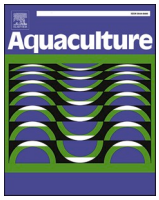
Aquaculture 599 (2025) 742144

Contents lists available at ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aquaculture



Genetic evaluation of nutritional traits in Malabar red snapper (*Lutjanus malabaricus*): Heritability and genetic correlations of fatty acid composition

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ARTICLE INFO

Keywords:
Malabar red snapper
Genetic parameters
Genetic correlations
Fatty acids
Selective breeding

ABSTRACT

The demand for nutritious seafood highlights aquaculture's role in global food security, with selective breeding now commonplace in many species as an approach to increase productivity and quality of farmed species. The Malabar red snapper (*Lutjanus malabaricus*) is a high-value marine species where there is interest in selective breeding to improve commercial traits. In this study genetic parameters associated with fatty acid composition were investigated in Malabar red snapper muscle fillet to understand if these traits would respond to genomic selection. The fatty acid profiles of 540 fish from a commercial farm in Singapore were analysed focusing on key components such as omega-3 and omega-6 fatty acids. A genomic relationship matrix, generated using 39,780 high-quality SNPs from a custom 70 K SNPs red snapper array, was employed in a linear mixed model to reveal heritable components of 15 fatty acid-related traits. Heritability for fatty acids ranged from 0.15 to 0.50. Polyunsaturated fatty acids (PUFA), n-3 omega fatty acids such as docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA) also showed moderate heritability of 0.32 and 0.29, respectively. DHA/EPA ($h^2 = 0.50$) and the sum of EPA and DHA ($h^2 = 0.46$) showed especially moderate-high heritability. High genetic correlations between levels of fatty acids were observed, including alpha-linolenic acid (ALA) with arachidonic acid (ARA; $r_g = 0.90$) and Oleic acid (OA; $r_g = 0.82$). This study demonstrated that variation in fatty acid levels are heritable and thus would respond to selection. The findings highlight the potential to enhance the nutritional quality of Malabar red snapper fillets through selective breeding, contributing to product quality and better health benefits for consumer.

1. Introduction

Aquaculture is increasingly recognized as a sustainable solution to meet the growing global demand for seafood, contributing significantly to food security and nutrition. Within this commercial sector, the cultivation of species with high nutritional quality, particularly those rich in essential fatty acids, is of great interest. Long-chain polyunsaturated fatty acids (LC-PUFAs), particularly the omega-3 PUFAs eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) are known for their significant health benefits, including their roles in biochemical and metabolic processes that enhance vision, brain development, and reduce the risks of several chronic diseases like cardiovascular disease, diabetes, and Alzheimer's (Brenna, 2016; Ghasemi Fard et al., 2019). Additionally, these n-3 omega PUFAs are associated with a lower risk of osteoporosis, rheumatoid arthritis, cognitive decline, neurological disorders, asthma, and potentially even certain cancers (Anderson and Ma, 2009; Harris et al., 2009; Simopoulos, 2008; Williams, 2000).

Consumer preferences are increasingly shifting towards healthier seafood options (Calder, 2017; Tocher, 2010). Fish are a crucial source of n-3 omega PUFAs, with a favourable omega-6/omega-3 ratio, and human nutritionists suggest they are essential in the diet at least twice a

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https://doi.org/10.1016/j.aquaculture.2025.742144
Received 30 September 2024; Received in revised form 5 January 2025; Accepted 8 January 2025
Available online 12 January 2025

week (Mraz et al., 2012; Rodrigues et al., 2017). Marine fish generally have higher n-3 omega PUFA levels than freshwater species, and fatty acid (FA) composition varies significantly due to several factors, including environmental conditions, nutrition and genetics (Dejana et al., 2017; Marković et al., 2016; Prchal et al., 2018). The PUFA content in fish varies by species and is highly influenced by diet since they cannot synthesize on their own (Sawyer et al., 2016). Omega-3 fatty acids are primarily synthesized by phytoplankton and bioaccumulate throughout the food chain (Zhang et al., 2024b). For every 100 g of fish fillet, wild Atlantic salmon (*Salmo salar*) contains high levels of omega-3 PUFAs (1.5–2.5 g of EPA + DHA), due to feeding on marine organisms rich in these fatty acids (i.e., sardines; *Clupea pilchardus* that het up to 3 g of EPA + DHA from feeding on plankton) while tilapia (*Oreochromis niloticus*), a species that feeds more on plant-based diets, has lower levels EPA + DHA (0.1–0.2 g). These fatty acids are essential for membrane fluidity, immune response, growth, and reproduction in fish (Glencross, 2009; Hemre et al., 2016; Tocher, 2010; Zhang et al., 2024b).

Among aquaculture species, the Malabar red snapper (*Lutjanus malabaricus*) is of interest due to its high market value and widespread consumer acceptance, especially in Southeast Asia (Purushothaman et al., 2024; Wang et al., 2019). Despite its economic importance, there has been limited research on the genetic parameters governing commercial traits of this species, with only those associated with growth and colour investigated to date (Liang et al., 2024; Poon et al., 2023). There have been no studies reporting on nutritional quality traits of Malabar red snapper. Understanding genetic parameters of fillet traits is interesting for future selective breeding programs, as though it is known diet influences the fatty acid content in many fish, demonstrating potential for a genetic response may be an alternative and/or complementary approach to enhance nutritional quality, thereby improving the species' market competitiveness, health benefits and supporting the sustainability of aquaculture practices (Dinh et al., 2023; Geng et al., 2017; Li et al., 2017; Liang et al., 2024; Purushothaman et al., 2024; Putri et al., 2021; Salini et al., 2006; Zhong et al., 2017). This study is the first to report the heritability of fatty acid composition in Malabar red snapper, addressing a key gap in the genetic understanding of its nutritional traits. These findings offer valuable insights to guide selective breeding programs aimed at enhancing both the nutritional quality and market value in this important food fish species.

