Heterosis and heritability estimates for the survival of the Pacific white shrimp (Litopenaeus vannamei) under the commercial scale ponds

LU Xia1, 2, LUAN Sheng1, 2, CAO Boxiang1, 2, SUI Juan1, 2, DAI Ping1, 2, MENG Xianhong1, 2, LUO Kun1, 2, KONG Jie1, 2*

1 Key Laboratory of Sustainable Utilization of Marine Fisheries Resources of Ministry of Agriculture, Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Qingdao 266071, China
2 Laboratory for Marine Fisheries Science and Food Production Processes, Qingdao National Laboratory for Marine Science and Technology, Qingdao 266071, China

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Abstract

The aim of the present study is to detect the potential of the base population from diallel crosses of eight introduced strains of the Pacific white shrimp (Litopenaeus vannamei) for improving the yield. Heterosis and heritability were estimated for pond survival at commercial farm conditions for the base population that included 207 full-sib families from a nested mating design by artificial insemination. Among all the hybrids, the heterosis ranged from –11.37% (UA1×UA2) to 20.53% (UA3×SIN) with an average of 0.953%. The results showed that more than half of the hybrids (51.85%) have negative heterosis for survival rate, but most of the hybrids with positive heterosis have high estimates. The high proportion of negative heterosis for survival rate reminds us that the survival trait also should be considered in the crossbreeding program to avoid yield decrease. However, high positive heterosis manifested in most of the hybrids for survival indicates the usefulness of these hybrids for improving the survival to obtain higher yield by crossbreeding in this breeding program. The heritability estimate for pond survival was 0.092±0.043 when genetic groups were included in the pedigree, and it was significantly different from zero (P<0.05). The results from this study also indicated that significant improvement for survival is possible through selection in L. vannamei.

Key words: heterosis, heritability, genetic group, pond survival, Pacific white shrimp, Litopenaeus vannamei

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1 Introduction

Selective breeding programs can improve culture performance of farmed shrimp (Gjedrem, 2012; Andriantahina et al., 2013; Campos-Montes et al., 2013), which have been conducted in several species, such as Penaeus japonicas (Hetzel et al., 2000), Oreochromis niloticus (Charo-Karisa et al., 2006), Fenneropenaeus chinensis (Zhang et al., 2011), Penaeus monodon (Kenway et al., 2006; Krishna et al., 2011; Sun et al., 2015), and Macrobrachium nirovenbergii (Luan et al., 2015). A base population with abundant genetic variation is the important foundation for executing a selection breeding program. In practice, diallel crossing with several populations is usually initially used to establish a base population with high genetic diversity. Subsequently, selective breeding programs were continuously conducted for several generations to improve the performance by selecting advantages and eliminating disadvantages over a long term of operation (Gall and Bakar, 2002; Martinez et al., 2006; Rezk et al., 2009).

Usually, selective breeding programs in the shrimp focused on growth, by which it has obtained substantial selection response for growth performance (Maluwa and Gjerde, 2006; Thanh et al., 2009; Lin et al., 2010; Ruan et al., 2013). Nevertheless, along with the deterioration in aquaculture environment, high mortality has greatly affected the total production yield in aquaculture. In the shrimp, to pursue a high pond survival rate at commercial farm conditions is crucial for reducing production cost and increasing income. So it is necessary to introduce survival into the breeding objective in the modern shrimp breeding programs to optimize the production yield (Luan et al., 2013). However, survival is possibly influenced by multiple environmental factors (such as cultivation density, water quality, and temperature etc.), and it has low genetic variation in farmed shrimp and fish breeding programs (Rye et al., 1990; Gitterle et al., 2005a, b; Vehviläinen et al., 2008; Luan et al., 2013). To date, shrimp has obtained slow and significant selection response in survival by selective breeding programs (Gitterle et al., 2007; Luan et al., 2013), although the survival of shrimp is significantly influenced by environments.

