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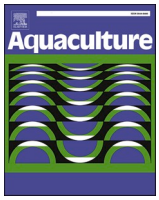

Genetic parameters and genotype by environment interaction for harvest traits of Malabar red snapper (*Lutjanus malabaricus*)

Bing Liang [a,b,*], Dean R. Jerry [a,d], Vu Nguyen [a], Xueyan Shen [a], Joyce Koh [a,c], Celestine Terence [a], Maria G. Nayfa [a,c], Maura Carrai [a], Purushothaman Kathiresan [a,c,e], Rachel Jia Wen Ho [a,c], Hazim Mohamed [a,c], Saraphina Dianne Rwei Qing Tneo [c], Grace Loo [c], Shubha Vij [a,c], Jose A. Domingos [a]

[a] *Tropical Futures Institute, James Cook University Singapore, 149 Sims Drive, 387380 Singaporechi, Singapore*
[b] *Marine Aquaculture Centre, Singapore Food Agency, 52 Jurong Gateway Road, JEM Office Tower, #14-01, 608550, Singapore*
[c] *School of Applied Science, Republic Polytechnic, 9 Woodlands Avenue 9, 738964, Singapore*
[d] *ARC Research Hub for Supercharging Tropical Aquaculture through Genetic Solutions, James Cook University, Townsville, QLD 4810, Australia*
[e] *Department of Preclinical Sciences and Pathology, Faculty of Veterinary Medicine, Norwegian University of Life Sciences, Ås 1433, Norway*

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ABSTRACT

Malabar red snapper (*Lutjanus malabaricus*) is a tropical fish farmed in Singapore and Southeast Asia. Currently, eggs are produced in open net cages without controlled breeding, and no breeding program exists. The industry needs access to high-quality eggs from genetically improved stocks, highlighting the importance of developing a breeding program. However, fundamental genetic information, such as heritability and genetic correlations, is needed before implementing such a program. In this study, 2547 Malabar red snappers were genotyped using a custom Axiom 70k Red Snapper SNP array across three different rearing sites in Singapore. The body weight (BW), total length (TL), body depth (BD), Fulton's condition factor (K), body shape index (BSI) and skin redness (CIELAB *a values; Cl_a) of the fish were collected at harvest when fish were 18 months old. The mean ± standard deviation (SD) of all fish samples were 635.1 ± 222.7 g (BW), 327.0 ± 39.4 mm (TL), 115.2 ± 14.4 mm (BD), 1.76 ± 0.23 (K), 3.63 ± 0.24 (BSI) and 4.6 ± 2.9 (Cl_a). Heritabilities (h^2), genetic correlations (r_g) and genotype by environment interactions (GxE interaction) were estimated using BLUPF90 with an animal mixed model using the genomic relationship matrix (GRM). Heritabilities were observed to be moderate for BW (0.29 ± 0.03), TL (0.30 ± 0.03), BD (0.39 ± 0.05), K (0.21 ± 0.03) and BSI (0.21 ± 0.03), but low for Cl_a (0.04 ± 0.02). High genetic correlations were present among both growth (BW, TL and BD, $r_g \geq 0.90$) and body-shape traits (K and BSI, $r_g = 0.91$), but lower for comparisons between growth (BW and BD) and body-shape traits (K and BSI) (0.21 ± 0.10 to 0.43 ± 0.09). These results indicate that both harvest growth traits and body shape of Malabar red snapper could be improved via selective breeding programs, although selection of fast growers might not maximize the genetic gain for K and BSI. In contrast, the low h^2 of red colouration suggested that environmental factors (e.g. dietary carotenoids) rather than genetic effects may be primarily responsible for the phenotypic variation observed in skin redness. Moderate GxE interactions were observed for BW (0.45 ± 0.25 to 0.60 ± 0.27), TL (0.31 ± 0.24 to 0.57 ± 0.27), BD (0.40 ± 0.24), K (0.36 ± 0.25 to 0.73 ± 0.91) and BSI (0.73 ± 0.26) among the three rearing sites, suggesting that a single breeding program may not deliver equal genetic gains for all farms alike, and that genomic selection algorithms should be trained on the rearing site where animals are to be farmed. In conclusion, the present study provided valuable information for the design of future selective breeding programs for Malabar red snapper.

* Corresponding author at: Tropical Futures Institute, James Cook University Singapore, 149 Sims Drive, 387380 Singaporechi, Singapore.
E-mail address: bing.liang@my.jcu.edu.au (B. Liang).

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1. Introduction

Singapore is a nation with limited land and natural resources and faces significant challenges in securing a stable food supply. As part of its food security vision to achieve 30 % of its nutritional needs locally by 2030, the country is increasingly turning to advanced technologies, including selective breeding, to enhance the productivity and resilience of its aquaculture industry. Malabar red snapper, also known as the Malabar Blood Snapper, is a species of marine fish belonging to the family Lutjanidae. It is found primarily in the Indo-Pacific region, particularly along the coasts of India, Southeast Asia, and Northern Australia (Fry et al., 2009). The species inhabits coral reefs and rocky substrates, and sexually matures at the age of three to five years with high fecundity.

Malabar red snapper holds significant economic value in Singapore's aquaculture sector. As a popular species in Southeast Asia, it is often sought after for its favourable taste, striking red colour, and high nutritional quality (Purushothaman et al., 2024), and the demand of farmed fish has been increasing due to a decrease in wild caught product (Pauly et al., 1998). However, the industry faces challenges such as inconsistent quality of fingerlings, slow growth rates and low survival rates, which call for more sustainable and efficient aquaculture practices. Genetic improvement through selective breeding offers a promising solution to these challenges by enhancing harvest traits such as growth, body shape, and skin colour. Selective breeding has been widely adopted in crop and livestock production (Georges et al., 2019; Marsh et al., 2021) and achieved great success in a number of key aquaculture species such as Atlantic salmon *Salmo salar* (Bangera et al., 2018), Nile tilapia *Oreochromis niloticus* (Joshi et al., 2020), common carp *Cyprinus carpio* (Palaiokostas et al., 2018), barramundi *Lates calcarifer* (Yue et al., 2023), black tiger shrimp *Penaeus monodon* (Vu et al., 2023) and pearl oyster *Pinctada maxima* (Kvingedal et al., 2010). These successes demonstrate that implementing genomic selection in Malabar red snapper is not only feasible but also has the potential to revolutionize the species' aquaculture in Singapore, contributing to both economic growth and sustainability in the industry.

