Hindawi
Aquaculture Research
Volume 2023, Article ID 8315364, 10 pages
https://doi.org/10.1155/2023/8315364

*Research Article*

# Heritability Estimates of Growth-Related Traits in Oriental River Prawns, *Macrobrachium nipponense*

**Hui Wang**,[1] **Yi Zhang**,[1,2] **Long Wang**,[1,2] **Tianyu Guan**,[1,2] **Guoliang Chang**,[1] **Nan Wu**,[1] **and Jiale Li**[2]

[1]*Jiangsu Engineering Laboratory for Breeding of Special Aquatic Organisms, Life Science School, Huaiyin Normal University, Huai'an 223300, Jiangsu, China*
[2]*College of Fisheries and Life Science, Shanghai Ocean University, Shanghai 201306, China*

Correspondence should be addressed to Hui Wang; hytcwhh@hytc.edu.cn

Received 18 August 2022; Revised 20 December 2022; Accepted 24 December 2022; Published 3 February 2023

Academic Editor: E. Ring



Breeding programs in oriental river prawn populations would benefit from a knowledge of heritabilities for growth-related traits to assess their potential for genetic improvement. This study reports the results of heritability estimation and evaluation of epistatic interactions for growth-related traits in oriental river prawn (*Macrobrachium nipponense*). The results showed that heritability estimates ($h^2$) were low to medium in magnitude, ranging between 0.10 (±0.02) and 0.22 (±0.01) for females and between 0.08 (±0.01) and 0.26 (±0.02) for males. The additive × additive epistasis was directional and synergistic for body weight (growth), body length, and two processing traits (abdominal meat weight and abdominal meat percentage). The presence of biallelic epistasis provides additional new information for the formulation of selection programs. Elimination of some sources of nonadditive effects from phenotypes can lead to more accurate genetic evaluations, and more desirable genetic gains could be achieved through the integration of heritability, additive effects (breeding values), and epistasis in oriental river prawns.

## 1. Introduction

The aquaculture industry of oriental river prawns is growing rapidly in China[1]. This species is very popular in the consumer market of the middle and lower reaches of the Changjiang River. Its total yield has reached 228,765 tons in 2021 alone [2], with its culture primarily concentrated in the Jiangsu and Zhejiang provinces. The sustainability of the aquaculture of oriental river prawn in China, nevertheless, is now confronting challenges. Genetic degradation of this species under culture has become a serious problem affecting yield and economic returns. Inbreeding, largely related to the biological features of prawns and seed production practices, are mainly responsible for this issue [3–5]. The seeds of oriental river prawns are produced in hatcheries through natural spawning. Brooder prawns may be wild-caught, but are more often selected from adult populations raised in grow-out ponds, and moreover, mature prawns often breed naturally in farmed ponds. Consequently, genetic degradation due to inbreeding often becomes established in cultured stocks. As a result, diminished growth/size at first maturity occurs. Oriental river prawn juveniles produced from pond-reared parents have a smaller average size than those produced from lake-collected berried females [4, 6, 7]. Although genetic improvement programs have been implemented through crossbreeding and selection in China to overcome the downsides incurred by inbreeding in oriental river prawns [1, 8], reliable genetic evaluation for this species is yet to be conducted.

Genetic evaluation allows for monitoring changes in genetic variation and gains for desired traits to be improved, and its accuracy depends upon how much nonadditive variation is removed from phenotypic variability and how large the sample size is [9–13]. Heritability estimates have been computed in commercial shrimp populations with different partitions of nonadditive components. Variation due to dominance may be confounded with additive genetic variation in estimates of heritability of *Penaeus monodon*

[14, 15], *Penaeus vannamei* [16–18], *Macrobrachium rosenbergii* [19–21], *Procambarus clarkii* [5], *Exopalaemon carinicauda* [22], and *Fenneropenaeus chinensis* [23]. In the study of Wang et al. [24], the dominance effect and its interaction with the environment were eliminated, but epistasis was confounded with additive variation in red swamp crayfish *P. clarkii*.

Epistasis, which describes the nonadditivity of effects between loci and acts as a source of genetic variation, should be a rule rather than an exception when estimating genetic parameters [9–12, 25–27]. Loci may interact in pairs or in groups of three or more. If a trait is affected by $n$ loci, the number of additive effects is $n$, whereas the number of biallelic epistatic effects is $n^2$. Thus, their cumulative effects may be large as $n$ increases irrespective of higher-order epistatic interactions such as triallelic epistasis. This points to the potential for significant epistasis in the expression of quantitative traits. In this sense, epistasis should not be neglected. Without epistatic effects partitioned out, estimates of heritability may be overestimated or inflated to varying degrees [10–13]. For example, Wang et al. [28] reported that the additive-by-additive interaction had a significant effect on body weight and body length in red common carp (*Cyprinus carpio*), whereas Joshi et al. [29] found that the additive-by-additive epistasis played a dominant role in *Oreochromis niloticus*. In addition, epistatic interactions play an important role in explaining the expression of heterosis [8, 30]. For a more accurate genetic evaluation, it is, therefore, necessary to examine the influence of epistasis. Although the presence of epistatic interactions has been suggested or implied in several aquatic animals, such as *Oncorhynchus mykiss* [31], *Argopecten purpuratus* [32], *Oreochromis aureus* [33], *Ictalurus punctatus* and *Ictalurus furcatus* [34], *Crassostrea gigas* [30, 35], and *Haliotis midae* [36], studies on epistasis in aquaculture species are very few. In particular, no results about epistasis have been reported in crustaceans.

Predicated on an incomplete diallel cross design and the analysis model that included additive, dominance, epistasis, and their interactions with the environment, the heritabilities, additive effects (breeding values), and additive × additive epistasis of nine growth-related traits of oriental river prawns were obtained in the present study. These results would contribute to a more reliable assessment of the genetic potential of this species and to more efficient improvement programs. To the authors' knowledge, this is the first report of heritabilities and epistatic interactions in oriental river prawn using an additive-dominance-epistasis model.

## 2. Materials and Methods

*2.1. Sourcing and Conditioning of Broodstock.* The broodstock prawns used for reproduction came from the Siyang aquafarm of Jiangsu Zhengfeng Fisheries Science & Technology Co., Ltd. (Jiangsu Province, China), where three strains of oriental river prawn are maintained: Gaoyou Lake strain (GY), Taihu Lake strain (TH), and Hongze Lake strain (HZ). The broodstock prawns demonstrated good vitality and were void of any exterior injury. The area of the earthen ponds for broodstock acclimation was 0.1 $hm^2$ (water depth 1.2 m). Harmful organisms in the ponds were eliminated by applying quicklime (0.15 $kg \cdot m^{-2}$ at a water depth of 10 to 15 cm) 10 days prior to stocking of broodstock. Water inflow to the ponds was filtered using a fine-mesh screen net to avert the entry of wild fish and other harmful organisms into the ponds. With a sufficient number of broodstock sampled and measured (Table 1), the parents were stocked at a density of 5 indiv. $m^{-2}$. Formula pelleted feed produced by Qingyuan Seashell Biotechnology Co., Ltd., Qingyuan, China (crude protein 43%, fat 7%) was fed to the prawns per day at 3 to 4% body weight daily to provide necessary nutrients for gonad development and to prevent aggressive behaviors such as cannibalism. Males were conditioned separately from females. Water temperature ranged between 22°C and 25°C and dissolved oxygen was over 5 $mg \cdot L^{-1}$. These technical steps ensured good conditioning of breeders and laid a solid foundation for spawning synchrony and high-quality seeds.

*2.2. Mating Design.* An incomplete diallel cross design was adopted in this study to realize the research objectives (Table 2). According to this mating design, the brooders of each combination were restocked (same density as above, and ♂ : ♀ = 1 : 3, standard body length >4 cm) in an earthen pond (0.1 $hm^2$ for each pond and water depth 1.2 m) for random mating. Each pond was planted with water weeds such as *Alternanthera philoxeroides*, *Hydrilla verticillate,* or *Potamogeton crispus* at the edges of the ponds to provide shelter for the breeders. It is necessary to make clear that due to the practical infeasibility to establish families (full- and half-sib) in oriental river prawn, the diallel cross design was adopted in the present study.

