



## **Genetic Insights and Trait Relationships in Domesticated Snakeskin Gourami (*Trichopodus pectoralis*): A Focus on Growth and Related Traits at Harvest**

### **Authors:**

Onprang Sutthakiet, Thanathip Suwanasopee, Uthairat Na-Nakorn and Skorn Koonawootrittriron\*

\*Correspondence: agrskk@ku.ac.th

**Submitted:** 15 February 2025; **Accepted:** 15 January 2026; **Published:** 12 February 2026

**To cite this article:** Onprang Sutthakiet, Thanathip Suwanasopee, Uthairat Na-Nakorn and Skorn Koonawootrittriron. (in press). Genetic insights and trait relationships in domesticated snakeskin gourami (*Trichopodus pectoralis*): A focus on growth and related traits at harvest (Early view). *Tropical Life Sciences Research*.

### **HIGHLIGHTS**

- Phenotypic variation, sexual dimorphism, and genetic parameters of six harvest traits were quantified in 8,345 domesticated snakeskin gourami at nine months of age.
- Females exhibited significantly greater body weight, corrected length, body depth, body thickness, and condition factor, confirming pronounced and economically relevant sexual dimorphism.
- Heritability estimates were low (0.059–0.190), but very high genetic correlations among growth traits (0.901–0.994) support effective multi-trait, sex-informed selection.

## EARLY VIEW

### **Genetic Insights and Trait Relationships in Domesticated Snakeskin Gourami (*Trichopodus pectoralis*): A Focus on Growth and Related Traits at Harvest**

<sup>1</sup>Onprang Sutthakiet, <sup>1</sup>Thanathip Suwanasopee, <sup>2</sup>Uthairat Na-Nakorn and <sup>1</sup>Skorn Koonawootrittriron\*

<sup>1</sup>Department of Animal Science, Faculty of Agriculture, Kasetsart University, Chatuchak, Bangkok, 10900, Thailand

<sup>2</sup>Department of Aquaculture, Faculty of Fisheries, Kasetsart University, Chatuchak, Bangkok, 10900, Thailand

\*Corresponding author: agrskk@ku.ac.th

Running title: Genetic Insights and Growth Traits in Snakeskin Gourami

**Submitted:** 15 February 2025; **Accepted:** 15 January 2026; **Published:** 12 February 2026

**To cite this article:** Onprang Sutthakiet, Thanathip Suwanasopee, Uthairat Na-Nakorn and Skorn Koonawootrittriron. (in press). Genetic insights and trait relationships in domesticated snakeskin gourami (*Trichopodus pectoralis*): A focus on growth and related traits at harvest (Early view). *Tropical Life Sciences Research*.

**Abstract:** Phenotypic variation in aquaculture species is shaped by genetic and environmental factors, influencing adaptability, growth performance, and commercial value. For the snakeskin gourami (*Trichopodus pectoralis*), a high-value species widely cultivated in Southeast Asia, integrated knowledge of the phenotypic and genetic relationships among key growth traits remains limited. This study aimed to quantify phenotypic variation, sexual dimorphism, and genetic parameters and to assess interrelationships among harvest traits to support selective breeding strategies. A total of 8,345 fish harvested at 9 months were measured for body weight (BW), total length (TL), corrected length (CL), body thickness (BT), body depth (BD), and Fulton's condition factor (K). Phenotypic analyses and a multi-trait animal model were applied to estimate variance components, heritability, common environmental effects ( $c^2$ ), and phenotypic and

genetic correlations. Females exhibited significantly larger size and greater trait variation than males, while most fish fell within the smaller commercial categories (XXS, XS, S). Heritability estimates were low (0.059–0.190), and  $c^2$  values ranged from low to moderate (0.063–0.214). Strong phenotypic and genetic correlations were detected among growth traits, except for a weak genetic association between TL and K. Overall, the pronounced sexual dimorphism, low heritability, and high trait interdependencies highlight the importance of multi-trait and sex-informed selection approaches to enhance growth efficiency and improve commercial outcomes in snakeskin gourami aquaculture.

**Keywords:** Snakeskin Gourami, Genetic Parameters, Body Composition Traits, Selective Breeding, Tropical Aquaculture

## INTRODUCTION

The snakeskin gourami (*Trichopodus pectoralis*) is a tropical freshwater fish species native to Southeast Asia (Ahmadi 2021), with Thailand being a major producer. In 2023, Thailand ranked fifth in national freshwater fish production, contributing 9,402 metric tons, valued at USD 17.45 million (Department of Fisheries [DOF] 2024). Cultivated for over six decades (Boonsom 1986), the species holds a unique position in niche markets, supported by both local and global trade in various product forms, including frozen, chilled, and live fish, as well as aquarium specimens. However, the most well-known product among consumers is salted-sundried fish, valued for its distinctive flavor and extended shelf life (DOF 2024).

Economically, snakeskin gourami commands a higher market value than many other tropical aquaculture species. In 2023, its fresh market price (USD 1.6–2.7/kg) exceeded that of Nile tilapia (*Oreochromis niloticus*, USD 1.6–2.0/kg) and broadhead catfish (*Clarias macrocephalus*, USD 1.1–1.4/kg), while the retail price of large, salted-sundried snakeskin gourami was nearly four times higher (USD 7.1–10.0/kg) (Talaad Thai 2025). Despite regional variability in production, the global demand for fish continues to outpace supply, driven by shifting consumption patterns, rising meat prices, and population growth. Consequently, closing this widening demand–supply gap requires sustainable, efficient aquaculture systems that ensure stable production and consistent product quality. Given the species' economic importance, optimizing production and strengthening breeding programs necessitate a comprehensive understanding of phenotypic variation and the interrelationships among economically relevant traits.

Like other whole-body sale fish, the consumer preference for snakeskin gourami extends beyond body weight (BW) and total length (TL) to include key body shape attributes influencing marketability. These traits include corrected length (CL), body thickness (BT), and body depth (BD), which are particularly relevant for processed fish products. Consumers favor a rounded or plump body shape, with BD and CL being the primary determinants of desirability, while BT represents the third-dimensional aspect of body form. Moreover, Fulton's condition factor (K) is a widely applied index in fisheries science for assessing body condition, as it relates body weight to length based on the conventional formula  $K = 100 \times W / L^3$  (Fulton 1904). This metric serves as an indicator of overall robustness, fitness, and morphological variation, and is useful for detecting deviations from expected weight-length relationships that may arise from genetic, environmental, or health-related influences (Froese 2006; Teubner et al. 2015). Importantly, variations in K are species-specific; thus, higher values (e.g.,  $K > 1$ ) do not universally signify superior condition, as morphological adaptations differ across species and populations (Ragheb 2023).

