



## Stability of muscle fatty acids and proximate composition across phenotypic traits in Malabar red snapper (*Lutjanus malabaricus*)

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### ABSTRACT

This study evaluated the influence of biological and phenotypic traits on the muscle nutritional composition of Malabar red snapper (*Lutjanus malabaricus*). A total of 540 farmed fish were analysed for fatty acids, ash, dry matter, and protein across sex, size, weight, health, and colour groups. Muscle lipids were dominated by saturated fatty acids (36.1%), followed by polyunsaturated (35.0%) and monounsaturated fatty acids (27.5%). Major fatty acids included oleic acid (22.7%), linoleic acid (15.5%), docosahexaenoic acid (11.7%), eicosapentaenoic acid (3.0%),  $\alpha$ -linolenic acid (1.1%), and arachidonic acid (0.22%). Across all traits, model explanatory power was low (adjusted  $R^2 = 0.01$ – $0.09$ ), and most predictors showed no significant effects. When significant associations were detected, effect sizes were small, typically representing changes of less than one percentage point. Proximate components (ash  $\sim$ 5.4%, dry matter  $\sim$ 94%, protein  $\sim$ 22%) also showed minimal variation across phenotypic groups. These results demonstrate that muscle fatty acid and proximate composition are highly stable across biological and phenotypic traits, providing robust baseline data for food composition assessment and supporting the nutritional consistency of farmed Malabar red snapper.

### 1. Introduction

Aquaculture has become the fastest-growing food production sector worldwide, now supplying nearly half of all seafood consumed globally and playing a vital role in enhancing global food and nutritional security (Casas et al., 2013; Kiron et al., 2022; Komissarov et al., 2018; Purushothaman et al., 2024a, 2025a; Thevasagayam et al., 2015). In Singapore, where land and natural resources are limited, aquaculture is central to the national goal of producing 30% of the country's nutritional needs locally by 2030, driving investment in advanced and sustainable production technologies (Vij et al., 2024). Within this context, the cultivation of nutritionally rich species, particularly those high in essential fatty acids, offers significant potential to strengthen both food resilience and the nutritional quality of locally farmed seafood.

The Malabar red snapper (*Lutjanus malabaricus*, hereafter referred to as red snapper) is a highly valued marine fish species widely distributed and cultured across Southeast Asia, particularly in Singapore, Malaysia, Indonesia, and Vietnam (Liang et al., 2026; Purushothaman et al.,

2025b, 2025c). Owing to its bright red pigmentation, firm texture, and rich taste, red snapper holds significant consumer appeal and contributes notably to the premium seafood market (Liang et al., 2025a, 2025b). In recent years, aquaculture production of red snapper has expanded to meet the increasing demand, as catches from wild stocks continue to decline due to overfishing and habitat degradation (Obi et al., 2025; Vij et al., 2024).

Our previous study showed that red snapper contains high levels of long-chain omega-3 polyunsaturated fatty acids (n-3 LC-PUFAs), particularly eicosapentaenoic acid (EPA, C20:5n-3) and docosahexaenoic acid (DHA, C22:6n-3), highlighting its strong nutritional potential (Purushothaman et al., 2024b). These fatty acids are known to play crucial roles in cardiovascular, neural, and visual health in humans, while also contributing to membrane stability and immune function in fish (Nigam et al., 2018; Tocher et al., 2019). Studies profiling seafood species have consistently shown that most marine fish, including snappers, contain higher proportions of  $\Sigma$ -3 PUFAs relative to  $\Sigma$ -6 PUFAs, emphasizing their importance as sources of health-promoting nutrients

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(Durmuş, 2019; Simopoulos, 2008).

Fish are an important component of the human diet due to their rich supply of macronutrients such as proteins, lipids, and minerals, along with essential micronutrients including vitamins and trace elements (Bezbaruah and Deka, 2021). These nutrients support vital metabolic functions and determine the overall nutritional and functional value of fish, allowing species to be ranked based on their contribution to human health and dietary quality (Ahmed et al., 2022).

The proximate composition of fish, which mainly consists of water, protein, fat, and minerals, is a reliable indicator of its nutritional quality, physiological condition, and overall health status (Begum et al., 2012; Ravichandran et al., 2011; Zhang et al., 2025). Variations in these components are influenced by several biological and environmental factors, including age, size, sex, habitat, feeding habits, and genetic background (Begum et al., 2016). Accurate compositional data are also essential for the development of national and international food composition databases, which support nutritional research, dietary assessment, and seafood quality evaluation.