*2.3. Hatching and Larviculture for $F_1$ Generation.* Mating in oriental river prawns is generally accomplished prior to spawning. Females begin to spawn within 24 hours after mating, and spawning occurs mostly at night [3]. During hatching, the egg-bearing of females was checked every 3 days. Broodstock prawns were fed with the feed as indicated above. The feeding amount was adjusted to 5 to 8% of their body weight. Water quality management was the same as described above. When the eyespots arose (fertilized eggs turned transparent and pale in color at this time), soybean milk was applied to enrich water and support natural diets (live zooplankton such as *Artemia*, rotifers, copepods, and cladocerans). Ample natural diets were used for the first feeding of hatched larvae to ensure larval yield. Egg hatching took approximately 3 weeks (from fertilization to hatching out as zoea). When hatching ended (all zoeal larvae left their mother and fended for themselves), broodstock prawns were removed from the hatching ponds using specialized tools such as ground cages and larval rearing commenced. Larvae began to feed on *Artemia nauplii* on the second day after hatching out. The density of *Artemia nauplii* was kept at a level equal to or larger than $10^4$ indiv. $L^{-1}$. The growth and feeding of larvae were

Table 1: Phenotypic means and coefficients of variation (CV) of nine growth-related traits of three oriental river prawn strains for 3 generations.

| Trait[1] | Females[2] | | | | | | Males[3] | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | | | CV (%) | | | Mean | | | CV (%) | | |
| | $F_0$ | $F_1$ | $F_2$ | $F_0$ | $F_1$ | $F_2$ | $F_0$ | $F_1$ | $F_2$ | $F_0$ | $F_1$ | $F_2$ |
| BW (g) | 2.06 | 2.06 | 2.05 | 22.10 | 21.34 | 20.13 | 2.44 | 2.35 | 2.21 | 26.54 | 27.85 | 23.62 |
| BL (mm) | 40.25 | 40.97 | 41.88 | 23.45 | 22.50 | 9.84 | 41.82 | 42.50 | 41.91 | 24.38 | 23.23 | 11.67 |
| CHL (mm) | 31.81 | 30.18 | 35.54 | 14.24 | 11.32 | 19.16 | 38.75 | 39.67 | 40.90 | 19.49 | 17.54 | 19.17 |
| CTL (mm) | 18.09 | 17.08 | 16.98 | 12.61 | 10.69 | 11.80 | 19.74 | 17.70 | 17.40 | 15.36 | 12.18 | 14.53 |
| CTW (mm) | 8.94 | 8.80 | 8.83 | 22.35 | 20.29 | 13.08 | 9.97 | 9.40 | 9.07 | 14.44 | 12.12 | 15.39 |
| SAW (mm) | 7.98 | 7.70 | 7.38 | 25.85 | 26.15 | 12.32 | 7.62 | 7.10 | 7.26 | 15.51 | 12.85 | 13.35 |
| SAH (mm) | 9.12 | 8.82 | 8.42 | 18.44 | 17.24 | 13.25 | 8.78 | 8.14 | 8.34 | 14.08 | 12.06 | 11.85 |
| TMW (g) | 0.75 | 0.66 | 0.78 | 24.67 | 23.87 | 21.00 | 0.81 | 0.75 | 0.81 | 25.84 | 26.99 | 20.23 |
| TMP (%) | 34.47 | 32.40 | 37.02 | 13.32 | 11.73 | 8.19 | 36.13 | 35.86 | 38.14 | 16.63 | 14.62 | 8.61 |

[1]BW, body weight; BL, body length; CHL, chela length; CTL, cephalothorax length; CTW, cephalothorax width; SAW, second abdominal segment width; SAH, second abdominal segment height; TMW, tail meat weight; TMP, tail meat percentage. [2]Sample size for females of generation $F_0$, $F_1$, and $F_2$ is 1693, 1686, 1711, respectively. [3]Sample size for males of generation $F_0$, $F_1$, and $F_2$ is 1679, 1724, 1736, respectively.

Table 2: Mating design of an incomplete diallel cross between three strains of *Macrobrachium* nipponense.

| Strain | GY♂ | TH♂ | HZ♂ |
|---|---|---|---|
| GY♀ | GY♀ × GY♂ | GY♀ × TH♂ | GY♀ × HZ♂ |
| TH♀ | | TH♀ × TH♂ | TH♀ × HZ♂ |
| HZ♀ | | | HZ♀ × HZ♂ |

*Note.* GY, Gaoyou lake strain; TH, Taihu lake strain; HZ, Hongze lake strain.

monitored each day. Dissolved oxygen was over 5 mg·L$^{-1}$, ammonia-N was less than 0.02 mg·L$^{-1}$, and the water temperature ranged from 24°C to 26°C during hatching and larval rearing.

*2.4. Grow-Out.* The larval development of oriental river prawns comprises 9 zoeal phases, which typically take about 3 weeks under the range of temperatures given above. When larvae metamorphose, they become post-larvae (PL, body length 0.9 to 1.1 cm), which are very analogous to adults in morphology and ecological habits. Then, the PL from each mating combination was placed into 3 polyethylene hapas (10 m × 6 m × 1.5 m, 100 mesh cm$^{-2}$) for 7 weeks, with a stocking density of 250 indiv. m$^{-2}$. There was a total of 27 hapas for 9 mating combinations. All hapas, which were set up in one earthen pond (2 hm$^2$), were 30 cm higher than the water surface and fastened to wood pillars to withstand the impact of winds and waves. One-quarter of each hapa area was planted with weeds for PL to inhabit. The PL was fed daily from 8:00 am to 9:00 am and from 4:00 pm to 5:00 pm. Prior to PL stocking, unwanted organisms (wild fish, frog eggs, and leeches) were eradicated from the ponds using quicklime. Water management was the same as described above; in particular, water quality was checked each day to prevent eutrophication and anoxia.

*2.5. Production of $F_2$ Generation.* Epistasis entails data from the $F_2$ generation, apart from those of $F_0$ and $F_1$ offspring [10–12]. Large numbers of $F_1$ progeny from each mating combination were sampled to become parents of $F_2$ males and females (grown separately; [10, 11]). Then, $F_1$ populations were sampled for data collection after water drainage. The production of $F_2$ began in early May 2020 through matings between males and females coming from within the same mating combination (♂ : ♀ = 1 : 3), and the growth of the $F_2$ populations ended in late Aug 2020. All technical measures used for the $F_2$ generation were roughly the same as those used for the $F_1$ generation.

*2.6. Data Collection.* The $F_1$ and $F_2$ generations were sampled in late August 2019 and 2020, respectively, to measure growth-related traits. These traits included body weight (BW, g); standard body length (tip of the rostrum to end of telson; BL, mm); chela length (CHL, mm); cephalothorax length (CTL, mm); cephalothorax width (CTW, mm); second abdominal segment width (SAW, mm), second abdominal segment height (SAH, mm); tail meat weight (TMW, g); and tail meat percentage (TMP, %), computed as the percentage of abdominal weight divided by body weight. A summary of these traits in the $F_0$, $F_1$, and $F_2$ generations is given in Table 1. A total of 10229 oriental river prawns were measured and sexed, including 1693 females and 1679 males in the $F_0$ generation, 1686 females and 1724 males in the $F_1$ generation, and 1711 females and 1736 males in the $F_2$ generation. All growth-related traits were measured to the nearest 0.01 mm (vernier caliper) or 0.01 g (electronic balance).

*2.7. Genetic Analysis Model.* The mixed linear model used to analyze males and females separately for each individual trait included additive, dominance, epistasis genetic effects, as

well as their interactions with the environment. The single-trait mixed model, in matrix notation [10, 11], was as follows:

$$\mathbf{p} = \mathbf{Xb} + \mathbf{U_A e_A} + \mathbf{U_D e_D} + \mathbf{U_{AA} e_{AA}} + \mathbf{U_{AE} e_{AE}} + \mathbf{U_{DE} e_{DE}} + \mathbf{U_{AAE} e_{AAE}} + \mathbf{H_B e_B} + \mathbf{e_\varepsilon}, \quad (1)$$

where $\mathbf{p}$ is the vector of records for each individual trait (BW, BL, CHL, CTL, CTW, SAW, SAH, TMW, and TMP); $\mathbf{X}$ is the coefficient matrix relating individual trait records to fixed effects; $\mathbf{b}$ is the vector of fixed effects including the overall mean $\mu$, pond effect, and year effect; $\boldsymbol{U}_\mathbf{A}$ is the coefficient matrix relating individual trait records to additive genetic effect; $\mathbf{e}_A$ is the vector of additive genetic effects, and $e_A \sim (0, \sigma_A^2\mathbf{I})$; $\mathbf{U_D}$ is the coefficient matrix relating individual trait records to dominance effects; $\boldsymbol{e_D}$ is the vector of dominance effects, and $\mathbf{e_D} \sim (0, \sigma_D^2\mathbf{I})$; $\mathbf{U_{AA}}$ is the coefficient matrix relating individual trait records to additive × additive epistatic effects; $\mathbf{e_{AA}}$ is the vector of additive × additive epistatic effects, and $\mathbf{e}_{AA} \sim (0, \sigma_{AA}^2\mathbf{I})$; $\mathbf{U_{AE}}$ is the coefficient matrix relating individual trait records to additive × environment interaction effect; $\mathbf{e_{AE}}$ is the vector of additive × environment interaction effects, and $\mathbf{e_{AE}} \sim (0, \sigma_{AE}^2\mathbf{I})$; $\mathbf{U_{DE}}$ is the coefficient matrix relating individual trait records to dominance × environment interaction effects; $\boldsymbol{e_{DE}}$ is the vector of dominance × environment interaction effects, and $\mathbf{e_{DE}} \sim (0, \sigma_{DE}^2\mathbf{I})$; $\mathbf{U_{AAE}}$ is the coefficient matrix relating individual trait records to additive × additive × environment interaction effects; $\mathbf{e_{AAE}}$ is the vector of additive × additive × environment interaction effects, and $\mathbf{e_{AAE}} \sim (0, \sigma_{AAE}^2\mathbf{I})$; $\boldsymbol{H}_\mathbf{B}$ is the coefficient matrix of hapa effects; $\boldsymbol{e}_\mathbf{B}$ is the vector of hapa effects, and $\mathbf{e_B} \sim (0, \sigma_B^2\mathbf{I})$; $\boldsymbol{e}_\varepsilon$ is the vector of residuals and $\mathbf{e}_\varepsilon \sim (0, \sigma_\varepsilon^2\mathbf{I})$; and $\boldsymbol{I}$ is the identity matrix. The above analysis model corresponded to the mating design used in the present study. Although this model did not account for additive genetic relationships among individuals, additive genetic relationships between individuals from 3 generations in this study were the same (no overlapping generations). These relationships were embedded into the mixed model by the diallel cross design [10, 11].