Heritability and genetic correlations among fatty acid related traits such as EPA, DHA, and their respective ratios (e.g., DHA/EPA and omega-6/omega-3 ratios) provide valuable insights into the potential for selective breeding. Studies on other aquaculture species, such as Nile tilapia (*O. niloticus*; $h^2 = 0$ to 0.39), Atlantic salmon (*S. salar*; $h^2 = 0.17$ to 0.46), common carp (*Cyprinus carpio;* $h^2 = 0.03$ to 0.37*),* and rainbow trout (*Oncorhynchus mykiss;* $h^2 = 0.02$ to 0.24), have shown varying degrees of heritability for these traits, highlighting the species-specific nature of genetic influences on fatty acid profiles (Blay et al., 2021; Horn et al., 2018; Leaver et al., 2011; Nguyen et al., 2010; Overturf et al., 2013; Prchal et al., 2018).

We have previously studied the nutritional value of Malabar red snapper in relation to fatty acids, protein, ash and moisture content (Purushothaman et al., 2024). The present study addresses the gap in knowledge related to the heritability and genetic correlation of key nutritional traits in the species, focusing on fatty acid composition. By leveraging on these genetic insights, the study seeks to provide a foundation for future genetic selective breeding programs aimed at enhancing the nutritional quality of the Malabar red snapper, thereby aligning with consumer preferences for healthier seafood options.

2. Materials and methods

2.1. Ethics statement

This study received approval from James Cook University's Institutional Animal Care and Use Committee (IACUC) under approval 2021-A010. All procedures were conducted in accordance with the guidelines of the National Advisory Committee on Laboratory Animal Research (NACLAR).

2.2. Sampling for proximate and SNP analysis

To increase the genetic diversity of the animals genotyped and phenotyped in this study, two months old Malabar red snapper fingerlings were simultaneously sourced from three commercial hatcheries: Johor, Malaysia; Kedah, Malaysia; and Singapore and pooled together into a single nursery tank before being transferred to the grow-out tanks. The current industry practices of Malabar red snapper hatcheries still rely on mass spawning techniques, where multiple males and females are allowed to naturally spawn in open sea cages. The fertilized eggs from these mass spawnings are collected from the surface of the sea cages and transferred to fertilized earthen ponds operating in green-water culture systems. These traditional systems rely on natural phyto- and zooplankton blooming to supply natural feeds to the larvae, followed by weaning them into formulated dry feeds to support early-stage development. After about four weeks, red snapper fingerlings in this study were then harvested from these ponds and packed into plastic bags to be transported to a floating barge farm located in the Eastern Johor Straight of Singapore. Upon arrival, the fingerlings were stocked into a 50 m^3 circular fiberglass tanks operating in flow-through system, with the raw seawater passing through a sand filter prior to reaching the tank and supplied with pure oxygen as needed. The environmental parameters in the tank during culture were as follows: water temperature of 29–31 °C, pH between 7.9 and 8.2, salinity between 27 and 30 ppt, and dissolved oxygen levels above 5 mg/L. At the time of transport from the hatchery to the farm, the overall mean and standard deviation of the fingerlings' body weight and total length were 6.7 ± 2.4 g and 6.7 ± 0.9 mm, respectively. Fish were fed a commercial pellet feed containing 44 % crude protein and 7 % crude fat (Uni-President, Dĩ An, Vietnam) four times per day, to satiation. At harvest time, approximately when fish were 18 months old, 604 animals were euthanized by immersion in 200 ppm Aqui-S and fillets were collected from adjacent the dorsal to tail fins (Fig. 1A). Also, fin tissues of these individuals were collected for genotyping. The average of body weight and total length with standard deviations of these samples were 452.9 ± 102.2 g and 289.0 ± 25.7 cm, respectively. Muscle flesh (approx. 15 g) from the fillet was subsampled as in Fig. 1B and stored at −80 °C for fatty acid profiling analysis. Collected tissues were placed in 96 well-plate containing 95 % ethanol. Each vial was labelled with the corresponding fish's identity and stored at −80 °C for downstream analysis.

In this study, we were not provided access to the broodstock from these commercial hatcheries; therefore, it was not possible to reconstruct the pedigrees or assess maternal effects. However, due to the small size of the snapper's pelagic eggs, maternal effects are considered unlikely to significantly influence the traits at harvest, as shown in previous studies (Domingos et al., 2013). Additionally, because in mass spawners offspring from different families are mixed from the fertilization stage and are communally reared throughout the culture cycle, there are no common environmental effects (as for species where strip spawning or single pair-mating practices are possible and families are reared separately during their early life stages).

2.3. Fillet fatty acid extraction and analysis

Fatty acid analysis of Malabar red snapper fillet samples was performed at the Sustainable Technology & Analytical Research (STAR) Laboratory of Republic Polytechnic of Singapore, following the method outlined by O'Fallon et al. (2007). Each 15 g sample was freeze dried for a week followed by grinding to determine moisture content. Subsequently, 0.5 g of ground sample powder was treated with C13:0 internal standard, 10 M KOH, and methanol, incubated at 55 °C, and then reacted with 24 M H_2SO_4. After forming fatty acid methyl esters (FAME),

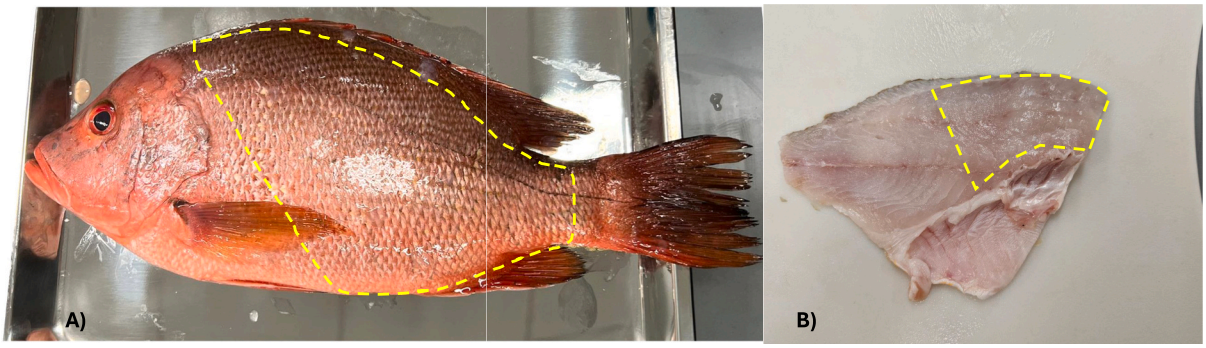

Fig. 1. Section of Malabar red snapper fillet that was collected for fatty acid analysis. (A) Fish, (B) fillet. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

extraction with hexane yielded samples which were stored at −20 °C until gas chromatography (GC) analysis. Using a SP2560 capillary column and flame ionization detector, fatty acids were quantified by comparing retention times with standards, providing percentages area of total fatty acids (Purushothaman et al., 2024).

