ablation in females was performed.

2.2. Production of families

Mature and ready to spawn female breeders were artificially inseminated using one male for every two females to produce full- and paternal half-sib families. Family origin was considered to avoid mating between sibs. These inseminated females were moved to individual spawning tanks where they spawned after 1 to 4 h. Their eggs were then collected in 10-l tanks, washed with iodine and placed back in the spawning tanks where they hatched with strong aeration conditions after 8–9 h. Originally 108 females and 54 males were used, but they only yielded 101 families. A record for every family included body weight of the male and female, number of obtained eggs and nauplii, as well as the number of nauplii cultured to growth.

2.3. Larvae culture

The larvae culture of every family and the control shrimp from the production area was done in 500-l tanks keeping one family per tank, using the regular procedures from the hatchery including a mixed diet of *Chaetoceros* sp., *Artemia* sp. and commercial larval diets. The initial density was 80 nauplii/l. Post-larvae were reared to the PL-5 stage, then counted to get survival estimates by weighing total biomass and counting the number of post-larvae in one gram. When post-larvae reached the PL-15 stage they were harvested to obtain total biomass, survival and mean weight. Post-larval rearing densities were adjusted to 1 post-larvae/l per tank. Post-larvae were then reared in the same tanks until they were around 1 to 3 g (averaging 2.54 g) and 70 to 90 days post-hatching. This size allowed us to tag them individually.

2.4. Tagging

Shrimp were injected with a colored elastomer tag (Northwest Marine Technology) to identify full-sib families. Two different tags per shrimp were injected using four different

colors (green, orange, purple and yellow) and five anatomical areas (second left and right abdominal segments, sixth left and right abdominal segments, and sixth dorsal abdominal segment). A total of 450 shrimps per family were tagged. This tagging identification allowed mixing of families in the ponds for performance evaluation.

2.5. Experimental design and stocking procedures

Once the shrimps were tagged they were stocked in four different ponds, two in the broodstock farm unit in Pozos (southern Sinaloa) and two in the broodstock farm unit in Guasave (northern Sinaloa). These two places were used in order to have different management environments. The dimensions of Pozos' ponds were 0.22 ha (47×47 m) with a column of water of 1.4 m. Water temperature ranged from 30 to 34 °C, and salinity ranged from 30 to 35 ppt. The dimensions of Guasave's ponds were 0.5 ha (100×50 m) with a column of water of 1.0 m. Water temperature ranged from 30 to 36 °C, and salinity ranged from 22 to 28 ppt. Feeding regimen in all ponds consisted of commercial pellets containing 35 to 40% protein. Originally, approximately the same number ($n=450$) of post-larvae from the 101 full-sib families were seeded in these four ponds. Two different densities were also used in both farm units (9.1/m² and 14.8/m² of tank floor). This experiment design allowed us to evaluate every family in every environment to obtain better estimates of the heritability and the mean family predicted breeding values for BW.

In addition, shrimp from both farm units of the hatchery, about a week of age younger than the tagged shrimp and with a mean body weight of 1 g, were used as a control group. The inclusion of the control shrimp allowed us to compare the stocks produced from mass selection procedures in the hatchery with those produced from the new family selection procedures performed the previous year to the experiment. These younger shrimp from the control group were also used to adjust the stocking densities in the experimental ponds.

2.6. Growth and harvest

During the growth period, the regular management practices in the two farm units were performed. These conditions are those mentioned for the experimental ponds regarding temperature, salinity and feeding regimen. The growth period lasted from 52 to 56 days. At this time the shrimps were harvested and individually weighed. Family origin and sex was identified and their condition was examined to check for individuals that were dead, molting, flaccid, or with evident deformities. Days from hatching to weighing ranged across families from 122 to 145 d with an average of 130 d. These differences (23 days to produce the 101 full-sib families) were related to management practices associated with the percentage of females ready to spawn per day. Six hundred forty non-tagged control shrimps from the four ponds were also weighed to obtain an estimate of their mean body weight at harvest. Management problems were reported in Guasave, particularly in the higher density pond. These problems caused a reduced survivability (21.8%), increased tagging code misidentification (non-existing codes were reported) (16.1%) and lack of sex identification (0.8%).

