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Research Article

Genetic gain, heritability, and phenotypic correlations of growth traits in the Whiteleg shrimp (*Penaeus vannamei*) during one generation of mass selection

Pasandideh R.[1*], Nazari M.A.[1], Yeganeh V.[1]

1Iranian Shrimp Research Center, Iranian Fisheries Science Research Institute (IFSRI), Agricultural Research, Education and Extension Organization (AREEO), Bushehr, Iran
*Correspondence: Rezapasandideh63@gmail.com

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Abstract

Mass selection is an effective strategy for improving growth traits in the *Penaeus vannamei*. In this study, two populations with distinct genetic backgrounds (Molokai and Mix) were subjected to mass selection, and growth and morphological traits including body weight, total length, muscle length, carapace length and width, and third abdominal segment depth were measured. Genetic parameters, phenotypic correlations, and selection responses were estimated to assess population structure and selection efficiency. The Mix population, due to higher genetic heterogeneity and potential heterosis effects, exhibited higher heritability (0.41±0.07 to 0.56±0.09) and faster response to selection. In contrast, the Molokai population, with a more fixed genetic base and greater phenotypic uniformity, showed lower heritability (0.13±0.03 to 0.38±0.07) but maintained long-term trait stability. Relative genetic gain for growth traits was higher in the Mix population (4.06% to 11.49%) compared to Molokai (1.17% to 5.58%), highlighting the efficiency of mass selection in genetically diverse populations. Mean female body weight was approximately 23.5% and 23% higher than males in the Molokai and Mix populations, respectively. Strong positive correlations (r up to 0.97) were observed between growth and morphological traits, enabling the development of multivariate selection indices to enhance selection accuracy. Overall, these findings suggest that strategic use of hybrid populations in early breeding stages can achieve faster genetic improvement, while fixed populations play a crucial role in maintaining long-term stability of economically important traits.

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Introduction

The Whiteleg shrimp (*Penaeus vannamei*) is one of the most important aquaculture species, accounting for approximately 70% of global shrimp production (FAO, 2022). In recent years, *P. vannamei* has become the predominant cultured shrimp species in the coastal provinces of Iran, with production reported at 60,631 and 45,473 tons in 2022 and 2024, respectively (Iranian Fisheries Statistical Yearbook, 2019–2023). Despite its advantages, such as rapid growth, favorable feed conversion ratio, and high survival, the performance of these traits in Iranian cultured populations has declined in recent years. This decline has been attributed to several factors including the non-native origin of the species, restrictions on broodstock importation, high costs of disease-free and genetically improved broodstock, and the consequent risks of increased inbreeding and reduced genetic diversity, which have been widely reported as major constraints in shrimp aquaculture systems worldwide (Gjedrem *et al.,* 2012; Zenger *et al.,* 2019; Shin *et al.,* 2023). Therefore, implementing structured breeding programs and providing selected broodstock is essential for achieving sustainable production in this industry.

Globally, extensive efforts have been made to improve economically important traits such as growth and disease resistance in *P. vannamei* (Caballero-Zamora *et al.,* 2015; Ren *et al.,* 2020; Shin *et al.,* 2023). Among these, growth traits are considered the primary targets in selective breeding programs for *P. vannamei*, as they are directly associated with production efficiency and economic profitability (Shin *et al.,* 2023). Reported heritability estimates for growth traits in *P. vannamei* are generally moderate to high. For instance, Castillo-Juárez *et al.* (2007) reported heritability of harvest weight in different culture environments ranging from 0.24±0.14 to 0.35±0.18 for univariate models and from 0.37±0.06 to 0.45±0.09 for multivariate models. Similarly, Sui *et al.* (2016) reported a heritability of 0.33±0.08 for harvest weight after two generations of selection. More recently, heritability estimates for growth traits at six months of age ranged from 0.39±0.15 to 0.81±0.10 (Sui *et al.,* 2024). These levels of heritability indicate a substantial additive genetic variation for growth traits in *P. vannamei* populations, making selection for these traits relatively efficient and effective (Shin *et al.,* 2023). This genetic potential has been practically realized in breeding programs worldwide; for example, after one generation of selection for growth, selected lines were approximately 21% heavier than the control group, indicating a high response to selection for harvest weight (Argue *et al.,* 2002). Similarly, Andriantahina *et al.* (2012) reported a 10.7% response to selection for body weight at five months in one generation. Review studies also indicate significant cumulative increases in mean body weight over multi-year periods, reflecting the long-term breeding potential. For example, the response to selection for mean harvest weight at 130 days increased by 18.4% between 2003 and 2010 (Castillo-Juárez *et al.,* 2015). On the other hand, some multi-trait breeding programs with varying selection intensities reported lower responses to selection for growth traits, highlighting that outcomes depend on

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program design and breeding objectives. For example, a multi-trait breeding program reported an average response of 4.2% for harvest weight (Gitterle *et al.,* 2007).