Quantifying the amount of genetic variation and determining the underlying genetic basis of phenotypic expression of commercially important traits, such as heritability, genetic correlations, and genotype by environment (GxE) interactions, are essential steps in designing an effective selective breeding program and developing high-performing strains for aquaculture. This is because heritability (h^2) estimates the proportion of phenotypic variance in a population that is attributable to additive genetic variance, indicating the extent to which trait performance/variation can be passed from parents to offspring. This metric is crucial as it is directly linked to the predicted response (R) to selection (Gjedrem and Baranski, 2009). Additionally, understanding genetic correlations (r_g) between traits provides important information on how selecting for one trait could lead to changes, positive or negative, in other traits due to shared genetic factors. Moreover, given the variability in commercial grow-out conditions across different farms, the performance of the animal may depend significantly on the interaction between its genotype and the environment, therefore understanding the GxE interactions in aquaculture breeding is also of great importance (Gjedrem and Baranski, 2009). Understanding these parameters enables breeders to set clear breeding objectives and optimize the design of selective breeding programs, which are crucial for advancing Singapore's aquaculture sector. By aligning with the country's goals of boosting aquaculture productivity and sustainability, well-designed breeding programs can develop high-yielding strains that are also suited to various farming environments.

Before this study, genomic resources and tools for Malabar red snapper were limited. To address this, a medium-density (70k) SNP array was developed as an initial step toward understanding the species' genetic makeup. Medium density arrays are now used as gold standard for advanced plant and animal breeding programs by offering a high number of SNP markers to capture detailed genetic variation in each individual, and are increasing being used as a cost-effective solution for aquaculture species (Rasal et al., 2024). In the present study, 2547 Malabar red snappers cultured at three different rearing sites were genotyped with a medium density SNP array and their body weight (BW), total length (TL), body depth (BD), Fulton's condition factor (K), body shape index (BSI) and intensity of red colouration (CIELAB *a values, CL_a) were measured at harvest size. BW, TL, and BD are key growth and size traits that directly influence the market value and yield of the fish. K, as an indicator of health and welfare, ensures that breeding candidates are resilient, productive, and less susceptible to disease. Meanwhile, BSI and CL_a reflect the shape and colour of the fish, which are crucial for market appeal, especially in Southeast Asia where cultural associations with red as a colour of prosperity can command higher prices. These combined yield-focused, health-focused, and appearance-focused traits assessments enhance the commercial value and consumer appeal of Malabar red snapper, directly supporting aquaculture goals for sustainable and high-quality production. The aim of this study is to lay the groundwork of future selective breeding programs for Malabar red snapper. Specifically, we aimed to quantify genetic parameters such as heritability, genetic correlations, and genotype by environment (GxE) interactions using the animal model in BLUPF90 in commercially important harvest traits in three different production environments. This study enhances the genetic understanding of Malabar red snapper, offering practical insights that meet industry requirements for consistently producing high-quality fingerlings. It achieves this by establishing a data-driven selective breeding framework.

2. Materials and methods

2.1. Ethics statement

The study was carried out at James Cook University in Singapore, following the approval from the Institute Animal Care and Use Committee (IACUC) under the reference number 2021-A010.

2.2. Experimental design and phenotypic data collection

In total, 28,000 2-month-old Malabar red snapper fingerlings were sourced from three hatcheries (Johor Malaysia M1, $n = 9955$; Kedah Malaysia M2, $n = 9955$; Singapore SG, $n = 8090$). The mean ± SD BW and TL of the fingerlings were 6.1 ± 1.0 g and 6.4 ± 0.5 cm for M1, 4.7 ± 1.2 g and 5.9 ± 0.5 cm for M2, and 9.3 ± 2.1 g and 7.7 ± 0.7 cm for SG, respectively. The overall mean ± SD of BW and TL of fish fingerlings across all three locations were 6.7 ± 2.4 g and 6.7 ± 0.9 mm. These fingerlings were mixed and stocked into two different commercial fish farming facilities in Singapore in January 2022: Farm 1 ($n = 14{,}000$), a sea-based farm using open net cages and Farm 2 (n = 14,000), a sea-based farm using tanks with flow-through seawater system. In addition, a second batch of fingerlings were acquired from an unspecified hatchery in Malaysia and stocked into tanks with flow-through seawater at the Singapore Food Agency's Marine Aquaculture Research Centre (MAC) in July 2022 ($n = 3000$). The seawater parameters at the three rearing sites were similar, with an annual range of 29–31 °C, pH 7.9–8.2 and salinity 27–30 ppt, respectively. Dissolved oxygen was in the range of 6–8 mg/L at Farm 1, while maintained above 5 ppm in the tank systems at Farm 2 and MAC. The fish were cultured at the three rearing sites according to the commercial company's or MAC's respective farming protocols and fed two to three times daily with commercial dry feed pellets containing 43–44 % crude protein, until the fish reached the target harvest size at approximately 1.5 years of age. The stocking density before harvest was about 3 kg/m^3 at Farm 1, 25 kg/m^3 at Farm 2 and 5 kg/m^3 at MAC. In total, 2579 fish were randomly sampled and phenotyped at Farm 1 ($n = 956$) and Farm 2 ($n = 955$) in May 2023, as well as at MAC ($n = 668$) in November 2023. Caudal fin clips (~5 mm^2

each) were collected and preserved in 95 % ethanol for subsequent DNA extraction and genotyping. Body weight (BW) and total length (TL) were measured using a Biomark® phenotyping station (Biomark LLC) comprising an electronic measuring board, an electronic scale and a tablet for recording. The intensity of red colouration (CIELAB *a values) was measured in a standardised area below the dorsal fin using a general colorimeter (JZ-300, M&A INSTRUMENTS INC) as shown in Fig. 1. Spinal deformities were identified by visual inspection and recorded as a binary trait (normal / deformed). Individual photographs of fish were captured with a standardised focal length and a reference object from a fixed distance using an Olympus® TG-6 camera. Body depth (BD) was measured manually based on the reference object of known length using ImageJ (Schneider et al., 2012). The sites for morphometric and skin redness measurement are shown in Fig. 1. Fulton's condition factor (K) was calculated using the formula $K = \frac{10^5 \times BW(g)}{TL(mm)^3}$ (Fulton, 1904), while the body shape index (BSI) was calculated with the formula $BSI = \frac{10 \times BD(mm)}{TL(mm)}$, following the methods described by Domingos et al. (2021).