2.7. Data edit

Dead shrimp (5.1%) and those with clear deformities (3.6%) were excluded from the genetic analysis. Percentage of dead and percentage of deformities were independent of family origin ($\chi^2_{101 \text{ d.f.}, 0.05}$). Shrimps lacking sex identification (0.1%) in the database or with family misidentification (7.3%) for different kind of typos like with BW>77.0 g (14 shrimp), reported with non-existing or duplicated codes (i.e., six sires were wrongly reported to have sibs with four dams each) were also excluded. It is important to mention that there were shrimp with more than one reason for exclusion (i.e., death, with deformities, lacking of sex identification, etc.). All these reasons led us to exclude a large number of shrimps, including all the full-sibs from 24 families. Final database consisted of 12,658 shrimp from 77 families, sibs from 48 sires and 77 dams. The number of records per family in the complete data set, farm unit, density, and farm unit by density pond are shown in Table 1.

2.8. Statistical and genetic analysis

Four different approaches were used to estimate variance components, heritability for body weight at harvest, and to predict the breeding values for all shrimps using mixed model methodology and restricted maximum likelihood (REML) methods with ASREML software (Gilmour et al., 2002): (1) a univariate animal model; (2) a univariate animal model with a common full-sib effect (c); (3) a multivariate animal model and (4) a multivariate animal model including correlated c effects within environments, where BW within farm unit by density pond environment was considered as a different trait. As only one generation of pedigreed data was available for analysis, the animal model including c effects is equivalent to a model with sires and dams nested within sires. Models (1) and (2) were applied to the whole data set and separately to each environment. Models included the significant ($P<0.05$) fixed effects of days post-hatching (as a covariate), sex (models 1 to 4), farm-unit-population density (models 1 and 2), as well as the animal

Table 1
Number of records per family in the complete data set, farm unit, density, and farm unit by density pond datasets

Data set	Number of full-sib families	Number of records per family		
		Mean	S.D.	Total
Complete	77	164.3	62.5	12658
Farm unit Pozos and lower density	77	73.9	26.1	5692
Farm unit Pozos and higher density	77	66.9	35.1	5155
Farm unit Guasave and lower density	69	15.1	10.5	1045
Farm unit Guasave and higher density	67	11.4	8.1	766

S.D.: standard deviation.

additive genetic effect and the residual as random effects (models 1 to 4). The covariate days post-hatching was included in the model in order to avoid overestimation of the animal genetic variance. A test statistic for comparing models, particularly to test for the existence of an effect common to full-sibs (a combined effect of tank environment, non-additive genetic and maternal effects) variance was obtained by computing twice the difference in log likelihoods between a complete model, where the variance common to full sibs is freely estimated, and a reduced model where it is constrained to be zero: the likelihood ratio statistic = $2(\log(lc) - \log(lr))$, where lc is the likelihood for the complete model and lr is the likelihood for the reduced model (e.g., Birkhead et al., 2005). This likelihood ratio statistic (LRT) is compared with a χ^2 distribution with one degree of freedom using a one-tailed region of rejection. This test was also used to compare the univariate animal model (with 3 (co) variances) versus the multivariate animal model (with 15 (co) variances, six for genetic, six for common environment and three for residual, since only three environments were considered in the final analysis) with a χ^2 distribution with 12 degrees of freedom. In matrix notation, the model used was:

$$Y = X\beta + Z_1u + Z_2c + e,$$

where

- Y vector of observations (body weight),
- β is the unknown vector of fixed effects,
- u is the unknown vector of random animal additive genetic effects, $u \sim N(0, \sigma^2_u A)$,
- c a random effect common to full-sibs (a combined effect of tank environment, non-additive genetic and maternal effects), $c \sim N(0, \sigma^2_c I)$,
- e is the vector of residual environmental random effects, $e \sim N(0, \sigma^2_e I)$,

X , Z_1 and Z_2 are known incidence matrices relating observations to fixed effects (sex, days post-hatching, location and density in the univariate approaches, or sex and days post-hatching in the multivariate approach), animal genetic effects and effects common to full-sibs other than additive genetics, respectively.