Mass selection-based breeding programs are widely applied in aquaculture due to their low cost, simplicity, rapid implementation, and suitability for high-fecundity species (Lind *et al.,* 2012). However, effective evaluation of these programs requires accurate estimates of genetic parameters, including genetic gain, realized heritability (h^2), and phenotypic correlations among traits, to determine selection efficiency and direction. These parameters can be influenced by various factors, including the structure of the base population, culture environment, and selection strategy. As no documented information exists regarding realized heritability and genetic gain from mass selection for growth traits in cultured *P. vannamei* populations in Iran, local studies are essential. Realized heritability, as the most reliable indicator for objectively assessing selection response, is directly calculated from the ratio of observed genetic gain to the applied selection differential, providing a more accurate representation of the population's genetic potential (Andriantahina *et al.,* 2012; Xu, 2022). Therefore, the present study aimed to estimate genetic gain, realized heritability, and phenotypic correlations of growth traits in *P. vannamei* during one generation of mass selection. The findings of this study could provide a solid scientific basis for designing effective and sustainable breeding programs for *P. vannamei* under Iranian aquaculture conditions.

Materials and methods

Populations of P. vannamei

This study was conducted on two populations of *P. vannamei*, namely Molokai (imported from Molokai Broodstock Company, USA) and Mix (a cross between Molokai and CP populations imported from Charoen Pokphand, Thailand). The experiment was carried out at the Persian Gulf Specific Pathogen-Free Shrimp National Research Center, Bushehr, Iran. Postlarvae (PL12) from each population were transferred to nursery tanks, and after the nursery phase, juveniles exhibiting clearly superior growth performance and good health status were preliminarily screened and transferred to grow-out ponds. The culture period lasted eight months, consisting of a 120-day grow-out phase (including the nursery stage) followed by a 120-day broodstocking phase. Shrimp were fed with commercial starter, grower, and broodstock diets formulated according to nutritional requirements. Feed management and water quality monitoring were conducted according to standard protocols to ensure similar rearing conditions in all ponds. To reduce stocking density near the end of the grow-out period (around four months of age), individuals within the top 20% of the weight distribution were retained, while the remaining shrimp were removed. The final stocking density was adjusted to 30 shrimp per m^2. For the Molokai population, two ponds were maintained, whereas the Mix population was maintained in a single pond. For each population, one pond was

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designated as the control group, in which selection was performed randomly. Shrimp health was routinely monitored using PCR-based diagnostic tests throughout the rearing period.

Measurement of growth traits

Phenotypic data on growth traits were collected from the first-generation shrimp between 2023 and 2024. Six morphometric traits were measured monthly using a digital balance and vernier caliper following Andriantahina *et al.* (2012):

1. Body weight (BW, g),
2. Total length (TL, cm): from the tip of the rostrum to the tip of the telson,
3. Muscle length (ML, mm): from the junction between the first abdominal segment and the carapace to the junction between the last abdominal segment and the telson,
4. Carapace length (CL, mm): from the posterior edge of the orbit to the posterior edge of the carapace,
5. Carapace width (CW, mm): measured at the midline of the carapace,
6. Third abdominal segment depth (TASD, mm): measured at the midline of the third abdominal segment (Fig. 1).

