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REVIEW ARTICLE

Genetic analysis of the Pacific white shrimp (*Litopenaeus vannamei*): heterosis and heritability for harvest body weight

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Abstract

The aim of this study was to estimate heterosis and heritability for harvest body weight of the Pacific white shrimp (*Litopenaeus vannamei)* measured at commercial farm conditions. Heterosis and heritability were estimated using a base population from diallel crosses of eight introduced strains. The base population included 9936 shrimp from 207 families that were produced with 188 sires and 172 dams using a nested mating design by artificial insemination. Heterosis was calculated basing on the least squares means (LSM) of harvest body weight. The results showed that most of the hybrids (75%) have positive heterosis for harvest body weight, which ranged from −13.36% (UA2 × UA5) to 13.80% (UA6 × UA5) with a mean of 2.41%. The high amount of heterosis manifested in the hybrids indicated the usefulness of these hybrids for improving the growth. Variance components and heritability for harvest body weight were estimated using an animal model. The heritability estimate for harvest body weight was 0.092 ± 0.082 (h^2) when genetic groups were excluded from the pedigree, but it was decreased when genetic groups were included in the pedigree (h^2_{group} = 0.066 ± 0.050), implying that there are strain additive genetic effect and heterosis in the base population. However, the heritability estimates for harvest body weight were significantly different from zero ($P < 0.05$) and there was no significant difference between h^2 and h^2_{group} ($P > 0.05$). The results from this study indicated that significant improvement for growth is possible through cross-breeding and selective breeding in *L. vannamei*.

Keywords: heterosis, heritability, genetic group, harvest body weight, Pacific white shrimp, *Litopenaeus vannamei*

Introduction

The Pacific white shrimp, *Penaeus* (*Litopenaeus*) *vannamei*, provided approximately 52% of the total penaeid shrimp output in the world, which distributed along the Pacific coast of the western American continent from Mexico to Peru (Huang, Yin, Ai, Huang, Li, Weng & He 2011). *L. vannamei* has been introduced into China since 1988, and now it has become a dominant farmed shrimp in China due to its high commercial value and many desirable traits. In China, the annual production of *L. vannamei* is approximately 1.2 million tons and its production value reached $4.4 billion, covering 70% of the total culture area and 80% of the shrimp output (Xiong, Zhao, Gao, Xie, Zhang & Chen 2011; Luan, Luo, Ruan, Cao, Wang, Du, Zhang & Kong 2013). Because *L. vannamei* is a non-native species in China, most culture stocks are produced using the introduced parents from the South American countries or closely cultured parents over multiple generations (Briggs, Funge-Smith, Subasinghe & Phillips 2005). Thus, it might bring possible risk for inbreeding depression of important economic traits due to the small effective population size after

cultivating populations for multiple generations (Donato, Manrique, Ramirez, Mayer & Howell 2005).

Genetic improvement programmes can increase the economic efficiency of farmed shrimp (Argue, Arce, Lotz & Moss 2002; Pérez-Rostro & Ibarra 2003a,b; Gitterle, Rye, Salte, Cock, Johansen, Lozano, Suárez & Gjerde 2005; Gitterle, Salte, Gjerde, Cock, Johansen, Salazar, Lozano & Rye 2005; Castillo-Juárez, Casares, Campos-Montes, Villela, Ortega & Montaldo 2007; Andriantahina, Liu & Huang 2013; Campos-Montes, Montaldo, Martínez-Ortega, Jiménez & Castillo-Juárez 2013). Selective breeding programmes have been conducted for several species, including *Fenneropenaeus chinensis* (Zhang, Kong, Luan, Wang, Luo & Tian 2011), *Penaeus monodon* (Kenway, Macbeth, Salmon, McPhee, Benzie, Wilson & Knibb 2006; Krishna, Gopikrishna, Gopal, Jahageerdar, Ravichandran, Kannappan, Pillai, Paulpandi, Kiran, Saraswati, Venugopal, Kumar, Gitterle, Lozano, Rye & Hayes 2011; Sun, Huang, Jiang, Yang, Zhou, Zhu, Yang & Su 2015), *Penaeus japonicas* (Hetzel, Crocos, Davis, Moore & Preston 2000), *Oreochromis niloticus* (Charo-Karisa, Komen, Rezk, Ponzoni, van Arendonk & Bovenhuis 2006) and *Macrobrachium rosenbergii* (Luan, Wang, Yang, Luo, Chen, Gao, Hu & Kong 2015). Selective breeding programmes for *L. vannamei* also have been conducted widely in the word and achieved remarkable results, by which its world production has increased to 45% in 2008 from 13% in 1993 (Gjedrem 2012). Genetic gain was 4.4% for harvest body weight and 12.4% for TSV survival after one generation (Fjalestad, Gjedrem, Carr & Sweeney 1997); the growth of a selected strain was 21% larger than the control strain after only one generation (Argue *et al.* 2002).