Experimental data for the nine growth-related traits of oriental river prawn were collected for two years. Thus, years were regarded as two different environments to account for genotype-environment interactions.

*2.8. Heritability Estimates and Additive Genetic Prediction.* Variances for the mixed genetic model were estimated using restricted maximum likelihood (REML). This method has been applied to solving various types of complicated genetic models [10–12]. Variances estimated by the mixed model for each trait were used to compute estimates of genetic variance components using the following formulae [10, 11]:

$$\widehat{\mathbf{V}}_\mathbf{A} = 2\widehat{\boldsymbol{\sigma}}_\mathbf{A}^2, \widehat{\mathbf{V}}_\mathbf{D} = \widehat{\boldsymbol{\sigma}}_\mathbf{D}^2, \widehat{\mathbf{V}}_\mathbf{AA} = 4\widehat{\boldsymbol{\sigma}}_\mathbf{AA}^2, \widehat{\mathbf{V}}_\mathbf{AE} = 2\widehat{\boldsymbol{\sigma}}_\mathbf{AE}^2, \widehat{\mathbf{V}}_\mathbf{DE} = \widehat{\boldsymbol{\sigma}}_\mathbf{DE}^2, \text{and } \widehat{\mathbf{V}}_\mathbf{AAE} = \mathbf{4}\widehat{\boldsymbol{\sigma}}_\mathbf{AAE}^2, \quad (2)$$

where $\widehat{\mathbf{V}}_\mathbf{A}$ is the estimate of additive genetic variance; $\widehat{\mathbf{V}}_\mathbf{D}$ is the estimate of dominance genetic variance; $\widehat{\mathbf{V}}_\mathbf{AA}$ is the estimate of additive × additive genetic variance; $\widehat{\mathbf{V}}_\mathbf{AE}$ is the estimate of the additive × environment interaction variance; $\widehat{\mathbf{V}}_\mathbf{DE}$ is the estimate of dominance × environment interaction variance; $\widehat{\mathbf{V}}_\mathbf{AAE}$ is the estimate of interaction variance between additive × additive and environment. Narrow-sense heritability ($h^2$) was estimated as the ratio of the additive genetic variance to the phenotypic variance ($\boldsymbol{V}_\mathbf{p}$), i.e., $h^2 = \widehat{\mathbf{V}}_\mathbf{A} / \widehat{\mathbf{V}}_\mathbf{p}$, $\widehat{\mathbf{V}}_\mathbf{p} = \sum_{\mathbf{i=1}}^{\mathbf{n}} (\mathbf{p_i} - \overline{\mathbf{p}})^2 / \mathbf{n} - \mathbf{1}$, where $p_i$ is the phenotypic record and $n$ is the sample size. The single-trait mixed model used here permits the estimation of variance components and heritabilities as well as the prediction of random effects [10–12, 37]. The best linear unbiased prediction (BLUP) was used to predict the additive and biallelic epistatic effects of the traits under consideration. A repeated sampling technique (Jackknife) was used to compute the standard errors of varying estimates and predictions, and parameters were tested using $t$ statistic for significance [10, 11]. All computations were conducted using QGAStation software (v 2.0, Zhejiang University, China).

## 3. Results

Survival rates ranged between 29.50% and 35.60% at the end of the growth period in generations $F_1$ and $F_2$. Differences in average survival among mating combinations and among hapas were not significant ($P > 0.05$). Between 10.50% and 12.10% of the females in the $F_1$ and $F_2$ generations were ovigerous. These females were excluded from the study because egg-bearing could retard their growth (i.e., heritabilities of growth-related traits in the ovigerous female population were not estimated in this study). In addition, no diseases occurred due to good management of the whole experimental process. Although there were lower survival rates in $F_1$ and $F_2$ generations, the progenies used for this study were sufficient.

*3.1. Description of $F_0$, $F_1$, and $F_2$ Generations.* The phenotypic means and coefficients of variation of the 9 growth-related traits of oriental river prawns in $F_0$, $F_1$, and $F_2$ generations are given in Table 1. These statistics were obtained based on samplings from three generations. Body weight and morphological traits (BL, CHL, CTL, and CTW) of males were higher than those of females. Two processing traits, TMW and TMP, of males were higher than those of females. Conversely, the SAW and SAH of females were higher than those of males. Second abdominal segment width and height are important for female fecundity. These two traits can form a ventral brood chamber in which eggs are carried. The higher the SAW and SAH, the greater the egg-bearing capacity. Relative phenotypic variations (coefficient of variation, CV%) varied from 8.19% to 27.85%.

*3.2. Variance Components.* Estimates of variance components of the 9 growth-related traits for females and males of oriental river prawn are shown in Tables 3 and 4. Variations of nearly all sources for the 9 growth-related traits were detected, but $\widehat{V}_{AAE}$ of TMW failed to be detected in both sexes; the additive × environment interaction variance ($\widehat{V}_{AE}$) of TMW was not detected in females, it was very small for males either. Values of estimated variance components varied with trait and sex. For example, $\widehat{V}_A$ of BW was $0.11 \pm 0.01\,g^2$ in females and $0.16 \pm 0.02\,g^2$ in males; the additive × additive genetic variance ($\widehat{V}_{AA}$) of BW was $0.05 \pm 0.01\,g^2$ in females and $0.10 \pm 0.01\,g^2$ in males. The additive-genetic variance ($\widehat{V}_A$) of CHL was $5.05 \pm 0.03\,mm^2$ in females and $7.01 \pm 0.05\,mm^2$ in males; the additive × additive genetic variance ($\widehat{V}_{AA}$) of CHL was $1.25 \pm 0.02\,mm^2$ in females and $1.45 \pm 0.02\,mm^2$ in males. The additive-genetic variance and additive × additive genetic variance ($\widehat{V}_A$ and $\widehat{V}_{AA}$) of TMW were $0.01 \pm 0.01\,g^2$ and $0.0056 \pm 0.01\,g^2$, respectively, in females, and were $0.02 \pm 0.01\,g^2$ and $0.006 \pm 0.01\,g^2$, respectively, in males. In contrast to the estimates of additive and epistatic genetic variances for other traits, those of TMW were the smallest.

*3.3. Estimates of Heritability.* Estimates of heritability for the 9 growth-related traits for females and males of oriental river prawn are given in Tables 5 and 6, respectively. Ratios of the other 6 variance components to phenotypic variances are also presented in the two Tables. All heritability estimates were obtained using the data collected at the time when the selection program was generally pursued in China [4, 5]. There exists sexual dimorphism in the oriental river prawn. Considering that selection pressure exerted on males is greater than that on females in this species during actual selective breeding, heritability estimation was undertaken within each sex of the oriental river prawn in this study. Heritability estimates for the 9 growth-related traits were statistically significant at a 5% level. Heritabilities were low to moderate in value and varied from 0.10 (±0.02) for CTW to 0.22 (±0.01) for BW in females and from 0.08 (±0.01) for SAW to 0.26 (±0.01) for BW in males. Heritabilities of BW, CTL, and two processing traits (TMW and TMP) stood within moderate ranges. The percentages of phenotypic variation explained by the $\widehat{V}_{AA}$ of BW, BL, CHL, CTL, SAW, SAH, TMW, and TMP were significant ($P < 0.05$), while the percentages of variation attributable to the $\widehat{V}_{AA}$ of CTW, SAW, and SAH statistically did not differ from zero in males ($P > 0.05$).