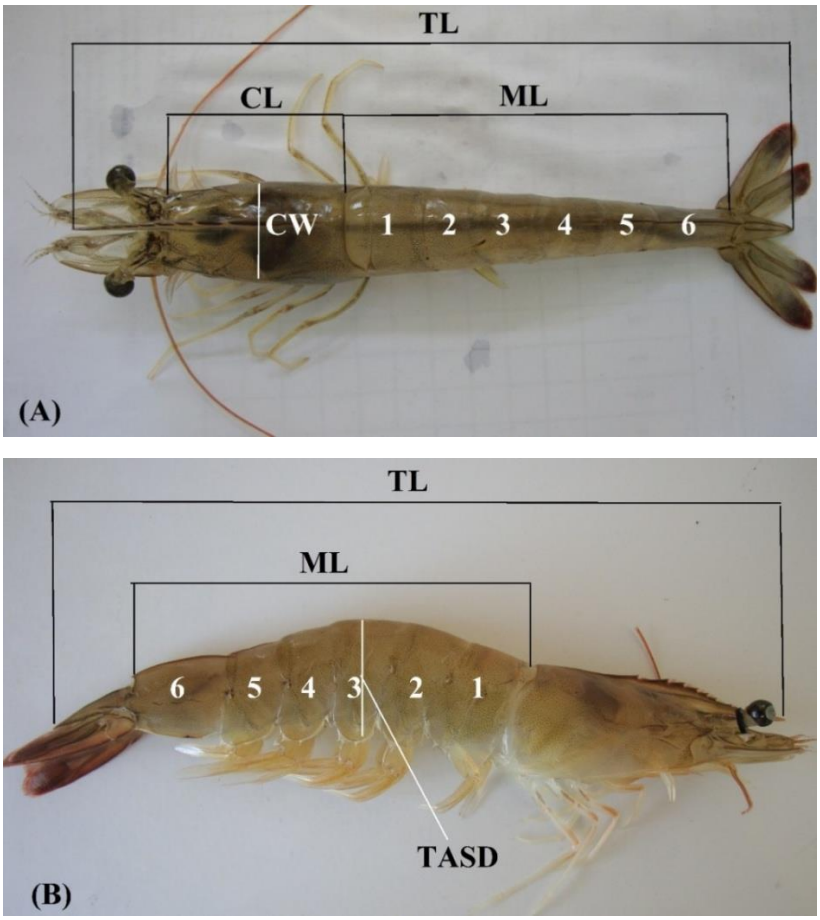

Figure 1: (A). Dorsal view of a *P. vannamei* individual with the morphometric measurements of growth-related traits. (B). Lateral view of a *P. vannamei* individual with the morphometric measurements of growth-related traits. TL: total length; ML: muscle length; CL: carapace length; CW: carapace width; TASD: third abdominal segment depth.

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Selection procedure

A mass selection breeding strategy was applied based on body weight, following Andriantahina *et al.* (2013). Each pond initially contained approximately 6,000 shrimp. During the rearing period, biometric sampling was conducted monthly by randomly collecting 40 shrimp per pond using feed trays. Phenotypic data for growth traits were recorded, and individuals within the top 20% of the weight distribution were identified using the standard z-score formula (Equation 1). In the control group, shrimp were selected randomly from the entire population weight range. At the end of the broodstocking period (8 months of age), individuals within the top 20% of the weight range in each population were selected as elite broodstock and transferred to the hatchery for producing the next generation. The remaining individuals were excluded from breeding.

$y = \mu + z\sigma$ Eq. 1

Where, y: body weight (g); μ: population mean (g); z: standardized selection intensity value; σ: population standard deviation (g).

Estimation of genetic and population parameters

For each trait, genetic gain (i.e., response to selection) was calculated as the difference between the mean of offspring from selected parents and that of offspring from control parents (Equation 2). Phenotypic data from the parental generation were used to estimate the phenotypic standard deviation required for calculating the selection differential. Accordingly, the selection differential was obtained using the selection intensity for the top 20% of the population (p=20%, i=1.3998) and the phenotypic standard deviation of the parental population (Equation 3). Realized heritability (h^2) was estimated as the ratio of the genetic response to the selection differential (Equation 4). Phenotypic correlations between traits were calculated using Pearson's correlation coefficient (Equation 5). Effective population size (Ne) was estimated based on the number of contributing males and females using Equation 6 (Hetzel *et al.,* 2000; Andriantahina *et al.,* 2012; Xu, 2022):

$R = \overline{X}_{\text{offspring } of\ selected} - \overline{X}_{\text{offspring of } control}$ Eq. 2

Where, R: genetic gain or response to selection (g); $\overline{X}_{\text{offspring } of\ selected}$: mean body weight of offspring from selected parents (g); $\overline{X}_{\text{offspring of } control}$: mean body weight of offspring from control parents (g).

$S = i \times \sigma_p$ Eq. 3

Where, S: selection differential (g); i: selection intensity (constant value of 1.3998 for top 20% selection); σ_p: phenotypic standard deviation of the parental population (g).

$h^2 = \frac{R}{S}$ Eq. 4

Where, h^2: realized heritability; R: genetic gain or response to selection; S: selection differential.

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$r_p = \frac{cov(X.Y)}{\sigma_X \sigma_Y}$ Eq. 5

Where, r_p: phenotypic correlation coefficient between traits *X* and *Y*; $cov(X.Y)$: covariance between the two traits; σ_X,σ_Y: standard deviations of traits *X* and *Y*, respectively.

$Ne = \frac{4Nm*Nf}{Nm+Nf}$ Eq. 6

Where, Ne: effective population size; Nm: number of selected males; Nf: number of selected females.