2.4. Genotype and phenotype quality control

Single Nucleotide Polymorphism (SNPs) were used to determine genomic relationships among fish sampled. SNPs were genotyped using a custom Axiom™ myDesign™ SNP array (ThermoFisher Scientific™) which comprised of 70,904 bi-allelic markers, designed from multiple geographical wild and farmed red snapper populations from Southeast Asia to Australia. All fin tissues stored in 95 % ethanol were sent for genotyping. Subsequently, genotypes in the form of CEL binary files were used to call SNPs. The default Axiom thresholds to call SNPs was adopted (i.e., retain SNP with call rate ≥ 97 % and disk call rate ≥ 82 % (Axiom, 2020). The SNP list of recommendations included the Poly High Resolution, No Minor Hom and Mono High Resolution. In other words, we excluded SNPs ranking as Off-Target Variant (OTV) and Call Rates Below Threshold. Moreover, considering high quality SNP with three separate and high-resolution clusters for each genotype (AA, AB and BB), the carefully visualization of SNP clusters were performed and stringent quality control parameters were set, resulting to further exclusion SNP with <99 % calling rates, minor allele frequency < 0.05 and Fisher's Linear Discriminant (FLD) values <7. Also, the SNPs having less than 10 counts of either AA, AB or BB were removed. This retained 39,780 SNPs and 540 samples. Subsequently, PLINK2 (Purcell et al., 2007) was used to export 540 fish and 39,780 SNP to the form of numerical genotypes (0, 1 and 2) for the subsequent analyses.

Quality control for phenotypic data was performed in Excel by visualizing the scatter plot between pair of traits to eliminate suspected outliers, including considering the mean and standard deviation to decide the cut-off points. This resulted in the actual number of phenotypes for genetic analyses retained for each trait (169–529 observations) as given in Table 1.

2.5. Estimation of genetic parameters

The linear animal mixed model equation was utilized to estimate genetic (co)variance components and subsequently estimate heritability (h^2), phenotypic (r_p) and genetic (r_g) correlations. Univariate analyses were employed to estimate the heritability of individual traits (Eq. 1), while bivariate analyses were conducted to determine genetic correlations between traits, utilizing an animal mixed model approach. All traits in this study were treated as continuous character fitting using the AI-REML algorithms in the BLUPF90 family program (Misztal et al., 2002). AI-REML accounts for the loss of degrees of freedom from fixed effects, ensuring unbiased estimates of genetic variance components.

Table 1
Summary statistics for fatty acid composition in the muscles of Malabar red snapper.

No	Trait Name	N	Min	Max	Mean	SD
1	SFA	502	32,06	39,93	36,09	1,33
2	PUFA	494	29,58	39,79	34,68	2,21
3	MUFA	505	20,12	33,15	27,48	2,25
4	PUFA/SFA ratio	529	0,76	1,35	0,98	0,11
5	Omega-6 (n-6FUFA)	445	17,65	20,98	19,22	0,66
6	Omega-3 (n-3FUFA)	495	10,55	19,86	15,28	1,81
7	Omega-6/Omega-3 ratio	428	0,96	1,58	1,26	0,14
8	DHA	525	6,93	19,89	11,67	2,4
9	EPA	458	2,51	3,49	3,01	0,2
10	DHA/EPA ratio	518	2,21	6,81	3,92	0,85
11	OA	503	17,02	26,48	22,68	1,63
12	LA	463	13,42	17	15,48	0,67
13	ALA	414	0,61	1,39	1,05	0,15
14	ARA	492	0,14	0,3	0,22	0,03
15	EPA + DHA	454	10,05	22,3	14,55	2,18

SFA: total saturated fatty acids; MUFA: total monounsaturated fatty acids; PUFA: total polyunsaturated fatty acid; DHA: docosahexaenoic acid; EPA: eicosapentaenoic acid; OA: oleic acid; LA: linoleic acid; ALA: alpha-linolenic acid; ARA: arachidonic acid; N: Number of observations; Min: Minimum value observed; Max: Maximum value observed; Mean: Mean value; SD: Standard deviation.

This approach is well-suited for the high-dimensional genomic relationship matrix derived from 39,780 SNPs used in this study, with computational efficiency and convergence (Strandén et al., 2024). The model notation can be expressed as:

$\boldsymbol{Y_{ij}} = \boldsymbol{\mu} + \boldsymbol{F_i} + \boldsymbol{g_j} + \boldsymbol{e_{ij}}$ (Eq.1).

where $\boldsymbol{Y_{ij}}$ represents the trait observations (i.e., PUFA or SFA levels) of the jth animal with ith fish body shape ranking, $\boldsymbol{\mu}$ is the population's overall mean, $\boldsymbol{F_i}$ denotes the fixed effect of body shape ranking at harvest of animal jth fitted as class factor covariate (good-looking or poor-looking as this may influence the fatty acid profile). The $\boldsymbol{g}$ and $\boldsymbol{e}$ stand for random and error terms with its variances denoted as σ^2_g and σ^2_e. Random additive genetic effect $\boldsymbol{g}$ and residual effect $\boldsymbol{e}$ are assumed to be normally distributed, with $\boldsymbol{a} \sim \boldsymbol{N}\left(\boldsymbol{0}, \boldsymbol{G}^*\sigma^2_g\right)$ and $\boldsymbol{e} \sim \boldsymbol{N}\left(\boldsymbol{0}, \boldsymbol{I}^*\sigma^2_e\right)$, where $\boldsymbol{G}$ and $\boldsymbol{I}$ are the genomic relationship matrix of 540 animals generated by 39,780 SNPs and identity matrix, respectively.