The Pacific white shrimp, Penaeus (Litopenaeus) vannamei, provided approximately 52% of the total penaeid shrimp production in the world (Lu et al., 2015), which distributed along the Pacific coast of the western American (Huang et al., 2011; Lu et al., 2015). In China, L. vannamei is a non-native species and most of the culture stocks are produced using the introduced limited number of parents or their offspring over multiple generations (Briggs et al., 2005a, b; Vehviläinen et al., 2008; Luan et al., 2013), which most likely to bring small effective population size. The small effective population
size of the base population would lead to inbreeding depression of important economic traits (De Donato et al., 2005). Consequently, the base population is particularly important for the selective breeding programs of L. vannamei in China. Growth is a very important trait in selective breeding programs of L. vannamei, as it is highly correlated with economic returns. In addition, the recently high mortalities from birth to harvest have caused large economic losses for farmers and the industry in L. vannamei (Lightner et al., 2012).

To improve the growth and survival of L. vannamei for increasing the production, a selective breeding program for the cultured L. vannamei was initiated at Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences in 2011. In this program, diallel crossing was performed to establish a base population with eight strains that were introduced from America and Singapore. Because the increase in selection response depends on the heritability of the aimed trait being selected for in the breeding program (Falconer and Mackay, 1996; Hertz et al., 2000), and genetic parameters are only applicable to the certain population and the environment where they are obtained (Ponzoni et al., 2005). Heterosis and heritability for the harvest body weight of the base population from the eight introduced strains has been estimated in our previous study (Lu et al., 2015). Heritability estimates for disease resistance and survival traits have been reported in several shrimp (Fjalestad et al., 1997; Argue et al., 2002; Gitterle et al., 2005b; Kenway et al., 2006; Krishna et al., 2011; Luan et al., 2013), but heritability estimates for survival at commercial farm conditions are scarce, and little information is available for L. vannamei. Consequently, the aim of the present study was to estimate heterosis and heritability of pond survival at commercial farm conditions, to investigate the potential of this base population for improving the total yield by increase pond survival.

2 Materials and methods

2.1 Production, rearing and tagging of families

The survival test was performed at the Mariculture Genetic Breeding Center of the Chinese Ministry of Agriculture (Qingdao, China). The base population was constructed with eight strains by an incomplete diallel cross experiment. The eight strains were separately introduced from different commercial companies in America and Singapore, containing Shrimp Improvement System Pte. Ltd (SINGAP), Shrimp Improvement System Hawaii LLC (HAWAII), University of Guam, CNAS (GUAMIS), Kona Bay Marine Resources, Waimaa Aquatic Lab (KONABA), the Oceanic Institute (OCEANA), Shrimp Improvement System Florida (SISMAM), and High Health Aquaculture Inc (HIGHHA). Two strains (OCEANA and OCEANA2) were introduced from OCEANA at different time. The origins of the stains were Singapore, Oahu, Guam, Kauai, Oahu, Miami and Hawaii, respectively. The pedigree of individuals in the eight strains was unknown. The base population contains 207 full-sib and 90 half-sib families from 188 sires and 172 dams (Table 1). The details for the production, rearing and tagging of families have been described in our previous study (Lu et al., 2015). Family reproduction and management for the families were shown in Table 2.

After six nauplii-stages that were three zoea-stages and three mysis-stages within 3 weeks, the hatched larvae became post-larvae. Larvae were fed commercial larval diets and a microalgae diet (Chaetoceros calcitrans, Thalassiosira fluviatilis, and Tetraselmis suecica) four times per day, and the amount and proportion were adjusted daily according to the different stages. When the mean body weight reached 3 g, 60 shrimp were randomly selected from each family for tagging with a unique family code by injecting Visible Implant Elastomer (VIE). The combination of the injected positions (three locations on the 6th abdominal segment and two locations on the 5th abdominal segment) and the colors of VIE (green, blue, orange, and red) was used for family tags, which allowed the mixing of the families in ponds to evaluate performance.

2.2 Survival test

After VIE tagging, 60 tagged shrimp of each family were assigned equally and randomly to two ponds (80 m² for each pond) with the same density. The 207 families were performed for survival test. During the test period, standard management practices were followed, which has been described in our previous study (Lu et al., 2015). After a period of 57 days for survival test, survival rate of each family was calculated as the ratio between its