Statistical analysis

In this study, growth data were collected from individual shrimp and used to compare growth traits between the Molokai and Mix populations. Data for the Molokai population were collected from two ponds, whereas data for the Mix population were collected from a single pond. Given that the objective of the study was to compare the phenotypic performance of the two populations, data from the two Molokai ponds were pooled to estimate the overall mean for this population. Mean growth traits were compared between the two populations using an independent-samples t-test at a significance level of $P < 0.05$ (PROC TTEST, SAS 9.4). Prior to the analysis, the assumptions of normality and homogeneity of variances were assessed using the Shapiro–Wilk and Levene's tests, respectively, and data were log-transformed when necessary. Descriptive statistics, including the mean, standard deviation, and coefficient of variation, were calculated for each trait in the first generation. In this analysis, each shrimp was considered an individual observation unit, and the numbers of observations differed between the two populations because of differences in the numbers of shrimp sampled. All statistical analyses were performed using SAS version 9.4.

Results

Descriptive statistics of body weight and selection thresholds

To establish a common criterion for selection based on body weight, phenotypic data from the two ponds of the Molokai population were pooled. Descriptive statistics of body weight in first-generation showed that the mean body weight of the Molokai population was significantly higher than that of the Mix population at 4 months of age ($P < 0.05$), whereas no significant difference was observed between the two populations at 8 months of age ($P > 0.05$). The selection threshold corresponding to the upper 20% of the population was also higher in the Molokai population than in the Mix population at both 4 and 8 months of age. In both populations, females exhibited a higher final body weight than males, with mean body weights approximately 23.5% and 23% greater than those of males in the Molokai and Mix populations, respectively. At the end of the broodstocking period (8 months), individuals within the top 20% of the body weight distribution were considered superior broodstock, from which 150 pairs (150 males and 150 females) were selected per population to produce the next generation. In parallel, control groups were formed by randomly selecting broodstock from the entire population without applying any selection criterion. Considering equal sex ratios, the effective population size (Ne) for each

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population was calculated as 300. Detailed means, standard deviations, and selection thresholds are presented in Table 1. Overall, both populations exhibited similar weight ranges, with Molokai showing a slightly higher growth tendency.

Descriptive statistics of morphometric traits

Descriptive statistics of the morphological traits of first-generation showed that, at 4 months of age, the mean total length (TL), carapace width (CW), and third abdominal segment depth (TASD) were significantly greater in the Molokai population than in the Mix population ($P < 0.05$), whereas no significant differences were observed between the two populations in mean muscle length (ML) or carapace length (CL) ($P > 0.05$). A similar pattern was observed at 8 months of age, with significantly greater mean TL and CW in the Molokai population compared with the Mix population ($P < 0.05$), while the differences in mean ML, CL, and TASD between the two populations were not statistically significant ($P > 0.05$). In addition, the Mix population exhibited higher coefficients of variation for most traits than the Molokai population, indicating greater phenotypic variability within the Mix population. Detailed means, standard deviations, and coefficients of variation for each trait at 4 and 8 months of age are presented in Table 2.

Table 1: Descriptive statistics of body weight and selection thresholds for shrimp populations at 4 and 8 months of age in the first generation. Values with different superscripts are significantly different ($P < 0.05$).

Pop	n	$\overline{X}_{BW}$ (g)	SD (g)	SE (g)	ST (z-score)	Minimum selection weight (g)	P - value
4 months							
Molokai	80	26.07[a]	3.65	0.40	0.84	29.13	
Mix	40	23.68[b]	2.83	0.44	0.84	26.06	0.0004
8 months							
Molokai (males)	31	36.00[a]	4.58	0.82	0.84	39.84	
Mix (males)	19	33.60[a]	3.95	0.90	0.84	36.91	0.0647
Molokai (females)	49	44.47[a]	7.30	1.04	0.84	50.60	
Mix (females)	21	41.35[a]	7.14	1.55	0.84	47.34	0.1036

Pop: Population; n = Sample size; $\overline{X}_{BW}$ (g) = Mean body weight (g); SD = Standard deviation; SE = Standard error; ST = Selection threshold (z-score at the 80th percentile).

Table 2: Comparison of morphological traits between Molokai and Mix shrimp populations at 4 and 8 months of age in the first generation. Values with different superscripts are significantly different ($P < 0.05$).

Trait	$\overline{X}_{Molokai\ Pop} \pm$ SD	% CV	$\overline{X}_{Mix\ Pop} \pm$ SD	% CV	P-value
4 months					
TL (cm)	14.37[a] ± 0.64	4.45	13.91[b] ± 0.70	5.03	0.0132
ML (mm)	74.09[a] ± 4.50	6.07	72.13[a] ± 4.62	6.41	0.1216
CL (mm)	33.46[a] ± 4.26	12.73	32.15[a] ± 2.05	6.38	0.1060
CW (mm)	16.56[a] ± 1.45	8.76	15.78[b] ± 0.88	5.58	0.0120
TASD (mm)	19.98[a] ± 1.30	6.51	18.97[b] ± 1.78	9.38	0.0143

