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Reducing Genotype-Environment Interaction Effects in a Genetic Improvement for *Liptopenaeus vannamei*

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Abstract: The genotype by environment interaction (G×E) might have crucial impacts on the performance and fitness of agricultural species, such as Pacific white leg shrimp (*Litopenaeus vannamei*). This study explores how enhancements in management practices can counteract G×E effects on growth traits. We analysed a selectively bred population of white leg shrimp spanning the latest two generations, encompassing 259 full-sib and half-sib families with 40,862 individual shrimp measured for body weight and total length. Our analysis revealed moderate genetic correlations (0.60 – 0.65) between trait expressions in pond and tank environments, a significant improvement compared to earlier generations. Employing the average information-restricted maximum likelihood (REML) approach in mixed model analysis showed significant differences in heritability (h^2) estimates between the two environments; however, the extent of these differences varied by trait (h^2 = 0.68 in pond *vs.* 0.37 in tank for weight, and 0.41 *vs.* 0.67 for length). Our results indicate that G×E effects on growth traits in this population of *L. vannamei* were moderate but biologically significant. Consistent with our previous estimates in this population, genetic correlations between body weight and total length remained high (close to one) in pond and tank environments. Our findings collectively demonstrate that management improvements targeting stocking density, aeration, water quality, feeds, and feeding regimes mitigated the G×E effects on two economically significant traits in this population of white leg shrimp.

Keywords: breeding program; genetic parameters; selection response; genotype and environment

Introduction

Genotype by environment interaction, G×E (Falconer and Mackay, 1996) denotes how genotypes respond differently to various environments, driven by intrinsic genetic and environmental factors. The differential response could stem from specific ambient conditions where animals or populations reside, or from intricate biological mechanisms encompassing gene interactions and epigenetic influences (Wu et al., 2023). Consequently, the G×E effects profoundly impact the performance and fitness of agricultural species, as extensively reported in both animals and plants (Napier et al., 2022; Fodor et al., 2023).

In aquaculture, extensive research has examined diverse G×E systems, covering various culture systems such as ponds, cages, tanks, lakes, or integrated rice-fish farming (Eknath et al., 2007; Thoa et al., 2016; Nguyen et al., 2017). Other studies also consider scales of production environment, e.g., smallholder to industrial operations (Trọng et al., 2013). Many nutritional factors such as diets, feed types, feeding schedules, and environmental or climatic stresses showed substantial G×E effects on important aquaculture species (Oikonomou et al., 2023; Torrecillas et al., 2023). Across species and systems, synthesized literature results (Nguyen, 2016; Sae-Lim et al., 2016) highlight the relevance of

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G×E effects, particularly when the selection environment in nucleus herds diverges from practical production settings (Khang et al., 2018; Gonzalez et al., 2022). Conversely, G×E effects diminish when environments align closely (Mengistu et al., 2020).

In white leg shrimp (*Litopenaeus vannamei*), past studies dissected the G×E effects based on farming locations (Castillo-Juárez et al., 2007) or interactions with stocking densities (Ibarra and Famula, 2008; Campos-Montes et al., 2009; Tan et al., 2017). Recent genetic evaluations of *L. vannamei* lines cultured in tank and pond environments revealed significant G×E impacts, hindering growth improvements under artificial selection (Nguyen et al., 2020).

To address these challenges without running multiple breeding programs, immediate enhancements in management practices focused on aeration, water quality, stocking density, feeds, and feeding regimes (Nguyen, 2024). These improvements aimed to mitigate G×E effects in this shrimp population's breeding program.

Thus, the primary objectives of this study were to evaluate how improvements in management practices can mitigate G×E effects on growth traits and to update genetic parameters for growth traits (weight and length) in the current shrimp population. Specifically, we explored whether trait inheritance (heritability) differed between pond and tank environments, whether G×E interaction effects remained significant for growth traits, and whether genetic relationships between weight and length changed between the two environments.