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

| Maternal | UA1 | UA2 | UA3 | UA4 | UA5 | UA6 | UA7 | SIN |
|---------|-----|-----|-----|-----|-----|-----|-----|-----|
| UA1     | 6   | 2   | 5   | 2   | 3   | 1   |     | 5   |
| UA2     | 8   | 1   | 1   | 1   | 1   | 1   | 1   | 2   |
| UA3     | 1   | 1   | 8   | 1   | 1   | 1   | 1   | 14  |
| UA4     | 2   | 1   | 2   | 13  | 4   | 5   | 4   | 35  |
| UA5     | 1   | 6   | 10  | 4   | 4   | 1   | 41  |
| UA6     | 5   | 7   | 4   | 10  | 5   | 1   | 34  |
| UA7     | 2   | 6   | 6   | 4   | 11  | 1   | 31  |
| SIN     | 7   | 1   | 1   | 1   | 1   | 10  | 1   | 22  |
| Total   | 32  | 14  | 16  | 40  | 27  | 28  | 21  | 207 |

Note: UA1 represents HAWAII, UA2 GUAMIS, UA3 KONABA, UA4 OCEANA, UA5 SISMAM, UA6 HIGHHA, UA7 OCEANA2, and SIN SINGAP.

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

| Synchronization of family production | Average days for rearing separately | Days for growth test | Harvest density/ind.·m⁻² |
|-------------------------------------|-------------------------------------|----------------------|--------------------------|
| Start date (D/M/Y)                  | End date (D/M/Y)                    | Days                | Stocking date (D/M/Y)    | Harvest date (D/M/Y)   | Days |                |
| 11/3/2012                           | 25/3/2012                           | 83                  | 5/6/2012                 | 1/8/2012               | 57   | 62              |
survived and initially tagged individuals.

2.3 Data analysis

Survival status during the test was recorded as “1” if a shrimp was alive or “0” if the shrimp was dead. An analysis of the descriptive statistics was conducted using the MEANS procedure in SAS software (SAS Institute Inc., 2005).

2.3.1 Heterosis estimate

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

$$H(\%) = \frac{MF_{ij} - \frac{1}{2}(MP_i + MP_j)}{\frac{1}{2}(MP_i + MP_j)} \times 100,$$  

(1)

where $MF_{ij}$ is the mean survival rate of the replications of $F_1$ crosses between the strain $P_i$ and $P_j$; $MP_i$ and $MP_j$ are the mean survival rate of the inbred offspring from parent strains of $P_i$ and $P_j$ respectively.

2.3.2 Variance components and heritability estimate

With respect to the calculation of variance components, animal and sire-dam models are statically equivalent, while animal threshold models may be severely biased (Luo et al., 2001). Therefore, a standard threshold (probit) and sire-dam model were preferred in the present study. The model was written as in ASReml (Gilmour et al., 2009).

$$\lambda_{ijlm} = \mu + s_i + d_j + f_{ij} + e_{ijlm},$$

$$y_{ijlm} = \begin{cases} 0 & \text{if } \lambda_{ijlm} \leq 0, \\ 1 & \text{if } \lambda_{ijlm} > 0, \end{cases}$$

(2)

where $y_{ijlm}$ is the survival statuses (1=alive and 0=dead) of the $m$th shrimp; $\lambda_{ijlm}$ is the underlying liability of $y_{ijlm}$, assumed to be a cumulative normal distribution; $\mu$ is the overall mean; $s_i$ and $d_j$ are the additive genetic effects of the $i$th sire and the $j$th dam; $f_{ij}$ is the random effect common to the $i$th full-sib family; $f \sim (0, I\sigma^2_f)$, which is a combination of the tank effect due to separate rearing of the full-sib families before mixed stocking and one quarter of the non-additive (dominance) genetic effect common to full-sibs; and $e_{ijlm}$ is the random residual error of the $m$th individual, with $e \sim (0, I\sigma^2_e)$. The residual variance of $\lambda$ was assumed to be 1. The phenotypic variance ($\sigma^2_y$) was the sum of $2\sigma^2_d$, $\sigma^2_f$ and $\sigma^2_e$. The $h^2$ was calculated as the ratio between $4\sigma^2_d$ and $\sigma^2_y$, while the common environment ($c^2$) was calculated as the ratio between $\sigma^2_f$ and $\sigma^2_y$.