*3.4. Prediction of Genetic Effects.* Predicted values of additive and epistatic (additive × additive) genetic effects of the 9 growth-related traits for females and males from 3 strains of oriental river prawn are provided in Tables 7 and 8, respectively. The additive genetic effects of BW, BL, CHL, CTL, CTW, TMW, and TMP were significant ($P < 0.05$). The epistatic genetic effects of BW, BL, CHL, TMW, and TMP were significant ($P < 0.05$), while those of CTL and CTW were nonsignificant ($P > 0.05$) in females and males. The additive and epistatic genetic effects for SAW and SAH were not detected in each sex of the 3 strains. For BW, the additive genetic effects in the HZ strain were greater than those in GY and TH strains in both sexes; the epistatic genetic effects in each sex of the 3 strains were all positive and favorable to growth. Additive and epistatic genetic effects for BL, CHL, TMW, and TMP were similar to those for BW.

## 4. Discussion

For more accurate genetic evaluation, the additive genetic variations of the 9 growth-related traits in oriental river prawn were estimated using an incomplete diallel cross design and a complex linear mixed model. Additive genetic variation is tightly enveloped by nonadditive variations, thus unveiling additive genetic variation is not an easy task [9, 12]. What matters the most is to estimate the additive genetic variation as accurately as possible [10, 11, 38]. The mere separation of dominance and dominance × environment interaction from phenotype may not suffice [24]. Empirical evidence confirmed the presence of epistasis in red common carp, *C. carpio* [28], and in Nile tilapia, *O. niloticus* [29]. Unlike the studies of Xu et al. [39] and Li et al. [40] in whiteleg shrimp, *P. vannamei*, of Kitcharoen et al. [37] and Luan et al. [41] in giant river prawn *M. rosenbergii* and analogous studies in other crustaceans, the variances due to additive × additive, additive × environment, and additive × additive × environment interactions were separated from the additive variance in the present study. Thus, relatively "cleaner" estimates of the additive genetic variations were obtained (Tables 3 and 4). For instance, the CHL variances attributable to dominance, additive × additive, dominance × environment, additive × environment, and additive × additive × environment were 5.02, 1.06, 4.13, 2.32, and $2.11\,mm^2$ in females, respectively, and 6.04, 1.51, 6.85, 2.78, and $2.46\,mm^2$ in males, respectively. These results clearly show the need for separating nonadditive sources of variation out of phenotypic variances. The heritability estimates of growth (body weight), body length, and two processing traits fell close to the lower end of the range (Tables 5 and 6). Only one report of heritability estimates of body weight and body length in 97-day-old oriental river prawn has been published to date [42]. Estimates obtained in

Table 3: Estimates of variance components (±SE) for nine traits in female *Macrobrachium nipponense* using the REML approach.

| Trait | $\hat{V}_A \pm$ SE | $\hat{V}_D \pm$ SE | $\hat{V}_{AA} \pm$ SE | $\hat{V}_{DE} \pm$ SE | $\hat{V}_{AE} \pm$ SE | $\hat{V}_{AAE} \pm$ SE | $\hat{V}_e \pm$ SE |
|---|---|---|---|---|---|---|---|
| BW (g) | 0.11 ± 0.01 | 0.08 ± 0.01 | 0.05 ± 0.01 | 0.05 ± 0.01 | 0.04 ± 0.01 | 0.04 ± 0.01 | 0.14 ± 0.02 |
| BL (mm) | 1.79 ± 0.03 | 2.32 ± 0.02 | 1.26 ± 0.02 | 2.02 ± 0.02 | 1.45 ± 0.02 | 0.70 ± 0.02 | 1.34 ± 0.03 |
| CHL (mm) | 5.05 ± 0.03 | 5.48 ± 0.04 | 1.25 ± 0.02 | 4.21 ± 0.03 | 1.43 ± 0.02 | 1.08 ± 0.01 | 6.02 ± 0.04 |
| CTL (mm) | 0.44 ± 0.02 | 0.37 ± 0.02 | 0.27 ± 0.02 | 0.40 ± 0.02 | 0.26 ± 0.02 | 0.22 ± 0.02 | 0.92 ± 0.02 |
| CTW (mm) | 0.18 ± 0.02 | 0.16 ± 0.02 | 0.08 ± 0.01 | 0.27 ± 0.02 | 0.12 ± 0.01 | 0.15 ± 0.02 | 0.86 ± 0.02 |
| SAW (mm) | 0.24 ± 0.02 | 0.30 ± 0.02 | 0.25 ± 0.02 | 0.28 ± 0.02 | 0.26 ± 0.02 | 0.19 ± 0.02 | 0.51 ± 0.02 |
| SAH (mm) | 0.17 ± 0.02 | 0.33 ± 0.02 | 0.16 ± 0.01 | 0.27 ± 0.02 | 0.16 ± 0.02 | 0.21 ± 0.02 | 0.28 ± 0.02 |
| TMW (g) | 0.01 ± 0.01 | 0.02 ± 0.01 | 0.0056 ± 0.01 | 0.02 ± 0.01 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.04 ± 0.01 |
| TMP (%) | 2.14 ± 0.03 | 2.06 ± 0.02 | 0.95 ± 0.03 | 1.76 ± 0.03 | 1.01 ± 0.02 | 1.05 ± 0.02 | 2.29 ± 0.02 |

*Note.* (1) Sample size = 5090 for all traits of interest. (2) BW, body weight; BL, body length; CHL, chela length; CTL, cephalothorax length; CTW, cephalothorax width; SAW, second abdominal segment width; SAH, second abdominal segment height; TMW, tail meat weight; TMP, tail meat percentage.

Table 4: Estimates of variance components (±SE) for nine traits in male *Macrobrachium nipponense* using the REML approach.

| Trait | $\hat{V}_A \pm$ SE | $\hat{V}_D \pm$ SE | $\hat{V}_{AA} \pm$ SE | $\hat{V}_{DE} \pm$ SE | $\hat{V}_{AE} \pm$ SE | $\hat{V}_{AAE} \pm$ SE | $\hat{V}_e \pm$ SE |
|---|---|---|---|---|---|---|---|
| BW (g) | 0.16 ± 0.02 | 0.06 ± 0.01 | 0.10 ± 0.01 | 0.08 ± 0.01 | 0.07 ± 0.01 | 0.05 ± 0.01 | 0.10 ± 0.01 |
| BL (mm) | 3.48 ± 0.04 | 3.32 ± 0.03 | 1.66 ± 0.02 | 3.31 ± 0.02 | 3.28 ± 0.02 | 2.44 ± 0.02 | 0.89 ± 0.02 |
| CHL (mm) | 7.01 ± 0.05 | 6.58 ± 0.04 | 1.45 ± 0.02 | 7.21 ± 0.04 | 1.69 ± 0.02 | 1.48 ± 0.02 | 5.35 ± 0.03 |
| CTL (mm) | 0.81 ± 0.03 | 0.76 ± 0.03 | 0.55 ± 0.02 | 0.68 ± 0.02 | 0.27 ± 0.02 | 0.41 ± 0.02 | 1.10 ± 0.02 |
| CTW (mm) | 0.22 ± 0.02 | 0.28 ± 0.02 | 0.06 ± 0.01 | 0.31 ± 0.02 | 0.20 ± 0.02 | 0.15 ± 0.01 | 0.33 ± 0.02 |
| SAW (mm) | 0.06 ± 0.01 | 0.11 ± 0.02 | 0.04 ± 0.02 | 0.14 ± 0.01 | 0.07 ± 0.01 | 0.08 ± 0.01 | 0.27 ± 0.02 |
| SAH (mm) | 0.09 ± 0.02 | 0.23 ± 0.02 | 0.03 ± 0.01 | 0.21 ± 0.02 | 0.06 ± 0.01 | 0.12 ± 0.01 | 0.25 ± 0.02 |
| TMW (g) | 0.02 ± 0.01 | 0.01 ± 0.01 | 0.006 ± 0.01 | 0.018 ± 0.01 | 0.01 ± 0.01 | 0.00 ± 0.00 | 0.058 ± 0.01 |
| TMP (%) | 3.15 ± 0.03 | 3.23 ± 0.02 | 1.02 ± 0.02 | 2.73 ± 0.02 | 1.11 ± 0.01 | 1.00 ± 0.01 | 3.08 ± 0.02 |

*Note.* (1) Sample size = 5139 for all traits of interest. (2) BW, body weight; BL, body length; CHL, chela length; CTL, cephalothorax length; CTW, cephalothorax width; SAW, second abdominal segment width; SAH, second abdominal segment height; TMW, tail meat weight; TMP, tail meat percentage.