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Trait	$\overline{X}_{Molokai\ Pop}$ ± SD	% CV	$\overline{X}_{Mix\ Pop}$ ± SD	% CV	P-value
8 months					
TL (cm)	17.20[a] ± 1.01	5.87	16.60[b] ± 1.09	6.57	0.0378
ML (mm)	81.96[a] ± 6.37	7.77	79.60[a] ± 6.44	8.09	0.1851
CL (mm)	41.41[a] ± 4.15	10.02	40.82[a] ± 4.53	11.10	0.6216
CW (mm)	19.41[a] ± 1.83	9.43	18.20[b] ± 2.41	13.24	0.0359
TASD (mm)	21.65[a] ± 2.12	9.79	21.45[a] ± 1.76	8.21	0.7141

BW = Body weight (g); TL = Total length (cm); ML = Muscle length (mm); CL = Carapace length (mm); CW = Carapace width (mm); TASD = Third abdominal segment depth (mm).
$\overline{X}_{Molokai\ Pop}$ = Mean of Molokai population; $\overline{X}_{Mix\ Pop}$ = Mean of Mix population; SD: Standard deviation; CV: Coefficient of variation.

Phenotypic correlations among growth traits

Phenotypic correlation analysis revealed that BW was positively and mostly significantly correlated (p<0.05) with all morphometric traits in both Molokai and Mix populations at four and eight months of age. Most morphometric traits were also positively and significantly intercorrelated, although a few correlations in the Molokai population were not significant (p>0.05). The strength and stability of correlations were generally higher in the Mix population. These results suggest that morphometric traits can serve as reliable indicators of growth and potential indirect selection criteria in shrimp breeding programs. Detailed correlation coefficients and corresponding P-values are provided in Tables 3 and 4.

Table 3: Phenotypic correlation matrix of growth traits in the Molokai shrimp population at 4 and 8 months of age in the F_1 generation. Above the diagonal: phenotypic correlation coefficients (r); below the diagonal: corresponding P-values. (p<0.05; Significant correlations).

Trait	BW	TL	ML	CL	CW	TASD
4 months						
BW	1	0.91	0.78	0.42	0.61	0.56
TL	0.0001	1	0.74	0.37	0.58	0.52
ML	0.0001	0.0001	1	0.28	0.41	0.51
CL	0.003	0.01	0.06	1	0.39	0.16
CW	0.0001	0.0001	0.005	0.008	1	0.25
TASD	0.0001	0.0002	0.0004	0.28	0.10	1
8 months						
BW	1	0.89	0.75	0.67	0.76	0.78
TL	0.0001	1	0.74	0.65	0.78	0.76
ML	0.0001	0.0001	1	0.53	0.46	0.66
CL	0.003	0.0002	0.003	1	0.68	0.77
CW	0.0001	0.0001	0.0007	0.0001	1	0.64
TASD	0.0001	0.0001	0.0001	0.0001	0.0003	1

BW = Body weight (g); TL = Total length (cm); ML = Muscle length (mm); CL = Carapace length (mm); CW = Carapace width (mm); TASD = Third abdominal segment depth (mm).

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Comparison of growth of selected shrimp between populations

Comparative analysis of selected male and female shrimp from Molokai and Mix populations indicated that, among males, BW, TL, ML, and CL were significantly higher in the Molokai population (p<0.05), while no significant differences were found in CW and TASD (p>0.05). In females, BW, TL, and CW were significantly greater in the Molokai population (p>0.05), whereas ML, CL, and TASD did not differ significantly between populations (p>0.05). Detailed mean values and significance levels are summarized in Table 5.

Analysis of genetic parameters of growth traits

Analysis of genetic parameters for growth traits in the first generation revealed that the response to selection (R) and realized heritability (h^2) were higher for all traits in the Mix population compared to the Molokai population. The relative genetic gain for growth traits ranged from 4.06% to 11.49% in the Mix population and from 1.17% to 5.58% in the Molokai population. The highest relative genetic gain (R%) was observed for BW, reaching 11.49% in the Mix and 3.29% in the Molokai population.

Table 4: Phenotypic correlation matrix of growth traits in the Mix shrimp population at 4 and 8 months of age in the F_1 generation. Above the diagonal: phenotypic correlation coefficients (r); below the diagonal: corresponding P-values. (p<0.05; Significant correlations).

Trait	BW	TL	ML	CL	CW	TASD
4 months						
BW	1	0.96	0.88	0.73	0.84	0.73
TL	0.0001	1	0.84	0.72	0.81	0.69
ML	0.0001	0.0001	1	0.71	0.78	0.73
CL	0.0001	0.0001	0.0001	1	0.76	0.40
CW	0.0001	0.0001	0.0001	0.0001	1	0.65
TASD	0.0001	0.0001	0.0001	0.009	0.0001	1
8 months						
BW	1	0.97	0.82	0.85	0.89	0.85
TL	0.0001	1	0.85	0.86	0.87	0.85
ML	0.0001	0.0001	1	0.75	0.73	0.82
CL	0.0001	0.0001	0.0001	1	0.83	0.76(0.0001)
CW	0.0001	0.0001	0.0001	0.0001	1	0.73
TASD	0.0001	0.0001	0.0001	0.0001	0.0001	1

BW = Body weight (g); TL = Total length (cm); ML = Muscle length (mm); CL = Carapace length (mm); CW = Carapace width (mm); TASD = Third abdominal segment depth (mm).