The base population was constructed with the diallel crosses of the eight introduced strains, so the strain additive genetic effect and heterosis from the crosses of the eight strains might increase genetic variability and inflate heritability estimate for survival rate (Díaz et al., 2002; Pieramati and Van Vleck, 1993; Nielsen et al., 2010; Maluwa and Gjerde, 2006; Nielsen et al., 2010). Consequently, in order to account for strain additive genetic effect and heterosis from the crosses, the eight strains were defined as eight genetic groups and included in the pedigree, and then used the GROUPS qualifier in ASReml for heritability estimating. The pedigree file began by identifying these groups, and the individuals of the base population have group identifiers as parents. 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.

The Z-score was used to test whether the heritability estimates was significantly different from zero (Nguyen et al., 2007):

$$Z = \frac{h^2}{\sqrt{\sigma^2}},$$

(3)

where $h^2$ was the heritability estimate for survival rate when the genetic groups were included in the pedigree, and $\sigma^2$ was its standard error. Significance for the analyses was established as $P<0.05$.

3 Results

3.1 Descriptive statistics

The survival rate of these families ranged from 63.33% to 100% with an average of 85.76%, and the distribution for the survival rate of the families was displayed in Fig. 1. It showed that survival rate varied substantially among the families according to survival rate of the families was displayed in Table 3. The survival rate of the paternal and maternal populations was displayed in Table 3. When the eight strains were used as male parents respectively, the order of their survival rate was UA6>UA7>US2>UA4>UA3>UA5>SIN>UA1; when they were used as female parents respectively, the order was UA3>UA6>UA5>UA1>UA2>UA4>SIN>UA7. Considering the paternal and maternal performance together, when UA6, UA3 and UA2 were used as parents, their offspring would have high survival rate.

The mean survival rate and heterosis of the crosses of the eight strains were presented in Table 4. Among the hybrids, the UA3×SIN has the highest mean survival rate (100%), which were 15.19% higher than the mean of all the hybrids; the UA1×UA2 has the lowest survival rate (77.05%), which was 10.72% lower than

![Fig. 1. The distribution of survival rate of all the 207 families.](image-url)
the mean of all the hybrids. Among the inbreds, the order of the mean survival rate was UA6>UA2>UA7>UA5>UA1>UA3>UA4>SIN.

The heterosis estimates for survival rate of the hybrids ranged from -11.37% (UA1×UA2) to 20.53% (UA3×SIN) with a mean of 0.95% (Table 4). The proportion of hybrids with positive heterosis is covered 48.15% of the hybrids. Combined with the heterosis estimates for body weight in our previous study of the same program (Lu et al., 2015), ten hybrids have positive heterosis for survival rate and body weight; ten hybrids have positive heterosis for body weight but negative heterosis for survival rate; three hybrids have positive heterosis for survival rate but negative heterosis for body weight; and four hybrids have negative heterosis for survival rate and body weight (Table 4).

### Table 3. Analysis for survival of paternal and maternal populations in Litopenaeus vannamei

| Populations | Male parents/% | Female parents/% | Mean/% |
|-------------|----------------|------------------|--------|
| UA6         | 90.44          | 87.53            | 88.99  |
| UA7         | 87.98          | 83.07            | 85.53  |
| UA2         | 87.42          | 85.90            | 86.66  |
| UA4         | 85.46          | 84.95            | 85.21  |
| UA3         | 85.07          | 88.65            | 86.86  |
| UA5         | 84.34          | 87.22            | 85.78  |
| SIN         | 83.33          | 83.71            | 83.52  |
| UA1         | 82.66          | 86.52            | 84.59  |