Despite its growing aquaculture potential, scientific research on red snapper remains limited compared to other marine species. Previous studies have primarily focused on growth performance and pigmentation traits (Poon et al., 2023), while nutritional and physiological parameters such as fatty acid, protein, and mineral composition have received less attention. Understanding these parameters is essential, as muscle biochemical composition is influenced by both intrinsic factors (e.g., sex, size, health, and coloration) and extrinsic conditions (e.g., diet, environment, and culture system). Furthermore, the nutritional composition of fish muscle is a critical determinant of both product quality and consumer acceptance, affecting flavor, texture, and health value. However, the extent to which phenotypic traits explain variability in muscle nutritional composition remains poorly quantified. Evaluating the predictive value of these traits is important for improving seafood quality assessment, aquaculture management, and the development of reliable food composition databases. With this rationale, the present study investigates the phenotypic variation in the muscle nutritional composition of red snapper, focusing on the influence of sex, size, weight, health status, and colour intensity. Using a large dataset of farmed individuals ( $n = 540$ ) and linear modelling approaches, this study evaluates the extent to which these phenotypic variables explain variation in muscle fatty acid and proximate composition. The findings aim to establish a baseline reference for the compositional consistency and nutritional quality of red snapper fillets, thereby supporting the development of selective breeding and nutritional optimization strategies for this emerging aquaculture species.

## 2. Materials and methods

### 2.1. Ethics statement

All experimental procedures involving Malabar red snapper (*Lutjanus malabaricus*) were carried out in accordance with established ethical standards for animal research. The study followed the ARRIVE (Animal Research: Reporting of In Vivo Experiments) guidelines and complied with the National Advisory Committee on Laboratory Animal Research (NACLAR) guidelines for the care and use of animals in Singapore.

All experimental procedures involving red snapper were approved by the Institutional Animal Care and Use Committee (IACUC) of the Singapore Food Agency (SFA) (Approval ID: 2021-A010). All animal handling followed the National Advisory Committee on Laboratory Animal Research (NACLAR) guidelines for the ethical use of animals in research.

### 2.2. Fish phenotyping

A total of 540 red snappers were collected from a Singapore Aquaculture Technologies farm located near the Johor Strait in Singapore

(Latitude 1.396°N, Longitude 103.972°E). All fish were reared under standardized farming conditions and fed a commercial pelleted diet containing 44% crude protein (Uni-President, Di An, Vietnam). All fish were sampled during a single production period and were maintained under uniform feeding and environmental conditions throughout the culture cycle. Prior to sampling, fish were anesthetized using Aquí-S. Morphometric data including body weight (BW), total length (TL), and color were recorded. Colour intensity (CIELAB  $a$  values) was measured in a standardized region below the dorsal fin using a handheld colorimeter (JZ-300, M&A Instruments Inc.); for more details, see (Liang et al., 2025a). Fish gender was assessed based on the visual presence of clearly identifiable testis or ovary upon dissection. Fish where gonads could not be visually sexed were sexually determined via histology (see Section 2.3); however, 3% of samples remained undetermined after histological sectioning and were classified as such (Fig. 1).

In addition to sex and colour, fish were categorized into several phenotypic characteristics. Fish were visually inspected and classified as healthy or deformed based on external morphology. Healthy fish showed normal body shape, symmetrical fins, intact eyes, and a straight vertebral axis. Deformed fish exhibited visible abnormalities such as shortened or compressed body shape, spinal curvature, fin deformities, or ocular abnormalities (e.g., missing or malformed eye). These classifications followed commonly described morphological indicators of deformities in cultured fish (Boglione et al., 2013b; Cobcroft and Battaglene, 2013) (Fig. 2).

All muscle samples were collected from the dorsal fillet region adjacent to the tail fin, immediately snap-frozen in liquid nitrogen, and stored at  $-80$  °C for subsequent fatty acid and proximate composition analyses. The detailed protocol has been described previously in Purushothaman et al. (2024b).

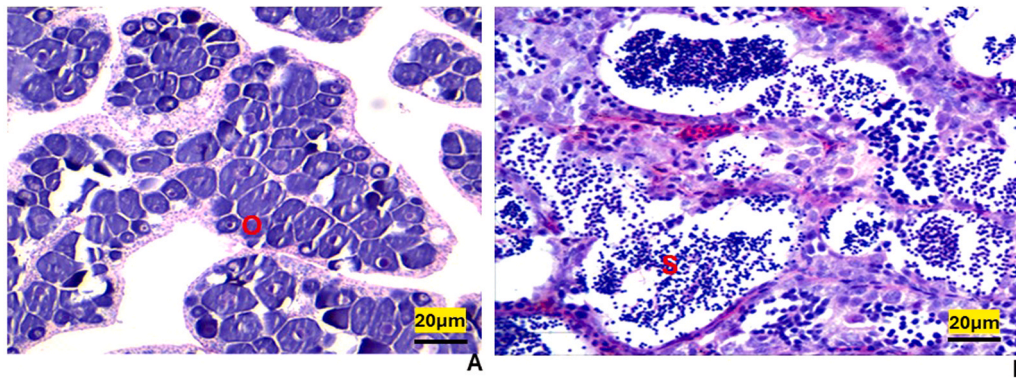
### 2.3. Gonadal histology for sex confirmation