Heritability estimates were determined by the ratio of additive genetic variance (σ^2_g) to the total phenotypic variance ($\sigma^2_g + \sigma^2_e$) (Henderson, 1984). Genetic correlation is the ratio between numerator covariance component of the two observed traits and the square root of the multiplication between the two genetic variances ($\frac{\sigma^2_{g12}}{\sqrt{\sigma^2_{g1} * \sigma^2_{g2}}}$) (Eq.2) (Henderson, 1984). The phenotypic correlation was computed according to Eq.2, but where each component was added by residuals (co)

variances ($\frac{\sigma^2_{g12}+\sigma^2_{e12}}{\sqrt{\left(\sigma^2_{g1}+\sigma^2_{e1}\right)*\left(\sigma^2_{g2}+\sigma^2_{e2}\right)}}$), where numbers 1 and 2 relate to trait1 and trait2, respectively.

3. Results

3.1. Overview of fatty acid composition

The composition of fatty acids (FAs) from 540 Malabar red snapper fillets are detailed in Table 1.

The aggregate fatty acid profile consisted of 36.1 % saturated fatty acids (SFAs), 27.5 % monounsaturated fatty acids (MUFAs) and 34.7 % polyunsaturated fatty acids (PUFAs). Oleic acid (OA) was the most abundant fatty acid, accounting for 22.7 % of total fatty acids and representing 82.5 % of all MUFAs present in fillet fat. Within polyunsaturated fatty acids (PUFAs), approximately 44.1 % were omega-3 fatty acids (n-3 PUFAs), and 55.4 % were omega-6 fatty acids (n-6 PUFAs). The most abundant omega-6 PUFA was linoleic acid (LA), which accounted for 15.5 % of the total fatty acids, representing around 44.6 % of all PUFAs and 80.5 % of omega-3 PUFAs. Docosahexaenoic acid (DHA) was the most prevalent omega-3 PUFA, constituting 76.4 % of omega-3 PUFAs and 33.7 % of total PUFAs. Alpha-linolenic acid (ALA) was the second most abundant omega-3 PUFA, accounting for 6.9 % of omega-3 PUFAs and 3.0 % of total PUFA content. The combined sum of EPA and DHA corresponded to 95.2 % of omega-3 PUFAs and 42.0 % of total PUFAs (Table 1).

3.2. Heritability estimates

Heritability estimates based on genomic information for individual fatty acids (FAs) and fatty acid groups are reported in Table 2. In total, 14 heritability estimates out of 15 fatty acid-related traits were significantly different from zero ($P < 0.05$) and ranged from $h^2 = 0.15 \pm 0.08$ to 0.50 ± 0.10 (Table 2). Within the different aggregated fatty acid groups, PUFAs and MUFAs exhibited the highest heritability ($h^2 = 0.37 \pm 0.10$ and 0.36 ± 0.10, respectively) than SFAs ($h^2 = 0.25 \pm 0.09$). Within the PUFAs, n-3 PUFAs (omega-3) demonstrated higher heritability ($h^2 = 0.26 \pm 0.08$) compared to n-6 PUFAs (omega-6; $h^2 = 0.17 \pm 0.09$). Among individual fatty acids, alpha-linolenic acid (ALA) ($h^2 = 0.32 \pm 0.10$) and DHA $h^2 = 0.32 \pm 0.09$), had the highest heritability followed by EPA ($h^2 = 0.29 \pm 0.10$), and oleic acid (OA) ($h^2 = 0.25 \pm 0.09$). Previous investigations attempting fitting fish body weight as covariate yielded nearly identical heritability values to the model without it, as previously shown for gilthead seabream (Horn et al., 2022) and common carp (Prchal et al., 2018). Therefore, results from the simpler model are reported.

Table 2
Heritability of fatty acid composition in the muscles of Malabar red snapper.

No	Trait name	σ^2_g	σ^2_e	*h2*	*se*
1	SFA	0.44	1.34	**0.25***	0.09
2	PUFA	1.82	3.11	**0.37***	0.10
3	MUFA	1.87	3.21	**0.36***	0.10
4	PUFA/SFA ratio	0.00	0.01	**0.39***	0.09
5	Omega-6 (n-6PUFA)	0.08	036	0.17	0.09
6	Omega-3 (n-3PUFA)	0.84	2.40	**0.26***	0.08
7	Omega-6/Omega-3 ratio	0.00	0.01	**0.23***	0.09
8	DHA	1.85	3.94	**0.32***	0.09
9	EPA	0.01	0.03	**0.29***	0.10
10	DHA/EPA ratio	0.37	0.36	**0.50***	0.10
11	OA	0.67	1.99	**0.25***	0.09
12	LA	0.09	0.35	**0.20***	0.09
13	ALA	0.01	0.01	**0.32***	0.10
14	ARA	0.00	0.00	**0.15***	0.08
15	EPA + DHA	2.19	2.58	**0.46***	0.10

The heritability (***h²***) in bold and *(Asterisk) indicated estimates had significantly different from zero ($P < 0.05$). σ^2_g: Genetic variance; σ^2_e: Error variance or residual variance, ***se***: standard error.

3.3. Phenotypic and genetic correlation among fatty acids

The phenotypic (r_p) and genetic correlations (r_g) between fatty acids traits were estimated (Figs. 2 and 3) and clustered based on their magnitudes, e.g., fatty acid-related traits in one standalone blue cluster were highly correlated. Phenotypic correlation magnitudes (Fig. 2) between all studied traits were significant estimates (P-value <0.05), except only for EPA + DHA vs. EPA. On the contrary, due to convergence of linear mixed models, there were many non-significant or not estimable genetic correlations between fatty acid traits such as between omega-6, EPA, ARA, ALA with other traits (values with cross sign).