Materials and Methods

1.1. Animal Population

The animals used in this study originated from a genetic improvement program for high growth at the Research Institute for Aquaculture No.3 (RIA3) in Vietnam. Briefly, the population was established in 2014, and the first generation was produced in 2015 (G1), from which animals (2-3 males and 4-6 females per family × 60 families) with the highest Estimated Breeding Value (EBV) for body weight were selected (Nguyen et al., 2020). The selection program continued until 2017. Between 2018 and 2021, the pedigreed population was maintained without any selection due to a lack of funding and the COVID-19 pandemic during this period. However, the genetic program resumed in 2022 and was ongoing in 2023, during which data were collected for this study. The same breeding protocol and selection procedures used in our previous study were implemented for these generations (2022 and 2023). Briefly, after data collection, genetic evaluation was performed using a linear mixed model that included fixed effects of generation, line, sex, environment, and age, as well as the random additive genetic effect of the individual animal, to estimate EBVs for body weight. Based on the EBV rankings, approximately two males and four females per family were selected to produce subsequent generations. Overall, one male was mated to two females of different families to avoid full-sib and half-sib matings and manage inbreeding. When mortality or breeding failure occurred, only full-sib families were available. Details of our breeding and rearing protocol are as follows.

1.1. Breeding and Rearing

During the breeding program, we used artificial methods to breed shrimp. This involved taking sperm packets from healthy adult males and inserting them into the thelycums of mature females with large red-green ovaries. These females, now carrying eggs, were moved to 300-liter tanks with specific water conditions (salinity 30‰, pH 8-8.5, oxygen >5mg/L, and temperature 28-29°C), one female per tank. Typically, spawning occurred at night within 1 to 4 hours, and the next morning, newly hatched larvae (45,000 - 90,000 per family) were collected and treated with formalin to disinfect them.

The larvae were then placed in separate tanks ($1m^3$) for rearing. After a day or two, a sample of 30,000 larvae from each family was transferred to larger tanks with a density of 60 larvae per Liter. These tanks maintained specific conditions (salinity 30‰, temperature 29-30°C, pH 8.2-8.6) and were

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fed a diet of Chaetoceros algae and synthetic food. As larvae grew, they were gradually transitioned to a commercial diet supplemented with vitamin C.

After reaching the post-larvae stage (about 25 days post-hatch), a sample of 10,000 individuals from each family was transferred to separate tanks (2.5m^3) and fed a commercial prawn pellet diet. After 1.5-2 months, when shrimp juveniles reached an average weight of 2 grams, they were tagged with visible implant elastomer tags for identification purposes. These tags were applied to the first left and sixth right segments of the prawns' abdomens, using six available colours to track their family lineage.

Once tagged, the juvenile prawns were acclimatized in a 1000-liter tank with aeration for three days before being transferred to communal grow-out tanks and ponds.

1.1. Test Environments and Data Recording

Pond: Marked shrimp from each family were divided into two groups: one group was raised in a pond with an area of 1,000 square meters, while the other was placed in tanks as described below. Only one pond was used for communal grow-out. Similar stocking density and feed were used in both tanks and ponds to minimize potential impacts of this factor on shrimp's growth. Specifically, unmarked shrimp were added to the grow-out ponds to maintain a commercial stocking density of 100 juveniles per square meter of water surface. Additionally, differences in tank and pond environments, as well as management practices such as aeration, water exchange, and water sources, were kept minimal. Water quality parameters and environmental factors are monitored weekly in both environments.

Tank environment: In every generation, tagged shrimp from all families were raised in three tanks, each with a capacity of 25,000 liters. An equal number of siblings from each family were randomly distributed among these tanks. To maintain an initial stocking density of 100 juveniles per square meter of water surface, surplus untagged juveniles were also raised alongside the experimental shrimp. These shrimp indviduals were fed a commercial dry pellet feed with 32% protein content four times a day (at 6 am, 11 am, 4 pm, and 10 pm), with the amount ranging from 3% to 5% of their body weight.