An alternative approach to improving the productivity of cultured stocks is via cross-breeding to exploit potential heterosis (hybrid vigour) in cross-bred offspring (Maluwa & Gjerde 2006). The use of cross-breeding offers two distinct and important advantages that were taking advantage of breed complementarity and non-additive effects (dominance and epistatic), thus leading to heterosis (hybrid vigour). This method, particularly diallel crossing was usually performed to establish a genetically diverse synthetic base population prior to the initiating a breeding programme. Selective breeding programmes were subsequently conducted for providing significant economic benefit over the long term of operation, as it is another method to cultivate good varieties by selecting advantages and eliminating disadvantages (Gall & Bakar 2002; Martínez, Kause, Mäntysaari & Mäki-Tanila 2006; Rezk, Ponzoni, Khaw, Kamel, Dawood & John 2009).

In the present study, a project aimed at establishing a genetic improvement programme for the cultured *L. vannamei* was initiated in 2011, for which eight strains were introduced from America and Singapore. Little is known about potential of heterosis for the diallel crosses of the eight introduced strains. In addition, the knowledge about the heritability for the desirable traits of the introduced strains is crucial for the selective breeding programme. Under such circumstances, it was necessary to detect the heterosis and heritability to ensure that our efforts are directed towards improving the desirable traits. Consequently, the aim of this study was to estimate the heterosis and heritability for the harvest body weight of the eight introduced strains to investigate the potential for a cross-breeding and selective breeding to improve growth in this species.

Materials and methods

Data structure on shrimp body weight

This breeding programme was performed at the Mariculture Genetic Breeding Center of the Chinese Ministry of Agriculture (Qingdao, China). In February 2012, eight strains of *L. vannamei* were introduced from America and Singapore. They were checked for different virus and bacteria by reverse transcriptase polymerase chain reaction, and only the virus-free individuals were used for further breeding. After a period of 1 month of isolation conservation and temporary rearing, the shrimps with healthy appearance were chosen and individually tagged using numbered rings placed on one ocular peduncle.

Production of families

In March 2012, the base population consisted of 207 families were produced through an incomplete diallel cross-experiment of the eight strains (Table 1). Briefly, the females and males with matured gonad were chosen carefully to maximize mating success. Females with orange ovaries that occupied a large area of the cephalothorax were preferred and reared separately in 170 L white

Table 1 Numbers of families produced from incomplete diallel crosses of eight strains of *Litopenaeus vannamei*

	Paternal								
Maternal	**UA5**	**UA4**	**SIN**	**UA3**	**UA1**	**UA6**	**UA2**	**UA7**	**Total**
UA5	10	6	1	–	5	4	1	4	31
UA4	4	13	1	3	7	9	2	4	43
SIN	–	1	10	1	7	1	1	1	22
UA3	–	1	1	8	1	1	1	1	14
UA1	2	5	5	2	6	3	–	1	24
UA6	4	7	1	1	5	10	1	5	34
UA2	1	1	2	1	1	1	8	1	16
UA7	6	6	–	1	2	4	1	11	31
Total	27	30	21	16	32	29	14	28	207

Table 2 Schedule of family production and management for *Litopenaeus vannamei*

Synchronization of family production			**Average days for rearing separately**	**Days for growth test**			
Start date (D/M/Y)	**End date (D/M/Y)**	**Days**		**Stocking date (D/M/Y)**	**Harvest date (D/M/Y)**	**Days**	**Harvest density (individuals m^{-2})**
11/3/2012	25/3/2012	15	83	5/6/2012	1/8/2012	57	62