However, genetic correlations (r_g) among fatty acids (FAs) clusters shared majority traits with phenotypic clusters. For examples, upper highly correlated cluster (upper blue) had SFA, ALA, OA, MUFA and ARA in both top triangles of half-matrices in phenotypic and genetic pyramids. Likewise, negatively correlated clusters in red had omega-3, omega-6, EPA + DHA, DHA/EPA, DHA/ALA, PUFA, PUFA/SFA and DHA. Here, PUFA was more strongly associated with omega-6 PUFAs ($r_g = 0.63$) than with omega-3 PUFAs ($r_g = 0.44$). SFAs were strongly correlated with omega-6/omega-3 PUFAs ($r_g = 1$). SFA also exhibited stronger correlations with MUFAs ($r_g = 0.86$) and moderate correlation with OA ($r_g = 0.68$). DHA, an individual omega-3 PUFA, was highly correlated with the combined total of EPA + DHA, omega-3 PUFAs and DHA/ ALA ($r_g = 1$; 0.99; 0.98, respectively). The omega-6/omega-3 ratio strongly correlated with SFAs, OA and MUFAs ($r_g = 1$; 0.95; 0.90, respectively) (Fig. 3).

4. Discussion

Selection for improvement in nutritional quality is of interest for aquaculture, as nutrition quality play a key role in determining product value and influencing consumer choices (Tan et al., 2022). It may also allow incorporation of lower cost ingredients into aquafeeds, which overall would lower costs of production without sacrificing nutritional quality of the fish product. In this study, we estimated genetic parameters for 15 fatty acids (FA) in muscle fillets of Malabar red snapper to inform future selective breeding programs for the species that might want to focus on increasing nutritional quality. By and large, we found that most FAs exhibited moderate heritability showing their potential to respond to selective breeding utilizing high density Axiom custom red snapper array.

4.1. Heritability estimates for fatty acid composition

This study revealed the significant heritability estimates for multiple fatty acid profiles in Malabar red snapper, particularly in the main fatty acid groups (SFA, MUFA, PUFA), and underscore the potential for selective breeding to enhance these nutritional traits in this species. Based on studies to date for aquaculture species, the heritability of nutritional quality traits varies from species to species (Nguyen et al., 2010; Overturf et al., 2013). Shrimp (*Litopenaeus vannamei*) heritability for all fatty acids ranged from 0 (omega-6) to 0.19 ± 0.07 (eicosadienoic acid), whereas heritability was found to be negligible (0.07 ± 0.05) for EPA, while low for DHA (0.12 ± 0.06) (Nolasco-Alzaga et al., 2018). In common carp (*C. cyprinus*), heritability of fatty acids ranged from 0.03 ± 0.10 to 0.37 ± 0.22, with $h^2 = 0.34 \pm 0.20$ for EPA and 0.03 ± 0.10 for DHA (Prchal et al., 2018). For tilapia (*O. niloticus*), FA heritability varied from $h^2 = 0$–0.39 ± 0.11, EPA $h^2 = 0.10 \pm 0.08$, and for DHA $h^2 = 0.004 \pm 0.07$ (Nguyen et al., 2010). In rainbow trout (*O. mykiss*), FA h^2 varied from $h^2 = 0.02 \pm 0.03$ to 0.24 ± 0.05, with $h^2 = 0.16 \pm 0.05$ for EPA (Blay et al., 2021). Finally, in the female Chinese mitten crab (*Eriocheir sinensis*), heritability for two of the most important FA was not