Despite existing research on the biological and physiological aspects of snakeskin gourami, including morphological development (Morioka et al. 2010) and genetic characterization (Gustiano et al. 2022), a comprehensive analysis of the phenotypic variation, correlation structures, and regression patterns among BW and other harvest-related traits remains unexplored. Phenotypic variation arises from multiple genetic and environmental sources, each carrying distinct implications for selection and adaptability (Graham 2021). Understanding the mechanisms driving these variations is essential for evaluating a trait's responsiveness to natural and artificial selection, as well as its adaptability to environmental changes (Naval-Sanchez et al. 2020). Moreover, investigating correlations and regression patterns among traits further enables prediction of population-level evolutionary trajectories, particularly within aquaculture breeding programs where multi-trait improvement is desired (Lickliter 2013). According to the principle of direct and correlated selection responses (Falconer & Mackay 1996), improvement in one trait can lead to genetic gains in another when the traits are positively correlated. In the context of snakeskin gourami, where marketable size and body conformation can be inferred from measurable traits such as BW, TL, CL, BD, and BT, understanding these correlations provides a scientific basis for enhancing both selection accuracy and selection intensity. Ultimately, such knowledge supports the development of more efficient and targeted breeding strategies to accelerate genetic gain.

This study aims to address a critical knowledge gap by examining the interrelationships among BW, TL, CL, BT, BD, and K in domesticated snakeskin gourami at the 9-month harvest

stage. Specifically, it evaluates phenotypic correlations, genetic associations, and regression patterns across sexes, providing insights into the functional relationships between growth and body composition traits. Additionally, this study underscores the significance of K as a biomarker linking fish conditions to biotic and abiotic factors. Beyond scientific inquiry, the findings offer practical implications for aquaculture breeding programs and production strategies, facilitating genetic improvement and optimizing marketable traits. Furthermore, while the market currently categorizes only salted-sundried snakeskin gourami, fresh market classifications remain undefined. By elucidating the variance components, genetic parameters, and trait relationships, this research contributes to a broader understanding of growth dynamics in domesticated snakeskin gourami, supporting sustainable aquaculture development and commercial optimization.

## **MATERIALS AND METHODS**

### **Experimental fish population**

This study utilized a comprehensive dataset comprising 8,345 individual records of farmed snakeskin gourami collected at the harvest stage, occurring at 270 days after hatching (DAH) or 9 months of age. The dataset encompasses multiple generations of domesticated populations, representing a structured breeding program. The baseline population ( $G_0$ ) was established between April 2018 and January 2019, followed by the first generation ( $G_1$ ), which was produced between September 2020 and June 2021, and the second generation ( $G_2$ ), cultivated from October 2021 to July 2022. The experimental populations were maintained and evaluated at the Kamphaeng Saen Fisheries Station at Kasetsart University, Kamphaeng Saen Campus, Nakhon Pathom Province, Thailand. The facility provided a controlled aquaculture environment, ensuring standardized rearing conditions across all generations. The study adhered to best aquaculture practices and ethical guidelines for the handling, management, and assessment of fish populations.

### **Production, nursing, and growth of fish**

The breeding process began with the selection of high-quality broodstock characterized by good health, active behavior, absence of deformities, and overall robust physical condition. Mature males and females used for spawning had an average body weight of  $111.97 \pm 44.51$  g and

140.49 ± 68.52 g, respectively. Prior to spawning, males and females were maintained separately in designated cages until they reached full reproductive maturity. Readiness for breeding was assessed using established morphological indicators, including soft, swollen abdomens in females and increased roughness of the gill opercular tubercles in males.

Selected brooders were introduced into 300-L cylindrical breeding tanks at a 1:1 male-to-female ratio (one pair per tank) to facilitate natural spawning. Each pair was maintained independently to preserve accurate family identity for pedigree recording and subsequent genetic evaluation. Following each confirmed spawning event, the male was paired with a new female within approximately 24 hours, enabling sequential spawning with multiple females while maintaining natural reproductive behavior.

After successful spawning, the breeding pairs were removed from the tanks, allowing the fertilized eggs to hatch undisturbed. Upon hatching, approximately 1,000 larvae were randomly sampled from each family and reared in separate 300 L cylindrical tanks for 15 days after hatching (DAH). At this stage, the juveniles were transferred to three identical rearing cages, each measuring 1 × 1 m with a depth of 1 m, at a stocking density of 150 individuals per cage. The fish were reared in cages submerged in earthen ponds, with a continuous-flow-through water system to maintain optimal water quality until 120 DAH, when they were individually tagged for identification.

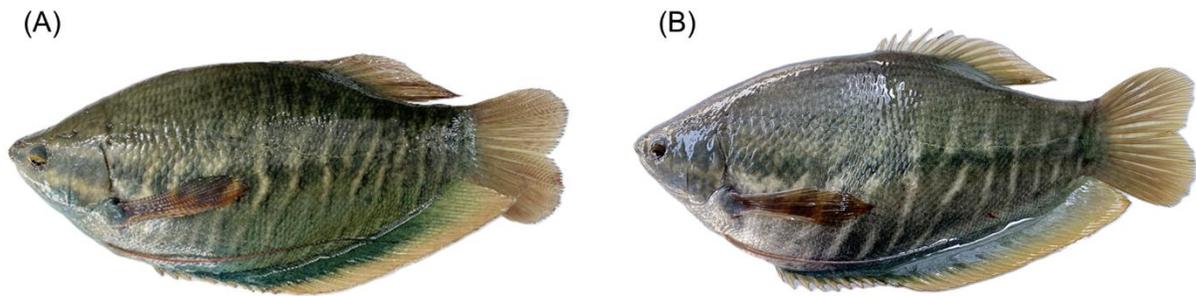
Following tagging, the fish were randomly stocked into larger grow-out cages, each measuring 5 × 5 m with a depth of 2 m, and fixed within a 0.32-hectare earthen pond with a continuous flow-through water supply. The stocking density was maintained at 15 fish/m<sup>2</sup> to support optimal growth conditions. Fish were reared under these conditions until the harvest age of 270 DAH, receiving a standardized feeding regimen (SFR) throughout the production cycle.

Feeding commenced upon complete yolk sac absorption. From 3 – 7 DAH, the fry were provided with an egg-yolk suspension as an initial nutrient source. Subsequently, from 5 – 10 DAH, the diet transitioned to live *Moina* spp., a natural zooplankton food source. From 8 – 15 DAH, fry were fed a finely ground fish meal containing 60% crude protein to support early growth. At 13 – 60 DAH, fish were gradually introduced to a small-sized commercial pelleted feed containing 40% crude protein (Higrade 9961, Charoen Pokphand Foods Public Company Ltd., Samut Sakhon, Thailand) to facilitate weaning onto formulated diets.

From 60 DAH until harvest at 270 DAH, the fish were fed a commercially formulated pelleted diet designed specifically for snakeskin gourami, containing 30% crude protein (Betagro 811, Betagro Public Co. Ltd., Lopburi, Thailand). The feeding rate was maintained at 3% of body weight per day, adjusted periodically based on observed growth performance.

## Data collection

Data was collected during the harvest session to obtain comprehensive morphometric and body composition measurements of domesticated snakeskin gourami. The sex of each fish was determined based on external morphological characteristics following established criteria (Chatchaiphan et al. 2019; Boonanuntanasarn et al. 2020). Males were identified by their pointed and elongated dorsal fin tips extending to the caudal peduncle and the presence of tubercles on the caudal peduncle. In contrast, females exhibited shorter and more rounded dorsal fin tips (Figure 1).