Table 5: Proportions and standard errors of phenotypic variation accounted for by variance components for the 9 growth-related traits in female *Macrobrachium nipponense*.

| Trait | $\hat{V}_A/\hat{V}_P \pm$ SE | $\hat{V}_D/\hat{V}_P \pm$ SE | $\hat{V}_{AA}/\hat{V}_P \pm$ SE | $\hat{V}_{DE}/\hat{V}_P \pm$ SE | $\hat{V}_{AE}/\hat{V}_P \pm$ SE | $\hat{V}_{AAE}/\hat{V}_P \pm$ SE | $\hat{V}_e/\hat{V}_P \pm$ SE |
|---|---|---|---|---|---|---|---|
| BW (g) | 0.22 ± 0.01** | 0.16 ± 0.08 | 0.10 ± 0.01* | 0.10 ± 0.02 | 0.08 ± 0.02 | 0.08 ± 0.02 | 0.26 ± 0.11 |
| BL (mm) | 0.16 ± 0.02** | 0.21 ± 0.07 | 0.12 ± 0.02* | 0.19 ± 0.01 | 0.13 ± 0.02 | 0.06 ± 0.02 | 0.13 ± 012 |
| CHL (mm) | 0.21 ± 0.02** | 0.22 ± 0.04 | 0.05 ± 0.01* | 0.17 ± 0.04 | 0.06 ± 0.01 | 0.04 ± 0.01 | 0.25 ± 0.09 |
| CTL (mm) | 0.14 ± 0.01** | 0.12 ± 0.05 | 0.09 ± 0.02* | 0.13 ± 0.02 | 0.09 ± 0.01 | 0.07 ± 0.02 | 0.30 ± 0.10 |
| CTW (mm) | 0.10 ± 0.02* | 0.09 ± 0.04 | 0.04 ± 0.01 | 0.15 ± 0.03 | 0.07 ± 0.02 | 0.08 ± 0.02 | 0.47 ± 0.15 |
| SAW (mm) | 0.12 ± 0.01* | 0.15 ± 0.06 | 0.12 ± 0.02* | 0.14 ± 0.02 | 0.13 ± 0.01 | 0.09 ± 0.02 | 0.25 ± 0.12 |
| SAH (mm) | 0.11 ± 0.02* | 0.21 ± 0.05 | 0.10 ± 0.02* | 0.17 ± 0.02 | 0.10 ± 0.03 | 0.13 ± 0.03 | 0.18 ± 0.10 |
| TMW (g) | 0.13 ± 0.01* | 0.22 ± 0.07 | 0.06 ± 0.01* | 0.18 ± 0.01 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.41 ± 0.10 |
| TMP (%) | 0.19 ± 0.01** | 0.18 ± 0.08 | 0.08 ± 0.02* | 0.16 ± 0.01 | 0.09 ± 0.01 | 0.09 ± 0.02 | 0.21 ± 0.12 |

*Note.* (1) * or ** indicates significance at 5% or 1% level. (2) Sample size = 5090 for all traits of interest. (3) BW, body weight; BL, body length; CHL, chela length; CTL, cephalothorax length; CTW, cephalothorax width; SAW, second abdominal segment width; SAH, second abdominal segment height; TMW, tail meat weight; TMP, tail meat percentage. (4) Only those parameters in the 2nd and 4th columns were tested.

this study are comparable to theirs. Due to the inability to analyze the maternal effect with incomplete diallel (cross design), it, if any, was confounded with the additive effects in the present study. Joshi et al. [29, 43] reported the presence of maternal effect on body weight at harvest, body depth, body length, and fillet weight in Nile tilapia, *O. niloticus*. Separation of various nonadditive sources of variation including the common environmental effect as well as larger sample sizes guarantees relatively more accurate genetic evaluation. The data from 3 generations of oriental river prawns were used for the separation of additive epistasis (Table 1). If the generation gap is larger, the experimental design used in this study may be unfeasible because this would take too long.

There are many possible types of epistasis. For biallelic epistasis, for example, there are 3 forms, i.e., additive × additive, additive × dominance, and dominance × dominance [26]. The last two epistatic interactions cannot be separated from phenotype based on the analysis model and mating design used in the present study, thus they were confounded with the additive effects. They are, however, generally ignored in genetic analyses of animals and plants due to their relatively weaker effects [10–12, 26, 27]. Since additive × additive epistasis is a type of genetic effect that can be modified through selection, it needs to

Table 6: Proportions and standard errors of phenotypic variation accounted for by variance components of the 9 growth-related traits in male *Macrobrachium nipponense*.

| Trait | $\hat{V}_A/\hat{V}_P \pm$ SE | $\hat{V}_D/\hat{V}_P \pm$ SE | $\hat{V}_{AA}/\hat{V}_P \pm$ SE | $\hat{V}_{DE}/\hat{V}_P \pm$ SE | $\hat{V}_{AE}/\hat{V}_P \pm$ SE | $\hat{V}_{AAE}/\hat{V}_P \pm$ SE | $\hat{V}_e/\hat{V}_P \pm$ SE |
|---|---|---|---|---|---|---|---|
| BW (g) | $0.26 \pm 0.02^{**}$ | $0.10 \pm 0.08$ | $0.16 \pm 0.05^{**}$ | $0.13 \pm 0.01$ | $0.11 \pm 0.02$ | $0.08 \pm 0.02$ | $0.16 \pm 0.08$ |
| BL (mm) | $0.19 \pm 0.01^{**}$ | $0.18 \pm 0.09$ | $0.09 \pm 0.06^{*}$ | $0.18 \pm 0.01$ | $0.18 \pm 0.02$ | $0.13 \pm 0.03$ | $0.05 \pm 0.03$ |
| CHL (mm) | $0.23 \pm 0.01^{**}$ | $0.21 \pm 0.09$ | $0.05 \pm 0.04^{*}$ | $0.22 \pm 0.02$ | $0.06 \pm 0.01$ | $0.05 \pm 0.01$ | $0.18 \pm 0.10$ |
| CTL (mm) | $0.18 \pm 0.02^{**}$ | $0.17 \pm 0.07$ | $0.12 \pm 0.06^{*}$ | $0.16 \pm 0.02$ | $0.05 \pm 0.01$ | $0.09 \pm 0.02$ | $0.23 \pm 0.12$ |
| CTW (mm) | $0.14 \pm 0.02^{**}$ | $0.18 \pm 0.08$ | $0.04 \pm 0.03$ | $0.20 \pm 0.01$ | $0.13 \pm 0.02$ | $0.10 \pm 0.02$ | $0.21 \pm 0.12$ |
| SAW (mm) | $0.08 \pm 0.01^{*}$ | $0.15 \pm 0.05$ | $0.02 \pm 0.01$ | $0.19 \pm 0.01$ | $0.09 \pm 0.03$ | $0.11 \pm 0.02$ | $0.36 \pm 0.13$ |
| SAH (mm) | $0.09 \pm 0.01^{*}$ | $0.23 \pm 0.06$ | $0.03 \pm 0.02$ | $0.21 \pm 0.01$ | $0.06 \pm 0.01$ | $0.12 \pm 0.02$ | $0.27 \pm 0.11$ |
| TMW (g) | $0.17 \pm 0.01^{**}$ | $0.07 \pm 0.05$ | $0.05 \pm 0.01^{*}$ | $0.15 \pm 0.02$ | $0.08 \pm 0.01$ | $0.00 \pm 0.00$ | $0.48 \pm 0.11$ |
| TMP (%) | $0.20 \pm 0.02^{**}$ | $0.21 \pm 0.05$ | $0.07 \pm 0.01^{*}$ | $0.18 \pm 0.03$ | $0.07 \pm 0.02$ | $0.06 \pm 0.01$ | $0.21 \pm 0.12$ |

*Note.* (1) * or ** indicates significance at 5% or 1% level. (2) Sample size = 5139 for all traits of interest. (3) BW, body weight; BL, body length; CHL, chela length; CTL, cephalothorax length; CTW, cephalothorax width; SAW, second abdominal segment width; SAH, second abdominal segment height; TMW, tail meat weight; TMP, tail meat percentage. (4) Only those parameters in the 2nd and 4th columns were tested.