The key improvement in management practices between generations in the two environments lies in the controlled outdoor field conditions for pond culture to match with the indoor system for tank culture. Specific improvements included the minimal stocking density differences, same duration of aeration, same commercial diet, similar time of feeding, minimal variations in water parameters (salinity level, temperature, and water exchange). Further detail is given in Supplementary Table S1. Despite these efforts, the differences were still observed in the pond environment, which exhibited greater variability in salinity levels (31.3±1.7 vs. 33.5±1.2, ‰) and slightly higher water temperatures (29±1.1 vs. 28±0.8°C, with a range of 25-33°C vs. 26-30°C) compared to the tank environment across the two generations.

Data collection: After approximately 184 days of grow-out, shrimp were harvested following pond drainage for body trait measurements. Individual shrimp was weighed using a digital scale with a precision of 0.1 grams, and their standard length (distance from eye orbit to telson) was measured using a ruler. At harvest, shrimp sex and pedigree information were recorded. A comprehensive dataset including all collected information was established for statistical and genetic analyses, as described in detail below.

1.1. Statistical Analysis

We conducted two main analyses: (i) analysing each environment separately, and (ii) combing data from both pond and tank environments.

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1.1.1. Separate Analysis of Tank and Pond Environments

In this analysis, genetic parameters (heritability and correlations) for traits studied were estimated using a mixed model that included both fixed and random effects as described in Equation 1.

$$y_{ijklm} = \mu + G_i + S_j + L_k + Age_l + a_m + e_{ijklm} \quad \text{[Equation 1]}$$

Here, y_{ijklm} represents observations of m^{th} individual (i.e., body weight and total length). The fixed effects of the model included generation (G_i, $i = 2$ corresponding to 2022 and 2023), sex (S_j, female and male) line (L_k including the selection line and control group), and age (Age_l) fitted as a linear covariate. The experimental conditions of rearing tanks were similar and hence, the effect of tanks was not statistically significant ($P > 0.05$). The random term was the additive genetic effect of individual shrimp, $a_m \sim (0, \mathbf{A}\sigma_a^2)$ where **A** is the numerator relationship matrix calculated from the pedigree traced back a previous generation. The residual error component of the model is represented by $e_{ijklm} \sim (0, \mathbf{I}\sigma_e^2)$ with **I** as the identity matrix. Under this model (Equation 1), var(**a**) = **G** = $\mathbf{A}\sigma_a^2$. The remaining effects are assumed to be distributed as var(**e**) = **R** = $\mathbf{I}\sigma_e^2$. The expectations of the random effects are zero, cov (**a**,**e**) = 0.

1.1.1. Combined Analysis of Both Tank and Pond Data

Combined analysis of both tank and pond data used a similar model to Equation 1. In addition to the fixed factors described above, the model also included the effect of environment. The full model is written as Equation 2.

$$y_{ijklnm} = \mu + G_i + S_j + L_k + E_l + Age_m + a_n + e_{ijklmn} \quad \text{[Equation 2]}$$

where y_{ijklm} indicates observations of m^{th} individual (i.e., body weight and total length). The fixed effects of the model include generation (G_i), sex (S_j), line (L_k), environment (E_l), and age (Age_m) fitted as a linear covariate. The random term was the additive genetic effect of individual shrimp, a_n. The residual error component of the model is denoted as e_{ijklmn}. The assumptions of this model were the same as described above for Equation 1.

For both analyses, the heritability for body traits (weight and length) was calculated as $h^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_a^2 + \hat{\sigma}_e^2}$ where $\hat{\sigma}_a^2$ is the additive genetic variance, and the residual variance ($\hat{\sigma}_e^2$).

The genetic and phenotypic correlations between weight (W) and length (L) were estimated as: $r = \frac{\sigma_{WL}}{\sqrt{\sigma_W^2}\sqrt{\sigma_L^2}}$, where the numerator represents covariance between the two traits and the denominator specifies the genetic or phenotypic variance of individual traits.