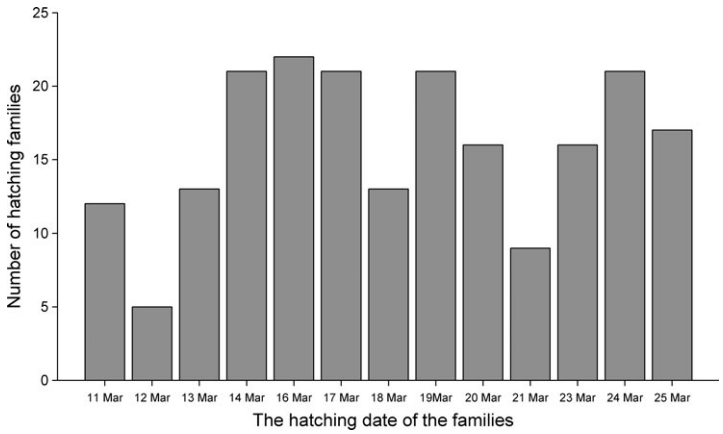

Figure 1 The distribution of the numbers of successfully hatched families at each hatching date.

tanks as breeding candidate to produce the families. Males with a healthy appearance and white, full spermatophores were obtained for mating with sexually receptive females. Full- and half-sib families were produced using a nested mating design by artificial insemination (two dams mating with one sire, and two sires mating with one dams). The inseminated female was moved back to individual spawning tank, and the spawned eggs were incubated in the spawning tank until hatching. After hatching, random samples of approximately 5000 larvae from each family were stocked into a separate 170 L larvae culture tank. In total, 207 full-sib and 90 half-sib families (40 paternal and 59 maternal half-sib families respectively) were successfully created using a total of 188 sires and 172 dams from the eight strains. Family reproduction and management for the families were shown in Table 2 and Fig. 1.

Larvae culture, tagging and growth test

The hatched larvae passed through six nauplii stages, that is three zoea stages and three mysis stages during a 3-week period before they became postlarvae. Larvae were fed a combination of food four times per day, which consisted of a microalgae diet (*Chaetoceros calcitrans*, *Thalassiosira*

fluviatilis and *Tetraselmis suesica*) and commercial larval diets. The amount and proportion of food were adjusted daily according to the different stages. The temperature of the larvae culture was maintained at 28 ± 0.5°C by a water bath outside each tank. Daily water exchanges increased according to the different stages. At the postlarvae 10 stage, random samples of 400 postlarvae per family were transferred to a separate 170 L tank for on-growing. Constant aeration and a 100% daily water exchange were provided. When the mean body weight reached 3 g, random samples of 60 shrimp from each family (totally 207 families) were tagged with a unique family code by injecting Visible Implant Elastomer (VIE). The combination of the colours of VIE (green, blue, orange, and red) and injected positions (five anatomical areas) were used to identify each family. This identification allowed the mixing of the families in ponds to evaluate performance.

After VIE tagging, two 80 m^{-2} earth ponds were used for rearing the tagged shrimp. About 60 tagged shrimp per family were assigned equally and randomly to the two ponds at the same density and with the same management environment. Standard management practices were followed during the growth test period. The feeding regimen consisted of feedstuff (contained 12% moisture, 42% crude protein and 17 crude ash) and fresh shellfish. The ponds had a water exchange rate varied from 15% to 30% of the total water volume per day, depending on the shrimp growth stage. All survived shrimp were harvested and measured the individual body weight after a growth test period of 57 days, and a total of 9936 shrimp were harvested.

Data analysis

The least squares means for harvest body weight

The least squares means (LSM) for harvest body weight were estimated using the mixed model. The model was formulated as follows:

$$y_{ijl} = \mu + S_i + \text{Family}_j(S_i) + b_1 \text{Wt}_l + e_{ij_l} \qquad (1)$$

where y_{ijl} is the obtained harvest body weight of the lth individual; μ is the overall mean harvest body weight; S_i is the fixed effect of the ith cross combination; Family_j (S_i) is the random effect of the jth full-sib family nested within the ith cross combination; Wt_l is the body weight of the lth animal before tagging (covariant), and b_1 is the regression coefficient; e_{ijl} is the random residual error of the lth individual.