To confirm sex, gonadal tissue samples were collected and fixed in 10% neutral-buffered formalin for 48 h and then processed using standard histological procedures (Purushothaman et al., 2016, 2021; Vij et al., 2020). Fixed tissues were dehydrated through a graded ethanol series (50–100%), cleared in xylene, and embedded in paraffin wax (Itani et al., 2023; Rocha et al., 2023). Transverse sections of 4–5  $\mu$ m thickness were prepared using a rotary microtome and mounted on glass slides (Hooft et al., 2024; Mensah et al., 2025). Slides were stained with hematoxylin and eosin (H&E) and examined under a Leica DM500 light microscope equipped with a Leica ICC50 HD digital camera (Leica Microsystems, Wetzlar, Germany).

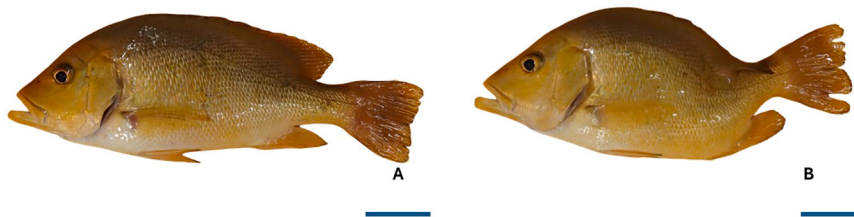
### 2.4. Fatty acid extraction and analysis

Muscle fatty acid profiles were analyzed following a modified one-step direct methylation method (O'Fallon et al., 2007a). Approximately 0.5 g of freeze-dried muscle powder was transferred into a 15 mL Falcon tube containing C13:0 internal standard (1.0 mL, 0.5 mg/mL in methanol), 10 N KOH (0.7 mL), and methanol (5.3 mL). Samples were incubated at 55 °C for 1.5 h, with manual shaking every 20 min to ensure complete hydrolysis and esterification. After cooling, 24 N H<sub>2</sub>SO<sub>4</sub> (0.58 mL) was added to catalyze methylation, followed by a second incubation for 1.5 h under identical conditions.

Fatty acid methyl esters (FAMES) were extracted using 3 mL of hexane, vortexed for 5 min, and centrifuged at 3000 rpm for 5 min. The upper hexane layer containing FAMES was transferred to GC vials and stored at  $-20$  °C until analysis. Chromatographic separation was performed using a SP-2560 capillary column (100 m  $\times$  0.25 mm  $\times$  0.20  $\mu$ m; Sigma-Aldrich) on a gas chromatograph equipped with a flame ionization detector (FID) and split injector (both at 250 °C). The oven was programmed at 140 °C for 5 min, ramped to 240 °C at 4 °C/min, and held for 25 min. Hydrogen served as the carrier gas (flow rate 1.12 mL/min; split ratio 15:1). Fatty acids were identified by comparing retention



**Fig. 1. Gonadal morphology of Malabar red snapper (*Lutjanus malabaricus*).** Representative histological sections of (A) female ovary and (B) male testis stained with hematoxylin and eosin (H&E). O: oocytes; S: spermatozoa. Scale bar = 20 µm.



**Fig. 2. Phenotypic comparison of healthy and deformed Malabar red snapper (*Lutjanus malabaricus*).** Representative images of (A) healthy fish exhibiting normal morphology and (B) deformed fish showing visible skeletal or morphological abnormalities. Images were captured under standardized lighting conditions. Scale bar = 5 cm.

times with a Supelco™ 37 Component FAME Mix standard (47885-U), and results were expressed as percentages of total identified fatty acids. The detailed protocol has been previously described in Purushothaman et al. (2024b). Fatty acids were identified using external reference standards. A Supelco™ 37 Component FAME Mix standard (Sigma-Aldrich, St. Louis, MO, USA; Catalogue No. 47885-U; purity  $\geq 99\%$ ) was used for fatty acid identification. Individual fatty acids were confirmed by comparing their retention times with those of the reference standards. C13:0 methyl ester (Sigma-Aldrich, USA) was used as an internal standard for quantification. Calibration curves were generated using serial dilutions of the FAME standard mixture to ensure linear detector response across the working concentration range. Method performance parameters, including detector linearity, limits of detection (LOD), and limits of quantification (LOQ), were consistent with those reported for previously published GC-FID fatty acid analytical methods (O'Fallon et al., 2007b; Purushothaman et al., 2024c). Detailed calibration data and standard information are provided in Supplementary Files S3–S5.