### Table 4. Analysis of heterosis for survival of eight strains in Litopenaeus vannamei

| Combination types | Population combinations | Orthogonal (♀ × ♂) | Reciprocal (♂ × ♀) | Mean | Heterosis/% |
|-------------------|-------------------------|--------------------|--------------------|------|-------------|
| Hybridized        |                         | 100.00             | 100.00             | 100  | 20.53       |
|                   | UA3×SIN                 | 100.00             | 93.33              | 96.67| 10.79       |
|                   | UA2×UA5                 | 83.33              | 100.00             | 91.67| 9.33        |
|                   | UA3×UA4                 | 91.67              | –                  | 91.67| 8.02        |
|                   | SIN×UA5                 | 90.00              | –                  | 90.00| 7.33        |
|                   | UA4×SIN                 | 85.00              | 91.67              | 88.34| 6.80        |
|                   | UA6×UA3                 | 100.00             | 86.67              | 93.34| 6.64        |
|                   | UA1×UA3                 | 88.33              | 91.67              | 90.00| 6.29        |
|                   | UA6×SIN                 | 93.33              | 85.00              | 89.17| 3.22        |
|                   | UA1×UA4                 | 80.67              | 92.33              | 86.50| 2.46        |
|                   | UA4×UA5                 | 88.33              | 83.75              | 86.04| 1.54        |
|                   | UA6×UA4                 | 90.00              | 86.90              | 88.45| 1.36        |
|                   | UA6×UA5                 | 90.83              | 86.67              | 88.75| 0.38        |
|                   | UA6×UA7                 | 91.25              | 86.00              | 88.63| 0.88        |
|                   | UA1×UA5                 | 82.00              | 86.67              | 84.34| 1.44        |
|                   | UA2×UA3                 | 81.67              | 88.33              | 85.00| 1.57        |
|                   | UA1×SIN                 | 81.90              | 82.00              | 81.95| 1.90        |
|                   | UA2×UA6                 | 93.33              | 81.67              | 87.50| 2.54        |
|                   | UA7×UA4                 | 88.75              | 77.78              | 83.27| 2.89        |
|                   | UA1×UA6                 | 83.33              | 86.67              | 85.00| 3.51        |
|                   | UA3×UA7                 | 66.67              | 98.33              | 82.50| 4.06        |
|                   | UA2×UA4                 | 85.00              | 80.00              | 82.50| 4.19        |
|                   | UA7×UA5                 | 87.92              | 78.33              | 83.13| 4.33        |
|                   | UA1×UA7                 | 82.50              | 80.00              | 81.25| 6.15        |
|                   | UA2×UA7                 | 78.00              | 90.00              | 82.50| 6.52        |
|                   | UA2×SIN                 | 80.00              | 77.50              | 78.75| 7.60        |
|                   | UA1×UA2                 | 77.05              | –                  | 77.05| 11.37       |
| Mean              |                         | 86.59              | 87.14              | 86.81| 0.95        |

### Note

1) Positive heterosis for survival rate and body weight; 2) positive heterosis for survival rate but negative heterosis for body weight; 3) positive heterosis for body weight but negative heterosis for survival rate; 4) negative heterosis for survival rate and body weight.

3.3 Variance components, heritability and common environmental effect

Estimates of variance components, heritability and the common environmental effects for the survival rate were presented in Table 5. When the genetic groups were included in the model, the heritability estimates ($h^2$) was 0.092±0.043. Although the heritability estimate was low, it was still significantly different from zero ($P<0.05$).
Table 5. Variance components and heritability estimates for survival in Litopenaeus vannamei

| Variance components | Heritability | Common environment $c^2$±SE |
|---------------------|-------------|-----------------------------|
| $2\sigma^2_{c}$     | 0.054       | 1.00                        |
| $\sigma^2_c$        | 0.122       | 1.176                       |
| $\sigma^2_p$        | 0.092±0.043 | 0.106±0.054                 |
| $\sigma^2_e$        | 0.106±0.054 |                             |

Note: $2\sigma^2_c$ is sire-dam variance; $\sigma^2_c$ is common environmental effect variance; $\sigma^2_p$ is residual variance; $c^2$ is common environment coefficient.

4 Discussion

In a selective breeding program, it is very important to make the testing environments emulate commercial conditions, which could enable the selected animals manifest the same traits under commercial conditions. Although pond survival in commercial conditions may not be intentionally selected for, it will inevitably change along with the inadvertent selection during a program (Doyle, 1983). In the present study, we detected the heterosis and heritability for survival rate under commercial conditions from the same base population used in our previous study (Lu et al., 2015).