The gender effects were not contained in the model, as part of the shrimp was too small to be identified the gender correctly when they were measured.

Heterosis estimate

The formulation for the heterosis of the hybrids from the eight introduced populations was written as:

$$H(\%) = \frac{M_{F_1} - \frac{1}{2}(M_{P_1} + M_{P_2})}{\frac{1}{2}(M_{P_1} + M_{P_2})} \times 100 \qquad (2)$$

where M_{F_1} is the mean LSM for harvest body weight of the replications of F_1 crosses between the strain P_1 and P_2; M_{P_1} and M_{P_2} are the mean LSM for harvest body weight of the inbred offspring from parent strains of P_1 and P_2 respectively.

Variance components and heritability estimate

The variance components of harvest body weight were estimated using the average information REML method in ASReml (Gilmour, Gogel, Cullis & Thompson 2009). The animal model was written in matrix notation as:

$$y_{kl}\mu + b * \text{Wt}_k + a_k + c_1 + e_{kl} \qquad (3)$$

where y_{kl} is the obtained harvest body weight of the kth individual; μ is the overall mean harvest body weight; Wt_k is the tagging body weight of the kth animal (covariant), and b is the regression coefficient; a_k is the additive genetic effect of the kth animal, $a \sim (0, A\sigma_a^2)$, where A is the additive genetic relationship matrix among all shrimp; c_l is the random effect common to the lth full-sib family, $c \sim (0, I\sigma_c^2)$, which is a combination of the tank effect due to separate rearing of the full-sib families before growth test and one quarter of the non-additive (dominance) genetic effect common to full-sibs; and e_{kl} is the random residual error of the kth individual, $e \sim (0, I\sigma_e^2)$.

The variance components for body weight were estimated including the common environmental effect (c) in the model. The additive (σ_a^2), common environmental (σ_c^2) and residual (σ_e^2) variances were estimated, whereas phenotypic variance (σ_p^2)

was the sum of all variance components. A complete pedigree in this breeding programme was available and used for the analysis. Heritability (h^2) was calculated as the ratio between σ_a^2 and σ_p^2, while the common environmental effect (c^2) was calculated as the ratio between σ_c^2 and σ_p^2.

As the base population was from the diallel crosses of the eight introduced strains, genetic variability and inflate heritability estimate for body weight might increase (Nielsen, Ødegård, Olesen, Gjerde, Ardo, Jeney & Jeney 2010). Consequently, eight genetic groups were included in the pedigree and used the !GROUPS qualifier in ASReml for heritability estimating (h^2_{group}) to account for heterosis from the crosses. The pedigree file began by identifying these groups, and the individuals of the base population have group identifiers as parents. In addition, to know the impact of heterosis from the crosses on heritability estimate, heritability was also estimated using the pedigree without genetic groups (h^2). The gender effects also were not contained in the model.

The Z-score was used to test whether the heritability estimates between h^2 and h^2_{group} were significantly different (Nguyen, Khaw, Ponzoni, Hamzah & Kamaruzzaman 2007):

$$Z = \frac{h^2 - h^2_{group}}{\sqrt{\left(\sigma_i^2 + \sigma_j^2\right)}} \quad (4)$$

where h^2_{group} and h^2 were the heritability estimates for harvest body weight when the genetic groups were included in the pedigree and excluded from the pedigree, respectively, and σ_i and σ_j were their respective standard errors. Significance for all analyses was established as $P < 0.05$.

Results

Descriptive statistics

The minimum, median, maximum and coefficients of variation for harvest body weight of each family were displayed in Fig. 2. The number of observations, simple means, minimum, maximum, standard deviation and coefficients of variation for harvest body weight among 207 families and overall 9936 individuals of *L. vannamei* are summarized in Table 3. The results showed that harvest body weight varied substantially within and among the families and overall individuals (Fig. 2; Table 3). The coefficients of variation for harvest body weight from each family ranged from 14.31% to 36.59% (Fig. 2b); it was 12.72% and 21.60% when calculated among family and overall individual respectively (Table 3). It had a higher variance when analysed at the individual level comparing to the family level, according to its higher standard deviation and coefficient of variation at the individual level (Table 3).