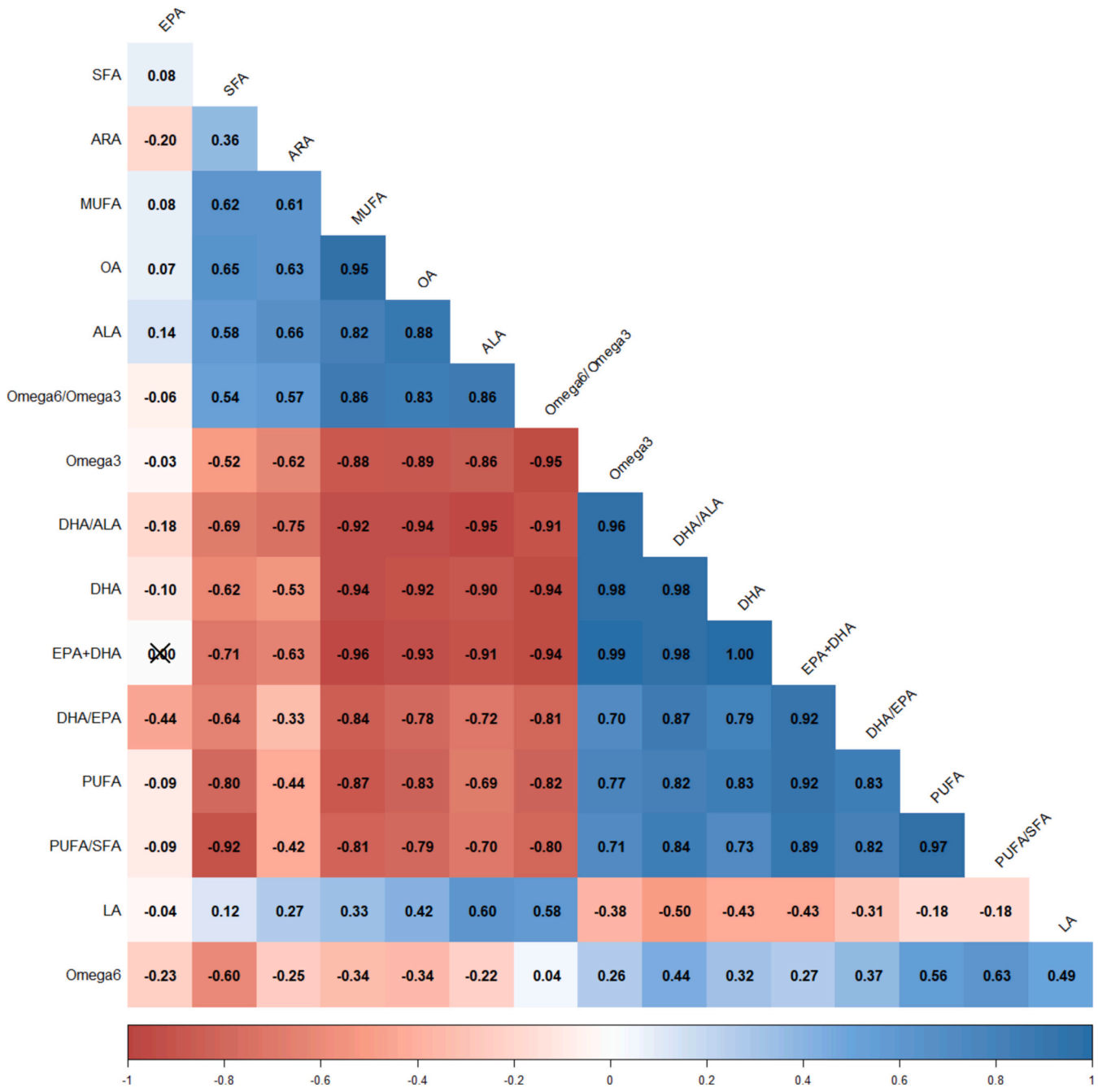

Fig. 2. Correlation matrix showing the phenotypic correlations between fatty acid composition in Malabar red snapper. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

significant, with $h^2 = 0.00 \pm 0.00$ for EPA and $h^2 = 0.03 \pm 0.07$ for DHA (Zhang et al., 2024a). Noted that in some of the study may of these estimates were not significant as large standard errors. In our study, a high content of DHA and EPA was found in the muscle of Malabar red snapper (*L. malabarius*), along with higher heritability for these fatty acids. Heritability observed in red snapper (*L. malabarius*) for EPA ($h^2 = 0.29$) was also much higher than in tilapia (*O. niloticus*) (Nguyen et al., 2010) and white leg shrimp (*L. vannamei*) (Nolasco-Alzaga et al., 2018), rainbow trout (*O. mykiss*) (Blay et al., 2021), Chinese mitten crab (*E. sinensis*) (Zhang et al., 2024a) and slightly higher than Atlantic salmon (*S. salar*) (Horn et al., 2018). However, the heritability of EPA in red snapper (*L. malabarius*) was slightly lower than that found in common carp (*C. cyprinus*) (Prchal et al., 2018). The heritability of DHA in Malabar red snapper (0.31) was significantly higher than in tilapia (*O. niloticus*) (Nguyen et al., 2010) and white legs shrimp (*L. vannamei*) (Nolasco-Alzaga et al., 2018), as well as in rainbow trout (*O. mykiss*) (Blay et al., 2021) and Chinese mitten crab (*E. sinensis*) (Zhang et al., 2024a). However, the heritability of DHA in Malabar red snapper was slightly lower than that found in common carp (*C. cyprinus*) (Prchal et al., 2018) and markedly lower than the estimates reported for Atlantic salmon (*S. salar*) (Horn et al., 2018). This variation in heritability estimates across species suggests that the additive genetic contribution to DHA and EPA content in Malabar red snapper is significant compared to many other aquaculture species, but still lower than common carp (*C. cyprinus*). Therefore, while Malabar red snapper shows promise for selective breeding programs targeting fatty acid content like EPA and DHA, the results highlight the need for a species-specific approach, considering the environmental and dietary factors that could influence