2.3. DNA extraction and genotyping

A subset of 2579 Malabar red snapper fin clips were sent to Neogen (New Zealand) for DNA extraction and genotyping with the custom 70k red snapper SNP array. DNA extraction from fin clips was performed using the sbeadex™ livestock kit (LGC Biosearch Technologies) following the manufacturer's manual. The concentration, purity and integrity of the extracted DNA were assessed using a NanoDrop spectrophotometer and 1 % agarose gel electrophoresis to confirm the suitability of the DNA for subsequent genotyping. DNA samples were genotyped on the GeneTitan™ MC Instrument (ThermoFisher Scientific™) following the Axiom™ Propel XPRES 384HT Workflow. The raw genotyping data (i.e., Cel files) were processed using Axiom Analysis Suite 5.3 with the Best Practices Genotyping Analysis Workflow using default settings with developed probes library. Recommended SNP lists was used to export the final SNP file with SNP call rate ≥ 0.97. Quality control was performed on individual samples with Dish Quality Control score (DQC) ≥ 0.82 and sample call rate (CR) ≥ 0.97. Further quality control was performed by PLINK 2.0 (www.cog-genomics.org/plink/2.0/) to keep biallelic SNPs with minor allele frequency > 10 % and SNP call rate ≥ 0.99, after which 56,378 (79.5 %) out of 70,874 SNPs remained for downstream data analysis.

2.4. Statistical analyses

The animal model was used with average information restricted/residual maximum likelihood (AIREMLF90) algorithm in BLUPF90 (Misztal et al., 2002) for the estimation of heritability, genetic and phenotypic correlations and GxE interactions of all traits. Heritability (h^2) was estimated fitting the single-trait animal model as in Eq. (I):

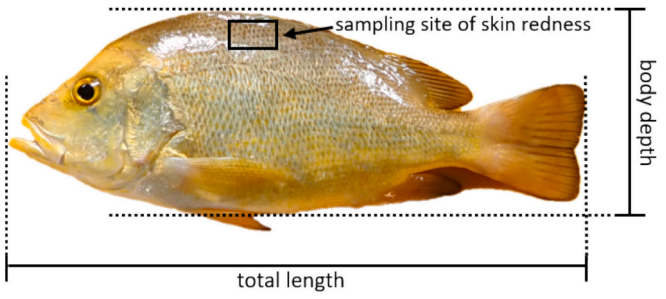

Fig. 1. Morphometric and skin redness measurement in Malabar red snapper. Black square indicates the sampling site of skin redness. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$$y_{ijk} = A_i + S_j + u_k + e_{ijk} \quad \text{(I)}$$

where $\boldsymbol{y_{ijk}}$ is an observation, $\boldsymbol{A_i}$ is the first fixed effect (i.e., rearing sites with three levels) for a farm $\boldsymbol{i}$, $\boldsymbol{S_j}$ is the second fixed effect (i.e., deformity with two levels), $\boldsymbol{u_k}$ is the additive genetic effect for an animal $\boldsymbol{k}$, and $\boldsymbol{e_{ijk}}$ is the residual effect.

The aim of this analysis was to calculate the additive genetic variance (σ_u^2) and the residual variance (σ_e^2). The heritability of traits was estimated as in Eq. (II):

$$h^2 = \frac{\sigma_u^2}{\sigma_u^2 + \sigma_e^2}. \quad \text{(II)}$$

where σ_u^2 is the variance of $\boldsymbol{u_k}$ and σ_e^2 is the variance of $\boldsymbol{e_{ijk}}$.

The standard error (S.E.) of the heritability was estimated using the Monte-Carlo method (Meyer and Houle, 2013) by adding the "se_covar_function" OPTION in BLUPF90. If $\boldsymbol{h^2}$ estimate subtract 1.96 x S.E. is ≤0 (at 95 % confidence interval), Likelihood Ratio Test (LRT) was performed to confirm if the estimates were significant. A simplified model without the genetic effect (as in Eq. III) was run to compare with the full model with genetic effect, and the -2logL (log-likelihood) value of the simplified model (***X***) and full model (***y***) was used for chi-square test with degrees of freedom equal to 1. The p value was calculated as "pchisq(x-y, 1, lower.tail=FALSE)/2" in R (Misztal et al., 2018), and insignificant estimates ($p \geq 0.05$) were labelled with "ns" in Table 2.

$$y_{ijk} = A_i + S_j + e_{ijk} \quad \text{(III)}$$

Genetic correlations (r_g) between traits were estimated using the 2-trait (bivariate) animal model as in Eq. (IV) and (V), which is an extension of the single-trait animal model shown above:

$$y_{ijk:1} = A_{i:1} + S_{j:1} + u_{k:1} + e_{ijk:1} \quad \text{(IV)}$$

$$y_{ijk:2} = A_{i:2} + S_{j:2} + u_{k:2} + e_{ijk:2} \quad \text{(V)}$$

where $\boldsymbol{y_{ijk}}$ is an observation, $\boldsymbol{A_i}$ is the first fixed effect (i.e., rearing sites with three levels) for a farm $\boldsymbol{i}$, $\boldsymbol{S_j}$ is the second fixed effect (i.e., deformity with two levels), $\boldsymbol{u_k}$ is the additive genetic effect for an animal $\boldsymbol{k}$, $\boldsymbol{e_{ijk}}$ is the residual effect, and ***1*** and ***2*** represent Trait ***1*** and Trait ***2***.

Genetic correlations between traits were estimated as in Eq. (VI):

$$r_g = \frac{cov(u_{k:1}, u_{k:2})}{\sqrt{\sigma^2_{u_{k:1}} \times \sigma^2_{u_{k:2}}}} \quad \text{(VI)}$$

where $\boldsymbol{u_{k:1}}$ is the genetic component of Trait ***1***, $\boldsymbol{u_{k:2}}$ is the genetic component of Trait ***2***, $\sigma^2_{u_{k:1}}$ is the variance of $\boldsymbol{u_{k:1}}$, and $\sigma^2_{u_{k:2}}$ is the variance of $\boldsymbol{u_{k:2}}$.

Phenotypic correlations between traits were estimated as in Eq. (VII):

$$r_p = \frac{cov(u_{k:1}, u_{k:2}) + cov(e_{ijk:1}, e_{ijk:2})}{\sqrt{\left(\sigma^2_{u_{k:1}} + \sigma^2_{e_{ijk:1}}\right) \times \left(\sigma^2_{u_{k:2}} + \sigma^2_{e_{ijk:2}}\right)}} \quad \text{(VII)}$$

where $\boldsymbol{e_{ijk:1}}$ is the residual component of Trait ***1***, and $\boldsymbol{e_{ijk:2}}$ is the residual component of Trait ***2***.