Assuming normality, we have

$$\begin{bmatrix} Y \\ u \\ c \\ e \end{bmatrix} \sim N \left(\begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} V & Z_1G & Z_2C & R \\ GZ_1' & G & 0 & 0 \\ CZ_2' & 0 & C & 0 \\ R & 0 & 0 & R \end{bmatrix} \right),$$

with $V = \text{var}(Y) = Z_1GZ_1' + Z_2CZ_2' + R$,

- G $gA = \text{var}(u)$, the genetic (co)variance matrix ($gA = \sigma^2_u A$),
- C $\text{var}(c)$, the full-sib common effects (co)variance matrix ($C = \sigma^2_c I$), and

$R = \text{var}(e)$, the residual effects (co)variance matrix ($R = \sigma^2_e I$).

Where g represents the additive genetic variance and A is the additive genetic relationship matrix among all the shrimps in the pedigree file. Pedigree file included full- and half-sib relationships but excluded relationships among their parents since they were unknown.

In the multivariate approach, body weight within environment was considered as a different trait and environmental covariances were restricted to zero. If we define G_o as the symmetric matrix containing variances of $(\sigma^2_{u_j})$ and covariances $(\sigma_{u_j u_k})$ among the animal effects for the four traits, then

$$\text{Var} \begin{bmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \end{bmatrix} = \begin{bmatrix} \sigma_{u_{11}}^2 & \sigma_{u_{12}} & \sigma_{u_{13}} & \sigma_{u_{14}} \\ & \sigma_{u_{22}}^2 & \sigma_{u_{23}} & \sigma_{u_{24}} \\ & & \sigma_{u_{33}}^2 & \sigma_{u_{34}} \\ \text{Symm} & & & \sigma_{u_{44}}^2 \end{bmatrix} \otimes A = G_o \otimes A = G,$$

where u_j is the vector of animal effects for the j th trait, while \otimes stands for the Kronecker product.

Based on the animal models, heritabilities were estimated as:

$$h^2 = \sigma_u^2 / (\sigma_u^2 + \sigma_e^2).$$

Genetic correlations among the BW within farm unit by density pond environment were calculated using the multivariate animal model as:

$$r_{u_{ij}} = \sigma_{u_{ij}} / (\sigma_{u_{ii}} \cdot \sigma_{u_{jj}})$$

For the univariate approach, mean family predicted breeding values were obtained as $1/2u_s + 1/2u_d$, where u_s and u_d are the estimated breeding values of the sire and the dam of every family, respectively, obtained from the solutions for the animal effects in the above mentioned animal models (Gilmour et al., 2002). For the multivariate approach and for ranking families in the selection program, mean family predicted breeding values were treated as an index giving the same economic weight to each environment and hence obtained as the simple average of the within-environment mean family predicted breeding values.

Since family selection is an important component for the shrimp industry genetic programs (Gjedrem, 2005), families were ranked using BW phenotypic means and using BW predicted breeding value means based on BLUP solutions. Spearman rank correlations and Pearson correlations between family phenotypic means and family breeding value means were also calculated.

BW least square mean from control group shrimp was compared to BW least square mean from the 77 families to roughly evaluate the effect of the selection program (comparing 2002 versus 2003 shrimp populations). This was done using a linear model and by adjusting for differences in age of the shrimps at harvest and the significant fixed effects already mentioned.

3. Results

BW means for sex, farm unit, density, and farm unit by density ponds are shown in Table 2. Overall BW phenotypic mean (S.D.) was 18.2 (2.4) g. Family BW means ranged from 15.5 to 22.5 g. Females were 0.50 g heavier (2.82%) than males ($P < 0.001$) which is consistent with other studies (Chow and Sandifer, 1991; Hansford and Hewitt, 1994; Argue et al., 2002; Pérez-Rostro and Ibarra, 2003a; Gitterle et al., 2005a). Farm unit–density environments differed in BW means ($P < 0.05$), with least square means that ranged from 17.0 to 19.5 g (Table 2). Higher density environments had lower BW mean than the corresponding lower density ones.