## 2.5. Proximate composition analysis

### 2.5.1. Moisture, protein, and ash

Moisture, protein, and ash contents were determined following AOAC (2016) procedures. Approximately 2 g of homogenized muscle tissue was oven-dried at 105 °C overnight to measure moisture content. The dried residue was incinerated at 600 °C for 4 h in a muffle furnace to estimate ash. Crude protein was determined by the Kjeldahl method, and total nitrogen content was multiplied by 6.25 to obtain crude protein. All values were reported as mean  $\pm$  standard deviation (SD) on a wet weight basis.

## 2.6. Statistical analysis

All analyses were conducted in R (version 4.3.3) (Team, 2020). To evaluate the influence of phenotypic traits on muscle composition, we fitted linear models:

$$\text{Response} = \beta_0 + \beta_1(\text{Length}) + \beta_2(\text{Weight}) + \beta_3(\text{Colour}) + \beta_4(\text{Health}) + \beta_5(\text{Sex}) + e$$

Response traits include fatty acid compositions and proximate traits. Length, weight, and colour score (CIELAB  $a^*$ ) were treated as continuous predictors, while sex and health status were included as categorical factors. Variance inflation factors (VIF) were used to assess multicollinearity; all predictors showed acceptable VIF values (1.00–2.22), showing no evidence of problematic collinearity. Model fit was evaluated using adjusted  $R^2$ , and residual standard error. For each fatty acid composition as well as proximate traits, we extracted regression coefficients, standard errors, and  $p$ -values. Statistical significance was interpreted in the context of effect sizes and overall model explanatory power. Given the large sample size ( $n = 540$ ), emphasis was placed on biological relevance rather than statistical significance alone. Each individual fish was treated as an independent biological replicate ( $n = 540$  for fatty acid analysis). For proximate composition analysis, replicate numbers for each group were specified in Table 2. All measurements were performed on individual samples without pooling.

## 3. Results

### 3.1. Morphometric traits

The sampled population ( $n = 540$ ) exhibited a broad but continuous range of body sizes, with total length averaging  $289 \pm 26$  mm (range: 195–362 mm) and body weight averaging  $453 \pm 102$  g (range: 175–800 g). Colour intensity (CIELAB  $a^*$ ) ranged from 0.1 to 23.4, with a mean of  $4.17 \pm 2.62$ . Sex distribution consisted of 63.0% females, 9.8% males, and 27.2% undetermined individuals. Based on external morphology, 63.9% of fish were classified as healthy and 36.1% as deformed. These descriptive statistics indicated that the dataset captured the natural phenotypic variation present in farmed Malabar red snapper and provided a robust basis for evaluating the influence of phenotypic traits on muscle nutritional composition.

### 3.2. Muscle fatty acid composition

A total of 540 fish were analyzed for the fatty acid (FA) composition of muscle tissue. The overall profiles were dominated by saturated fatty acids (SFAs), followed by polyunsaturated fatty acids (PUFAs) and monounsaturated fatty acids (MUFAs). Among individual fatty acids, oleic acid (OA), arachidonic acid (ARA),  $\alpha$ -linolenic acid (ALA), linoleic acid (LA), eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA), and the n-6/n-3 ratio were the most abundant components of the muscle lipid fraction. Please see Purushothaman et al. (2024b) (see Table 1 and Supplementary File S1 & S2 for details of the analyses).