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Table 5: Comparison of growth traits between selected male and female shrimp from the Molokai and Mix populations at 8 months of age (F_1 generation).

Trait	$\overline{X}_{Molokai\ Pop}$	$\overline{X}_{Mix\ Pop}$	P-value
Selected Males			
BW (g)	43.75[a]	38.86[b]	0.0001
TL (cm)	17.05[a]	16.32[b]	0.0003
ML (mm)	88.70[a]	80.37[b]	0.0499
CL (mm)	38.50[a]	35.95[b]	0.0002
CW (mm)	18.62[a]	18.05[a]	0.1244
TASD (mm)	21.30[a]	20.42[a]	0.0928
Selected Females			
BW (g)	52.25[a]	48.71[b]	0.0065
TL (cm)	18.09[a]	17.46[b]	0.0008
ML (mm)	92.25[a]	90.25[a]	0.0819
CL (mm)	41.97[a]	41.97[a]	1.0000
CW (mm)	21.57[a]	20.92[b]	0.0475
TASD (mm)	23.02[a]	22.60[a]	0.3144

Differences between populations within each sex were tested by t-test; values with different superscripts are significantly different (p<0.05).
BW = Body weight (g); TL = Total length (cm); ML = Muscle length (mm); CL = Carapace length (mm); CW = Carapace width (mm); TASD = Third abdominal segment depth (mm).
$\overline{X}_{Molokai\ Pop}$ = Mean of Molokai population; $\overline{X}_{Mix\ Pop}$ = Mean of Mix population.

Other traits, including TL, ML, CL, CW, and TASD, also exhibited higher responses to selection and heritability in the Mix population, although to a lesser extent than BW. The realized heritability of BW was estimated at 0.48 in the Mix population and 0.14 in the Molokai population, confirming the higher potential of the Mix population to respond to selection for this trait. Other growth traits showed moderate to high realized heritability values (0.13–0.56). Detailed values of parental means, phenotypic standard deviations, selection differentials, means of selected and control offspring, selection responses, and realized heritability estimates for each trait are presented in Table 6.

Table 6: Genetic parameters of growth traits in Molokai and Mix populations of *P. vannamei* at 8 months of age (F1 generation).

Trait	Pop	$\overline{X}_P$	σp	i	S	$\overline{X}_{SO}$	$\overline{X}_{CO}$	R	h²	SE(h²)	R%
BW (g)	Molokai	40.52	6.72	1.3998	9.41	40.73	39.39	1.33	0.14	0.03	3.29
	Mix	43.38	7.39	1.3998	10.35	37.67	32.68	4.98	0.48	0.08	11.49
BL (cm)	Molokai	16.29	1.06	1.3998	1.49	17.05	16.85	0.20	0.13	0.03	1.25
	Mix	16.79	0.85	1.3998	1.19	16.55	15.87	0.68	0.56	0.09	4.06
ML (mm)	Molokai	84.01	4.74	1.3998	6.64	81.21	80.22	0.98	0.14	0.03	1.17
	Mix	79.89	8.22	1.3998	11.50	79.60	73.14	6.45	0.56	0.09	8.08
CL (mm)	Molokai	38.87	5.70	1.3998	7.98	41.57	40.02	1.55	0.19	0.04	3.99
	Mix	39.95	4.14	1.3998	5.80	40.82	38.40	2.42	0.41	0.07	6.05
CW (mm)	Molokai	19.22	2.46	1.3998	3.44	19.78	18.80	0.98	0.28	0.06	5.14
	Mix	19.81	1.64	1.3998	2.30	18.20	17.00	1.20	0.52	0.09	6.05
TASD (mm)	Molokai	20.67	2.15	1.3998	3.01	21.57	20.42	1.15	0.38	0.07	5.58
	Mix	20.91	3.06	1.3998	4.28	21.45	19.16	2.28	0.53	0.09	10.91

BW = Body weight (g); TL = Total length (cm); ML = Muscle length (mm); CL = Carapace length (mm); CW=Carapace width (mm); TASD = Third abdominal segment depth (mm).
Pop = Population; $\overline{X}_P$ = Mean of parents; σp = Phenotypic standard deviation; i = Selection intensity; S = Selection differential; $\overline{X}_{SO}$ = Mean of selected offspring; $\overline{X}_{CO}$ = Mean of control offspring; R = Genetic gain; h² = Heritability; SE(h²) = Standard error of heritability; R% = Genetic gain relative to parental mean.