Heritabilities and c estimates within environment based on the univariate approach are presented in Table 3, while those obtained based on the multivariate animal model approach are shown in Table 4. Univariate analysis within environment without c effects in the model showed important differences among estimates, particularly with a very low heritability for the Guasave farm unit and higher density environment. When c effects were included in these univariate models, the heritability for Guasave farm unit and higher density was equal to zero.

The univariate approach for the complete data set when common environment and non-additive genetic effects were excluded from the model resulted in a BW heritability (S.E.) of 0.45 (0.06), and in 0.47 (0.06) when the Guasave farm unit and higher density environment was excluded. The inclusion of c effects in the model reduced the heritability estimate (S.E.) to 0.27 (0.16) and c (S.E.) was 0.07 (0.07) but the c effect

Table 2

Number of records, mean, standard deviation (S.D.), coefficient of variation (C.V), minimum and maximum for body weight in grams at 130 days post-hatching in the complete data set, as well as by sex, and farm unit by density pond

Data set	Number of Records	Mean	S.D.	C.V.	Min	Max
Complete	12,658	18.2	2.4	13.0	8.4	30.0
Excluding farm unit Guasave and higher density	11,892	18.2	2.4	13.0	9.5	30.0
<i>Sex</i>						
Males	6425	18.0 ^a	2.3	12.6	8.4	29.8
Females	6233	18.5 ^b	2.5	13.3	10.0	30.0
<i>Environment</i>						
Farm unit Pozos and lower density	5692	19.5 ^a	2.2	11.3	15.5	30.0
Farm unit Pozos and higher density	5155	17.0 ^c	1.8	10.9	9.5	29.6
Farm unit Guasave and lower density	1045	18.4 ^b	1.9	10.6	10.2	25.1
Farm unit Guasave and higher density	766	18.0 ^b	2.3	12.7	8.4	29.3

Based on the univariate analysis, means (least square means) within fixed effect with different letter are statistically different ($P < 0.05$).

Table 3

Heritability (h^2) and a combined non-additive genetic with common environment effect (c) estimates for body weight at 130 days post-hatching in *Penaeus (Litopenaeus) vannamei* for the complete data set and for within farm unit by density pond environment, using univariate animal models*

Data set	Model 1		Model 2		c	S.E.
	h^2	S.E.	h^2	S.E.		
Complete	0.45	0.06	0.27	0.16	0.07	0.07
Excluding farm unit Guasave and higher density	0.47	0.06	0.33	0.17	0.08	0.06
Farm unit Pozos and lower density	0.48	0.06	0.35	0.18	0.06	0.08
Farm unit Pozos and higher density	0.43	0.06	0.24	0.14	0.08	0.08
Farm unit Guasave and lower density	0.50	0.10	0.32	0.23	0.08	0.11
Farm unit Guasave and higher density	0.15	0.08	0.00	0.00	0.13	0.03

* Model 1 excluded the c effect. Both models included the fixed effects of sex, and age. Complete data set analysis included also farm unit by density pond environment as a fixed effect.

S.E.: standard error.

inclusion was not significant ($P > 0.15$). When the multivariate animal model was used, heritabilities remained variable and with convergence problems related to Guasave farm unit and higher density environment which had a heritability essentially equal to zero or out of the parameter space (negative values), regardless of the inclusion or not of the c effect in the model. Based on these results and in the mentioned problems in Sections 2.6 and 2.7, regarding Guasave farm unit and higher density quality data, a new analysis excluding these data subset was made.

Comparison between the univariate animal model that excluded the Guasave and higher density environment and the corresponding multivariate animal model, based on LRT, was significant ($P < 0.001$). The inclusion of the c effects in this multivariate model reduced the magnitude of BW heritabilities

Table 4

Heritability (h^2) and a combined non-additive genetic with common environment effect (c) estimates for body weight at 130 days post-hatching in *Penaeus (Litopenaeus) vannamei* using a multivariate animal model

Data set	Model 1		Model 2		c	S.E.
	h^2	S.E.	h^2	S.E.		
Farm unit Pozos and lower density	0.49	0.07	0.43	0.07	0.02	0.001
Farm unit Pozos and higher density	0.46	0.07	0.37	0.06	0.03	0.001
Farm unit Guasave and lower density	0.52	0.09	0.45	0.09	0.03	0.001

Model 1 excluded the c effect. Both models included the fixed effects of sex, and age.