### 3.3. Linear model analysis of fatty acid traits

To formally evaluate the effects of phenotypic traits on muscle fatty acid composition, linear models were fitted for each fatty acid using length, weight, colour score, health status, and sex as predictors. A summary of significant predictors and model fit statistics is presented in Table 3. Across all traits, adjusted  $R^2$  values were low (0.01–0.09), indicating that phenotypic variables explained only a small proportion of the variability in muscle fatty acid composition. Most predictors were not statistically significant ( $p > 0.05$ ), and when significant associations were detected, the effect sizes were small. For example, weight showed weak associations with PUFA (estimate =  $-0.007$ ,  $p = 0.019$ ) and MUFA (estimate =  $+0.005$ ,  $p = 0.016$ ), while length was associated with Omega-6 (estimate =  $-0.025$ ,  $p < 0.001$ ). These changes corresponded to less than one percentage point variation in the respective fatty acids. Health status was associated with EPA (estimate =  $+0.136$ ,  $p = 0.005$ ) and ALA (estimate =  $-0.126$ ,  $p = 0.004$ ), but the magnitude of these effects remained small relative to the overall trait means. Sex effects were detected for n-6 and LA, again representing differences of less than one percentage point. Colour score showed no significant associations with any fatty acid trait. Collectively, these results indicate that muscle fatty acid composition remains highly stable across phenotypic traits, with phenotypic variation explaining only minor differences (Table 3 and Supplementary File S1 & S2).

### 3.4. Proximate composition

Linear models for ash, dry matter, and protein content also showed minimal influence of phenotypic traits, with adjusted  $R^2$  values between 0.00 and 0.03. Most predictors were non-significant ( $p > 0.05$ ), and no trait consistently explained variation in proximate composition. Ash content averaged  $\sim 5.4\%$ , dry matter  $\sim 94\%$ , and protein  $\sim 22\%$ , with narrow ranges across all phenotypic groups. These results indicate that proximate composition is physiologically conserved and largely independent of sex, size, weight, colour, or health status (Table 2 and Supplementary File S1 & S2).

### 3.5. Gonadal maturity and external health condition of Malabar red snapper

Gonadal morphology analysis revealed clearly differentiated ovaries

**Table 1**

Fatty acid composition of Malabar red snapper (*Lutjanus malabaricus*) across phenotypic groups. Values are presented as mean  $\pm$  standard deviation (SD). 'n' indicates the number of biological replicates per group (n = 540 biological replicates).

Factor	Group	n	ALA (Mean $\pm$ SD)	LA (Mean $\pm$ SD)	ARA (Mean $\pm$ SD)	OA (Mean $\pm$ SD)	EPA (Mean $\pm$ SD)	DHA (Mean $\pm$ SD)	n-3 (Mean $\pm$ SD)	n-6/n-3 Ratio (Mean $\pm$ SD)
Sex	Male	52	1.0 $\pm$ 0.4	16.6 $\pm$ 2.0	0.2 $\pm$ 0.1	21.1 $\pm$ 6.3	2.9 $\pm$ 0.6	11.4 $\pm$ 3.2	15.3 $\pm$ 2.4	1.3 $\pm$ 0.2
	Female	339	0.9 $\pm$ 0.4	15.8 $\pm$ 2.0	0.2 $\pm$ 0.1	21.8 $\pm$ 4.6	3.0 $\pm$ 0.5	11.6 $\pm$ 3.0	15.7 $\pm$ 2.5	1.3 $\pm$ 0.2
	Unknown	146	0.9 $\pm$ 0.4	15.8 $\pm$ 2.4	0.2 $\pm$ 0.1	21.5 $\pm$ 4.9	3.0 $\pm$ 0.4	11.8 $\pm$ 2.6	15.8 $\pm$ 2.3	1.3 $\pm$ 0.2
Health	Healthy	343	0.9 $\pm$ 0.4	15.8 $\pm$ 1.7	0.2 $\pm$ 0.1	21.6 $\pm$ 5.0	3.1 $\pm$ 0.4	11.7 $\pm$ 2.9	15.7 $\pm$ 2.3	1.3 $\pm$ 0.2
	Deformed	194	1.0 $\pm$ 0.4	16.1 $\pm$ 2.7	0.2 $\pm$ 0.1	21.6 $\pm$ 4.7	2.9 $\pm$ 0.6	11.5 $\pm$ 3.1	15.7 $\pm$ 2.6	1.3 $\pm$ 0.3
	All population	540	0.9 $\pm$ 0.4	15.9 $\pm$ 1.6	0.2 $\pm$ 0.2	21.6 $\pm$ 4.6	3.0 $\pm$ 0.4	11.6 $\pm$ 2.6	15.7 $\pm$ 2.2	1.3 $\pm$ 0.2

**Table 2**

Proximate composition of Malabar red snapper (*Lutjanus malabaricus*) across phenotypic groups. Values are presented as mean  $\pm$  standard deviation (SD). 'n' indicates the number of biological replicates per group (n = 540 biological replicates).