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Discussion

In recent decades, selective breeding programs in *P. vannamei* have been recognized as one of the most effective strategies to enhance growth performance and production efficiency in the aquaculture industry. Descriptive statistics of body weight in the Molokai and Mix populations revealed that although the mean body weight was significantly higher in the Molokai population at 4 months of age, no significant difference was observed between the two populations at 8 months of age. This pattern indicates overall similarity in growth performance between the two base populations and relative uniformity of rearing conditions. The marginal tendency of the Molokai group toward higher body weight may be attributed to its prior selection history and early genetic improvement for faster growth, whereas the Mixed population originated from the admixture of multiple genetic sources aimed at increasing diversity. Generally, responses to selection for growth traits in *P. vannamei* become evident only after several consecutive generations. For instance, Castillo-Juárez *et al.* (2015) reported an 18.4% increase in mean body weight over seven generations of selection in an improved *P. vannamei* strain. At eight months of age, the difference in mean body weight between sexes was remarkable, with females being significantly heavier than males in both populations. This pattern is consistent with the findings of Argue *et al.* (2002), who reported that *P. vannamei* females were on average 12.7% larger than males after only one generation of selection. However, part of the higher body weight observed in females at eight months of age may be associated with sex-specific maturation and gonadal development in addition to somatic growth.

In the present study, the selection threshold was determined based on the top 20% of the population, calculated according to the normal distribution of body weight. Similarly, Andriantahina *et al.* (2013) selected the top 40% of females and 20% of males based on body weight to produce the next generation in *P. vannamei*. In the current work, the selection threshold for the top 20% of individuals in the Molokai population was also higher, which is consistent with its greater mean body weight and indicates that selection in this group was primarily directed toward individuals with superior growth performance.

At the end of the broodstocking phase (8 months), individuals within the top 20% of the body weight distribution were considered superior broodstock, from which 150 pairs (150 males and 150 females) were selected per population, resulting in an effective population size (Ne) of approximately 300 individuals per stock. Maintaining a sufficiently large effective population size is essential to preserve genetic diversity and to minimize the rate of inbreeding in mass selection programs for aquatic species. The estimated Ne in this study was in agreement with the recommendations of Bentsen and Olesen (2002), who suggested a minimum threshold to avoid genetic bottlenecks and inbreeding depression in subsequent generations.

Evaluation of morphological traits in the first generation indicated that the Molokai

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population generally showed superior morphological performance compared with the Mix population across all measured traits, although some differences were not statistically significant. Such consistent phenotypic advantages may indicate underlying genetic potential that could be further evaluated and exploited through targeted selection in subsequent generations. In mass selection programs, even relatively subtle phenotypic differences may become progressively reinforced through continued selection, potentially leading to cumulative genetic gains over successive generations (Gjedrem and Baranski, 2010). Morphometric traits such as ML and TASD have been recognized as indirect indicators of growth performance in *P. vannamei* (Andriantahina *et al.,* 2012; Shin *et al.,* 2023).

The lower coefficients of variation (CV %) observed in the Molokai population across most traits and at both ages indicated greater phenotypic uniformity within this group. This may reflect a more stabilized genetic composition and better environmental control during rearing. However, from a breeding perspective, maintaining adequate phenotypic and genetic variation is essential for effective selection response. Therefore, a low CV is only desirable if sufficient additive genetic variance is preserved (Falconer and Mackay, 1996; Gjedrem and Baranski, 2010). In contrast, the higher dispersion observed in the Mix population likely resulted from its heterogeneous genetic background derived from the cross between different base stocks, which can enhance phenotypic variance and, consequently, the capacity for selection response during early generations (Xu, 2022).

Phenotypic correlations among growth-related traits were notably stronger and more consistent in the Mix population (r up to 0.97), whereas the Molokai population exhibited slightly weaker or, in some cases, non-significant correlations. This difference in correlation strength can be attributed to the genetic structure and origin of each population. The Mix population, being a product of two distinct genetic sources, likely exhibited structured heterogeneity, which increases phenotypic variance and reveals stronger trait interrelationships, particularly when traits are under common genetic control (Xu, 2013). Conversely, the more uniform genetic background of the Molokai population may result in weaker correlations if environmental variance predominates or the phenotypic range is narrow (Falconer and Mackay, 1996). Moreover, the strong correlations among morphometric traits and body weight indicate synergistic relationships that could support the construction of multivariate selection indices to improve selection accuracy (Hasan *et al.,* 2022; Soler *et al.,* 2024). The higher stability of correlations at eight months compared with four months suggests that these relationships become more established at later growth stages, enhancing the reliability of indirect selection criteria. This pattern agrees with observations from industrial breeding programs in Ecuador (Shin *et al.,* 2023), where morphometric traits were effectively used as complementary indicators for late-stage growth selection in *P. vannamei*.