Table 7: Predicted values of additive and epistatic (additive × additive) genetic effects for nine traits in three strains of female *Macrobrachium nipponense* using the BLUP approach.

| Trait | GY strain | | TH strain | | HZ strain | |
|---|---|---|---|---|---|---|
| | Additive | Epistatic | Additive | Epistatic | Additive | Epistatic |
| BW (g) | $-0.08 \pm 0.01^{*}$ | $0.10 \pm 0.04^{*}$ | $-0.09 \pm 0.03^{*}$ | $0.15 \pm 0.02^{*}$ | $0.17 \pm 0.03^{**}$ | $0.18 \pm 0.03^{**}$ |
| BL (mm) | $-0.07 \pm 0.02^{*}$ | $0.13 \pm 0.02^{**}$ | $-0.05 \pm 0.01^{*}$ | $0.17 \pm 0.02^{**}$ | $0.12 \pm 0.02^{**}$ | $0.16 \pm 0.02^{**}$ |
| CHL (mm) | $-0.12 \pm 0.02^{**}$ | $0.07 \pm 0.01^{*}$ | $-0.08 \pm 0.01^{*}$ | $0.06 \pm 0.01^{*}$ | $0.20 \pm 0.04^{**}$ | $0.10 \pm 0.02^{*}$ |
| CTL (mm) | $-0.06 \pm 0.01^{*}$ | $-0.01 \pm 0.01$ | $-0.09 \pm 0.02^{*}$ | $-0.03 \pm 0.01$ | $0.15 \pm 0.02^{**}$ | $-0.03 \pm 0.02$ |
| CTW (mm) | $-0.05 \pm 0.01^{*}$ | $-0.03 \pm 0.01$ | $-0.02 \pm 0.01$ | $-0.05 \pm 0.03$ | $0.07 \pm 0.01^{*}$ | $-0.02 \pm 0.01$ |
| SAW (mm) | $0.00 \pm 0.00$ | $0.02 \pm 0.01$ | $0.00 \pm 0.00$ | $0.04 \pm 0.02$ | $0.00 \pm 0.00$ | $-0.04 \pm 0.01$ |
| SAH (mm) | $0.00 \pm 0.00$ | $0.04 \pm 0.01$ | $0.00 \pm 0.00$ | $0.03 \pm 0.01$ | $0.00 \pm 0.00$ | $-0.03 \pm 0.01$ |
| TMW (g) | $-0.07 \pm 0.01^{*}$ | $0.10 \pm 0.02^{*}$ | $-0.06 \pm 0.01^{*}$ | $0.08 \pm 0.02^{*}$ | $0.13 \pm 0.01^{*}$ | $0.07 \pm 0.02^{*}$ |
| TMP (%) | $-0.09 \pm 0.02^{*}$ | $0.15 \pm 0.03^{**}$ | $-0.05 \pm 0.01^{*}$ | $0.18 \pm 0.04^{**}$ | $0.14 \pm 0.03^{**}$ | $0.12 \pm 0.03^{**}$ |

*Note.* (1) GY, Gaoyou lake strain; TH, Taihu lake strain; HZ, Hongze lake strain. (2) BW, body weight; BL, body length; CHL, chela length; CTL, cephalothorax length; CTW, cephalothorax width; SAW, second abdominal segment width; SAH, second abdominal segment height; TMW, tail meat weight; TMP, tail meat percentage. (3) * or ** indicates significance at 5% or 1% level.

Table 8: Predicted values of additive and epistatic (additive × additive) genetic effects for nine traits in three strains of male *Macrobrachium nipponense* using the BLUP approach.

| Trait | GY strain | | TH strain | | HZ strain | |
|---|---|---|---|---|---|---|
| | Additive | Epistatic | Additive | Epistatic | Additive | Epistatic |
| BW (g) | $-0.07 \pm 0.01^{*}$ | $0.11 \pm 0.04^{*}$ | $-0.08 \pm 0.01^{*}$ | $0.13 \pm 0.03^{**}$ | $0.15 \pm 0.02^{**}$ | $0.12 \pm 0.03^{**}$ |
| BL (mm) | $-0.09 \pm 0.02^{*}$ | $0.15 \pm 0.03^{**}$ | $-0.07 \pm 0.01^{*}$ | $0.12 \pm 0.04^{**}$ | $0.16 \pm 0.03^{**}$ | $0.14 \pm 0.05^{**}$ |
| CHL (mm) | $-0.16 \pm 0.03^{**}$ | $0.13 \pm 0.02^{**}$ | $-0.10 \pm 0.02^{*}$ | $0.10 \pm 0.02^{*}$ | $0.26 \pm 0.04^{**}$ | $0.17 \pm 0.03^{**}$ |
| CTL (mm) | $-0.10 \pm 0.02^{*}$ | $-0.02 \pm 0.01$ | $-0.08 \pm 0.01^{*}$ | $-0.04 \pm 0.01$ | $0.18 \pm 0.03^{**}$ | $-0.02 \pm 0.01$ |
| CTW (mm) | $-0.07 \pm 0.01^{*}$ | $-0.03 \pm 0.01$ | $-0.02 \pm 0.01$ | $-0.03 \pm 0.01$ | $0.09 \pm 0.01^{*}$ | $-0.03 \pm 0.01$ |
| SAW (mm) | $-0.01 \pm 0.01$ | $0.00 \pm 0.00$ | $0.00 \pm 0.00$ | $0.00 \pm 0.00$ | $0.01 \pm 0.01$ | $-0.02 \pm 0.01$ |
| SAH (mm) | $0.00 \pm 0.00$ | $0.00 \pm 0.00$ | $-0.02 \pm 0.01$ | $0.00 \pm 0.00$ | $0.02 \pm 0.01$ | $-0.04 \pm 0.01$ |
| TMW (g) | $-0.05 \pm 0.01^{*}$ | $0.18 \pm 0.03^{**}$ | $-0.06 \pm 0.01^{*}$ | $0.08 \pm 0.04^{*}$ | $0.11 \pm 0.02^{*}$ | $0.10 \pm 0.02^{*}$ |
| TMP (%) | $-0.11 \pm 0.02^{**}$ | $0.20 \pm 0.04^{**}$ | $-0.09 \pm 0.02^{*}$ | $0.17 \pm 0.03^{**}$ | $0.20 \pm 0.03^{**}$ | $0.18 \pm 0.03^{**}$ |

*Note.* (1) GY, Gaoyou lake strain; TH, Taihu lake strain; HZ, Hongze lake strain. (2) BW, body weight; BL, body length; CHL, chela length; CTL, cephalothorax length; CTW, cephalothorax width; SAW, second abdominal segment width; SAH, second abdominal segment height; TMW, tail meat weight; TMP, tail meat percentage. (3) * or ** indicates significance at 5% or 1% level.

be analyzed together with additive and dominance effects [12]. Therefore, only additive × additive epistasis (biallelic) was examined in this study using the experimental data of 3 generations of oriental river prawns (Table 1). Results given in this study showed that the existence of additive × additive epistasis was dependent on traits and was directional (Tables 7 and 8). For instance, the additive × additive epistasis, although not significant, was negative for cephalothorax length and width. In contrast, the additive × additive epistasis was positive for body weight, body length, and chela length in both sexes of oriental river prawn, indicating that the loci underlying these traits interacted epistatically in a synergistic manner. Moreover, the

additive × additive epistasis for traits with higher heritabilities was relatively larger. For instance, the heritability of body weight for females was 0.22 ± 0.01, and the additive × additive epistasis ratio for this trait was 0.10 ± 0.04, 0.15 ± 0.02, and 0.18 ± 0.03 in the Gaoyou strain, Taihu strain, and Hongze strain of oriental river prawn, respectively. This is because higher levels of additive variation occurred [12, 13]. Additive × additive epistasis was detected in other aquatic animals. For instance, Wang et al. [28] concluded that synergistic additive × additive epistasis was present for the body weight and body length of the red common carp, *C. carpio*. Palti et al. [33] reported strong synergistic epistasis between two microsatellite marker loci (UNH159 and UNH216), where an additional deleterious mutation could greatly decrease the fitness of blue tilapia *O. aureus*. Results presented in this study are analogous to those of these two studies, but they are inconsistent with those of Pante et al. [31], who implied no presence of additive × additive interaction for growth (body weight at harvest) of rainbow trout, *O. mykiss*. Based upon the linkage disequilibrium between many candidate loci under molecular-driven selective breeding, Dale-Kuys et al. [36] suggested the occurrence of possible epistatic interactions in the genome of South African abalone (*H. midae*) but did not demonstrate the directionality and magnitude of the epistatic interactions. In this study, the additive × additive epistasis was also synergistic for two processing traits (tail meat weight and tail meat percentage) in both sexes of oriental river prawns (Tables 7 and 8). This result is similar to that of Argue et al. [34], who found that greater epistatic interactions could significantly increase the dress-out percentage and fillet percentage in channel catfish *I. punctatus*. Results of this study indicate that epistasis is an important genetic basis for economic traits such as body weight (growth) and processing traits in oriental river prawns. For Mendelian traits such as coloration, similar results regarding the existence of epistasis have also been reported in a couple of aquatic species. Winkler et al. [32] suggested the existence of a dominant epistasis that governs the general pattern of coloration in scallop *A. purpuratus*. Ge et al. [35] found an epistatic effect of shell background color on shell foreground pigmentation in Pacific oyster, *C. gigas*.