Group	Category	n	Ash (Mean $\pm$ SD)	Dry matter (Mean $\pm$ SD)	Protein (Mean $\pm$ SD, %)
Sex	Male	18	5.7 $\pm$ 0.6	93.7 $\pm$ 4.8	22.2 $\pm$ 0.4
	Female	118	5.4 $\pm$ 0.8	94.5 $\pm$ 3.6	22.0 $\pm$ 0.6
	Unknown	40	5.5 $\pm$ 0.5	93.4 $\pm$ 5.0	22.0 $\pm$ 0.4
Health status	Healthy	120	5.4 $\pm$ 0.8	93.9 $\pm$ 4.8	22.0 $\pm$ 0.5
	Deformed	56	5.6 $\pm$ 0.7	94.7 $\pm$ 1.9	22.0 $\pm$ 0.6
	All population	540	5.4 $\pm$ 0.8	94.2 $\pm$ 4.1	22.0 $\pm$ 0.5

**Table 3**

Summary of linear model results for fatty acid traits in Malabar red snapper (n = 540 biological replicates). Only statistically significant predictors ( $p < 0.05$ ) are shown. Adjusted  $R^2$  values indicate model explanatory power.

Trait	Significant predictors	Estimate ( $\beta$ coefficient)	p-value	Adjusted $R^2$	
ALA	Weight	0.00075	0.0438	0.0442	
ALA	Health (Healthy)	-0.126	0.00434	0.0442	
DHA	Weight	-0.00848	0.00126	0.0229	
DHA.ALA	Health (Healthy)	17.9	0.0348	0.0122	
DHA.EPA	Weight	-0.00268	0.00344	0.0685	
DryMatter	Weight	0.0171	0.0151	0.0325	
EPA	Health (Healthy)	0.136	0.00503	0.0654	
EPA.DHA	Weight	-0.00816	0.00304	0.0169	
LA	Length	-0.0276	0.000446	0.0368	
LA	Weight	0.00574	0.00227	0.0368	
LA	Sex (Male)	0.839	0.00781	0.0368	
MUFA	Weight	0.00506	0.0165	0.0679	
Omega3	Weight	-0.00507	0.0198	0.0187	
Omega6	Length	-0.0251	0.000197	0.0877	
Omega6	Sex (Male)	0.551	0.0402	0.0877	
Omega6.	Length	-0.0021	0.00628	0.033	
Omega6.	Omega3	Weight	0.000525	0.00426	0.033
Omega6.	Omega3	Sex (Male)	0.062	0.0446	0.033
PUFA	Weight	-0.00714	0.0186	0.0483	
PUFA.SFA	Weight	-0.000217	0.0191	0.083	

ALA – Alpha-linolenic acid; LA – Linoleic acid; ARA – Arachidonic acid; EPA – Eicosapentaenoic acid; DHA – Docosahexaenoic acid; MUFA – Monounsaturated fatty acids; PUFA – Polyunsaturated fatty acids; SFA – Saturated fatty acids.

and testes, with females showing well-developed oocytes and males displaying organized testicular lobules indicative of active reproductive status (Fig. 1). Assessment of fish condition showed distinct differences between healthy and deformed individuals, where deformed fish exhibited visible external abnormalities that were not present in the healthy phenotype, suggesting potential developmental or environmental impacts (Fig. 2).

#### 4. Discussion

The present study provides a comprehensive evaluation of the nutritional composition of red snapper muscle. Overall, fatty acid, protein, ash, and dry matter contents remained relatively consistent across a wide range of phenotypic traits, despite detectable statistical associations in some models. Linear regression models showed that phenotypic variables explained only a small proportion of the variation in fatty acids, with adjusted  $R^2$  values ranging from 0.01 to 0.09. Even when statistically significant associations were detected, effect sizes were small and unlikely to be biologically meaningful. Overall, these findings highlight the nutritional consistency of Malabar red snapper muscle across diverse phenotypic characteristics. These results indicate that phenotypic traits account for only a small fraction of the variability in muscle fatty acid composition within the studied population.

##### 4.1. Fatty acid composition and biological variation

In this study, sex-related differences in muscle fatty acids were minimal. Linear models detected small effects of sex on linoleic acid (LA) and omega-6 fatty acids, with males showing slightly higher mean values than females. However, the magnitude of these differences was less than one percentage point, suggesting limited biological relevance despite statistical significance. Such small variations may reflect minor differences in lipid metabolism between sexes but are unlikely to substantially affect the nutritional quality of the muscle tissue. Previous studies have suggested that females may require higher levels of long-chain omega-3 fatty acids during reproductive development to support oocyte maturation and embryo formation (Bogevik et al., 2024; Izquierdo et al., 2001; Johnson et al., 2017). Consistent with this, females in the present study showed marginally higher DHA and EPA levels, whereas males exhibited slightly higher ALA and LA, although these differences remained minimal in cultured red snapper.