The least squares means of harvest body weight

The LSM for harvest body weight of the paternal and maternal populations was displayed in Table 4. When the eight strains were used as male parents respectively, the order of their LSM for harvest body weight was SIN > UA3 > US2 > UA5 > UA1 > UA6> UA4 > UA7; when they were used as female parents respectively, the order was UA3 > SIN > UA1 > UA2 > UA5 > UA7 > UA6 > UA4. Considering the paternal and maternal performance together, when SIN and UA3 were used as male or female parents, their offspring would have growth advantages.

The mean LSM and heterosis for harvest body weight of the crosses of the eight strains were presented in Table 5. The mean LSM for harvest body weight of the hybrids (11.12 g) was higher than the inbreds (10.89 g). Among all the hybrids, the UA2 (♂) × UA3 (♀) has the highest mean LSM for harvest body weight (12.91 g), which were 16.10% higher than the mean of all the hybrids; the UA1 (♂) × UA7 (♀) has the lowest LSM for harvest body weight (9.33 g), which was 16.10% lower than the mean of all the hybrids. Among the inbreds, the order of the LSM for harvest body weight was UA3 > SIN > UA2 > UA5 > UA1> UA7 > UA4 > UA6.

The heterosis estimates for harvest body weight of the hybrids ranged from -13.36% to 13.80% with a mean of 2.41%, among which UA6 × UA5 has the highest heterosis and UA1 × UA7 has the lowest heterosis (Table 5). The proportion of hybrids with positive heterosis was larger, which covered 75% of the hybrids. The heterosis in most of the hybrids was considerable, indicating that most of the hybrids were superior to their parents in the harvest body weight. There were no crosses for UA5 × UA3 in this experiment, so their crosses should be produced for further detecting their growth performance and heterosis.