Because the variation ascribable to additive × additive epistasis is heritable, it, in conjunction with additive variation, should be taken into account when formulating an improvement program. Predicated on the results of the present study (Tables 5 and 8), heritabilities, additive × additive epistasis, and additive genetic effects can provide detailed information for the traits to be improved, which may result in additional genetic gains when implementing selection programs. According to the directionality of additive × additive epistasis, the traits that have higher heritability, additive effects, and synergistic epistatic interactions can be considered candidates for improvement. In this study, for example, the breeding value (additive effect) and additive × additive epistasis for body weight in the Hongze Lake strain of oriental river prawn were relatively higher, 0.17 ± 0.03 g and 0.18 ± 0.03 g, respectively, for females and 0.15 ± 0.02 g, and 0.12 ± 0.03 g, respectively, for males. Hence, if this strain were selected as the parents, preferable genetic gains would be garnered. For the body weight of oriental river prawn in the Gaoyou Lake and Taihu Lake strains, the higher synergistic additive × additive epistasis would also result in better genetic gains if taking the two strains as parents for selective breeding, albeit with relatively lower additive effects. Although significant synergistic additive × additive epistasis and additive effects occurred with two processing traits, it was very difficult for them to be directly selected or improved. The epistatic interactions, additive effects, and heritabilities of other traits, such as cephalothorax length, cephalothorax width, and second abdominal segment width and height, were absent or had very low values, thus they would be of little benefit to the selection program.

The choice of mating design is very important when estimating genetic parameters for aquaculture species [44]. The nested design has been used by many researchers such as Pérez-Rostro and Ibarra [16], Li et al. [5], and Joshi et al. [29]. A diallel cross design, however, was used in this study because the establishment of families and identification of individuals in oriental river prawn was impracticable due to the biological characteristics of this species. Although genetic markers can be used to construct families, the cost would be prohibitively high for this study. Thus, the individual animal model used by some researchers such as Joshi et al. [43] and Cardoso et al. [45] was not appropriate for the data analysis in this study. In many aquaculture species, individual animal identification is a challenge, which was the case in the current study. This is because the oriental river prawn is morphologically very small, and ecdysis takes place about 20 times throughout its life [46]. This would explain why strategic mating designs could be used to try to devise selection programs in oriental river prawns. The diallel design has been widely applied to genetic assessment in many aquaculture species, such as red common carp, *C. carpio* [28]; giant river prawn, *M. rosenbergii* [19, 47, 48]; Pacific oyster, *C. gigas* [49]; red swamp crayfish, *P. clarkii* [24, 50]; and pearl oyster, *Pinctada fucata* [46]. Based upon the single-trait mixed genetic analysis model utilized in this study, the diallel design can be used for genetic evaluation of oriental river prawn using the specific approach of Zhu [10, 11]. Since the genetic linkage map for the oriental river prawn has yet to come out, genomic information was not utilized for the genetic assessment of the oriental river prawn in the present study.

## 5. Conclusion

The existence of ample additive genetic variation is a prerequisite for desirable genetic gains for traits to be improved in selective breeding. Thus, it is necessary to make an accurate genetic assessment of the existing additive genetic variation in a population prior to developing a selection program. In the present study, due to sufficiently large sample sizes, the additive × additive epistasis, other nongenetic effects, and their interactions with the environment were accounted for when estimating additive genetic variance and breeding values. There was greater relative additive genetic variation for body weight (growth) and processing traits to be utilized for the selective breeding of oriental river prawns. The level of epistasis varied according to the trait of

interest. The genetic determinism of these traits depends quantitatively on not only significant additive genetic effects but also synergistic epistatic interactions. The epistatic interactions provided new information on the genetic determinism of growth-related traits in oriental river prawns. Desirable genetic gains for this commercial species would be achieved for traits such as growth with superior additive genetic effects and synergistic epistatic interactions.

## Data Availability

The data that support the findings of this study are available from the corresponding author upon request.

## Ethical Approval

The animal experiments in this project were approved by the Animal Care and Use Committee of Huaiyin Normal University (20170315001A), Jiangsu Province, China.

## Conflicts of Interest

The authors declare that they have no conflicts of interest.

## Authors' Contributions

Hui Wang performed conceptualization, methodology, formal analysis, writing of original draft, editing, and revision; Yi Zhang, Long Wang, and Tianyu Guan performed data curation, used the software, and validated the manuscript; Guoliang Chang and Nan Wu gave the experimental design and performed the methodology; and Jiale Li performed conceptualization, supervision, and review.

## Acknowledgments

This research was financed by the following grants: Jiangsu Collaborative Innovation Center of Regional Modern Agriculture & Environmental Protection, Huaiyin Normal University (No. HSXT2-107), Shanghai Science and Technology Innovation Action Plan (Agriculture) (No. 19391900900), Jiangsu Province Agricultural Science and Technology Independent Innovation Fund Project (No. CX(18)2016), and the Science and Technology Program of Huaiyin Normal University (No. 31WH000).

## References

[1] H. T. Fu, "Breeding and extension of new freshwater shrimp strain *Macrobrachium nipponense*," *Scientific Fish Farming*, vol. 3, pp. 26-27, 2020.

[2] D. Wang and F. X. Wu, *China Fishery Statistical Yearbook*, pp. 20–30, China Agriculture Publishing House, Beijing, China, 2021.

[3] M. N. Kutty and W. M. Miao, "Culture of the oriental river prawn Macrobrachium nipponense," in *Freshwater Prawns: Biology and Farming*, M. B. New, W. C. Valenti, J. H. Tidwell, L. R. D'Abramo, and M. N. Kutty, Eds., pp. 475–483, John Wiley & Sons, West Sussex, UK, 2010.

[4] J. L. Li, L. S. Chen, and Q. G. Liu, "Problems and countermeasures for further development of the aquaculture industry of *Macrobrachium nipponense*," *Fisheries Science & Technology Information*, vol. 38, no. 6, pp. 315–319, 2011.

[5] F. Li, Z. M. Gu, X. L. Li et al., "Estimates of genetic parameters for growth-related traits of the red swamp crayfish, *Procambarus clarkii*," *Aquaculture International*, vol. 24, pp. 1–10, 2016.

[6] Q. H. Song and Y. F. Zhao, "New advances for the breeding of oriental river prawn (*Macrobrachium nipponense*) and crab (*Eriocheir sinensis*) in China," *Scientific Fish Farming*, vol. 5, pp. 13–17, 2016.

[7] Q. H. Song and Y. F. Zhao, "Analysis for the status quo of aquaculture industry of the oriental river prawn (*Macrobrachium nipponense*) in China," *Scientific Fish Farming*, vol. 6, pp. 13–16, 2018.

[8] H. T. Fu, Y. S. Gong, Y. Wu, P. Xu, and C. J. Wu, "Artificial interspecific hybridization between *Macrobrachium* species," *Aquaculture*, vol. 232, no. 1–4, pp. 215–223, 2004.

[9] D. S. Falconer and T. F. C. Mackay, *Introduction to Quantitative Genetics*, Pearson Education Limited, Edinburgh Gate, Harlow, England, 1996.

[10] J. Zhu, *Analysis Methods for Genetic Models*, China Agriculture Publishing House, Beijing, China, 1996.

[11] J. Zhu, "Diallel analysis for an additive-dominance model with genotype-by-environment interaction effects," in *Handbook of Formulas and Software for Plant Geneticists and Breeders*, M. S. Kang, Ed., pp. 39–50, Food Products Press, New York, NY, USA, 2003.

[12] M. Lynch and B. Walsh, *Genetics and Analysis of Quantitative Traits*, Sinauer Associates, Sunderland, MA, USA, 1998.

[13] B. Walsh and M. Lynch, *Evolution and Selection of Quantitative Traits*, Sinauer Associates, Inc., Oxford University Press, Oxford, UK, 2018.

[14] M. Kenway, M. Macbeth, M. Salmon et al., "Heritability and genetic correlations of growth and survival in black tiger prawn *Penaeus monodon* reared in tanks," *Aquaculture*, vol. 259, no. 1-4, pp. 138–145, 2006.

[15] M. M. Sun, J. H. Huang, S. G. Jiang et al., "Estimates of heritability and genetic correlations for growth-related traits in the tiger prawn *Penaeus monodon*," *Aquaculture Research*, vol. 46, no. 6, pp. 1363–1368, 2015.

[16] C. I. Pérez-Rostro and A. M. Ibarra, "Heritabilities and genetic correlations of size traits at harvest size in sexually dimorphic Pacific white shrimp (*Litopenaeus vannamei*) grown in two environments," *Aquaculture Research*, vol. 34, no. 12, pp. 1079–1085, 2003.

[17] G. R. Campos-Montes, H. H. Montaldo, A. Martínez-Ortega, A. M. Jiménez, and H. Castillo-Juarez, "Genetic parameters for growth and survival traits in Pacific white shrimp *Penaeus* (*Litopenaeus*) *vannamei* from a nucleus population undergoing a two-stage selection program," *Aquaculture International*, vol. 21, no. 2, pp. 299–310, 2013.

[18] J. C. Zhang, F. J. Cao, J. Y. Liu, and R. P. Yuan, "Genetic parameters for growth and survival traits in *Litopenaeus vannamei* at different ages," *Aquaculture International*, vol. 25, no. 5, pp. 1901–1911, 2017.