Similar to $\boldsymbol{h^2}$, if $\boldsymbol{r_g}$ or $\boldsymbol{r_p}$ estimate subtract 1.96 x S.E. is ≤0, a Likelihood Ratio Test (LRT) was performed to confirm if the estimates were significant by comparing the full model to one in which the cov($\boldsymbol{u_{k:1}}$, $\boldsymbol{u_{k:2}}$) was constrained to 0 for $\boldsymbol{r_g}$; or both cov($\boldsymbol{u_{k:1}}$, $\boldsymbol{u_{k:2}}$) and cov($\boldsymbol{e_{ijk:1}}$, $\boldsymbol{e_{ijk:2}}$) were constrained to 0 for $\boldsymbol{r_p}$ (Wilson et al., 2010). The -2logL (log-likelihood) value of the simplified model (***X***) and full model (***y***) was used for chi-square test with 1 degree of freedom. The p value was calculated as "pchisq(x-y, 1, lower.tail=FALSE)/2" in R (Misztal et al., 2018), and insignificant estimates ($p \geq 0.05$) were labelled with "ns" in Table 3.

Genotype by environment interactions between rearing sites (i.e. $\boldsymbol{r_g}$

between rearing sites) were estimated using the 2-trait (bivariate) animal model as in Eq. (VIII) and (IX).

$$y_{jk:1} = S_{j:1} + u_{k:1} + e_{jk:1} \quad \text{(VIII)}$$

$$y_{jk:2} = S_{j:2} + u_{k:2} + e_{jk:2} \quad \text{(IX)}$$

where $\boldsymbol{y_{ijk}}$ is an observation, $\boldsymbol{S_j}$ is the fixed effect (i.e., deformity with two levels), $\boldsymbol{u_k}$ is the additive genetic effect for an animal **k**, $\boldsymbol{e_{ijk}}$ is the residual effect, and ***1*** and ***2*** represented rearing Site ***1*** and rearing Site ***2***.

GxE between rearing sites was estimated as in Eq. (X):

$$\boldsymbol{r_g} = \frac{cov(\boldsymbol{u_{k:1}}, \boldsymbol{u_{k:2}})}{\sqrt{\boldsymbol{\sigma^2_{u_{k:1}}} \times \boldsymbol{\sigma^2_{u_{k:2}}}}} \quad \text{(X)}$$

where $\boldsymbol{u_{k:1}}$ is the additive genetic effect of a trait at rearing Site ***1***, and $\boldsymbol{u_{k:2}}$ is the additive genetic effect of the same trait at rearing Site ***2***, $\boldsymbol{\sigma^2_{u_{k:1}}}$ is the variance of $\boldsymbol{u_{k:1}}$, and $\boldsymbol{\sigma^2_{u_{k:2}}}$ is the variance of $\boldsymbol{u_{k:2}}$. Similar LRT was performed if GxE estimate subtract 1.96 x S.E. is ≤ 0 by comparing the full model to one in which the cov($\boldsymbol{u_{k:1}}, \boldsymbol{u_{k:2}}$)was constrained to 0.

3. Results

Out of the 2579 samples (956 from MFG, 955 from SAT, and 668 from MAC) collected for harvest traits and genotyped by the 70k SNP array, 2547 (98.8 %) samples (946 from MFG, 948 from SAT, and 653 from MAC) passed the sample Quality Control thresholds of DQC $\geq$ 0.82 and sample Call Rate $\geq$ 0.97. Specifically, the mean $\pm$ SD of sample Call Rate of samples passing QC was 99.6 % $\pm$ 0.2 %. Descriptive statistics of phenotypic traits and the number of fish records per trait at the three rearing sites are summarized in Table 1 and Supplementary Table S1. The percentage of available records per trait per rearing site ranged from 98.5 to 100 % for all traits except for Cl_a, whereby obvious data outliers (possibly caused by equipment inaccuracy) were removed through a two-step quality control. Firstly, outliers with Cl_a value >20 or < −10 were removed after visual inspection of the data distribution; then the extreme reads were removed by keeping data between mean $\pm$ 2SD (i.e., 2.4–11.8). This resulted in 2420 out of 2547 samples for subsequent analysis of the Cl_a trait. Additionally, a technical issue caused 867 photos to be saved unsuccessfully, leading to 87 % missing data for body depth and body shape index traits at Farm 1, 1.5 % at Farm 2, and 0.9 % at MAC. As a result, the BD and BSI traits at Farm 1 were excluded from further analyses, while the data from Farm 2 and MAC were retained for subsequent analysis.

3.1. Genetic parameters

Heritability estimates for growth traits (BW, TL and BD) at the three rearing sites (except BD was not available at Farm 1) ranged from 0.33 $\pm$ 0.07 to 0.44 $\pm$ 0.06, with the overall h^2 estimated from 0.29 $\pm$ 0.03 to 0.39 $\pm$ 0.05 (Table 2). h^2 estimates for K and BSI ranged from 0.31 $\pm$ 0.08 to 0.38 $\pm$ 0.07 except that the h^2 estimate for K at Farm 1 was much lower (0.09 $\pm$ 0.04). The h^2 estimates of Cl_a ranged from 0.00 $\pm$ 0.00 to 0.07 $\pm$ 0.04 with the overall h^2 estimate being 0.04 $\pm$ 0.02. Thus, Cl_a was not included for genetic correlations analyses between traits and rearing sites due to a small genetic component apparently contributing to the phenotypic variability of this trait. High phenotypic and genetic correlations were observed between BW, TL and BD (0.90 $\pm$ 0.02 to 0.99 $\pm$ 0.01), as well as between K and BSI (r_p = 0.71 $\pm$ 0.01 and r_g = 0.91 $\pm$ 0.04) across three rearing sites, while the phenotypic and genetic correlations between one of the growth-related traits (BW, TL and BD) and one of the shape-related traits were moderate to low (−0.05 $\pm$ 0.02 to 0.43 $\pm$ 0.02; Table 3).

Table 1
Descriptive statistics for body weight (BW), total length (TL), body depth (BD), Fulton's condition factor (K), body shape index (BSI) and intensity of red colouration (Cl_a) of harvest-size Malabar red snapper.