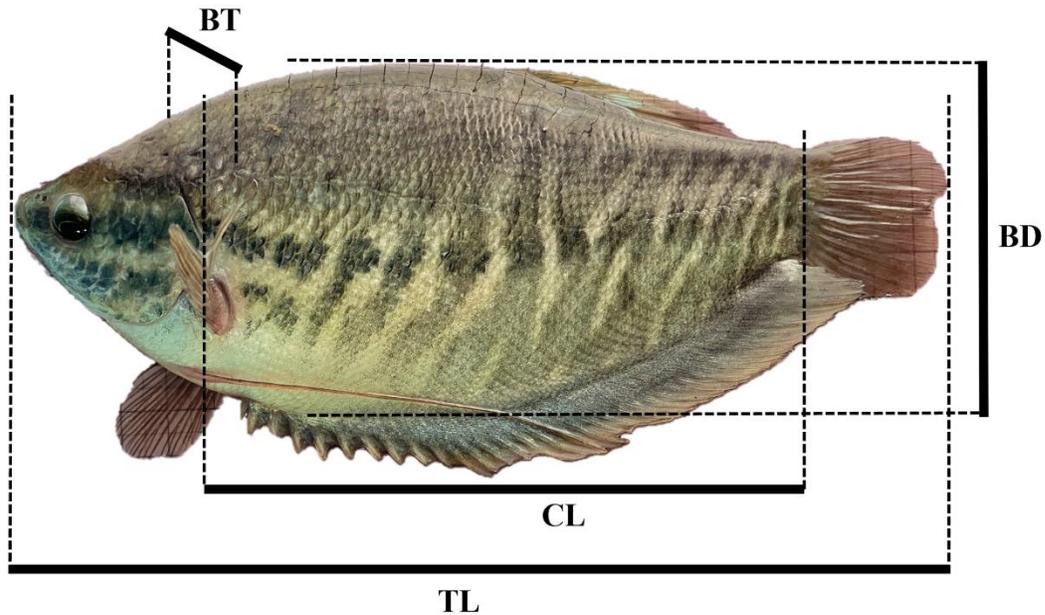


**Figure 1:** Male (A) and female (B) snakeskin gourami

A total of 8,345 fish were measured for key morphometric traits, including total length (TL) and body weight (BW). TL was recorded to the nearest 1 mm using a standard measuring board (Figure 2), while BW was recorded to the nearest 0.01 g using a digital scale. Additional body shape traits, including corrected length (CL), body thickness (BT), and body depth (BD), were measured using digital image analysis. Each fish was photographed individually using a high-resolution digital camera, ensuring standardized positioning to minimize measurement errors. Image processing and precise centimeter-based morphometric assessments were performed using the GNU Image Manipulation Program (Kimball & Mattis 2023), following the methodology outlined by Sutthakiet et al. (2020).

Fulton's condition factor (K; Fulton 1904) was calculated to assess fish body condition and shape using the standard formula:  $K = (BW \times 100)/TL^3$ , where BW is body weight (g) and TL is the total length (cm). This index provides insights into the overall health and well-being of the fish.

All procedures involving live fish handling, measurement, and data collection followed ethical standards. The study received approval from the Institutional Animal Care and Use Committee of Kasetsart University under approval number ACKU65-FIS-001, ensuring compliance with ethical guidelines for the humane treatment of aquatic species used in research.



**Figure 2:** Measurement for the total length (TL), corrected length (CL), body thickness (BT) and body depth (BD) of the snakeskin gourami

### **Classification of snakeskin gourami sizing**

Fresh snakeskin gourami were classified by weight per kilogram, based on a modified system from Yensuk (2005), to facilitate standardized analyses in both research and market contexts. The classification includes seven distinct categories: XXL ( $\geq 250$  g; 3 – 4 fish/kg), XL (250 – 200 g; 4 – 5 fish/kg), L (167 – 200 g; 5 – 6 fish/kg), M (111 – 167 g; 6 – 9 fish/kg), S (83 – 111 g; 9 – 12 fish/kg), XS (83 – 62 g; 12–16 fish/kg), and XXS (< 62 g; > 16 fish/kg). This structured framework supports consistent evaluation of size-related variations in growth traits and market suitability, contributing to a clearer understanding of phenotypic diversity within domesticated snakeskin gourami populations.

### **Statistical analyses**

All data related to BW, TL, CL, BT, BD, and K underwent comprehensive statistical analyses. Initially, normality tests were performed to assess data distribution, followed by the computation of descriptive statistics for all traits. An analysis of variance (ANOVA) was conducted to examine the effects of sex, with multiple comparisons performed using Bonferroni's post hoc test.

To model the phenotypic response of body weight, the following statistical model was applied:

$$y_{ijklm} = \mu + \text{Gen}_i + \text{Cage}_{j(i)} + \text{Sex}_k + b(\text{DAH}_l) + e_{ijklm}$$

Where  $y_{ijkl}$  represents the phenotypic value of body weight at harvest,  $\mu$  is the population mean,  $\text{Gen}_i$  is the fixed effect of generations ( $i = G_0, G_1$  and  $G_2$ ),  $\text{Cage}_{j(i)}$  is the collection point at harvest ( $j = 1, \dots, 27$ ), which is nested within generation ( $\text{Gen}_i$ ),  $\text{Sex}_k$  is the fixed effect of sex ( $k = \text{male, female}$ ),  $b(\text{DAH}_l)$  is the continuous covariate representing days after hatching ( $l = 234, 235, \dots, 284$ ), where  $b$  is the regression coefficient, and  $e_{ijkl}$  denotes the residual error.

All results were expressed as least squares means (LSMeans)  $\pm$  standard error (SE) to provide an accurate estimation of the studied variables. Pearson's correlation coefficients were computed to assess trait interrelationships, and trendlines were analyzed to evaluate the linear associations among them. Statistical significance was set at  $\alpha = 0.05$  (95% confidence level), and all analyses were conducted using SAS software (SAS 2016).

A multiple-trait animal model was implemented to estimate genetic parameters for growth traits, incorporating significant fixed effects (generation ( $\text{Gen}_i$ ), collection point nested within generation ( $\text{Cage}_{j(i)}$ ), and sex ( $\text{Sex}_k$ )) as well as a continuous covariate (days after hatching ( $b(\text{DAH}_l)$ )). The model accounted for random environmental effects, which capture environmental influences shared among full-sib families.

Genetic parameter estimation was performed using the average information-restricted maximum likelihood (AI-REML) procedure in ASReml software (Gilmour *et al.* 2002). The statistical model was defined as follows:

$$y = Xb + Zu + Wc + e$$

Where  $y$  is the vector of phenotypic observations for each trait (BW, TL, SL, BD, BT and K);  $b$  is the vector of fixed effects, which includes cage effects (collection point at harvest, nested within generation, DAH (continuous covariate), sex (male or female) and generations ( $G_0, G_1$  and  $G_2$ );  $u$  is the vector of random additive effects of individual fish; and  $c$  is the vector of common full-sib

family effects, which account for shared environmental influences during early family rearing (15 – 120 DAH) and maternal effects, such as egg size and cytoplasmic inheritance,  $e$  is the vector of residual effects, representing unexplained variation.  $X$ ,  $Z$ , and  $W$  are incidence matrices that link phenotypic observation ( $y$ ) to the corresponding fixed effects ( $b$ ), random additive genetic effects ( $u$ ), and common environmental effects ( $c$ ).