To assess genotype by environment interaction, we employed multivariate model and treated trait expressions in tank and pond as a separate character; and hence, there is no phenotypic correlation between trait expressions between the two environments. The genetic correlation between homologous trait expressions in tank and pond was estimated as: $r = \frac{\sigma_{TP}}{\sqrt{\sigma_T^2}\sqrt{\sigma_P^2}}$ where σ_{TP} is the estimated additive genetic covariance of weight or length between tank (T) and pond (P), and σ_T^2 and σ_P^2 are the additive genetic variances of weight (or length) in tank and pond, respectively.

All the statistical analyses were conducted using ASReml software (Gilmour et al., 2015), and convergence was achieved in both univariate and multivariate models used to analyse body weight and total length.

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Results

1.1. Characteristics of the Population and Data Structure

In each generation, we produced 120 full-sib families, from which progeny were sampled for performance testing in tanks and ponds. Although fewer progeny were tested in generation 2023 compared to 2022, the sample size remained substantial in each testing environment. Totally, 40,862 shrimp indviduals were performance tested when combining data from both tank and pond environments (Table 1).

Table 1. Data structure and pedigree.

Generation	Environment	Dam	Sire	Full-sibs (half-sibs)	No of progeny
G8 (2021 – 2022)	Pond	102	86	100 (32)	12425
	Tank	102	86	100 (32)	12425
	Both	102	86	100 (32)	24,850
G9 (2022 – 2023)	Pond	120	104	96 (31)	8009
	Tank	120	104	96 (31)	8009
	Both	120	104	96 (31)	16,018
Both G8 and G9	Pond	222	190	196 (63)	20431
	Tank	222	190	196 (63)	20431
	Both	222	190	196 (63)	40,862

1.1. Descriptive Statistics

The average body weight of the population in combined tank and pond environments was 19.8g. The shrimp raised in ponds exhibited faster growth compared to those in tanks (Table 2). Although the standard deviation was similar between the two environments, the coefficient of variation for body weight was higher in tanks than in ponds (60.6% *vs.* 53.7%). Similar patterns of results were also observed for total length (Table 2).

Table 2. Basic statistics (number of observations *n*, raw mean, standard deviation SD and coefficient of variation CV) for body traits.

Trait	Environment	n	Mean	SD	CV (%)
Weight, g	Pond	16259	19.747	4.1	53.7
	Tank	8176	19.879	2.6	60.6
	Both	24435	19.791	3.7	53.8
Length, mm	Pond	16260	136.73	11.1	58.2
	Tank	8176	138.06	3.5	86.3
	Both	24436	137.17	9.3	58.4

1.1. Heritability

The variance components and heritability estimates for two key growth traits, body weight, and total length, are presented in Table 3. For body weight, genetic variances were higher in ponds compared to tanks, while environmental variances were similar between the two environments. Consequently, the heritability of body weight was greater in ponds than in tanks (0.68 vs. 0.37). In contrast, a different pattern was observed for total length. Despite in ponds total length exhibiting greater genetic variance than tanks, the environmental variance was significantly higher in ponds. When considering both environments together, the heritabilities for both weight and length were high (0.76 and 0.74, respectively).

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Table 3. Heritability (±S.E.) for body traits.

Trait	Environment	Genetic variance	Environmental variance	Phenotypic variance	Heritability
Weight	Pond	12.04	5.71	17.75	0.68 ± 0.04
	Tank	2.42	5.11	7.53	0.37 ± 0.03
	Both	12.31	3.94	16.25	0.76 ± 0.04
Length	Pond	32.46	47.01	79.47	0.41 ± 0.04
	Tank	16.61	8.16	24.77	0.67 ± 0.08
	Both	63.92	22.70	86.62	0.74 ± 0.04

1.1. Correlations

The genetic correlations between body weight and length were consistently high and approached unity (0.95 – 0.99) across pond, tank, and combined environments. Correspondingly, at the phenotypic level, these traits exhibited strong correlations ranging from 0.85 to 0.92 (refer to Table 4). Overall, both phenotypic and genetic correlations between weight and length didn't differ between the two environments.