Health status also showed limited influence on fatty acid composition. Regression analysis detected a small association between health status and EPA (estimate = 0.136,  $p = 0.005$ ) as well as ALA (estimate = -0.126,  $p = 0.004$ ). However, the observed effect sizes were small relative to the overall fatty acid concentrations, indicating that external morphological condition likely explain only a minor portion of lipid variability. Slightly higher EPA levels in healthy red snapper may reflect its role in anti-inflammatory processes, as omega-3 fatty acids regulate inflammatory pathways, influence gene expression, and support immune balance (Bodur et al., 2025). EPA exerts potent anti-inflammatory and modulatory effects, influencing multiple physiological pathways and contributing to the maintenance of metabolic health and the prevention of diet-related diseases (Banaszak et al., 2024; Poggioli et al., 2023). The stable DHA levels across all groups further indicate consistent membrane structural integrity and cellular function, suggesting that EPA variability may serve as a sensitive indicator of immune condition and metabolic status in red snapper. Across all phenotypic groups, the n-6/n-3 PUFA ratio in red snapper muscle remained consistently low, averaging  $\sim 1.27$  (range 1.26–1.32). This balanced ratio is within the range considered optimal for human health, as higher n-6/n-3 ratios have been linked to increased inflammatory responses and metabolic dysfunctions (Abdelhamid et al., 2020; Mariamenatu and Abdu, 2021; Simopoulos, 2008). In contrast, a balanced ratio around 1:1–2:1 supports anti-inflammatory pathways and improved cardiovascular outcomes through enhanced synthesis of eicosanoids derived from omega-3 fatty acids (Simopoulos, 2011; Wijendran and Hayes, 2004). Furthermore, recent nutrigenomic studies have highlighted that elevated n-6/n-3 ratios are associated with increased risk of depression and chronic inflammation, underscoring the functional importance of maintaining lower ratios in the human diet (Wang et al., 2022). Collectively, the favorable n-6/n-3 ratio observed in red snapper muscle indicates that this species provides a nutritionally beneficial lipid profile with potential to support metabolic and mental health when included in

the human diet. The consistently low ratio observed in this study further supports the nutritional value of Malabar red snapper as a source of health-promoting fatty acids.

Body size and weight showed weak statistical associations with several fatty acid traits. Weight was associated with small changes in several lipid classes including PUFA (estimate = -0.007,  $p = 0.019$ ) and MUFA (estimate = +0.005,  $p = 0.016$ ). These minor shifts may reflect metabolic scaling, where larger individuals allocate more lipids toward energy storage, while smaller fish maintain relatively higher levels of structural membrane lipids such as long-chain PUFAs (Aksakal et al., 2023; Marques et al., 2021; Tocher, 2003). Length was also associated with small changes in n-6 fatty acids (estimate = -0.025,  $p < 0.001$ ) and LA (estimate = -0.028,  $p < 0.001$ ). These changes represented less than one percentage point of the respective fatty acids. However, the small magnitude of these effects suggests that overall fatty acid composition remains largely conserved across body size ranges and lengths.

Colour intensity showed no significant association with fatty acid composition. The regression models indicated that the colour score was not a significant predictor for any fatty acid trait, suggesting that pigmentation differences are largely independent of muscle lipid metabolism in this species. This observation agrees with Vo et al. (2023), who reported that pigmentation in Atlantic salmon was primarily influenced by carotenoid metabolism and not by variations in fatty acid profiles. However, Lin et al. (2024) demonstrated that dietary lipid composition could modulate carotenoid deposition and pigmentation intensity, suggesting that, under certain dietary conditions, lipid metabolism may indirectly influence pigmentation outcomes. Together, these findings indicate that while dietary lipids may affect pigment assimilation, intrinsic colour variation in Malabar red snapper is likely independent of muscle fatty acid composition.

The generally low adjusted  $R^2$  values observed across all regression models suggest that phenotypic traits explain only a small proportion of the variability in muscle fatty acid composition. This indicates that other factors, such as diet formulation, metabolic regulation, or environmental conditions, may play a greater role in determining lipid composition in cultured red snapper. Overall, the fatty acid composition of red snapper muscle remained largely stable across all phenotypic groups, with only minor variations reflecting subtle differences in metabolism, energy allocation, and immune regulation.