Rearing Site	*n*	BW (g)[a]	TL (mm)	BD (mm)	K	BSI	Cl_a
		756.4	346.5		1.76		5.9
Farm 1	946	(224.0)	(36.1)	N.A.	(0.15)	N.A.	(2.8)
		560.1	307.7	112.6	1.87	3.67	3.6
Farm 2	948	(191.4)	(36.0)	(13.4)	(0.27)	(0.27)	(2.4)
		568.2	326.8	116.0	1.58	3.55	4.3
MAC	653	(183.8)	(34.7)	(13.6)	(0.15)	(0.15)	(3.2)
		635.1	327.0	115.2	1.76	3.63	4.6
All	2547	(222.7)	(39.4)	(14.4)	(0.23)	(0.24)	(2.9)

[a] mean (SD); N.A., not available.

Table 2
Heritability estimates ($\pm$ SE) of body weight (BW), total length (TL), body depth (BD), Fulton's condition factor (K), body shape index (BSI) and intensity of red colouration (Cl_a) in the skin of harvest-size Malabar red snapper at three rearing sites (Farm 1, Farm 2 and MAC).

h^2	BW	TL	BD	K	BSI	Cl_a
h^2 (Farm 1)	0.36 $\pm$ 0.07	0.33 $\pm$ 0.07	N.A.	0.09 $\pm$ 0.04	N.A.	0.06 $\pm$ 0.04
h^2 (Farm 2)	0.41 $\pm$ 0.07	0.42 $\pm$ 0.07	0.44 $\pm$ 0.06	0.38 $\pm$ 0.07	0.32 $\pm$ 0.06	0.07 $\pm$ 0.04
h^2 (MAC)	0.39 $\pm$ 0.08	0.43 $\pm$ 0.08	0.39 $\pm$ 0.08	0.32 $\pm$ 0.08	0.31 $\pm$ 0.08	0.00 $\pm$ 0.00^{ns}
h^2 (all)	0.29 $\pm$ 0.03	0.30 $\pm$ 0.03	0.39 $\pm$ 0.05	0.21 $\pm$ 0.03	0.33 $\pm$ 0.05	0.04 $\pm$ 0.02

ns: not significant; N.A., not available.

3.2. Genotype by environment interactions

G $\times$ E interactions of five traits (BW, TL, BD, K and BSI) across three rearing sites (Farm 1, Farm 2, and MAC) are presented in Table 4. Overall, moderate to high GxE interactions were observed for all traits among the three rearing sites, ranging from 0.31 $\pm$ 0.24 to 0.73 $\pm$ 0.26, and GxE interactions between Farm 2 and MAC were generally lower than the other site pairs. BW showed moderate to strong G $\times$ E interactions across site pairs, with correlations of 0.55 $\pm$ 0.12 between Farm 1 and Farm 2, 0.60 $\pm$ 0.27 between Farm 1 and MAC, and 0.45 $\pm$ 0.25 between Farm 2 and MAC. TL exhibited similar interactions, with moderate correlations of 0.56 $\pm$ 0.13 between Farm 1 and Farm 2, and 0.57 $\pm$ 0.27 between Farm 1 and MAC, but the GxE interaction of TL between Farm 2 and MAC was low and non-significant (0.31 $\pm$ 0.24). In addition, high GxE interactions were observed between Farm 2 and MAC for BSI (0.73 $\pm$ 0.26), and between Farm 1 and MAC was observed for K (0.73 $\pm$ 0.91, although not statistically significant according to LRT). (Table 4).

Table 3
Genetic correlations (below diagonal) and phenotypic correlations (above diagonal) ($\pm$ SE) for body weight (BW), total length (TL), body depth (BD), Fulton's condition factor (K), body shape index (BSI) and skin redness (Cl_a) of Malabar red snapper.

	BW	TL	BD	K	BSI	Cl_a
BW		0.94 $\pm$ 0.00	0.94 $\pm$ 0.00	0.23 $\pm$ 0.02	0.22 $\pm$ 0.03	−0.01 $\pm$ 0.02
TL	0.97 $\pm$ 0.01		0.90 $\pm$ 0.00	−0.05 $\pm$ 0.02	−0.01 $\pm$ 0.03^{ns}	−0.03 $\pm$ 0.02
BD	0.99 $\pm$ 0.01	0.90 $\pm$ 0.02		0.25 $\pm$ 0.02	0.43 $\pm$ 0.02	−0.11 $\pm$ 0.03
K	0.21 $\pm$ 0.10	−0.03 $\pm$ 0.1^{ns}	0.31 $\pm$ 0.11		0.71 $\pm$ 0.01	0.01 $\pm$ 0.02^{ns}
BSI	0.31 $\pm$ 0.10	0.05 $\pm$ 0.1^{ns}	0.43 $\pm$ 0.09	0.91 $\pm$ 0.04		−0.07 $\pm$ 0.03
Cl_a	N.A.	N.A.	N.A.	N.A.	N.A.	

ns: not significant; N.A., not available.

Table 4
Estimates of Genotype by Environment interaction (± SE) between the three rearing sites for body weight (BW), total length (TL), body depth (BD), Fulton's condition factor (K) and body shape index (BSI).

Traits	r_g between Farm 1 and Farm 2[a]	r_g between Farm 1 and MAC	r_g between Farm 2 and MAC
BW	0.55 ± 0.12	0.60 ± 0.27	0.45 ± 0.25
TL	0.56 ± 0.13	0.57 ± 0.27	0.31 ± 0.24^{ns}
BD	N.A.	N.A.	0.40 ± 0.24^{ns}
K	0.50 ± 0.38	0.73 ± 0.91^{ns}	0.36 ± 0.25^{ns}
BSI	N.A.	N.A.	0.73 ± 0.26

ns: not significant; N.A., not available.