In this program, the survival rate of 92.6% of the hybirding combinations and all of the inbreeding combinations was higher than 80%, suggesting that these strains have good performance on pond survival. In addition, most of the positive heterosis for survival rate was considerable (Table 4), among which the highest heterosis estimate (20.53%) was higher than that detected for the body weight (13.80%, Lu et al., 2015). The observed high positive heterosis for survival rate indicated that these hybrids were superior to their parents in the survival rate and it is an advantage to obtain higher yield in this breeding program by crossbreeding. The high positive heterosis (4%–25%) for survival in hybrids also has been obtained by crossbreeding with two wild strains and two farmed strains in common carp (Nielsen et al., 2010). However, more than half of the hybrids (51.85%) have negative heterosis for pond survival rate in the present study, which was higher than the proportion for body weight (25.93%) from the same hybrids (Lu et al., 2015). In addition, 37% of the hybrids have negative heterosis for survival rate and positive heterosis for body weight. Thus it can be seen that it is very important to estimate the heterosis of the pond survival rate, and it reminds us that the pond survival also should be taken into account in the crossbreeding program to avoid yield decrease, because the breeding program usually more focused on growth. Fortunately, 37% of the hybrids have positive heterosis for both body weight and survival rate, indicating these hybrids were the preferred selection for improving production yield.

Three main causes were most likely responsible for the present high proportion of negative heterosis for survival rate. First, the eight strains have been domesticated and selected for multiple generations before they were introduced, which has led to inbreeding depression for survival trait due to the small effective population size (De Donato et al., 2005). Second, the pond survival might be easily influenced by environmental factors and the performance was not stable in different environments. Third, it was worth to notice that some of the hybrids only consisted of one family (Table 1), and there were no crosses for UA5×UA3 in this experiment, which might lead to bias for the estimations. So it was necessary to produce more families for further verifying their survival performance and heterosis.

The heritability estimate for survival rate in the present study was low (0.092±0.043), but it was significantly different from zero ($P<0.05$). Low heritability estimates for survival also have been obtained in other farmed shrimp and fish, such as the giant fresh water prawn (0.007 to 0.066) (Luan et al., 2015), abalone (0.04) (Jonasson et al., 1999), Nile tilapia (0.03–0.14) (Charo-Karisa et al., 2006; Rezk et al., 2009), Atlantic salmon (0.04–0.09) (Standal and Gjerde, 1987; Rye et al., 1990; Jonasson, 1993), rainbow trout (0.08) (Rye et al., 1990; Vehviläinen et al., 2008), chinook salmon (0.05) (Witlher et al., 1987), and turbot (0.06–0.12) (Wang et al., 2010). The heritability estimates for survival might be influenced by many factors, such as different populations, growing conditions, ages, density, and methodological problems (Rye et al., 1990; Korkeila et al., 1991; Murray et al., 1993; Elvingson and Johannson, 1993; Ng et al., 2006; Zhang et al., 2008; Sahoo et al., 2010; Luan et al., 2013). It would be very important to improve the accuracy of selection even though the heritability for survival was found to be low (Gitterle et al., 2005a, b).

The heritability for survival actually might be low in aquaculture, but three main causes were most likely responsible for the present low heritability. First, low heritability might due to low genetic variation in the introduced strains that have been domesticated and selected for multiple generations, because domestication and selection would increase the genetic homogeneity and reduce the genetic variability (Sbordoni et al., 1986; Doyle, 1983; Biern et al., 2000; Li et al., 2006; Freitas et al., 2007). Especially, decline of genetic variability in the population of L. vannamei has been detected using microsatellite and pedigree information in the previous study (Vela-Avituá et al., 2013). Second, the low heritability estimates might from low genetic ties between the families, which could lead to the fact that the $c^2$ could not be partitioned effectively. Because there were fewer half-sib families in the tested base population. Third, the survival rate might not be a suitable index for heritability estimates of survival trait, as it was family record rather than individual record (Castillo-Juárez et al., 2007). Therefore, to better estimate heritability for survival, a larger number of dams per sire to produce more half-sib families and individual survival data (such as individual survival time) would be considered in the future study.

5 Conclusions

We established a breeding program to improve growth and survival in the Pacific white shrimp, Litopenaeus vannamei. In this program, high proportion of negative heterosis (51.85%) for survival rate reminds us that the pond survival rate should be taken into account in the crossbreeding program to avoid yield decrease. However, most of the positive heterosis for survival rate was considerable, indicating that it is an advantage to obtain higher yield in this breeding program by crossbreeding. Heritability estimate for survival rate in the present study was low, which was consistent with other studies for survival in aquaculture. However, it was still significantly different from zero ($P<0.05$). Consequently, genetic gain for survival could be obtained in future by crossbreeding and selective breeding by increasing the selection intensity.

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