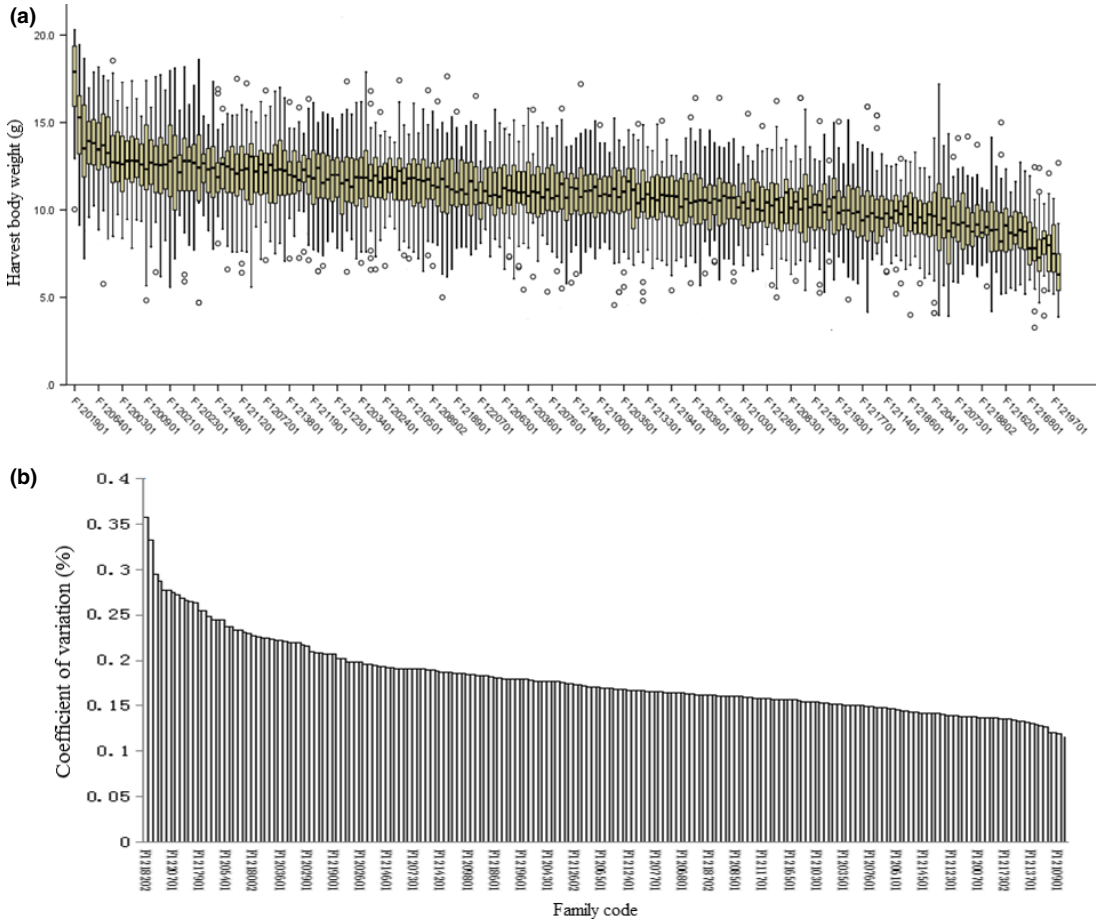

Figure 2 (a) Box plot of harvest body weight of all the families. The 25th (up line), median (inside line) and 75th (bottom line) percentiles of each family are plotted as boxes. The minimum, maximum and outliers are shown as -, - and O respectively; (b) The coefficients of variation for harvest body weight of all the families.

Variance components, heritability and common environmental effect

Estimates of variance components, heritability and the common environmental effects for the harvest body weight were presented in Table 6. When the genetic groups were excluded from the pedigree, the heritability estimate for harvest body weight was 0.092 ± 0.082; however, when the genetic groups were included in the pedigree, the heritability estimate was decreased to 0.066 ± 0.050. Although the heritability estimates were low, they were still significantly different from zero ($P < 0.05$) and there was no significant difference between h^2_{group} and h^2 ($P > 0.05$).

Discussion

Many studies have indicated that the cross-breeding and selective breeding could greatly improve the performance in aquaculture (Hines 1976; Olesen, Gjedrem, Bentsen, Gerdje & Rye 2003; Rezk

Table 3 Descriptive statistics for harvest body weight in *Litopenaeus vannamei*

	N	Mean (g)	Minimum (g)	Maximum (g)	SD	CV (%)
Family level	207	11.50	6.60	17.22	1.34	12.27
Individual level	9936	11.50	2.10	20.80	2.36	21.60

N, number of observations; SD, standard deviation; CV, coefficient of variation.

Table 4 Analysis of LSM for harvest body weight of paternal and maternal populations in *Litopenaeus vannamei*

Populations	Male parents (g)	Female parents (g)	Mean (g)
SIN	12.16	11.41	11.79
UA3	11.50	11.98	11.74
UA2	11.35	11.21	11.28
UA5	11.23	11.17	11.20
UA1	10.80	11.36	11.08
UA6	10.76	10.49	10.63
UA7	10.38	10.79	10.59
UA4	10.62	10.47	10.34

et al. 2009; Thanh, Ponzoni, Nguyen, Vu, Barnes & Mather 2009), as aquatic animals have higher coefficient of variation for growth, such as body weight of giant freshwater prawn (24–35%) (Thanh *et al.* 2009), rainbow trout (17–56%) (INGA 1997), giant freshwater prawn (20–50%) (Luan, Yang, Wang, Luo, Zhang, Gao, Hu & Kong 2012), Atlantic salmon (25–76%) (Jonasson 1993; Gjerde, Pante & Baeverfjord 2005) and channel catfish (22%) (INGA 1997). In the present study, the coefficient of variation for harvest body weight of *L. vannamei* ranged from 14.31% to 36.59%, which has provided important precondition and foundation for improving its growth per-

Table 5 Analysis of the LSM and heterosis for harvest body weight of eight strains in *Litopenaeus vannamei*