4. Discussion

Phenotypic and genetic parameters of economically important traits are crucial for defining the breeding goals and establishing a selective breeding program (Gjedrem, 2005). In this study, we report the first heritability estimates for harvest-size Malabar red snapper (average BW = 635.1 g) reared across three sites in Singapore, focusing on body weight (BW), total length (TL), body depth (BD), Fulton's condition factor (K), body shape index (BSI) and intensity of red skin colouration (Cl_a). The results highlighted several key findings. Firstly, all growth-related traits, including BW, TL and BD exhibited moderate heritability with h^2 ranging from 0.29 ± 0.03 to 0.39 ± 0.05. These results generally agreed with the heritability reported in other aquaculture fish species. For example, the h^2 estimates of body weight in barramundi ranged from 0.21 to 0.42 (Domingos et al., 2013; Jerry et al., 2022). Moderate to high heritability for body weight were also reported for European seabass (*Dicentrarchus labrax*; h^2 = 0.38 to 0.44) (Dupont-Nivet et al., 2008) and rainbow trout (*Oncorhynchus mykiss*; h^2 = 0.32 to 0.49) (Kurta et al., 2023). In addition, both phenotypic and genetic correlations followed a similar trend and showed high values (greater than 0.9) among all growth-related traits (i.e., BW, TL, and BD) in Malabar red snapper. These results are consistent with studies on other tropical fish species farmed in Singapore and Southeast Asia, where strong correlations above 0.8 were reported, including barramundi in two separate studies (Domingos et al., 2013; Ye et al., 2017), Nile tilapia (Rutten et al., 2005), and catfish *Clarias gariepinus* (Srimai et al., 2019). Therefore, given the high correlations between W, TL and BD, any of those independent measurements serve as a proxy for growth of Malabar red snapper, depending on the ease of data collection (i.e. use of weighing scales in floating fish farms are challenging depending on the wind and sea conditions). In contrast, phenotypic and genetic correlations between growth-related traits and shape-related traits (i.e., K and BSI) were moderate to low in Malabar red snapper, ranging from −0.05 ± 0.02 to 0.43 ± 0.02. This range is comparable to the above mentioned fish species, with values reported from 0.07 to 0.61 (Domingos et al., 2013) and − 0.27 to 0.23 in barramundi (Ye et al., 2017), and from −0.20 to 0.72 in catfish (Srimai et al., 2019). Although the overall h^2, r_g and r_p of BD and BSI were calculated based on BD data from Farm 2 and MAC due to missing BD data from Farm 1, the sample size at Farm 2 and MAC comprising in total 1601 fish samples (63 % of the full sample size) for BD trait was large and representative. Additionally, since BD is typically highly correlated with BW and TL, and K is determined by both traits, K can also serve as a proxy for overall body shape assessment (Ragheb, 2023). The values of K at Farm 1 (1.76) fell within the range observed at Farm 2 (1.87) and MAC (1.58), suggesting that the fish at Farm 2 shared comparable morphological characteristics with those at Farm 1 and MAC. Therefore, the potential impact of missing BD data at Farm 1 on the overall h^2, r_g and r_p of BD and BSI should be minimal. Overall, our results suggest that growth-related traits can be effectively improved through conventional selection within a well-designed breeding programme. However, selection for growth is unlikely to yield a substantial response in K or BSI.

Moderate heritability (0.21 to 0.33) was observed for condition factor (K) and Body Shape Index (BSI) in Malabar red snapper, which are generally higher than those reported in barramundi (h^2 K = 0.14 to 0.21, h^2 BSI = 0.20 to 0.24) (Jerry et al., 2022) and Nile tilapia (*Oreochromis niloticus* h^2 K = 0.04, h^2 mid-sagittal plane = 0.08) (Trọng et al., 2013), and comparable to those reported in common sole (*Solea solea*; h2 shape = 0.34) (Blonk et al., 2010) and gourami (*Trichopodus pectoralis*; h2 BSI = 0.40) (Sutthakiet et al., 2020). These findings underscore the suitability of K and BSI as candidate traits for enhancement in selective breeding programs aimed at improving the overall body condition and shape of Malabar red snapper for better health and marketability, although their inclusion as an additional breeding objective might slow the genetic response for improved harvest weight.

On the other hand, the moderate heritability of K and BSI suggests that these traits are more influenced by environmental factors, highlighting the importance of optimized feeding, rearing conditions, and effective disease management in enhancing these traits. The genetic correlation between K and BSI was high (r_g = 0.91 ± 0.04), indicating that Malabar red snapper with higher depth to length ratio (i.e., "wider" fish) tends to be "fatter" (or in good nutritional condition).

An interesting observation was that the heritability of Fulton's condition factor (K) at Farm 1 was much lower (h^2 = 0.09 ± 0.04) than those at Farm 2 (h^2 = 0.38 ± 0.07) and MAC (h^2 = 0.32 ± 0.08). Condition factor is a measure used in fisheries and aquaculture to assess the health and well-being of fish, and it is a ratio that describes the condition or "fatness" of a fish (Fulton, 1904). Although artificial dry pellets were used across all the three rearing sites, a key difference between Farm 1 and both of Farm 2 and MAC was the fish culturing systems used, i.e., Farm 2 and MAC utilised closed containment tank systems while Farm 1 utilised open net cage systems whereby small wild fish could freely enter the net cages holding farmed Malabar red snapper. Thus, the red snapper cultured at Farm 1 had access to both artificial pellets and potentially wild fish as food, while the fish at Farm 2 and MAC fed only on pellets. This assumption was supported by observations of small wild fish in the Malabar red snapper stomachs during fish dissection for another project at Farm 1 (unpublished observation), and farm staff also frequently observed red snapper preying on wild fish in the net cages. Consequently, compared to fish at Farm 2 and MAC, it is likely that environmental factors, such as the availability of wild fish as natural food, played a larger role in the increased condition factor (K) observed in fish at Farm 1. This greater environmental influence may have reduced the contribution of genetic factors, leading to lower heritability (h^2) estimates at Farm 1. Furthermore, this might also explain why fish at Farm 1 grew faster overall than fish at Farm 2 and MAC after the same grow-out duration (mean ± SD of BW at Farm 1 = 756.4 ± 224.0, Farm 2 = 560.1 ± 191.4, MAC = 568.2 ± 183.8; Table 1). In addition to these findings, it is important to consider the broader implications of selecting for body shape and condition traits. Improving K and BSI could lead to higher market value and consumer acceptance, as fish with desirable body shape and better condition often fetch premium prices. Furthermore, better body condition is typically associated with enhanced health and robustness, which could translate into improved survival rates and feed efficiency in aquaculture systems. As selective breeding continues to develop, integrating these traits into a comprehensive breeding strategy will be critical for optimizing both production efficiency and product quality in Malabar red snapper.