##### 4.2. Ash, dry matter, and protein composition

The proximate composition of Malabar red snapper muscle was stable across all groups. Ash content averaged approximately 5.4%, while dry matter ( $\approx 94\%$ ) and protein ( $\approx 22\%$ ) showed only minor variation across individuals. These stable values are consistent with the very low explanatory power of the linear models (adjusted  $R^2 = 0.00$ – $0.03$ ), indicating that phenotypic variables had negligible influence on proximate composition, and are comparable with previous reports in reef-associated fishes (Begum et al., 2012; Ravichandran et al., 2011). Slightly higher ash in males and deformed fish may relate to minor osmoregulatory adjustments or bone mineral deposition (Boglione et al., 2013a, 2013b; Cahu et al., 2003), whereas higher dry matter in females and heavier fish reflects greater tissue density and lipid accumulation (Begum et al., 2012; Elvingson and Sjaunja, 1992). As the nutritional profiles of deformed fish were comparable to those of normal individuals, the observed deformities are unlikely to be associated with muscle nutrient composition and may instead reflect developmental or genetic factors commonly reported in cultured fish populations (Boglione et al., 2013b; Cobcroft and Battaglene, 2013). The overall narrow range of variation highlights stable water and mineral balance in muscle tissue, supporting the view that these traits are physiologically conserved.

#### 4.3. Nutritional and practical implications

From a food-quality perspective, the consistency of fatty acid, protein, and mineral composition across biological traits underscores the nutritional reliability of Malabar red snapper as a seafood product. Stable concentrations of essential fatty acids (EPA and DHA) ensure that consumers receive predictable omega-3 benefits, while uniform protein and ash content support consistent textural and nutritional quality. For aquaculture producers, this compositional stability suggests that phenotypic variability, whether in size, sex, or colour, has minimal impact on product nutritional value, simplifying grading and processing decisions.

Furthermore, the results contribute valuable baseline data for selective breeding and feed optimization strategies aimed at enhancing the nutritional profile of farmed fish. Maintaining such stable nutrient composition is critical for consumer acceptance, export consistency, and labeling accuracy within the aquaculture industry.

#### 4.4. Overall interpretation

Overall, the present study demonstrates that phenotypic traits, including sex, body size, colour and external health status, have limited influence on the muscle fatty acid and proximate composition of farmed Malabar red snapper. The regression analyses indicate that these variables explain only a small proportion of nutritional variability, supporting the conclusion that muscle composition is largely conserved across individuals within the studied population. The lack of clear nutritional differences between healthy and deformed fish further suggests that the observed morphological deformities are unlikely to be driven by muscle nutrient composition and may instead arise from genetic factors or developmental and handling stresses during early life stages, as reported in cultured marine fish (Boglione et al., 2013b; Cobcroft and Battaglene, 2013). Because all fish were sampled from a single aquaculture facility during a defined production period and were fed the same commercial diet, the present study did not account for potential seasonal, dietary, or ontogenetic influences that may also affect muscle nutritional composition. This compositional consistency reinforces the value of red snapper as a nutritionally reliable aquaculture species and provides an important baseline for future studies investigating dietary, genetic, or environmental influences on fish muscle quality.

#### 5. Conclusion

Linear modelling of 540 individuals showed that phenotypic traits, including sex, length, weight, colour intensity, and external health status, explained only a small proportion of the variation in muscle fatty acids and proximate composition in Malabar red snapper. Across fatty acid traits, model explanatory power was low (adjusted  $R^2 = 0.01-0.09$ ), while proximate composition showed even lower values (adjusted  $R^2 = 0.00-0.03$ ). Although some predictors reached statistical significance, effect sizes were consistently small and generally represented changes of less than one percentage point in individual fatty acids. Given the large sample size analysed, the statistical models had sufficient power to detect small differences, indicating that the limited effects observed reflect genuine biological consistency rather than insufficient statistical power. Overall, these findings demonstrate that muscle nutritional composition remains relatively consistent across phenotypic traits in cultured Malabar red snapper. The study provides robust baseline data for food composition databases and supports the nutritional reliability of farmed red snapper as a valuable seafood product for aquaculture production and consumer markets.

#### CRedit authorship contribution statement

**Domingos Jose:** Writing – review & editing, Resources, Project

administration, Methodology, Investigation, Funding acquisition. **Bing Liang:** Writing – review & editing, Visualization, Validation, Formal analysis. **Jiun-Yan Loh:** Writing – review & editing, Visualization, Validation, Formal analysis. **Vu Nguyen:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation. **Kathiresan Purushothaman:** Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Shubha Vij:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition.

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#### Declaration of Competing Interest

The authors declare no competing interests.

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#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.jfca.2026.109133](https://doi.org/10.1016/j.jfca.2026.109133).

#### Data availability

Data will be made available on request.

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