S.E.: standard error.

Table 5

Genetic correlation estimates (and their standard errors) among BW at 130 days post-hatching for *Penaeus (Litopenaeus) vannamei* within farm unit by density pond environments using a multivariate animal model that includes the *c* effect

Environment	Farm unit Pozos and higher density	Farm unit Guasave and lower density
Farm unit Pozos and lower density	0.86 (0.04)	0.83 (0.07)
Farm unit Pozos and higher density		0.80 (0.08)

estimates and using LRT was also significant ($P < 0.001$). Genetic and phenotypic correlations among farm unit by density ponds BW from multivariate analysis are presented in Table 5.

BW family breeding value means from multivariate analysis ranked from -2.07 to 2.15 g. The Spearman rank correlation and the Pearson correlation between raw family phenotypic means and family predicted breeding values from multivariate analysis were both 0.93.

The BW least square mean of the shrimp coming from mass selection that was used as a control group was 1.45 g lighter (8.0%) ($P < 0.01$) than the BW least square mean from the 77 families representing the new generation of brood stock shrimp where a combined family and within family selection was performed the previous year to this experiment.

4. Discussion

To our knowledge, our heritability estimates for BW are the first ones obtained based on a factorial designed experiment, with a large data set, and using a multivariate animal mixed model methodology (preliminary results based on the univariate approach were presented by Castillo-Juarez, 2004). Heritabilities within farm unit by density pond environment based on the univariate approach, with the exception of Guasave higher density environment, were relatively similar across environments whether *c* was included in the model or not. Some reduction in heritabilities with the presence of *c* in the model was observed. On the other hand, *c* estimates were low but significant (LRT., $P < 0.01$) and remained nearly the same across farm unit by density pond environments (Table 3). The observed differences between h^2 estimates across the four environments led us to consider an analysis using a multivariate animal model approach, where BW within farm unit by density pond environment was considered as a different trait.

As it was mentioned, this multivariate animal model had convergence problems related to Guasave farm unit and higher density. Reasons for convergence problems might be related to low quality data in the conflicting

environment and/or genotype by environment interaction effect. For this reason we decided to run a multivariate analysis excluding the data from Guasave farm unit and higher density. The exclusion of this environment had no effects on the overall mean and the standard deviation for BW (Table 2). Our nested structure with only two dams per sire did not allow us to separate the spawning tank effect from the dam effect but models excluding *c* lead to over-estimation of heritabilities for additive direct effects. An interesting finding was that the *c* estimates were close to zero across farm unit by density pond environments (Table 4) and heritabilities for the three remaining environments were more similar, higher and with lower standard errors. Likelihood ratio test showed an important difference between the multivariate animal model that included the *c* effect and the one that excluded it ($P < 0.001$). This indicated that the *c* effects are important at 130 d post-hatching and showed that although the estimated *c* effects were very small (0.02 to 0.03), models that excluded them overestimated heritabilities. Based on log-likelihood values, results showed too that the multivariate animal model approach fitted the data better than the univariate one and that *c* effects can be reduced by replicating the families in several environments (i.e., with different density, salinity, temperature and management practices), which is similar to Maluwa et al. (2006) findings in Tilapia.

These results are also evidence of some heterogeneity of genetic variability for BW at 130 days post-hatching. But the degree of this heterogeneity is greatly reduced using a multivariate approach and excluding the Guasave farm unit and higher density environment. They show that the selection for BW will yield different genetic gain depending on environment, similar to what has been observed for other yields in farm and aquatic animals (Castillo-Juarez et al., 2000; Castillo-Juarez et al., 2002; Coman et al., 2002; Maluwa et al., 2006; Saillant et al., 2006). Consistently with these genotype by environment effects, genetic correlations among farm unit by density pond environments BW ranged from 0.80 to 0.86 (Table 5) and the approximate upper confidence interval limits of these genetic correlations differed from 1.0. Relatively high genetic correlations between environments indicate that there is no evidence for “true” genotype by environmental interactions (Montaldo, 2001), but results from unreplicated assays for BW in shrimp might be confounded with the environmental conditions and *c* effects. In the multivariate model analysis *c* effects were highly correlated between environments ranging from 0.93 to 0.94 in this study, which may indicate that common effects arising from group rearing of full sibs (i.e., tank effects) may be important up to 130 days post-hatching for BW in shrimp.