In recent decades, the appearance traits of skin pigmentation have gained significant value in commercial fish species such as red strain tilapia (*Oreochromis* spp.), Blue Back rainbow trout (*Oncorhynchus mykiss*), red skin common carp (*Cyprinus carpio*) (see Colihueque and Araneda, 2014 and references herein) and barramundi (Marcoli et al., 2024). Similarly, skin redness (Cl_a) is also an important commercial trait for Malabar red snapper, which increases its value in the marketplace. The red colouration in fish skin is usually determined by the amount of pteridines and carotenoids in pigment-containing cells such as xanthophores and erythrophores; however, most fish cannot biosynthesize carotenoids and have to obtain them through natural or formulated

artificial feeds (Poon et al., 2023; Rajasingh et al., 2006). In this study, Cl_a at all three rearing sites (overall $h^2 = 0.04 \pm 0.02$) showed very low to negligible heritability, indicating that environmental factors such as dietary carotenoids might be the primary contributors to the observed phenotypic variation in skin redness, rather than genetic effects. Therefore, farm management practices and optimized feeding protocols are key to controlling skin redness in Malabar red snapper. Astaxanthin, a valuable carotenoid responsible for the pink-red coloration in the fins, skin, muscles, and gonads of many aquatic species, is commonly used in aquaculture to enhance skin pigmentation (Maoka, 2011). Effective astaxanthin dosages vary across species, including 50–200 mg/kg feed for rainbow trout (Noori and Razi, 2018), 30 mg/kg for red sea bream *Pagrus major* (Kurnia et al., 2007), 75 mg/kg for large yellow croaker *Larimichthys croceus* (Yi et al., 2014), and 100–200 mg/kg for olive flounder *Paralichthys olivaceus* (Pham et al., 2014). These treatments generally span a few weeks to allow for the bioaccumulation of astaxanthin in the skin. Based on these findings, a finishing feed containing 30–200 mg/kg of astaxanthin could be used to enhance the skin redness of Malabar red snapper to the desired level before harvest. In addition, while measuring multiple locations on fish skin could provide additional insights into colour variation across the body, it would significantly increase both the time and resources required to process fish in an industry setting where fish were destined for sale. For studies involving high-throughput assessments, consistency in a single defined area offers a pragmatic balance between detail and feasibility, ensuring a focus on representative colour data across specimens. Thus, standardizing measurements at one location is a common and practical approach in similar aquaculture research (Colihueque, 2014; Poon et al., 2023). If study of colour variation analysis is the primary research objective (e.g. on the study of dietary carotenoids) and sample sizes are smaller, multi-location measurements to address body-wide colour patterns may be useful.

Generally, GxE interactions <0.8 are considered to be of biological significance due to low accuracies of estimated breeding value for production performance when the genetic correlation between breeding and production environments was below this number (Su et al., 2020). However, this statistical-based value of 0.8 should not be used as the only factor to decide whether a single breeding programme should be split into two or more breeding programs tailored to specific environments, because running multiple small breeding programmes usually requires more investment and higher operating costs than running a single large breeding programme. Assuming we temporarily disregard the concern of costs, a 'break-even correlation' can also be used as a criterion to evaluate different breeding strategies. A break-even correlation is defined as the intersection of genetic correlations between different environments when the genetic gain of different breeding strategies is equal. Compared to that in livestock breeding, the break-even correlation in fish is expected to be higher because fish have higher fecundity, and sib testing is usually used for selection in fish instead of progeny testing in livestock. Therefore, the break-even correlation in fish was expected to be ≥ 0.7 (Sae-Lim et al., 2013) based on the break-even correlations reported in a dairy cattle breeding programme which ranged from 0.61 (Mulder et al., 2006) to 0.70 (James, 1961). In this study, low to moderate positive GxE interactions for growth-related traits (0.31 ± 0.24 to 0.60 ± 0.27) were observed across the three rearing sites. This implies that Malabar red snapper broodstock selected for faster growth at one rearing site are expected to lead to positive genetic responses at the other rearing sites; however, these genetic gains may not realise their full potential at the other sites. Using multiple breeding programs, where candidates are measured and selected within each specific environment, would maximize genetic gains, but the commercial implementation of this strategy would incur significantly higher investment and operational costs (Jerry et al., 2022). This challenge could be addressed by several strategies based on previous studies (Domingos et al., 2021; Gjerde et al., 2014; Jerry et al., 2022; Kause et al., 2003; Martinez et al., 2006; Sae-Lim et al., 2016). One approach is to centralize the Malabar red snapper broodstock at a land-based, high-biosecurity facility for disease-free seed production, while simultaneously establishing test stations at each rearing site for accurate performance tracking. While phenotyping and genotyping costs may increase due to the need for data collection across multiple environments, the overall operational expenses (e.g. candidate broodstock management, hatchery and nursery production, breeding value estimation, and selection processes) are minimized. This unified strategy, ensures resource efficiency and enables flexibility for breeding across multiple environments as needed. For Malabar red snapper, by treating traits recorded at different rearing sites as different traits, the estimated breeding values (EBVs) of these site-specific traits can be incorporated into a single selection index, and index weights can then be assigned based on the production volume at each site. This ensures that genetic improvements are concentrated where they will have the most significant economic impact, optimizing profitability for stakeholders. This approach eliminates the necessity of maintaining multiple breeding nuclei across rearing sites, thereby reducing operational complexity and ensuring cost-effectiveness. At the same time, it prioritizes broodstock selection for sites with higher production volumes, enabling the breeding program to focus genetic improvements where they will have the greatest economic impact, while making it more accessible to a broader range of producers. Additionally, if only a single breeding program based on traits recorded at one primary rearing site is feasible, increasing selection intensity could also help maintaining high genetic gain across environments. However, appropriate control measures must be implemented to ensure that inbreeding rates remain within acceptable levels. These strategies enable breeding programs to adaptively manage GxE interactions, maximizing genetic potential while balancing investment and operational cost.

An intriguing observation was that although both Farm 2 and MAC used flow-through tank systems compared to Farm 1's open net cage system, r_g between Farm 2 and MAC for BW, TL and K were the lowest, indicating that farming systems might not be the primary factor for the levels of genotype re-ranking. The lower r_g between Farm 2 and MAC might be due to Farm 2 being on a floating structure in the sea whereby the movement of current might affect the stability of the tanks, compared to the stable land-based facility at MAC. Other environmental factors such as diet, stocking density, water quality, physical stressors, microbiota, disease effects and farm practices might also have contributed to the GxE interaction as reported in previous studies on barramundi (Domingos et al., 2021), olive flounder *Paralichthys olivaceus* (Li et al., 2019) and sole *Solea solea* (Mas-Muñoz et al., 2013).