Table 4. Phenotypic and genetic correlations between body weight and length in pond, tank and in both environments.

Generation	Environment	Phenotypic correlation	Genetic correlation
Both G8 and G9	Pond	0.93 ± 0.006	0.97 ± 0.005
	Tank	0.85 ± 0.009	0.95 ± 0.001
	Both	0.92 ± 0.004	0.99 ± 0.001

1.1. Genotype by Environment Interactions

Table 5 presents genetic correlations for homologous body traits between pond and tank environments as a measure of genotype-environment interaction (G×E). The results are shown for each of the two generations separately and when combined. In the generation produced in 2022, the genetic correlations between homologous traits were negative, indicating potential G×E effects despite large standard errors associated with the estimates. However, in the generation produced in 2023, where improved management practices (stocking density, aeration, feeds and feeding regimes and water parameters) were implemented, the genetic correlations between trait expressions in tanks and ponds were remarkedly higher and significant ($P < 0.001$). Similar results were observed when data from both generations were combined, suggesting that the implementation of improved management practices may have contributed to mitigating the G×E interaction effects in this population of Pacific white leg shrimp.

Table 5. Genetic correlations between pond and tank environments.

Generation	Trait	Genetic correlations between the two environments
G8 (2021 – 2022)	Weight	-0.149 ± 0.117
	Length	-0.072 ± 0.126
G9 (2022 – 2023)	Weight	0.61 ± 0.09
	Length	0.52 ± 0.13
Both G8 and G9	Weight	0.65 ± 0.04
	Length	0.60 ± 0.05

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Discussion

The presence of G×E interaction in our study indicates a need to refine breeding strategies that consider both genetic potential and environmental influences on phenotypic traits in this population of white leg shrimp. Genetic effects, measured by genetic correlations between trait expressions in tank and pond environments, were moderate (0.60 – 0.65) but significantly different from one in the latest two generations. We aimed to reduce environmental variability in the latest generation within each rearing system by controlling five main factors: similar stocking density, synchronous aeration, same feeds and feeding regimes and less variable water parameters. Standardizing environmental conditions in tank and pond reduced confounding effects and improved the accuracy of genotype-environment evaluations in the latest generation compared to earlier stages of the breeding program. These improvements may have contributed to the reduced G×E effects on growth traits in this population of white leg shrimp, although other factors may have been involved. While the improvements were observed, the G×E interaction remained biologically significant, as genetic correlations of homologous traits differed from 0.8 or unity (Robertson, 1961), which reflect re-ranking G×E effects, i.e., breeding candidates are ranked differently in tank and pond. Our previous evaluations of the between-environment genetic correlations of growth traits were low (-0.39 to 0.03) when two different statistical models (sire-dam or standard animal model) were employed (Nguyen et al., 2020). These results, along with our current findings, align with published estimates across aquaculture species from fish (de Araújo et al., 2020) to crustaceans (Van Sang et al., 2020) and molluscs (Barros et al., 2018) when tank and pond were used for on growing. Studies in other species using diverse testing systems, such as sea cage *vs.* tank in Asian seabass (Khang et al., 2018) or monoculture *vs.* polyculture in catla and rohu carps (Hamilton et al., 2023), also showed the existence of G×E effects on growth traits. However, when testing environments are similar, these effects were less significant, as demonstrated in Neotropical fish pacu, *Piaractus mesopotamicus* (Freitas et al., 2021).

In addition to the re-ranking effects mentioned earlier, the G×E interaction in this shrimp population was attributed to scaling effects, which refer to differences or heterogeneities in variance components for growth traits between tank and pond environments. This was supported by the observed differential heritability of both weight and length in tank versus pond conditions. The scaling effect was eliminated after data transformation. For instance, when square root transformation was used, the phenotypic variances for body weight were 4.45 g^2 in tank and 4.42 g^2 in pond. Similar results were also observed when logarithmic method was tested. Our previous study pointed it out that the scaling G×E effects due to variance heterogeneity on genetic gain were not significant, such as less than 6% for body weight. It was also less economically important compared to the re-ranking effects. A thorough assessment of the genetic enhancement program for common carp estimated the economic loss resulting from re-ranking G×E interactions to be around US$11-20 million relative to only US$3-5 million due to scaling effects (Ponzoni et al., 2008).

In the present study, we focused on improving five environmental parameters (aeration, water quality, stocking density, feeds, and feeding regimes). While applying the same feeds, feeding regimes, and stocking density across environments and generations are simple and straightforward, managing environmental and water parameters such as reducing water temperature in the pond by increasing frequency of water exchange and volume remains challenging. There are also many other management practices such as housing conditions and environmental factors (e.g., ambient temperature or climate index) that should be considered in future studies. Furthermore, the G×E effects should be re-estimated to confirm the current findings when more data from multiple generations are accumulated. Due to breeding failure and mortality of brookstock, the numbers of half-sib families were limited to allow fitting additional random effects to obtain accurate genetic parameters for weight and length in this population. Advanced statistical procedures can also mitigate the G×E impacts on production traits of this shrimp population. One option is to test animals in multiple environments representative of target production conditions to identify genotypes that consistently perform well or genotype-environment combinations that maximize trait expression. This method, combined with genomic information, also enables breeders to accurately predict individual genetic merit, considering G × E effects and selecting genotypes with improved stability

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across environments. Apart from the multivariate approach used in our study, there are advanced statistical methods and modelling techniques (such as factor analysis and reaction norm models) to identify stable genotypes or genomic regions less influenced by environmental variation (Madsen et al., 2024; Raunsgard et al., 2024). Tailoring breeding objectives and selection criteria based on specific target environments or production systems prioritizes genotypes that perform well under relevant environmental conditions, promoting adaptation and resilience. Regardless of the approach to be employed, evaluation of genotype performance across a range of environments before widespread deployment in commercial production would help identify genotypes with consistent performance and reduces the risk of economic loss in genetic improvement programs for white leg shrimp and other aquaculture species.

Concluding Remarks

Improvements in management practices have helped mitigate the G×E interaction effects in this population of Pacific white leg shrimp, as shown by the moderate genetic correlations for two key growth traits between ponds and tanks. Heritabilities for body weight and total length were generally moderate in both testing environments, although the differences in the estimates between tanks and ponds varied by trait. However, the heritability estimates may have been somewhat biased upwards, due to the existing pedigree structure that does not allow to include additional random effects such as common full-sib families. Overall, our results suggest that the current shrimp population will continue to respond to selection. However, future programs should further enhance other management and husbandry practices to improve the G×E impacts and maximize production and revenue for the shrimp sector.

Scheme 1. Differences in management practices between pond and tank in generations or years of selection (2022 and 2023).

Generation	Parameter	Pond	Tank
G8 (2022)	Stocking density (juveniles per m^2 surface water)	60 due to mortality	100
	Aeration	Paddlewheel (morning)	Aerator (full day)
	Feeds	Home-made diet	Commercial diet
	Feeding regime	3 – 5%	3 – 5%
	Water parameters		
	Salinity level (ppt)	27 – 36	30 – 35
	Water temperature (°C)	25 – 33	26 – 30
	Water exchange	3 – 5% water addition every 4 days	50% every 2 days
G9 (2023)	Stocking density (juveniles per m^2 surface water)	Approx. 70	100
	Aeration	Paddlewheel (full day)	Aerator (all day)
	Feeds	Same commercial diet	Same commercial diet
	Feeding regime	Same 4 times daily	Same 4 times daily
	Water parameters		
	Salinity level (ppt)	31.3 ± .17	33.5 ± .12
	Water temperature (°C)	26 – 32	26 – 30
	Water exchange	15 – 20% water addition every 4 days	50% every 2 days

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