Combination types	Population combinations	Mean of LSM (g)			
		Orthogonal (♂ × ♀)	Reciprocal (♀ × ♂)	Mean	Heterosis(%)
Hybridized combinations	UA6 × UA5	11.77	11.47	11.62	13.80
	UA2 × UA3	12.91	10.87	11.89	13.66
	UA2 × UA4	12.14	10.94	11.54	13.27
	UA6 × UA3	12.05	12.03	12.04	11.43
	UA1 × UA2	12.08	–	12.08	11.05
	UA6 × UA7	11.30	9.93	10.62	10.35
	UA2 × UA7	11.57	10.90	11.24	7.33
	UA1 × UA6	11.09	11.54	11.31	7.25
	UA4 × SIN	11.81	11.00	11.40	6.38
	UA6 × SIN	11.33	11.53	11.43	5.61
	SIN × UA5	11.87	–	11.87	5.35
	UA3 × SIN	12.25	11.63	11.94	4.35
	UA6 × UA4	10.52	10.64	10.58	3.34
	UA1 × UA4	11.05	11.30	11.17	3.24
	UA7 × UA5	11.12	10.37	10.74	3.21
	UA4 × UA5	10.96	10.29	10.62	2.31
	UA2 × SIN	11.52	11.68	11.60	2.23
	UA1 × UA3	11.49	11.11	11.30	1.30
	UA1 × SIN	11.37	11.73	11.55	1.05
	UA2 × UA6	10.41	10.20	10.31	0.59
	UA1 × UA5	10.36	10.79	10.57	−4.64
	UA3 × UA7	10.61	11.53	11.07	−5.66
	UA3 × UA4	10.40	11.32	10.86	−6.97
	UA2 × UA5	9.92	11.11	10.52	−8.82
	UA7 × UA4	9.60	10.73	10.17	−9.48
	UA7 × SIN	9.68	–	9.68	−13.23
	UA1 × UA7	9.33	11.57	10.45	−13.36
Mean		11.13	11.09	11.12	2.41
Inbred combinations	UA3 × UA3	–	–	11.82	–
	SIN × SIN	–	–	11.65	–
	UA2 × UA2	–	–	10.89	–
	UA5 × UA5	–	–	10.88	–
	UA1 × UA1	–	–	10.86	–
	UA7 × UA7	–	–	10.67	–
	UA4 × UA4	–	–	10.54	–
	UA6 × UA6	–	–	9.81	–
Mean				10.89	–

Table 6 Variance components and heritability estimates for harvest body weight in *Litopenaeus vannamei*

	Variance components			Heritability		Common environment
	σ_a^2	σ_c^2	σ_e^2	σ_p^2	$h^2 \pm$ SE	$c^2 \pm$ SE
h^2_{group}	0.293	0.073	4.098	4.465	0.066 ± 0.050	0.016 ± 0.024
h^2	0.466	0.560	4.034	5.064	0.092 ± 0.082	0.111 ± 0.046

h^2_{group} and h^2 were the heritability estimates for harvest body weight when the genetic groups were included in the pedigree and excluded from the pedigree respectively; σ_a^2 = additive genetic variance; σ_c^2 = common environmental effects variance; σ_e^2 = residual variance; c^2 = common environment coefficient.

formance by cross-breeding and selective breeding. The results indicated that the eight introduced strains have great selective potential and could be used to produce base population in our breeding programme.

The heterosis for harvest body weight in most of the hybrids was considerable, and 75% of the hybrids have positive heterosis (Table 5). The observed high positive heterosis for body weight would be an advantage to obtain higher yield in the breeding programme. The present highest heterosis estimate for harvest body weight (13.80%) was higher than that detected in other studies reported in *L. vannamei* (3.74% to 11.72%) (Lin, Shen, Zhang, Hu & Liang 2010; Ruan, Luo, Luan, Kong, Xu, Chen & Chen 2013). The high amount of heterosis might be generated by the accumulation of favourable dominant alleles and masking of deleterious effects of recessive alleles by their dominant alleles in the hybrids (Crow 1952; Hill, Becker & Tigerstedt 1998) and superiority of heterozygotes at some of the loci to both the relevant homozygotes (Sprague 1983). In general, the high amount of heterosis manifested in the hybrids indicated the prevalence of dominant gene action in controlling the body weight and the usefulness of the hybrids for improving the growth (Xiao, Li, Yuan & Tanksley 1995; Falconer & Mackay 1996). However, it was worth to notice that some of the hybrids only consisted of one family, which might lead to bias for the estimations, and it was necessary to produce more families for further verification.