Assessment of genetic parameters based on family structures has been a common approach in livestock and aquaculture breeding programs, which can provide additional insights when combined with genomic-based methods. One limitation of this study is that the pedigree information of fish samples was not available for family-based assessment of genetic parameters, due to the current practice in hatcheries in Singapore and Malaysia of mass spawning untagged Malabar red snapper in open sea cages. However, previous studies have demonstrated that GRMs inferred from SNP data can more precisely capture the genetic relationships between individuals compared to pedigree data (Wang and Da, 2014). This is because genomic-based approaches directly measure the genetic variation in each individual, while the pedigree-based approach estimates relatedness among individuals based on recorded family relationships (i.e. assuming a fixed relationship value of 0.5 for parent-offspring and full-sibs, a 0.25 for grandparent-grandchildren and half-sibs, and so on), without accounting for Mendelian sampling effects and random genetic variations (such as independent assortment of chromosomes or recombination) which causes genetic differences among individuals, such as full-sibs, despite shared parentage. For example, the prediction accuracies of breeding value estimation for traits of interest using GBLUP were higher than those using PBLUP in Chinese shrimp *Fenneropenaeus chinensis* (Liu et al., 2023), Arctic Charr *Salvelinus alpinus* (Palaiokostas et al., 2020),

barramundi (Jerry et al., 2022), European Sea Bass *Dicentrarchus labrax* and the Gilthead Sea Bream *Sparus aurata* (Griot et al., 2021). These findings underscore that genomic-based approaches offer greater accuracy than pedigree-based methods for estimating individual genetic variation using direct genotype data.

Maintaining genetic diversity throughout the reproductive cycle is essential for successful breeding programs in aquaculture, as it can maintain and continue the genetic improvement while reducing risks of inbreeding depression, which may negatively impact survival, growth, and disease resistance (Keys et al., 2004; You and Hedgecock, 2019). Malabar red snapper is a mass-spawning species, whereby males and females randomly mate with multiple partners within a single tank. This often leads to skewed broodstock contributions and high family size variance, potentially reducing effective population size (*Ne*) and increasing inbreeding rates (ΔF), as observed in other mass-spawning species such as gilthead seabream (Cameron Brown et al., 2005) and barramundi (Loughnan et al., 2013). To keep the increase of inbreeding rates within a low level (about 1 % per generation), Bentsen and Olesen (2002) recommended a minimum of 50 broodstock pairs with 30–50 progeny per pair being tested. In addition, the high variance in family sizes also requires greater genotyping efforts to capture smaller families. For instance, Domingos et al. (2014) found that 10 % of barramundi offspring needed to be genotyped to capture the top-performing individuals from all families, although genotyping the top 1.5 % of individuals which represented 75 % of families was recommended for better cost-effectiveness. Other measures for enhancing genetic diversity in Malabar red snapper breeding programs may include importing genetically diverse founders from different regions, pairing genetically distant individuals, monitoring parental contributions over multiple spawning events, and synchronizing spawning across tanks (Loughnan et al., 2013; Wong et al., 2023). These strategies help to maintain a broad genetic diversity in long term for sustainable breeding programmes.

Implementing selective breeding programmes often demands significant investment and resources, making it challenging for individual farmers to undertake on their own. As a result, breeding programmes are typically carried out by farm cooperatives, associations, or private breeding companies, often with backing from government agencies (Gjedrem, 2005). Efficient breeding programs have demonstrated a high benefit-to-cost ratio. For example, studies in sheep, cattle, and pigs reported cost/benefit ratios ranging from 1:5 to 1:50 (Gjedrem, 2005). A baseline study of a gilthead seabream breeding program in Greece also found that the program became profitable within five years, with an annual operating cost of €127,845 including major expenses like infrastructure, feed, labour and genotyping services (Janssen et al., 2018). Advancement in genomic resources and tools, including the 70k red snapper SNP array, have paved the way for implementing genomic selection in Malabar red snapper in Singapore. The SNP array not only allows for the calculation of Estimated Breeding Values (EBVs), which is a basis for accurately selecting future broodstock, but also aids in parentage assignment, tracking genetic diversity, and Genome-Wide Association Studies (GWAS), contributing to a more effective and sustainable breeding program. Despite these advancements, several challenges remain, including securing suitable land with access to high-quality seawater for breeding facilities, establishing reliable protocols for spawning Malabar red snapper in tanks, managing disease in both the spawning nucleus and grow-out populations, improving survival rates during larviculture, and better understanding the species' nutritional requirements. With continued research and development, there is strong potential for the red snapper farming industry to grow and flourish, contributing to a more sustainable and profitable aquaculture sector in Singapore.

5. Conclusions

Based on the genetic analyses for harvest traits of Malabar red snapper at three rearing sites, heritability of both growth-related traits (BW, TL and BD) and shape-related traits (K and BSI) were moderate and suitable for genetic improvement, while skin redness could be primarily determined by environmental factors such as dietary carotenoids instead of genetic effects. The high genetic correlation between traits within the growth-related trait group (BW, TL and BD) and the shape-related trait group (K and BSI) implied that high genetic gains could be achieved for all traits within the same group during a selective breeding programme, and more easily measured trait within each group could be used for data collection. In contrast, moderate genetic correlation between traits in growth-related and shape-related groups suggested that traits in different groups could be selected separately based on the breeding goals for maximised genetic gains. Moderate GxE interaction suggested that offspring could be sent to specific rearing site for training of genomic selection algorithms separately for more accurate genomic predictions, while broodstock fish should be kept in a facility with good biosecurity and resources for producing high-quality and disease-free eggs. With the advent of genomic resources and tools for Malabar red snapper, the genetic parameters and genotype-by-environment interaction for harvest traits reported in this study have laid the groundwork for implementing genomic selection in the species in Singapore.

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CRediT authorship contribution statement

Bing Liang: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Dean R. Jerry:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Vu Nguyen:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Xueyan Shen:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Joyce Koh:** Writing – review & editing, Investigation. **Celestine Terence:** Writing – review & editing, Investigation. **Maria G. Nayfa:** Writing – review & editing, Investigation. **Maura Carrai:** Writing – review & editing, Investigation. **Purushothaman Kathiresan:** Writing – review & editing, Investigation. **Rachel Jia Wen Ho:** Writing – review & editing, Investigation. **Hazim Mohamed:** Writing – review & editing, Investigation. **Saraphina Dianne Rwei Qing Tneo:** Writing – review & editing, Investigation. **Grace Loo:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Shubha Vij:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Jose A. Domingos:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare no competing interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2025.742247.

Data availability

Data will be made available on request.

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