Phenotypic variance ( $V_p$ ), additive genetic variance ( $V_a$ ), common full-sib family variance ( $V_c$ ) and residual variance ( $V_e$ ) of a particular trait, and covariance between traits were estimated from the model. Heritability ( $h^2$ ) and common environmental effect ( $c^2$ ) as derived as  $h^2 = \frac{V_a}{V_p} = \frac{V_a}{V_a+V_c+V_e}$  and  $c^2 = \frac{V_c}{V_p} = \frac{V_c}{V_a+V_c+V_e}$ , respectively.

The genetic correlation ( $r_{p/g}$ ) between all traits was calculated as follows: For  $r_{p/g(xy)} = \frac{COV_{p/g(xy)}}{\sqrt{V_{p/g(x)}V_{p/g(y)}}$ . For estimating genetic correlation ( $r_g$ ) and phenotypic correlation ( $r_p$ ),  $COV_{p/g(xy)}$  is the phenotypic and genetic covariance between two traits ( $x$  and  $y$ );  $V_{p/g(x)}$  and  $V_{p/g(y)}$  are the phenotypic and genotypic variance of traits  $x$  and  $y$  (Falconer & Mackay 1996).

## RESULTS

### Characteristic of the snakeskin gourami population

This study analyzed 8,345 domesticated snakeskin gourami, consisting of 3,344 males and 5,001 females from 251 full-sib families, derived from 179 sires and 219 dams across three generations. The survival rate averaged  $71.57\% \pm 20.16\%$ , with a sex ratio of 1:1.5 favoring females.

Phenotypic traits exhibited substantial variation. BW ranged from 18.00 to 203.56 g (mean  $73.22 \pm 26.83$  g), TL from 10.80 to 21.83 cm (mean  $16.47 \pm 1.69$  cm), and CL from 5.65 to 14.03 cm (mean  $9.87 \pm 1.22$  cm). BT varied from 0.98 to 3.29 cm (mean  $2.11 \pm 0.31$  cm), while BD ranged from 3.00 to 8.97 cm (mean  $5.43 \pm 0.88$  cm). K spanned 0.83 to 2.63 (mean  $1.57 \pm 0.24$ ), reflecting differences in body shape and condition.

Least squares means (LSMeans) of measured traits at harvest indicated significant differences between males and females (Table 1). Females exhibited significantly larger BW ( $82.24 \pm 0.65$  g) compared to males ( $64.03 \pm 0.69$  g,  $P < 0.01$ ). Similarly, TL was significantly greater in females ( $16.91 \pm 0.04$  cm) than in males ( $16.31 \pm 0.04$  cm,  $P < 0.01$ ). The CL, representing the marketable portion of the fish after excluding the head length, was also significantly longer in females ( $10.25 \pm 0.03$  cm) than in males ( $9.55 \pm 0.03$  cm,  $P < 0.01$ ).

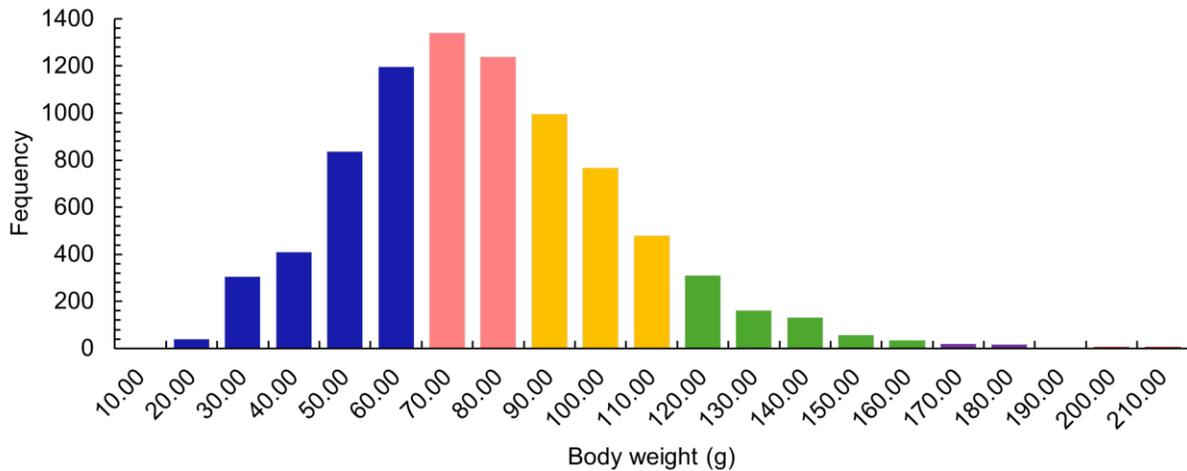
**Table 1:** The least square means  $\pm$  standard error of body weight (BW), total length (TL), corrected length (CL), body thickness (BT), body depth (BD), and condition factor (K) at harvest of all sex, male and female snakeskin gourami

Traits	N	Male	N	Female
BW (g)	3344	64.71 $\pm$ 0.60 <sup>b</sup>	5001	84.89 $\pm$ 0.56 <sup>a</sup>
TL (cm)	3241	16.39 $\pm$ 0.04 <sup>b</sup>	4909	16.99 $\pm$ 0.04 <sup>a</sup>
CL (cm)	3070	9.76 $\pm$ 0.03 <sup>b</sup>	4676	10.47 $\pm$ 0.03 <sup>a</sup>
BT (cm)	3344	1.98 $\pm$ 0.01 <sup>b</sup>	5001	2.24 $\pm$ 0.01 <sup>a</sup>
BD (cm)	3190	5.14 $\pm$ 0.02 <sup>b</sup>	4809	5.69 $\pm$ 0.02 <sup>a</sup>
K	3241	1.42 $\pm$ 0.01 <sup>b</sup>	4909	1.62 $\pm$ 0.01 <sup>a</sup>

Note: Least square means comparison was done by Bonferroni post hoc test. The different superscript letters were significantly different from each other ( $P < 0.0001$ ).

Morphometric traits related to body shape followed a similar trend. Females had significantly greater BT (2.24  $\pm$  0.01 cm) compared to males (1.98  $\pm$  0.01 cm,  $P < 0.01$ ). Likewise, BD was significantly larger in females (5.71  $\pm$  0.01 cm) than in males (5.16  $\pm$  0.02 cm,  $P < 0.01$ ), indicating a more rounded body shape preferred in the market. The condition factor (K) was also significantly higher in females (1.64  $\pm$  0.01) than in males (1.44  $\pm$  0.01,  $P < 0.01$ ), reinforcing the observation that females tend to have a more robust body conformation.

At the nine-month harvest stage, the snakeskin gourami population was categorized into six commercial size groups: XL, L, M, S, XS, and XXS (Figure 3). The size distribution revealed that despite the relatively short cultivation period compared to traditional farming practices (which extend to 12 – 13 months), BW was widely distributed across size classes. The XXS category constituted the largest proportion of the population (36.25%), potentially serving as stock for further growth in separate ponds or for processing into secondary products. Males comprised 50.51% of this group, whereas females accounted for 26.87%, indicating that a substantial fraction of the male population had slower growth rates.



**Figure 3:** A distribution of body weight (g) for the domestic snakeskin gourami population, segmented into various size categories. Each color represents a different size category: blue for XXS, pink for XS, yellow for S, green for M, purple for L, and red for XL.