[19] N. M. Thanh, N. H. Nguyen, R. W. Ponzoni, N. T. Vu, A. C. Barnes, and P. B. Mather, "Estimates of strain additive and non-additive genetic effects for growth traits in a diallel cross of three strains of giant freshwater prawn (*Macrobrachium rosenbergii*) in Vietnam," *Aquaculture*, vol. 299, no. 1–4, pp. 30–36, 2010.

[20] D. Hung, N. H. Nguyen, R. W. Ponzoni, D. A. Hurwood, and P. B. Mather, "Quantitative genetic parameter estimates for body and carcass traits in a cultured stock of giant freshwater

prawn (*Macrobrachium rosenbergii*) selected for harvest weight in Vietnam," *Aquaculture*, vol. 404–405, pp. 122–129, 2013.

[21] B. R. Pillai, P. L. Lalrinsanga, R. W. Ponzoni et al., "Phenotypic and genetic parameters for body traits in the giant freshwater prawn (*Macrobrachium rosenbergii*) in India," *Aquaculture Research*, vol. 48, no. 12, pp. 5741–5750, 2017.

[22] M. D. Li, J. T. Li, K. P. Shi et al., "Estimation of heritability and genetic correlation of saline-alkali tolerance in *Exopalaemon carinicauda*," *Progress in Fishery Sciences*, vol. 42, no. 1, pp. 117–123, 2021.

[23] J. Sui, S. Luan, K. Luo et al., "Genetic parameters and response to selection of harvest body weight of the Chinese shrimp *Fenneropenaeus chinensis*, after five generations of multi-trait selection," *Aquaculture*, vol. 452, pp. 134–141, 2016.

[24] W. Hui, W. Long, S. Wenjing et al., "Estimates of heritability based on additive-dominance genetic analysis model in red swamp crayfish, Procambarus clarkii," *Aquaculture*, vol. 504, pp. 1–6, 2019.

[25] J. M. Cheverud and E. J. Routman, "Epistasis and its contribution to genetic variance components," *Genetics*, vol. 139, no. 3, pp. 1455–1461, 1995.

[26] O. Carlborg and C. S. Haley, "Epistasis: too often neglected in complex trait studies?" *Nature Reviews Genetics*, vol. 5, no. 8, pp. 618–625, 2004.

[27] W. G. Hill, M. E. Goddard, and P. M. Visscher, "Data and theory point to mainly additive genetic variance for complex traits," *PLoS Genetics*, vol. 4, no. 2, Article ID e1000008, 2008.

[28] C. H. Wang, S. F. Li, Z. G. Liu et al., "Genetic analysis of epistatic effects of growth traits in red common carp," *Journal of Fishery Sciences of China*, vol. 13, no. 4, pp. 573–578, 2006.

[29] R. Joshi, T. H. E. Meuwissen, J. A. Woolliams, and H. M. Gjøen, "Genomic dissection of maternal, additive and non-additive genetic effects for growth and carcass traits in Nile tilapia," *Genetics Selection Evolution*, vol. 52, pp. 1–13, 2020.

[30] D. Hedgecock, D. J. McGoldrick, and B. L. Bayne, "Hybrid vigor in Pacific oysters: an experimental approach using crosses among inbred lines," *Aquaculture*, vol. 137, no. 1–4, pp. 285–298, 1995.

[31] M. R. Pante, B. Gjerde, and I. McMillan, "Effect of inbreeding on body weight at harvest in rainbow trout, *Oncorhynchus mykiss*," *Aquaculture*, vol. 192, no. 2–4, pp. 201–211, 2001.

[32] F. M. Winkler, B. F. Estévez, L. B. Jollán, and J. P. Garrido, "Inheritance of the general shell color in the scallop *Argopecten purpuratus* (Bivalvia: pectinidae)," *Journal of Heredity*, vol. 92, no. 6, pp. 521–525, 2001.

[33] Y. Palti, A. Shirak, A. Cnaani, G. Hulata, R. R. Avtalion, and M. Ron, "Detection of genes with deleterious alleles in an inbred line of tilapia (*Oreochromis aureus*)," *Aquaculture*, vol. 206, no. 3–4, pp. 151–164, 2002.

[34] B. J. Argue, Z. J. Liu, and R. A. Dunham, "Dress-out and fillet yields of channel catfish, *Ictalurus punctatus*, blue catfish, *Ictalurus furcatus*, and their $F_1$, $F_2$ and backcross hybrids," *Aquaculture*, vol. 228, no. 1–4, pp. 81–90, 2003.

[35] J. L. Ge, Q. Li, H. Yu, and L. F. Kong, "Mendelian inheritance of golden shell color in the Pacific oyster *Crassostrea gigas*," *Aquaculture*, vol. 441, pp. 21–24, 2015.

[36] R. C. Dale-Kuys, R. Roodt-Wilding, and C. Rhode, "Genome-wide linkage disequilibrium in South African abalone, *Haliotis midae*, and implications for understanding complex traits," *Aquaculture*, vol. 523, Article ID 735002, 2020.

[37] N. Kitcharoen, W. Rungsin, S. Koonawootrittriron, and U. Na-Nakorn, "Heritability for growth traits in giant freshwater prawn, *Macrobrachium rosenbergii* (de Mann 1879) based on best linear unbiased prediction methodology," *Aquaculture Research*, vol. 43, no. 1, pp. 19–25, 2012.

[38] W. G. Hill, "Understanding and using quantitative genetic variation," *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 365, no. 1537, pp. 73–85, 2010.

[39] R. W. Xu, Z. Y. Qian, X. L. Liu, Z. Lu, J. D. Ren, and F. S. Yang, "Genetic parameter estimation for growth traits of Pacific white shrimp (*Litopenaeus vannamei*)," *Journal of Fisheries of China*, vol. 37, no. 5, pp. 672–678, 2013.

[40] W. J. Li, S. Luan, K. Luo et al., "Genetic parameters and genotype by environment interaction for cold tolerance, body weight and survival of the Pacific white shrimp *Penaeus vannamei* at different temperatures," *Aquaculture*, vol. 441, pp. 8–15, 2015.

[41] S. Luan, G. Yang, J. Wang et al., "Genetic parameters and response to selection for harvest body weight of the giant freshwater prawn *Macrobrachium rosenbergii*," *Aquaculture*, vol. 362-363, no. 363, pp. 88–96, 2012.

[42] Y. Y. Jia, Z. M. Gu, Y. J. Yang, and X. M. Huang, "Initial family construction and heritability estimates for growth-related traits in *Macrobrachium nipponense*," *Journal of Zhejiang Ocean University*, vol. 34, no. 2, pp. 154–160, 2014.

[43] R. Joshi, J. A. Woolliams, T. H. E. Meuwissen, and H. M. Gjøen, "Maternal, dominance and additive genetic effects in Nile tilapia; influence on growth, fillet yield and body size traits," *Heredity*, vol. 120, no. 5, pp. 452–462, 2018.

[44] Y. Li and R. W. Ponzoni, "Some aspects of design and analysis of selection programmes in aquaculture species," *Journal of Animal Breeding and Genetics*, vol. 132, no. 2, pp. 169–175, 2015.

[45] A. J. d. S. Cardoso, C. A. L. d. Oliveira, E. C. Campos, R. P. Ribeiro, G. J. d. F. Assis, and F. F. e. Silva, "Estimation of genetic parameters for body areas in Nile tilapia measured by digital image analysis," *Journal of Animal Breeding and Genetics*, vol. 138, no. 6, pp. 731–738, 2021.

[46] J. Chen, H. Luo, Z. Q. Zhai et al., "Estimates of additive and non-additive genetic effects on growth traits in a diallel cross of three strains of pearl oyster (*Pinctada fucata*)," *Aquaculture International*, vol. 29, no. 3, pp. 1359–1371, 2021.

[47] N. M. Thanh, R. W. Ponzoni, N. H. Nguyen, N. T. Vu, A. C. Barnes, and P. B. Mather, "Evaluation of growth performance in a diallel cross of three strains of giant freshwater prawn (*Macrobrachium rosenbergii*) in Vietnam," *Aquaculture*, vol. 287, no. 1–2, pp. 75–83, 2009.

[48] B. R. Pillai, K. D. Mahapatra, R. W. Ponzoni et al., "Genetic evaluation of a complete diallel cross involving three populations of freshwater prawn (*Macrobrachium rosenbergii*) from different geographical regions of India," *Aquaculture*, vol. 319, no. 3–4, pp. 347–354, 2011.

[49] X. S. Yin and D. Hedgecock, "Bayesian hierarchical modeling of yield in incomplete diallel crosses of the Pacific oyster *Crassostrea gigas*," *Aquaculture*, vol. 510, pp. 43–50, 2019.

[50] W. Hui, S. Wenjing, W. Long et al., "Genetic determination of processing traits in the red swamp crayfish, *Procambarus clarkii* (Girard)," *Aquaculture*, vol. 529, Article ID 735602, 2020.