The number of published results on genetic parameters for body weight in *P. vannamei* is not large. Our multivariate heritability estimates (0.37 to 0.45, averaging 0.42) are larger than REML estimates of 0.17 ± 0.06 (Pérez-Rostro and Ibarra, 2003a), and in the range when compared to 0.20 ± 0.17 (Pérez-Rostro and Ibarra, 2003b), $0.20 \pm .04$ to 0.21 ± 0.04 (Gitterle et al., 2005b), and 0.24 ± 0.05 (Gitterle et al., 2005a), although smaller than those found by Argue et al. (2002) from 0.71 ± 0.15 to 0.84 ± 0.43 and Pérez-Rostro et al. (1999) from 0.89 ± 0.18 to values like 1.32 ± 0.18 . The latter estimate out of the parameter space (i.e., with $h^2 > 1$), probably because of confounded maternal and cage effects and the use of ANOVA related techniques. Our heritability estimates are larger than most of the published results. This may be due, at least partially, to the mixed origin of our 1998 base population. In any case, differences in the magnitude of the published heritability estimates may also arise from the number of selected generations, the kind of selection program (familiar, mass, etc.) and the selection intensity applied in the different breeding programs of the populations analyzed. Proportionally, the standard errors of our heritability estimates are smaller than all the others found in the literature. This may be due not only to the relatively large number of full sibs per family involved (Table 1), but to the multivariate animal model methodology and the breeding structure (full and half sibs) of our experimental design used to estimate them.

The sharp reductions in heritabilities with the inclusion of the *c* effects in within-environmental effects might indicate a confounding effect between additive and non-additive genetic and maternal effects included in *c*, similarly to what has been observed in salmon (Rye and Mao, 1998; Martínez et al., 1999). In disagreement with Argue et al. (2002) who found no evidence for maternal genetic (nor non-additive genetic) effects for this trait, our univariate and multivariate animal model results (very small although significant *c* combined effects) are consistent with those presented by Gitterle et al. (2005a). These authors, using an animal model methodology, also found a small, although significant, influence of maternal effects that were confounded with non-additive genetic effects, when analyzing data yield under standard commercial conditions, indicating that either one or both of these genetic effects might exist for body weight in shrimp, in some environmental production conditions.

The lower BW least square mean of the shrimp coming from mass selection and used as a control group when compared to the BW least square mean from the 77 families representing the new generation of breed stock shrimp (1.45 g) indicates that the breeding program is yielding important results. In any case, this difference is

not a clean estimate of the genetic gain, since differences in age between the two populations may be were not properly adjusted by the simple linear model used.

5. Conclusions

Our heritability estimates for BW are the first ones obtained for a North American shrimp population under commercial-like conditions, based on a designed experiment, and using a multivariate animal mixed model methodology. Our heritability estimates are of a relatively large magnitude, implying that a large genetic gain for harvest weight is expected in the short term if this trait is included in selection programs under environment conditions similar to those of our study.

Genetic correlations between environments lower than unity are evidence of genotype by environment interaction for BW at 130 days post-hatching. Under our experimental conditions when the multivariate animal model analytical approach was used, common environment effects were small for this trait, but their exclusion caused overestimation of heritabilities showing there are some confounding effects between genetic and common environment effects. To better estimate BW at 130 days post-hatching heritabilities, genetic maternal and common environment effects, a larger number of dams per sire is needed, to yield more half-sib families and have them replicated in several environments.

The rather high rank and simple correlation estimated between predicted family breeding value means and raw family means shows that, for a heritability magnitude like the one found for harvest weight at 130 d post-hatching, when a large number of full sibs per family are involved, and under environmental conditions similar to those in our study, there is only a medium risk of miss selecting the better families in a breeding program if BLUP solutions were neglected.

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