The XS category, representing 32.11% of the population, was particularly relevant for salted-sundried fish production. Males comprised 34.99% of this category, while females comprised 29.91%, suggesting that both sexes contributed significantly to this commercial segment. The S category, encompassing 23.29% of the population, included a predominant proportion of females (30.59%) compared to males (12.38%), highlighting the superior growth performance of females at this stage.

The M category accounted for 7.92% of the population, with females (12.08%) outnumbering males (2.06%), further emphasizing female-biased growth patterns. The L size category, representing 0.43% of the population, marked the threshold for substantial profitability, as larger fish commanded premium market prices. Within this group, females (91.7%) greatly outnumbered males (8.3%). Finally, the XL category, the least frequent size class (0.10% of the population), held the highest commercial value, with females (75.0%) also predominating over males (25.0%), underscoring the economic advantage of achieving larger fish sizes through optimized growth management.

The observed growth patterns and size distribution suggest that sex-based growth differentiation plays a crucial role in commercial production strategies for domesticated snakeskin gourami. The predominance of smaller-sized males in the early harvest stage highlights the potential for sex-specific management strategies, including selective breeding or sex-biased rearing systems, to enhance production efficiency. Additionally, the economic significance of

larger fish sizes, particularly the L and XL categories, underscores the importance of refining feeding regimes, optimizing stocking densities, and extending rearing periods to maximize profitability. These findings from this study provide a comprehensive characterization of growth dynamics in domesticated snakeskin gourami, offering valuable insights for aquaculture breeding programs and commercial production strategies to improve yield and market value.

### **Relationship between the measured harvest traits**

The comprehensive analysis revealed significant positive correlations among all measured traits in all sexes, ranging from 0.26 – 0.90 (Table S1). The results indicated significant positive correlations between BW and TL, BD, CL and BT (0.90, 0.87, 0.86 and 0.84,  $P < 0.01$ ). This implies that fish with greater BW tend to exhibit greater values regarding TL, BD, CL and BT. A statistically significant correlation (0.61,  $P < 0.01$ ) was observed between BW and K, indicating that animals with a larger BW tend to have a higher K. A strong positive connection between TL and both CL and BD (0.86 and 0.79,  $P < 0.01$ ) was also observed, indicating that deeper fish and longer for meat length are likely to have a longer TL. Conversely, this information could be valuable in understanding the K of the fish. Moderate positive correlations with BT, BD, CL and TL (0.55, 0.54, 0.46, 0.36 and 0.26,  $P < 0.01$ ) were found in this study, suggesting that an increase in these dimensions corresponds to an elevation in K. These observations significantly enhance our comprehension of the intricate interrelationships among these traits within the snakeskin gourami population.

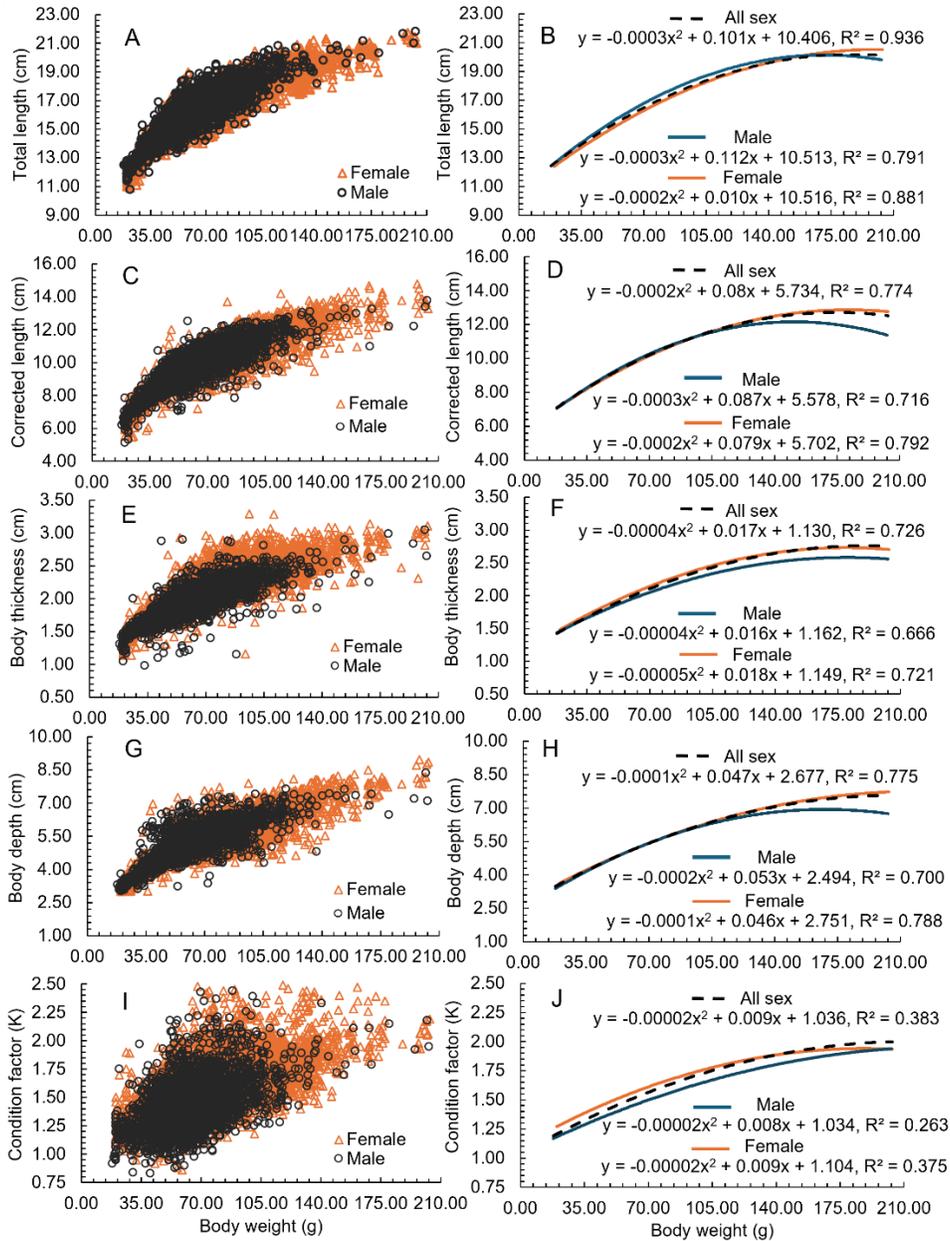
Table 2 and Figure 4 show significant positive correlations among various morphometric traits of male and female snakeskin gourami, with notable distinctions between both sexes. For males, BW demonstrates strong positive correlations with TL (0.87,  $P < 0.01$ ), CL (0.82,  $P < 0.01$ ), and BD (0.82,  $P < 0.01$ ). Body thickness strongly correlates positively with BW (0.80,  $P < 0.01$ ). Conversely, the correlation between BW and K is moderate (0.51,  $P < 0.01$ ). These findings are visually supported by scatter plots (Figure 4A, 4C, 4E, 4G and 4I) that show a more compact distribution of these traits among males compared to the broader dispersion observed in females. Females exhibit stronger correlations for BW with TL (0.92,  $P < 0.01$ ), CL (0.87,  $P < 0.01$ ), BD (0.88,  $P < 0.01$ ), and BT (0.83,  $P < 0.01$ ), with a moderately positive correlation with K (0.60,  $P < 0.01$ ). Additionally, both sexes show strong correlations between TL and BD (males = 0.76; females = 0.84;  $P < 0.01$ ), indicating a consistent relationship between length and depth across sexes. The correlations between BD and K are moderate (males = 0.42, females = 0.54;  $P < 0.01$ ), and between TL and K are low (males = 0.07, females = 0.31;  $P < 0.01$ ). This suggests a