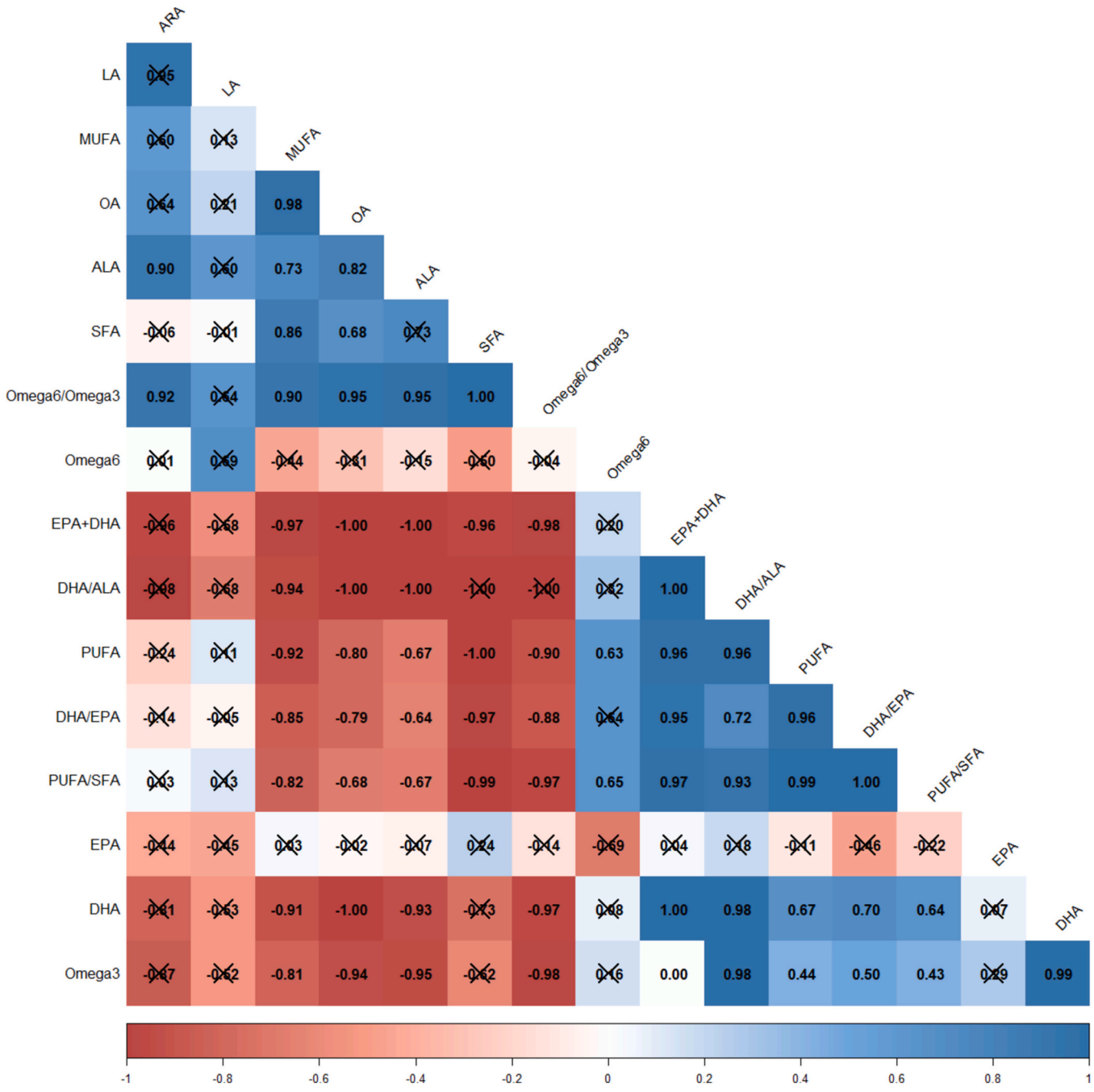

Fig. 3. Correlation matrix showing the genetic correlations between fatty acid composition in Malabar red snapper. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

these traits.

The DHA/EPA in Malabar red snapper exhibited a higher heritability ($h^2 = 0.50$) compared to Chinese mitten crab (*E. sinensis*) ($h^2 = 0.07$). This ratio is crucial in evaluating the nutritional quality and associated health benefits of seafood since DHA and EPA each uniquely contribute to overall health. A higher DHA/EPA has been linked to improved cardiovascular health, enhanced brain function, and stronger anti-inflammatory responses (Calder, 2017; Glencross, 2009; Purushothaman et al., 2024; Simopoulos, 2008; Tocher, 2010; Zhang et al., 2024a). In addition, Malabar red snapper showed higher omega-3 PUFA heritability than in Chinese mitten crab and common carp (*C. cyprinus*) (Prchal et al., 2018; Zhang et al., 2024a), which indicated a strong genetic influence on the complementary accumulation of these beneficial fatty acids. This suggested that selective breeding programs could effectively enhance the omega-3 PUFA content, improving their nutritional value and offering greater health benefits to consumers. Such high heritability also implied that omega-3 PUFA traits were less susceptible to environmental variation, making them reliable targets for genetic improvement.

4.1.1. *Implications for breeding programs*

Given the heritability estimates observed for EPA and DHA, Malabar red snapper presents a valuable opportunity for selective breeding programs aimed at improving these nutritional traits. The significant genetic variation observed implies that targeted selection could lead to substantial improvements in the fatty acid profile of farmed individuals of the species. Practical breeding strategies, like genomic selection, offer significant advantages over traditional breeding methods. This is since

genomic selection uses genome-wide markers to predict the genetic potential of breeding candidates, enabling faster and more efficient selection by reducing the reliance on phenotypic testing (Yáñez et al., 2023; Zenger et al., 2019). This approach is especially useful for complex traits, like fatty acid composition, which are inherently tedious to quantify. In contrast, traditional phenotypic selection is slower, less accurate, and more prone to environmental influences (Gjedrem and Baranski, 2010). Breeding strategies could focus on selecting individuals with higher levels of beneficial fatty acids to enhance the overall nutritional quality of the fish. For example, incorporating genomic selection techniques could accelerate the breeding process by identifying individuals with favourable genetic profiles for fatty acid composition (Blay et al., 2021; Hua et al., 2019; Khatkar, 2017; Yáñez et al., 2023; Zenger et al., 2019). Moreover, as the heritability of DHA/EPA was notably high ($h^2 = 0.50$), selective breeding could also be directed towards optimizing this ratio to improve the health benefits associated with omega-3 fatty acids. This could not only enhance the nutritional value of Malabar red snapper, but also meet consumer demand for healthier seafood options (Gjedrem and Baranski, 2010). This study provides the first evidence of significant heritability for important fatty acid traits such as DHA and EPA levels in Malabar red snapper. By identifying these genetic components, this research sets a foundation for selective breeding programs that can enhance the nutritional value of this commercially important species.

4.1.2. Strategies for selective breeding without family structuring

One major challenge in implementing selective breeding for Malabar red snapper is the potential lack of family structuring in breeding populations, making family-based selection unfeasible. This is especially common in aquaculture systems that utilize mass spawning techniques to produce the next generation of fish. However, genomic selection can still be effectively applied in such systems. Unlike traditional methods that rely on pedigree information, genomic selection uses high-density molecular markers across the genome to predict an individual's breeding value based on their genetic profile (Daetwyler et al., 2008; Meuwissen et al., 2001). This approach does not require family structures and can be implemented in large, mass-spawning populations, where tracking individual family lines would be impractical. In genomic selection, genomic estimated breeding values (GEBVs) are estimated by leveraging the genetic relatedness between individuals, which can then be used for controlling inbreeding depression. This would make the selective breeding program a long-term run, even when the pedigree is not available. For example, tools such as EVA (Henryon et al., 2015) and optiSel (Wellmann, 2019) are designed for this purpose, in which GEBVs and genomic relationship matrices can be utilized for optimum contribution selection of the next generations. These approaches enable the identification of genetically superior individuals without the need for explicit family structuring, thereby circumventing the limitations of mass spawning systems.

Additionally, the phenotype collection required for fatty acid profiling poses another challenge, as it involves sacrificing individuals to obtain fillet samples. To address this, non-invasive or minimally invasive methods, such as near-infrared reflectance spectroscopy (NIR), could be considered for future studies. NIR has demonstrated utility in predicting fatty acid composition in various fish species, including Atlantic salmon (*Salmo salar*) and Gilthead seabream (*Sparus aurata*) (Difford et al., 2021; Elalfy et al., 2021). Such techniques offer a promising avenue for real-time phenotype collection in live individuals. Combining these advanced phenotyping methods with genomic tools could significantly enhance the feasibility and efficiency of selective breeding programs for Malabar red snapper, thereby supporting sustainable aquaculture practices for this economically important species.