The previous studies indicated that additive genetic variance would be decreased when genetic groups were included in the model (Pieramati & Van Vleck 1993; Díaz, Moreno & Carabaño 2002). In this study, the base population was produced by eight strains, and the inclusion of the eight genetic groups in the pedigree has decreased the heritability estimate for harvest body weight (Table 6), implying that there were strain additive genetic effect and heterosis in the base generation. The strain additive genetic effects and heterosis for harvest body weight were also detected in the base populations of Nile tilapia (*Oreochromis shiranus*) (Maluwa & Gjerde 2006) and common carp (*Cyprinus carpio*) (Nielsen *et al.* 2010).

Genetic parameters are only applicable to the certain population and the environment where they are obtained (Ponzoni, Hamzah, Tan & Kamaruzzaman 2005). In the present study, the heritability estimate for harvest body weight was lower than the REML estimates in other farmed shrimp species, shuch as *L. vannamei* (0.13–0.65) (Carr, Fjalestad, Godin, Swingle, Sweeney & Gjedrem 1997; Fjalestad, Carr, Lotz, Sweeney & Gjedrem 1997; De Donato, Cabrera, Ramirez, Manrique, Markham, Howell, Lodeiros & Graziani 2001), *Fenneropenaeus chinensis* (0.44–0.74) (Zhang *et al.* 2011) and *Penaeus monodon* (0.10–0.56) (Benzie, Kenway & Trott 1997; Kenway *et al.* 2006; Krishna *et al.* 2011). However, it was higher than the estimates reported in *Macrobrachium rosenbergii* (0.055) (Luan *et al.* 2012). The differences between those heritability estimates reported previously and that found in the present study for body weight could be due to multiple factors of genetic or environmental origin, such as different populations, growing conditions, ages, gender and methodological problems (Korkeila, Kaprio, Rissanen & Koskenvuo 1991; Elvingson & Johansson 1993; Jarayabhand, Uraiwan, Klinbunga, Tassanakajon, Srimukda, Pattanachan, Panakulchaiwit & Menasveta 1998; Ng, Sham, Paterson, Chan & Kung 2006).

In particular, the low heritability for harvest body weight in the present study might be due, at least in part, to low genetic variation in the introduced strains. Because the strains have been domesticated and selected for multiple generations before they were introduced. The domestication and selection would increase the genetic homoge-

neity and reduce the genetic variation (Doyle 1983; Sbordoni, De Matthaeis, Cobolli-Sbordoni, La Rosa & Mattoccia 1986; Bierne, Beuzart, Vonau, Bonhomme & Bedier 2000; Li, Li, Wang, He & Liu 2006; Freitas, Calgaro & Galetti 2007). Another reason for the low heritability estimates might be from low genetic ties between the families, which could lead to the fact that the c^2 could not be partitioned effectively. The low heritability estimate, also likely because of the short growth test period (57 days), which would lead to individuals' growth potential has not been fully expressed in the common environment. To better estimate heritability for harvest body weight, a larger number of dams per sire are needed to produce more half-sib families, and a longer growth test period was also necessary (Castillo-Juárez *et al.* 2007).

Conclusion

We established a breeding programme to improve growth in the Pacific white shrimp, *Litopenaeus vannamei*. The heterosis estimates for harvest body weight in most of the hybrids of the eight strains were considerable, and 75% of the hybrids have positive heterosis, indicating that it was useful for improving the growth to obtain higher yield by cross-breeding in this breeding programme. The inclusion of genetic groups in the pedigree has decreased the heritability estimate for harvest body weight, implying that there are strain additive genetic effect and heterosis in the base generation. Heritability estimate for the harvest body weight in the present study was in general lower than those reported in other selection breeding programmes for shrimp growth. The lower heritability estimate was most likely caused by low genetic variation in the population, as the strains have been domesticated and selected for multiple generations before they were introduced. Even so, higher genetic gain for growth could be obtained in future by cross-breeding and selective breeding by increasing the selection intensity.

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