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Comparison of selected breeders across the two populations revealed that the response to selection for growth traits was not only population-dependent but also partially sex-dependent. In the Molokai population, key growth traits improved in both sexes, yet the pattern of differences between males and females was not identical. Sex-dependent variation in selection response may stem from physiological differences, growth rates, and genetic sensitivity of traits between males and females, as also reported by Andriantahina *et al.* (2013) and Sui *et al.* (2024). The significant differences observed in traits such as BW and TL in both sexes indicate the effectiveness of selection in the Molokai population, likely due to its more uniform genetic structure and history of continuous selection. In contrast, the Mix population, resulting from the cross of two distinct genetic sources, may still be undergoing genetic reorganization and allele frequency adjustments, leading to a more variable and less stabilized response to selection (Xu, 2013; Xu, 2022). The lack of significant differences in traits such as TASD and CL, particularly in females, may reflect lower heritability, environmental effects, or the absence of focused selection on these traits. This highlights the need for careful multivariate selection index design when selecting for multiple traits simultaneously (Falconer and Mackay, 1996; Hasan *et al.,* 2022; Soler *et al.,* 2024).

Analysis of genetic parameters for growth traits indicated that both realized heritability (h^2) and selection response (R) were markedly higher in the Mix population compared with the Molokai population. The relative genetic gains for growth traits in the Mix population ranged from 4.06% to 11.49%, whereas in the Molokai population they ranged from 1.17% to 5.58%. This difference highlights the higher potential for selection response in the Mix population and reflects its greater additive genetic variance. Previous studies have reported moderate to high heritability values (0.25–0.73) for growth traits in *P. vannamei* (Ren *et al.,* 2022; Wang *et al.,* 2024; Sui *et al.,* 2024), which aligns with the observations from the Mix population in this study. For instance, Ren *et al.* (2022) reported mean heritability ranging from 0.373 to 0.486 for body weight, emphasizing that environmental conditions and selection design can cause wide fluctuations in these parameters. Similarly, Wang *et al.* (2024) reported heritability estimates in the moderate to high range (0.256–0.441), consistent with our findings.

The higher heritability observed in the Mix population can be attributed to several factors. First, the Mix population originates from a cross between two genetically distinct sources, which can lead heterogeneity and heterosis in the F1 generation, enhancing the potential for selection response (Lu *et al.,* 2017). Second, combining diverse genetic sources may temporarily increase additive variance in traits and elevate heritability estimates, a phenomenon observed in other populations derived from interline or intersource crosses (Lamkey and Edwards, 1999; Buskirk and Willi, 2006). Third, the higher phenotypic dispersion seen in the Mix population reflects a broader range of additive genetic variance for growth traits. This increased genetic variation supports

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the capacity for selection response in traits such as BW and ML, resulting in higher empirical heritability estimates ($h^2 = R/S$) in this population (Falconer and Mackay, 1996; Xu, 2013). In contrast, the Molokai population, with a more stabilized origin and higher phenotypic uniformity, displayed lower genetic variance for growth traits. Although this results in lower heritability, it contributes to maintaining trait stability and uniformity in subsequent generations. These findings are in agreement with Fernández *et al.* (2014), who indicated that a reduced level of genetic diversity within the base population may constrain the overall response to selection.

Conclusion

The results of this study demonstrate that both Mix and Molokai populations of *P. vannamei* possess significant genetic potential for selective breeding aimed at improving growth traits. The Mix population, with its composite origin and higher genetic heterogeneity, exhibited greater additive variance and heritability, providing a higher capacity for rapid response to selection. This underscores the efficiency of mass selection in populations with greater genetic diversity. Conversely, the Molokai population, with a more stabilized genetic background and higher phenotypic uniformity, exhibited lower but more stable heritability, which is beneficial for maintaining consistent economic trait performance over the long term. These findings suggest that utilizing composite populations during early breeding stages can enhance genetic variation and accelerate growth improvements, while employing stabilized populations in later generations helps maintain performance stability and genetic homogeneity. Strategically combining both population types could achieve an optimal balance between short-term genetic gain and long-term sustainability in *P. vannamei* breeding programs. Furthermore, integrating mass selection with advanced genetic evaluation models, such as BLUP or GBLUP, in subsequent generations can improve prediction accuracy and genetic stability. Overall, the study confirms that even within a single generation, mass selection can produce meaningful genetic progress in growth traits of *P. vannamei*, providing a solid foundation for future selective breeding programs.

Conflicts of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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