4.2. Genetic and phenotypic correlations

Strong genetic correlations, whether positive or negative, among different fatty acids are beneficial as they enable the selection of traits with the highest heritability. ARA exhibited a significant strong positive genetic correlation with omega-6/omega-3 ratio ($r_g = 0.92$) and ALA ($r_g = 0.90$), which may be attributed to their shared metabolic pathways and roles in lipid metabolism, as both are synthesized from similar precursor fatty acids. ARA, an omega-6 fatty acid, competes with Omega-3 for the same desaturase and elongase enzymes, leading to interconnected outcomes, while ALA (omega-3) serves as a precursor to longer-chain fatty acids. The positive correlation between the omega-6/omega-3 ratio and ARA levels has been observed in studies of PUFA content across species (Nakamura and Nara, 2004; Schmitz and Ecker, 2008). Moreover, common regulatory genes likely influence the production of both omega-6, omega-3 and ARA, leading to this high correlation (Brenner, 1977; Jump, 2002; Nakamura and Nara, 2004).

DHA demonstrated significant positive genetic correlations with the combined levels of EPA + DHA ($r_g = 1$), which can likely be attributed to DHA levels weighing the sum of the index but also due to the interconnected biosynthetic pathways and shared enzymatic processes. Both EPA and DHA are derived from the same precursor, alpha-linolenic acid, through a series of desaturation and elongation reactions that involve common enzymes, such as delta-5 and delta-6 desaturases. The genetic and environmental factors that regulate the production of DHA often similarly influence EPA synthesis due to these shared pathways. As a result, when DHA levels are increased, EPA levels tend to rise as well, reflecting the strong genetic and phenotypic correlations observed (Jump, 2002; Tocher, 2010). This interconnectedness implies that selective breeding strategies targeting higher EPA levels could simultaneously enhance DHA, thereby improving the overall Omega-3 fatty acid profile in the species (Brenner, 1977; Calder, 2017; Tocher, 2010). This dual benefit is particularly advantageous in aquaculture, where enhancing the nutritional quality of fish through selective breeding is a key objective. (Simopoulos, 2002; Tocher, 2010; Calder, 2017; Brenna, 2009).

The omega-6/omega-3 ratio showed significant positive genetic correlations with ALA (0.95) and SFA (1), due to the competitive nature of their metabolic pathways. Both omega-6 and omega-3 fatty acids rely on shared enzymes like delta-6 desaturase for their conversion into longer-chain polyunsaturated fatty acids, including ALA. The competition for these enzymes can lead to a specific balance between omega-6 and omega-3 fatty acids, which influences the levels of ALA. Genetic factors that increase ALA synthesis may also impact the omega-6/omega-3 ratio, accounting for the observed correlations. SFAs serve as precursors in the biosynthesis of both omega-6 and omega-3 fatty acids, and the enzymes involved in these pathways, such as elongases and desaturases, are shared among these fatty acid types. Additionally, environmental factors such as diet, which influence the intake of omega-6 and omega-3 precursors, further explain these correlations, as they can alter enzyme activity and fatty acid metabolism (Calder, 2017; Papanikolaou et al., 2014; Simopoulos, 2008; Swanson et al., 2012; Tocher, 2010). The significant positive correlations of omega-6/omega-3 ratio with ALA and SFA suggest a strong genetic influence on fatty acid metabolism, making these traits promising targets for selective breeding. Optimizing these ratios through genetic selection could enhance the nutritional quality of aquaculture species, benefiting human health.

5. Conclusion

This study provides valuable insights into the heritability and genetic correlations of nutritional traits in the Malabar red snapper (*L. malabaricus*), with a focus on fatty acid composition. Our results demonstrate that individual fatty acids, particularly polyunsaturated fatty acids (PUFAs), exhibit significant genetic variation, with heritability ranging from $h^2 = 0.15 \pm 0.08$ to 0.50 ± 0.10. Notably, n-3 PUFAs (omega-3) show higher heritability compared to n-6 PUFAs (omega-6), and the DHA/EPA ratio demonstrates strong heritability, highlighting its

potential as a target for selective breeding. The observed genetic correlations among different fatty acids further clarify the genetic architecture underlying these traits. These findings highlight the potential for selective breeding to enhance the nutritional quality of Malabar red snapper, aligning with consumer preferences and supporting sustainable aquaculture practices. This research establishes a foundation for future genetic improvement efforts in this economically valuable species, contributing to the advancement of aquaculture and the production of high-quality seafood.

Funding

This work was funded by the Singapore Food Story (SFS) R&D Programme in 'Sustainable Urban Food Production' (NRF-000190-00; Proposal ID: SFSRNDSUFP1–0097 "Developing genetic resources for red snapper, an important marine food fish for Singapore").

CRediT authorship contribution statement

Kathiresan Purushothaman: Formal analysis, Data curation, Conceptualization, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. **Nguyen Thanh Vu:** Formal analysis, Data curation, Conceptualization, Methodology, Investigation, Writing – review & editing. **Saraphina Dianne Tneo Rwei Qing:** Methodology, Investigation, Writing – review & editing. **Joyce Koh:** Methodology, Investigation, Writing – review & editing. **Muhammad Hazim Bin Mohamed:** Methodology, Investigation, Writing – review & editing. **Rachel Ho Jia Wen:** Methodology, Investigation, Writing – review & editing. **Bing Liang:** Methodology, Investigation, Writing – review & editing. **Grace Loo:** Visualization, Resources, Supervision, Funding acquisition, Project administration, Writing – review & editing. **Jose A. Domingos:** Visualization, Resources, Supervision, Funding acquisition, Project administration, Writing – review & editing. **Dean R. Jerry:** Conceptualization, Visualization, Resources, Supervision, Funding acquisition, Project administration, Writing – review & editing. **Shubha Vij:** Conceptualization, Visualization, Resources, Supervision, Funding acquisition, Project administration, Writing – review & editing.

Declaration of competing interest

The authors declare no competing interests.

Data availability

The data that has been used is confidential.

Acknowledgements

We would like to thank Nurul Nabiha Bte Rosman, Nur Nabiilah Bte Azlan, Dinie Hasya Bte Ahmadwi, Nur Humaira Bte Kamarudin, and Lim Hui Si for their invaluable efforts in optimizing the protocol for high-performance liquid chromatography.

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