sexual dimorphism influence on the relationship between size and condition. The trendline analyses in Figure 4B reveal that males tend to have longer total length than females at weights below 145 g. In contrast, heavier females are typically longer of CL (Figure 4D) and rounder/plum (BD; Figure 4H) than males of comparable weight, where females consistently demonstrate greater BT (Figure 4F) and K (Figure 4J) across all weight ranges. Collectively, these data show significant sexual dimorphism in body morphology and condition, with females typically showing stronger correlations among measured traits. This suggests potential gender-specific adaptive strategies or differential growth patterns in snakeskin gourami, which are crucial for targeted breeding and management practices in aquaculture.

**Table 2:** Pearson correlation matrix and *p*-value for body weight (BW), total length (TL), corrected length (CL), body thickness (BT), body depth (BD), and condition factor (K) at harvest, differentiated by gender (male in the upper diagonal and female in the lower diagonal).

Traits	BW (g)	TL (cm)	CL (cm)	BT (cm)	BD (cm)	K
BW (g)		0.87**	0.82**	0.80**	0.82**	0.51**
TL (cm)	0.92**		0.82**	0.75**	0.76**	0.07**
CL (cm)	0.87**	0.88**		0.72**	0.77**	0.31**
BT (cm)	0.83**	0.81**	0.77**		0.70**	0.40**
BD (cm)	0.88**	0.84**	0.84**	0.75**		0.42**
K	0.60**	0.31**	0.47**	0.52**	0.54**	

Note: \*\* represents  $P < 0.0001$



**Figure 4:** The scatter plots and trendlines illustrating the relationship between body weight and total length (A and B), corrected length (C and D), body thickness (E and F), body depth (G and H), and condition factor (I and J) for all sex, male and female.

### Heritability and common environmental effect

The variance components, heritability and common environmental effect of snakeskin gourami farmed population are shown in Table 3. The results demonstrate the presence of significant

additive genetic variation for all the traits analyzed. The heritability for body weight was  $0.190 \pm 0.077$ , representing the highest estimate among the traits while still relatively low. Notably,  $V_p$  and  $V_e$  are considerably larger than  $V_a$ . Heritability estimates were also low for other traits, including TL, CL, BD and BT, ranging from  $0.059 \pm 0.037$  for BT to  $0.147 \pm 0.060$  for BD, with all estimates exhibiting low standard errors. Common environmental effects ( $c^2$ ) were observed at low to moderate levels, spanning  $0.063 \pm 0.016$  to  $0.214 \pm 0.035$ , with low standard errors, highlighting the reliability of these estimations.

**Table 3:** Phenotypic variance ( $V_p \pm SE$ ), additive genetic variance ( $V_a \pm SE$ ), common full-sib family variance ( $V_c \pm SE$ ), heritability ( $h^2 \pm SE$ ) and common environmental effect ( $c^2 \pm SE$ ) of body weight (BW), total length (TL), corrected length (CL), body thickness (BT), body depth (BD) and condition factor (K) at harvest for snakeskin gourami farmed populations.

Traits	$V_p \pm SE$	$V_a \pm SE$	$V_c \pm SE$	$h^2 \pm SE$	$c^2 \pm SE$
		87.640 ±	98.869 ±		
BW	461.823 ± 16.460	36.824	16.814	0.190 ± 0.077	0.214 ± 0.035
TL	1.835 ± 0.050	0.149 ± 0.092	0.365 ± 0.055	0.081 ± 0.496	0.199 ± 0.027
CL	0.973 ± 0.030	0.076 ± 0.045	0.162 ± 0.026	0.078 ± 0.045	0.166 ± 0.025
BT	0.058 ± 0.001	0.003 ± 0.002	0.008 ± 0.001	0.059 ± 0.037	0.136 ± 0.021
BD	0.454 ± 0.013	0.070 ± 0.028	0.070 ± 0.012	0.147 ± 0.060	0.148 ± 0.026
K	0.035 ± 0.001	0.002 ± 0.001	0.002 ± 0.001	0.069 ± 0.035	0.063 ± 0.016

### Genetic and phenotypic correlations

Table 4 reveals strong genetic correlations among key growth traits of snakeskin gourami at harvest. Genetic correlations between BW and other traits (TL, CL, BT, BD, and K) were exceptionally high (ranging from 0.901 to 0.994), indicating shared genetic control over these traits. However, the genetic correlation between K and TL was notably weaker (0.232). Phenotypic correlations followed a similar pattern but were generally lower, ranging from 0.494 to 0.868. The condition factor (K) exhibited relatively weak phenotypic correlations with TL (0.086) and CL (0.139).

**Table 4:** Phenotypic correlations ( $r_p$ , above diagonal), and genetic correlations ( $r_g$ , below diagonal) among body weight (BW), total length (TL), corrected length (CL), body thickness (BT), body depth (BD) and condition factor (K) of snakeskin gourami at harvest

Traits	BW	TL	CL	BT	BD	K
BW		0.868 ± 0.005	0.833 ± 0.006	0.755 ± 0.007	0.805 ± 0.007	0.494 ± 0.011
TL	0.994 ± 0.021		0.930 ± 0.002	0.713 ± 0.008	0.764 ± 0.007	0.086 ± 0.016
CL	0.978 ± 0.026	0.982 ± 0.018		0.705 ± 0.008	0.715 ± 0.009	0.139 ± 0.015
BT	0.986 ± 0.027	0.904 ± 0.062	0.990 ± 0.001		0.643 ± 0.010	0.377 ± 0.012
BD	0.901 ± 0.016	0.940 ± 0.047	0.891 ± 0.076	0.936 ± 0.068		0.358 ± 0.012
K	0.990 ± 0.001	0.232 ± 0.001	0.990 ± 0.001	0.996 ± 0.144	0.990 ± 0.001	

## DISCUSSION

The size of the harvested snakeskin gourami in our study, ranging from 13 – 14 fish per kilogram, aligns with the previous report (Chatchaiphan et al. 2019) given under similar conditions. This disparity can be attributed to our higher stocking density (15 fish/m<sup>2</sup>) compared to the more typical 3 – 5 fish/m<sup>2</sup> used in commercial ponds (Sampantarak et al. 2004; Chatchaiphan et al. 2019). However, it notably differs from commercially cultured fish, which typically range from 5 – 6 fish per kilogram, and from wild populations (Ahmadi 2021; Sutthakiet et al. 2024). It's worth noting that farmers have observed size differences between male and female populations. While female populations are generally more desirable and productive, sexual size dimorphism has emerged as an economically important trait (Boonanuntasarn et al. 2020; Nakharuthai et al. 2022). The skewed sex ratio observed in this snakeskin gourami population mirrors findings reported by previous research, indicating a predominance of females within the population (Chatchaiphan et al. 2019; Nakharuthai et al. 2022). Furthermore, this population was reared under experimental conditions and harvested at 9 months old. The expected snakeskin gourami market size ranged from XL to XS categories, depending on what product they would process, such as crispy fried fish, seasoning mixed snacks, and salted-sundried fish (Waiprib et al. 2016).

There was more significant variation among BW and various harvest traits in females than males. Behavioral interactions and nutritional factors influence size variation in snakeskin

gourami. Interestingly, the BW distribution of snakeskin gourami reported in wild populations from Indonesia exhibited a similar pattern (Ahmadi 2021). Improved culture conditions can reduce the need for stressful and labor-intensive grading operations. However, it is essential to recognize that size distributions can be activated in favorable environments and may not be directly comparable due to differences in management and timing. In addition, the distribution graph of BW encompassed a wide range of sizes, suggesting the potential of producing robust growth offspring by simple selection.

## **Heritability**

Heritability represents the proportion of  $V_p$  attributable to  $V_a$ . High heritability indicates that trait expression is strongly influenced by genetics, whereas low heritability suggests a greater contribution of environmental factors. In this study, heritability estimates for all traits were low, with BW showing the highest additive genetic contribution (0.190), followed by BD (0.147). TL (0.081), CL (0.078), K (0.069), and BT (0.059) exhibited minimal additive genetic influence, highlighting the substantial role of environmental variation in shaping these traits.

The low heritability estimates observed here fall within the range commonly reported for growth traits across aquatic species, including low (0.056–0.21; Luan et al. 2012; Domingos et al. 2013; Phuc et al. 2021; Liu et al. 2022), moderate (0.21–0.40; Blonk et al. 2010; Trùng et al. 2013; Fu et al. 2016; Dufflocq et al. 2017), and high (>0.40; Charo-Karisa et al. 2007; Gheyas et al. 2009; Li et al. 2019) heritability categories. However, the values reported herein were lower than those previously documented for snakeskin gourami, including the base population estimate (0.37) by Sutthakiet et al. (2019) and the realized heritability (0.42) reported by Chatchaiphan et al. (2019). Importantly, all estimates except for TL exhibited low standard errors, supporting the reliability of the results.

Despite the low magnitudes, the estimated heritabilities demonstrate that sufficient additive genetic variation exists to support genetic improvement in growth and body-shape traits through selective breeding. Low heritability does not preclude genetic progress; rather, it reflects a larger proportion of environmental influence while still allowing additive genetic variance to be exploited for selection response (Falconer & Mackay 1996).

The common environmental effect ( $c^2$ ), which encompasses shared environmental influences, maternal effects, and other non-additive components, ranged from low to moderate (0.063–0.214). These values are consistent with previous reports in aquaculture species (Srimai et al. 2019; Vu et al. 2019; Phuc et al. 2021) and indicate that early rearing environments and

family-specific conditions contributed meaningfully to phenotypic variation. Accounting for  $c^2$  is essential in breeding program design, as failure to do so may inflate heritability estimates and lead to inaccurate predictions of genetic gain (Lozano-Jaramillo et al. 2020).

The heritability estimates presented in this study are interpreted strictly within the narrow-sense genetic evaluation framework, in which phenotypic variance is decomposed into additive genetic and environmental components. These values do not imply differences in inbreeding levels, as brooders were individually tagged and matings among related individuals were actively avoided. Consequently, the assessment of inbreeding patterns or their theoretical relationships with heritability, as described in some BLUP selection scenarios, was beyond the scope of this study. The results, therefore, reflect additive genetic contributions under controlled mating conditions where inbreeding was minimized.

### **Correlations and relationships**

The relationship between BW was moderately to highly correlated with various body composition traits in this domesticated snakeskin gourami population. Females displayed significantly greater relationships with these variables than males. Moreover, females exhibit various body shapes, including a narrow shape (long TL with a small BD) and a plump shape (long TL with a wide BD). Fish growth tends to be correlated with body size. As fish grow, they generally increase in weight, length, and depth. This pattern can lead to strong correlations between BW and other size-related measurements. These findings suggest that BD, given its strong correlation with BW and moderate correlation with K, could be a crucial criterion for future selective breeding programs. CL, the total length minus the head length, which is pertinent to the marketable portion of processed snakeskin gourami, also showed significant differences between sexes, with females exhibiting a higher mean CL than males. BT followed a similar pattern, with females displaying greater thickness than males, further emphasizing the pronounced sexual dimorphism in physical form, which holds economic implications for targeted breeding and management strategies.

Fulton's condition factor is proportional to weight and length as an indicator of health, well-being, fitness (Teubner *et al.* 2015), and body shape (Firdaus *et al.* 2018) of the fish. The larger the factor, the better the condition. It was determined by factors such as feed availability, stocking density, parasitic infestations, and environmental conditions. The overall K result from this study ranged from 0.83 – 2.63 with an average of  $1.57 \pm 0.24$ . The K value in females showed significantly more rounder/plump compared to males in this domesticated population, and this pattern was also observed in a wild population (Ahmadi 2021). Moreover, several studies of Nile

tilapia have shown that a K greater than 1.0 implies good fish health (Anani & Nunoo 2016). Normally, the K would remain the same when they got older if the proportion of BW and TL would not change (Firdaus *et al.* 2018). However, both high values of BD and K could be considered plump body shape indicators. Our analysis revealed consistently low correlations between K and TL across all sexes.

The high genetic correlation between growth and related traits aligned with previous reports (e.g. Vu *et al.* 2019; Srimai *et al.* 2020; Phuc *et al.* 2021; Liu *et al.* 2022). The strong genetic correlation indicates that selecting for enhanced development, particularly body weight (BW), is expected in correlated improvements in body dimensions, including TL, CL, BD, and BT. Such correlations are beneficial for breeding programs aiming to improve multiple traits simultaneously, as they allow for the indirect selection of difficult or costly traits to measure. However, a notable exception in this study was the unexpectedly low  $r_g$  between TL and condition factor (K), which deviates from the general trend reported in an earlier study (Srimai *et al.* 2020). While the genetic correlation between growth traits is typically high due to shared genetic control, the low  $r_g$  between TL and K suggests that distinct genetic factors may influence these traits. This finding may be attributed to the different ways in which TL and K are measured. TL reflects overall body length, while K is an indicator of body condition, especially plumpness of the fish (Froese 2006), fish's health and well-being, which is more affected by body depth and thickness relative to length (Knaepkens *et al.* 2002; Oyebola *et al.* 2022).

## **Implication**

This study emphasizes the need for a comprehensive approach to selective breeding programs for snakeskin gourami, including BW, TL, CL, BT, BD, and K. Moreover, the inclusion of BT and CL in selection indices could provide a more holistic approach to understanding body structure dynamics, aligning breeding objectives more closely with market demands and consumer preferences. The observed sexual dimorphism, where females exhibit larger sizes, is economically significant (Boonanuntanasarn *et al.* 2020). The study stresses a holistic approach, acknowledging the influence of unanalyzed factors like sex and cage conditions. Recommendations include expanding trait analysis to dimensions like body thickness and volume to complete a whole-body structure, drawing from studies in other fish species (Reis Neto *et al.* 2014; Fu *et al.* 2016; Joshi *et al.* 2018).

Although the heritabilities of growth and related traits are low, meaningful genetic improvement remains achievable over successive generations. In practical settings, phenotypic

(individual) selection offers the most straightforward and most accessible starting point for snakeskin gourami breeders, as it relies on routine measurements and requires only minimal infrastructure. As breeding programs mature, however, the presence of additive genetic variance in this population justifies the adoption of more advanced selection strategies. Estimating genetic parameters facilitates the design of more effective selection schemes, and implementing EBV-based individual or family selection can substantially enhance selection accuracy and genetic gain, particularly when supported by reliable pedigree recording, tagging systems, and controlled environmental conditions. Collectively, these considerations provide a strong foundation for developing progressive, productive breeding programs to improve growth performance and body conformation in snakeskin gourami for commercial aquaculture.

The moderate  $c^2$  values observed in this study highlight the importance of managing shared environmental conditions, such as hatchery practices, stocking density, and water quality, to minimize environmental variation that may mask genetic potential. Additionally, these findings underscore the potential benefit of incorporating selection to account for maternal effects in the genetic evaluation process. By doing so, breeders can obtain more precise estimates of genetic parameters and ensure that selection decisions are grounded in actual genetic merit rather than environmental variability.

The genetic correlations observed in this study highlight the potential for designing breeding programs that target both growth performance and desirable body conformation. While growth rate and final body weight are important economic traits for improving feed efficiency and production sustainability, body-shape attributes, particularly those reflected by Fulton's condition factor (K), also play a critical role in market acceptance and pricing for snakeskin gourami. The strong correlations among BW and key morphological traits suggest that selection strategies can be structured to enhance growth and body form simultaneously. However, because K reflects aspects of body robustness not fully captured by linear measurements such as TL, direct consideration of K may be necessary when specific body conformation is a breeding objective. For consumer-driven markets where fish size categories and body proportions influence product value, integrating both BW and K into a multi-trait selection index would allow breeders to balance improvements in growth efficiency with consistency in body shape, thereby aligning genetic progress with commercial requirements.

Addressing size variation within the cultured population is another practical consideration for breeding programs. The introduction of uniform rearing protocols and improved management practices, such as size grading and optimal stocking density, can minimize size disparities.

Producing a more uniform size distribution benefits farmers and processors by reducing waste during processing and enabling more consistent product marketing.

Despite the valuable insights provided by this study, several limitations should be acknowledged. Notably, using higher stocking density and shorter culture periods compared to commercial production systems may limit the generalizability of the results to other populations or aquaculture environments. Consequently, caution should be exercised when applying these findings to broader breeding programs for snakeskin gourami or other species. Further validation of the genetic parameters obtained under commercial production conditions is recommended to ensure the robustness of selection strategies.

## **CONCLUSION**

This study revealed substantial phenotypic variation and strong genetic relationships among key growth and body-shape traits in domesticated snakeskin gourami. Despite low heritability estimates, the presence of additive genetic variance and high genetic correlations indicates that meaningful genetic improvement is achievable. Pronounced sexual dimorphism highlights the need to account for sex effects in selection schemes. The integration of traits such as corrected length and body thickness into multi-trait selection indices can help balance improvements in growth performance and market-relevant body conformation. Together, these findings provide a practical foundation for designing more efficient breeding programs and enhancing the commercial value and production consistency of snakeskin gourami in tropical aquaculture systems.

## **ACKNOWLEDGEMENTS**

The authors thank the Kamphaeng Saen Fisheries Station, Kasetsart University, Thailand, for providing research facilities and technical support. This study was supported by the Graduate School Fellowship Program of Kasetsart University, the Distinguished Research Professor Project (DPG5980003; TRF FY 2016) funded by Thailand Science Research and Innovation, and the Kasetsart University Research and Development Institute (KURDI; FF(KU) 3.65).

## AUTHORS' CONTRIBUTIONS

Onprang Sutthakiet: Data collection, data curation, statistical analysis, interpretation of results, and manuscript drafting.

Thanathip Suwanasopee: Data interpretation and critical revision of the manuscript.

Uthairat Na-Nakorn: Conceptual guidance, supervision, and critical revision of the manuscript.

Skorn Koonawootrittriron: Study conceptualization and design, genetic and statistical analysis, interpretation of results, supervision, and manuscript revision.

All authors read and approved the final version of the manuscript.

## REFERENCES

- Ahmadi. (2021). Morphometric characteristic and condition factor of snakeskin gourami (*Trichogaster pectoralis*) from Sungai Batang swamp, Indonesia. *Iranian Journal of Ichthyology* 8(1): 19–29. <https://doi.org/http://doi.org/10.22034/iji.v8i1.301>
- Anani F and Nunoo F K E. (2016). Length-weight relationship and condition factor of Nile tilapia, *Oreochromis niloticus* fed farm-made and commercial tilapia diet. *International Journal of Fisheries and Aquatic Studies* (28 Jan 2024): 647-650. <https://doi.org/https://api.semanticscholar.org/CorpusID:55506374>
- Blonk R J W, Komen J, Tenghe A, Kamstra A and van Arendonk J A M. (2010). Heritability of shape in common sole, *Solea solea*, estimated from image analysis data. *Aquaculture* 307(1–2): 6–11. <https://doi.org/http://doi.org/10.1016/j.aquaculture.2010.06.025>
- Boonanuntanasarn S, Jangprai A and Na-Nakorn U. (2020). Transcriptomic analysis of female and male gonads in juvenile snakeskin gourami (*Trichopodus pectoralis*). *Scientific Reports* 10(1): Article 5240. <https://doi.org/http://doi.org/10.1038/s41598-020-61738-0>
- Boonsom J. (1986). Aquaculture practices, planning and extension in Thailand. Bangkok: FAO. Chapter 12, Pla solid (*Trichogaster pectoralis* Regan): a life history and manual for culture. <https://www.fao.org/3/ac231e/AC231E12.htm>. (accessed on 26 May 2023).
- Charo-Karisa H, Bovenhuis H, Rezk M A, Ponzoni R W, van Arendonk J A M and Komen H. (2007). Phenotypic and genetic parameters for body measurements, reproductive traits and gut length of Nile tilapia (*Oreochromis niloticus*) selected for growth in low-input earthen ponds. *Aquaculture* 273(1): 15–23. <https://doi.org/http://doi.org/10.1016/j.aquaculture.2007.09.011>

- Chatchaiphan S, Thaithungchin C, Koonawootrittriron S and Na-Nakorn U. (2019). Responses to mass selection in a domesticated population of snakeskin gourami, *Trichopodus pectoralis*, Regan 1910, and confounding effects from stocking densities. *Aquaculture* 498: 181–186. <https://doi.org/https://doi.org/10.1016/j.aquaculture.2018.08.029>
- Department of Fisheries (DOF). (2022). Fisheries Statistics of Thailand. Fisheries Development Policy and Planning Division, Department of Fisheries, Bangkok, Thailand.
- Department of Fisheries (DOF). (2024). Statistics of Freshwater Aquaculture Production 2023. Department of Fisheries, Bangkok, Thailand.
- Domingos J A, Smith-Keune C, Robinson N, Loughnan S, Harrison P and Jerry D R. (2013). