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Genotype-by-environment interaction in white shrimp associated with White Spot Disease

Interacción genotipo por ambiente en camarón blanco asociada a Síndrome de Mancha Blanca

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ABSTRACT

This study aimed to estimate the genotype-by-environment interaction for body weight (BW) and harvest survival (HS), in the presence and absence of White Spot Disease (WSD) in two genetic lines of *Penaeus vannamei* (Growth -GRO- and resistance to WSD-RES-). The heritability for BW in the GRO line was 0.05 ± 0.16 in the presence of WSD and 0.35 ± 0.15 in the absence, while for the RES line it was 0.26 ± 0.07 and 0.49 ± 0.08 in the presence and absence of WSD, respectively. The genetic correlations for BW between environments were -0.17 ± 0.60 for GRO and 0.89 ± 0.09 for RES. The heritability for HS in GRO was 0.01 in both environments and the genetic correlation was not estimable, while, for RES, the heritabilities were 0.06 ± 0.04 and 0.11 ± 0.06 in the absence and presence of WSD, respectively, additionally, the genetic correlation it was not significant. Although the linear model suggests a genotype-by-environment interaction, the estimates propose independence of the same characteristic between environments, and the correlations between characteristics for the resistance line propose to independently select the characteristics when WSD is present.

Keywords: *Penaeus vannamei*, heritability, additive genetic correlation, body weight, survival

RESUMEN

Este estudio tuvo como objetivo estimar la interacción genotipo por ambiente para peso corporal (PC) y supervivencia a cosecha (SC), en presencia y ausencia de Síndrome de Mancha Blanca (SMB) en dos líneas genéticas de *Penaeus vannamei* (Crecimiento -CRE- y resistencia a SMB -RES-). La heredabilidad para PC en la línea CRE fue 0.05 ± 0.16 en presencia de SMB y 0.35 ± 0.15 en ausencia, mientras que para la línea RES fueron 0.26 ± 0.07 y 0.49 ± 0.08 en presencia y ausencia de SMB, respectivamente. Las correlaciones genéticas para PC entre ambientes fueron -0.17 ± 0.60 para CRE y 0.89 ± 0.09 para RES. La heredabilidad para SC en CRE fue 0.01 en ambos ambientes y la correlación genética no fue estimable, mientras que, para RES, las heredabilidades fueron 0.06 ± 0.04 y 0.11 ± 0.06 en ausencia de y presencia de SMB, respectivamente, adicionalmente, la correlación genética no fue significativa. Aunque el modelo lineal sugiere una interacción genotipo por ambiente, los estimados proponen independencia de la misma característica entre ambientes y, las correlaciones entre características para la línea de resistencia proponen seleccionar de manera independiente las características cuando SMB esté presente.

Palabras clave: *Penaeus vannamei*, heredabilidad, correlación genética aditiva, peso corporal, supervivencia.

INTRODUCTION

The world production of Pacific white shrimp (*Penaeus vannamei*) has been based on the production of genetic lines that have been selected for growth and general survival (Campos-Montes *et al.*, 2009; Caballero-Zamora *et al.*, 2015; Yuan *et al.*, 2018). At the same time, the production units have been affected by several diseases with high rates of morbidity and mortality (Trang *et al.*, 2019); among them, the White Spot Disease (WSD) (Hernández-Llamas *et al.*, 2016).

The control of WSD has been a difficult goal and it has been decided to add selection criteria related to the resistance of this disease to the selection objective of Genetic Breeding Programs (GBP) in penaeids (Ødegård *et al.*, 2011; Huang *et al.*, 2012; Klinger and Naylor, 2012; Caballero-Zamora *et al.*, 2015). In this idea, it is important to have adequate estimators of heritability (h^2) and genetic correlation (r_G) for the formulation of selection strategies. These genetic parameters, estimated under natural sprouting conditions, can provide important information to be considered in GBPs. Some authors have estimated the heritability for body weight in the presence of WSD between 0.09, using outbreak information and 0.21 from a controlled challenge (Gitterle *et al.*, 2005b; Caballero-Zamora *et al.*, 2015).

Regarding heritability for survival in the WSD presence, it has been estimated between 0.01 and 0.21 in controlled challenge studies based on different statistical models and infection protocols (Gitterle *et al.*, 2005b; Gitterle *et al.*, 2006a; Gitterle *et al.*, 2006b), and as 0.06 in natural outbreak conditions of WSD (Caballero-Zamora *et al.*, 2015). Instead, the estimation of these parameters for the same trait in different environments can be interpreted as a genotype-environment interaction (GEI). GEI can modify the estimation of h^2 and r_G between selection criteria, causing inaccurate responses to selection and alterations in the ordering of breeding candidates (Sae-Lim *et al.*, 2016).

In *P. vannamei*, previous studies have searched GEI for body weight at harvest (BW) between locations or planting densities under commercial conditions, without finding evidence (Ibarra and Famula, 2008; Campos-Montes *et al.*, 2009). However, Caballero-Zamora *et al.* (2015) observed effects of GEI for body weight at 19 weeks of age among populations that grew in the presence or in WSD absence under commercial conditions. Regarding GEI for general harvest survival (HS), no studies have reported effects of GEI.

Concerning the r_G for weight and survival in shrimp, some studies have estimated the r_G between BW and HS in the absence of any disease between -0.49 and 0.56 (Campos-Montes *et al.*, 2013); while Caballero-Zamora *et al.* (2015) report that it was not possible to estimate this correlation in the presence of WSD, due to the loss of information structure derived from the high mortality in the population. On the other hand, there is no information on how these r_G are modified for weight and survival across different environments in

shrimp production. Therefore, it is important to estimate these genetic parameters (h^2 and r_G) in the presence or absence of WSD for the optimal design of GBPs.

Therefore, the objective of this study was to estimate the effects of GEI for BW and HS in two commercial environments (presence or absence of a natural outbreak of WSD), in two genetic lines of Pacific white shrimp (*Penaeus vannamei*), one selected for growth and another with a history of WSD resistance.

MATERIAL AND METHODS

The data were obtained from a Production Company of shrimp larvae located in northwestern Mexico. The records included shrimp from the 2016 production cycle. The shrimp were raised under commercial conditions in three ponds: two ponds were located on two farms established in Sonora state (Kino and Marea Alta); which presented a natural outbreak of WSD (WSD-presence), where the diagnosis was made from the symptoms and macroscopic changes typical of WSD ([Stentiford and Lightner, 2011](#)), during the production cycle and confirmed by PCR analysis. The third pond was located in Los Pozos community, Sinaloa (Pozos), where strict biosafety procedures were carried out and no symptoms of WSD were detected, nor was there a positive diagnosis by PCR (WSD-absence).

A line selected since 1998 for growth and HS (GRO), and another line with a history of resistance to WSD (RES) was used. The families considered from each line in this study had a maximum of 25% genes from the other line ([Gallaga-Maldonado et al, 2020](#)), and were analyzed independently. For the GRO line, 7,679 records from matings between 49 fathers and 69 mothers (families) were analyzed. For the RES line, 9,519 records were used with the progeny of 63 fathers and 91 mothers (families). The female to male ratio was 1.4 in both lines. The pedigree information included animals born since 2002 for GRO and since 2014 for RES.

Origin and development of genetic lines

The GRO and RES lines were formed in 1998 and 2014 respectively. The GRO line was produced using shrimp from Mexico, Venezuela, Colombia, the United States, and Ecuador. The RES line is composed of shrimp with a history of resistance to WSD from Ecuador, Panama and the United States and since 2014. A more specific description of the creation of the genetic lines can be found in [Gallaga-Maldonado et al. \(2020\)](#) and [Campos-Montes et al. \(2020\)](#).

Family management

The families were produced by artificial insemination, using a ratio of one male for every two females to form half-sib families. The inseminated females spawned in individual tanks for the counting of nauplii per family (full siblings); those spawning with less than

25,000 nauplii being discarded for the next stage. The feeding in the larval stages was based on commercial micro-pellets with 40% to 50% protein and 8% to 10% fat, *Chaetoceros microalgae*, *Spirulina* spp., and *Artemia* spp., and the constitution of the diet was adapted to each stadium. The full sib families were kept in the same pond until they were marked around 60 days of age (weighing between 2 and 3 grams), using colored elastomers (Northwest Marine Technology™), in the last abdominal segment of the shrimp and whose color combination worked as family identification.

Management of growing ponds

Ten days after tagging, an average of 36 shrimp per family were stocked in each pond. The ponds of Sonora (WSD-presence) were of sand of 0.20 ha, with a water column of 1.4 m, at an average temperature of 32 °C and an average salinity of 33 gL⁻¹. The daily water exchange rate ranged from 5 to 20%. The food offered had a protein percentage between 34 and 40% at a rate of 3% of the total biomass in the pond. The stocking density in both ponds was 16 organisms/m². In Sinaloa (WSD-absence) a 4 x 16 m concrete pond was used, with a water column of 2 m and a planting density of 70 m². The water temperature was maintained at 30 °C with a salinity of 35 gL⁻¹, constant aeration and a daily water exchange rate of 4 to 5%. The amount of daily food offered (35 - 40% protein); it was calculated as 6% of its biomass.

Data collection for body weight at 130 days of age and survival from 70 to 130 days

After 70 days after sowing, all the organisms were recovered from the ponds, and from each one the family of origin, sex and body weight were identified. The information of individuals with deformities, without reliable identification or undefined sex was eliminated. For the estimation of the HS, the animals recovered at the end of the period were considered as alive (1) and the animals not recovered, considering the difference between the living organisms of each family and those sown, as dead (0).

Information analysis

To compare the productive behavior between both lines in both scenarios (WSD-presence and WSD-absence), the following linear model was considered:

$$y_{ijk} = \mu + L_i + S_j + LS_{ij} + e_{ijk}$$

Where, y_{ijk} is the vector of observations of BW or HS, μ is the mean of the population for the variable of interest (HS or BW), L_i is the effect of the i-th line (GRO, RES), S_j is the effect of the j-th environment (WSD-presence, WSD-absence), LS_{ij} is the effect of the interaction between the line and pond health status, and $e_{ijk} \sim N(0, \sigma^2_e)$. Sex and the pond were also included on BW. To determine differences between line and environment combinations, a Tukey test ($\alpha = 0.05$) was used.

The genetic parameters for BW and HS were estimated for each line, using an animal model and restricted maximum likelihood, with the ASReml software. Considering the

criteria for approximation of a binomial distribution to a normal distribution (Schader and Schmid, 1989; Emura and Yu-Ting, 2018), normality was assumed in the HS analysis; the model used was:

$$y = X\beta + Zu + Wf + \varepsilon$$

Where, y is the vector of observations of (BW or HS) of both environments, β is the vector of fixed effects of each characteristic, u is the vector of random additive genetic effects of the animal, $u \sim MVN(0, G)$, where $G = V \otimes A$, where V is a symmetric matrix containing the (co) variances between the effects of same family animals for the characteristics in the two environments, and A is a matrix of additive relationships; \otimes is the Kronecker product, environmental residuals, f is the unknown vector of the common family effect for all characteristics, $f \sim MVN(0, F)$; where, $F = C \otimes I$, where, C is a matrix of co (variances) of common family environment effects, only for BW, and I is an identity matrix of appropriate order, and ε is the vector of effects random, $\varepsilon \sim MVN(0, R)$, where, $R = E \otimes I$, where, E is the matrix of co (variances) of the residual effects that contains the covariances between the two characteristics, and I is an identity matrix of appropriate order, with σ_2^e as the residual variance.

Finally, X , Z , and W are known incidence matrices that relate the observations to the fixed effects (which varied depending on the trait analyzed), the genetic effects of the animal, and common family environment effects, respectively. The genetic correlations between both characteristics in the line-pond combination were estimated with ASReml, using bivariate models and with the same model, but considering the y vector of information from BW and HS. No restrictions were used in the covariance structure and common family environment effects were considered independent.

In estimating the genetic parameters for BW, the fixed effects included in the model were: sex, age at harvest linear and quadratic, additionally in the case of WSD-presence; the pond effect was included (Kino and Marea Alta). Regarding the HS for the affected ponds, the only fixed effect considered was that of the pond in WSD-presence; while in the WSD-absence environment, no fixed effect was considered.

The phenotypic variance for each characteristic was estimated as the sum of the variance components of the random effects (animal genetic and common family). The h^2 was estimated as phenotypic variance proportion that is due to the additive genetic variance, and the r_G was estimated as the covariance divided by the product of the corresponding standard deviations. The statistical significance of the estimated parameters was based on the confidence intervals (95%), constructed with their standard errors, assuming normality. The existence of GEI was determined when r_G between environments was less than 0.80 (Sae-Lim *et al.*, 2016).

Finally, to analyze whether the behavior of the characteristics between genetic lines was similar. A comparison of the estimated r_G was made in each line (Nguyen *et al.*, 2016), such comparison was made by means of a Fisher's Z transformation (Rosenthal *et al.*, 1992) implemented in the “Cocor” package in R (Diedenhofen and Musch, 2014), a significance test for the difference between 2 correlations, based on dependent groups with 1 variable in common. For a better understanding, a diagram of the estimated genetic correlations per line is presented in Figure 1.

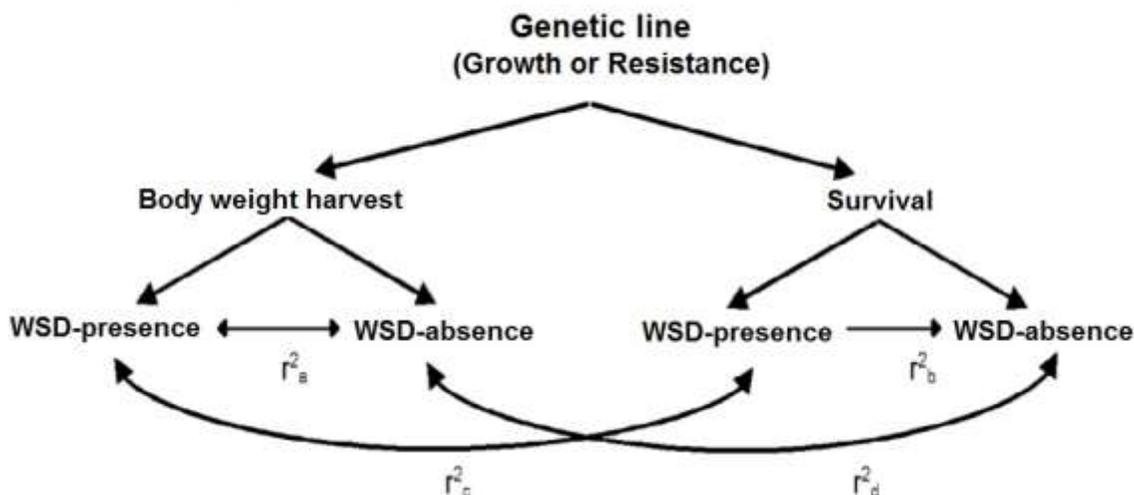


Figure 1. Scheme of the genetic correlations estimated in the study by genetic line

r_a^2 and r_b^2 = Genetic correlation between environments (WSD-presence and WSD-absence) within each characteristic. r_c^2 = Genetic correlation between WSD environments-presence of the two characteristics. r_d^2 = Genetic correlation between WSD environments-absence of the two characteristics

RESULTS AND DISCUSSION

Comparison of productive behavior between lines

Descriptive statistics for BW and HS in each genetic line (GRO and RES), within environment (WSD-presence, WSD-absence) are shown in Table 1. At the same time, Figures 2 and 3 show the LSM of both lines (GRO and RES), through the environments for BW and HS. These results show differences in HS, where the GRO line has a low HS in WSD-presence; while the shrimp of the RES line have a lower HS in WSD-presence. Additionally, there is line-by-environment interaction ($P < 0.0001$) in the two characteristics. These line-by-environment interactions highlight the importance of considering the probability of occurrence of WSD disease, when the line is chosen in the genetic improvement program (Sae-Lim *et al.*, 2016).

Table 1. Number of individuals (n) and least squares means for body weight and survival rate to harvest in the growth line and in the Resistance line, in the presence and absence of White Spot Disease

Environment	Line	Body Weight (g)		Survival Rate	
		n	LSM ± se	n	LSM ± se
WSD-presence	RES	2,524	12.80 ± 0.07 ^a	6,414	0.45 ± 0.01 ^a
	GRO	294	8.75 ± 0.06 ^b	5,494	0.06 ± 0.01 ^b
WSD-absence	RES	2,838	11.91 ± 0.17 ^c	3,105	0.82 ± 0.01 ^c
	GRO	1,926	13.75 ± 0.05 ^d	2,185	0.88 ± 0.01 ^d

LSM: least squares means, se: standard error.

*The different literals within the columns indicate statistically significant differences

TUKEY (α = 0.05).

Heritability for body weight at harvest

The heritabilities for BW in both lines are shown in Table 2. The common family environment effects were 0.05 in both lines. The inclusion of these effects in all the models reduced the estimation of the additive variance, according to what was presented by other authors (Campos-Montes *et al.*, 2013; Montaldo *et al.*, 2013). The heritabilities in WSD-absence were consistent with those reported by authors such as Tan *et al.* (2017), Trang *et al.* (2019) and Ren *et al.* (2020), despite the fact that the latter did not consider common family environment effects in its model; however, these heritability estimates were higher than those reported by other authors (Li *et al.*, 2015; Zhang *et al.*, 2017; Yuan *et al.*, 2018). On the other hand, the heritabilities for WSD-presence are similar to those estimated by Caballero-Zamora *et al.* (2015), who also used data from a natural outbreak of WSD.

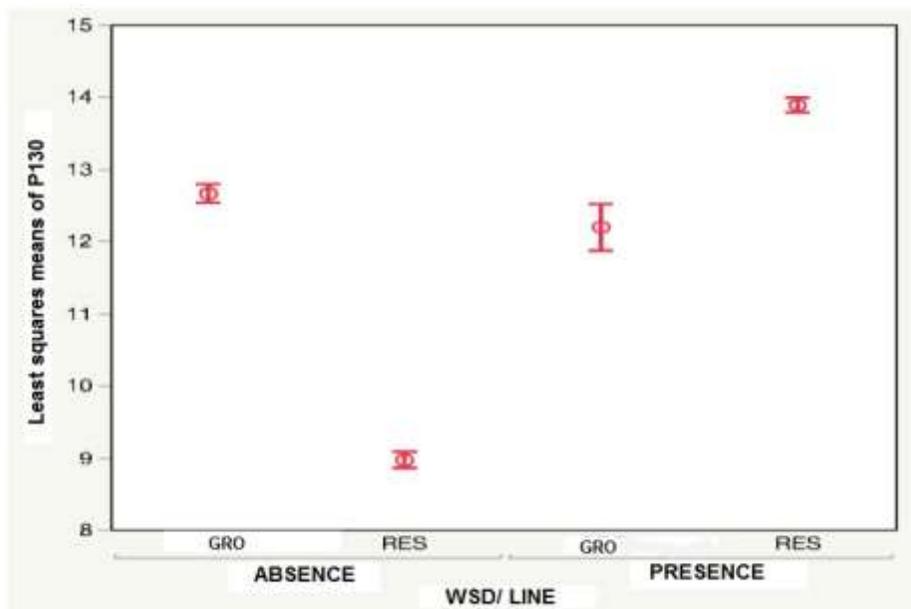


Figure 2. Least squares means for body weight at harvest in the growth lines and resistance to WSD, in the presence and absence of SMB in *P. vannamei*

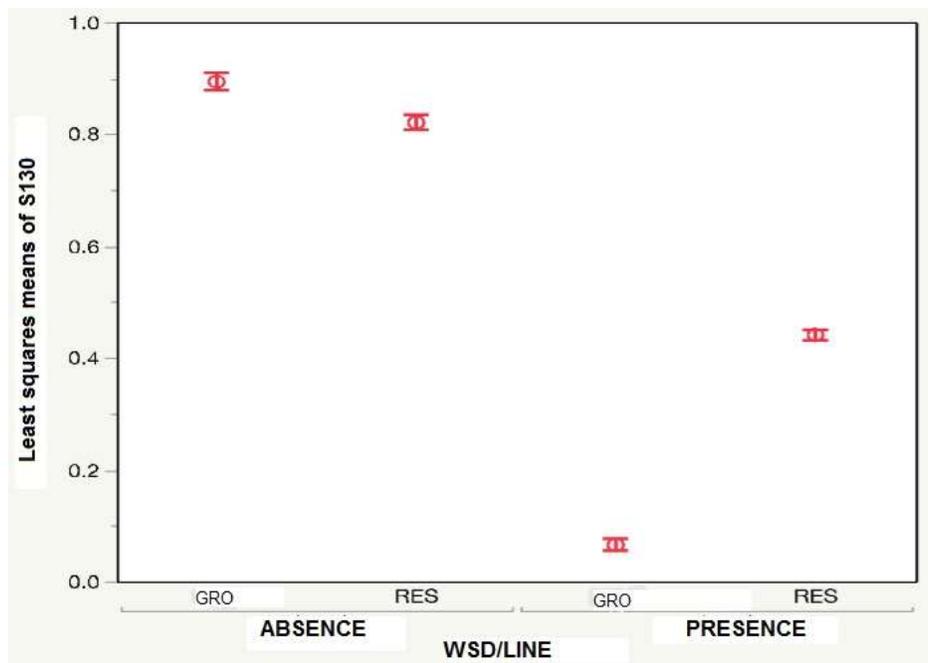


Figure 3. Least squares means for harvest survival in growth lines and resistance to WSD, in the presence and absence of WSD in *P. vannamei*

In the GRO line, the difference between the heritabilities for WSD-presence (0.05 ± 0.16) and WSD-absence (0.35 ± 0.15), can be an indicator of heterogeneity of variances (Sae-Lim *et al.*, 2016). In this case, in addition to changes in the additive genetic variance, the source of this heteroscedasticity may be contained in changes in the environmental variance due to the microenvironmental sensitivity of the individuals. In the case of WSD-presence, it is important to mention that the low precision in the estimate of h^2 may be due to the data structure resulting from the high mortality. In the RES line, the heritability estimates for BW were higher than for GRO; in addition to having better precision. On the other hand, the estimate of h^2 in WSD-presence (0.26 ± 0.07) is lower than in WSD-absence (0.49 ± 0.08), as in the GRO line, and the estimators of this line were consistent with other authors (Luan *et al.*, 2015; Sui *et al.*, 2016; Zhang *et al.*, 2017 and Yuan *et al.*, 2018).

Table 2. Heritability and additive genetic correlations for body weight in growth and resistance lines by environment *

	Environment	WSD-presence	WSD-absence
Growth Line	WSD- presence	0.05 ± 0.16	-0.17 ± 0.60
	WSD- absence		0.35 ± 0.15
	WSD- presence	0.26 ± 0.07	0.89 ± 0.09
Resistance Line	WSD- absence		0.49 ± 0.08

*Estimated by bivariate analysis. Genetic correlations are shown in bold

Variations in heritability estimators for BW may be the result of the microenvironmental sensitivity of individuals (Sae-Lim *et al.*, 2016). Given the above, it is important to note that these changes in heritability can alter the response prediction accuracy to selection.

Genetic correlations for BW

The estimated r_G for the BWs between environments in the GRO line was negative and not significant ($P > 0.05$) (-0.17 ± 0.60); although in estimates with preliminary models (data not shown) it was consistently negative. The imprecise value of the estimate may be a low value consequence of the additive genetic variance of WB in WSD-presence. It complicates the evaluation of GEI effects in this line; while in the RES line, this correlation was not different from 1 ($P > 0.05$) (Table 2); noting that the additive genetic effects for BW are very similar in the two environments (Sae-Lim *et al.*, 2016). In other words, there is no GEI effect on RES for BW. Considering that both lines were under the same environmental management conditions and exposed to the same pathogen (WSD), it is possible to consider that the differences in the estimators of both lines are the result of the low HS rate of the GRO line. In several studies GEI was not detected when considering environmental conditions, such as planting density (Campos-Montes *et al.*, 2009; Tan *et al.*, 2017) or cultivation location (Sui *et al.*, 2016). Other works report possible effects of GEI for BW, considering the point values of the r_G estimators. However, their standard errors do not allow defining them as significantly different from one or zero (Caballero-Zamora *et al.*, 2015; Li *et al.*, 2015; Nguyen *et al.*, 2020).

Heritability for survival to harvest in both genetic lines

The heritability and additive genetic correlations for HS in the genetic lines are shown in Table 3. Regarding the common family effects, these were considered independent between environments for each characteristic, and varied between 0.02 and 0.04. The estimated heritabilities for HS in WSD-presence were 0.01 and 0.11 for GRO and RES respectively; the previous ones are similar to those reported by other authors in the presence of WSD (Gitterle *et al.*, 2005a; Caballero-Zamora *et al.*, 2015); however, they were lower than those estimated by Li *et al.* (2015) and Trang *et al.* (2019); both in WSD controlled challenges. The results of the HS model were consistent with estimates, using univariate models, considering a binomial distribution (results not shown).

Table 3. Heritability and additive genetic correlations for survival in growth lines and resistance by environment *

	Environment	WSD-presence	WSD- absence
Growth line	WSD -presence	0.01 ± 0.02	0.00
	WSD - absence		0.01 ± 0.03
Resistance line	WSD -presence	0.11 ± 0.06	0.10 ± 0.40
	WSD- absence		0.06 ± 0.04

*Estimated using bivariate models
Genetic correlations are shown in bold

The heritabilities for HS in WSD-absence were 0.01 ± 0.03 in GRO and 0.06 ± 0.04 in RES concordant with other estimators for overall survival (Campos-Montes *et al.*, 2013; Zhang *et al.*, 2017; Ren *et al.*, 2020), but lower than those presented by Lu *et al.* (2017), Luan *et al.* (2020), and Tan *et al.* (2017), where the effect of a common family environment was not included, which could have generated an overestimation of the genetic parameters.

The heritabilities in GRO were essentially zero in both environments, 0.01 ± 0.02 in SMB-presence and 0.02 ± 0.03 in WSD-absence, which represents minimal possibilities of genetic advancement by selection for this characteristic in both scenarios, which is consistent with other authors (Gitterle *et al.*, 2005a; Campos-Montes *et al.*, 2013; Li *et al.*, 2015; Lu *et al.*, 2017). The minimum advance by selection could be related to the difficulty in the estimation due to the mortality rate by the statistical models (Vehviläinen *et al.*, 2008), a very low genetic proportion in the survival expression, or possibly, the damage in the structure of genetic family relationships when WSD was present.

The estimated heritabilities for HS in RES were 0.11 ± 0.06 and 0.06 ± 0.04 , for WSD-presence and WSD-absence, respectively (Table 3); which were not statistically different from those estimated for the GRO line. The h^2 for HS in WSD-presence was higher than that estimated by Caballero-Zamora *et al.* (2015) 0.06 and that reported by Gitterle *et al.* (2005b), who calculated values between 0.03 and 0.07. The h^2 for WSD-absence was concordant with other estimators for general survival in the same species (Campos-Montes *et al.*, 2013; Zhang *et al.*, 2017; Ren *et al.*, 2020).

The heritabilities of HS for both environments were consistent in both lines (Table 3), suggesting that there is no compression of the additive variance, in the lines, associated with the environment (Sae-Lim *et al.*, 2016). The genetic correlations between HS in WSD-presence and WSD-absence were not different from zero ($P > 0.05$), coinciding with that reported by Vehviläinen *et al.* (2010) in another aquatic species, which may suggest that survivals in both environments are independent characteristics, as suggested by Thoa *et al.* (2015).

Genetic correlations between body weight and harvest survival

The genetic correlations by environment between BW and HS are shown in Table 4. For the estimation of these correlations, the common family effect was considered independent between environments.

Table 4. Genetic correlations within lines (Growth and Resistance) between body weight to harvest (BW) and harvest survival for environments in the presence or absence of WSD

	WSD- presence	WSD- absence
Growth line	ne*	-0.09 ± 0.92
Resistance line	0.04 ± 0.16	0.57 ± 0.20

*Not estimable

The genetic correlation between the two characteristics could not be estimated in WSD-presence in the GRO line, possibly due to the affectation in the structure of the information associated with the high mortality presented in that line; whereas, for the RES line, it was not different from zero (0.04 ± 0.16), agreeing with the results of [Caballero-Zamora *et al.* \(2015\)](#). In the case of WSD-absence for the GRO line, the r_G was not different from zero (-0.09 ± 0.92), unlike the one estimated in the RES line which was 0.57 ± 0.20 , which was consistent with that estimated by [Campos-Montes *et al.* \(2013\)](#), in commercial ponds, in the absence of SMB (0.56 ± 0.10). The r_G estimated in the RES line was higher than that reported by [Yuan *et al.* \(2018\)](#), [Gitterle *et al.* \(2005a\)](#), and [Zhang *et al.* \(2017\)](#). The differences between the genetic correlations in RES may be an indicator of changes in the variance components possibly associated with GEI, in turn related to the corresponding covariance, which would have implications in the response to correlated selection ([Sae-Lim *et al.*, 2016](#)).

Some authors highlight the importance of the creation of genetic lines in aquaculture ([Nguyen *et al.*, 2016](#)), the results of this study suggest that the selection indices for BW should take into account the genetic line used in the genetic improvement program. On the other hand, the estimation of genetic parameters related to BW must consider the presence of endemic diseases, such as WSD in shrimp culture and visualize HS in the presence and absence of WSD as independent characteristics, in both genetic lines.

In addition to changes in heritabilities and genetic correlations in both lines, their productivity was different in the environments studied, which could be interpreted as an indicator of phenotypic plasticity, which may be common in marine organisms as suggested by [Munday, \(2013\)](#). It can be understood as the expression of different phenotypes in individuals with the same genotype, but under different environmental conditions ([Munasinghe and Seneviratha, 2015](#)). Consequently, this phenotypic plasticity effect should be considered in shrimp genetic improvement programs, ensuring that the performance environments to be analyzed are as close to the production conditions as possible ([Nguyen *et al.*, 2016](#)).

CONCLUSIONS

The results of the linear model suggest differences between the lines, both for body weight and for survival across environments; however, the estimates of the genetic correlations do not allow considering GEI effects within the line in both characteristics, which would indicate that they are independent. Furthermore, the genetic correlations between the characteristics of the resistance line propose to treat them as independent variables, when WSD is present in the environment.

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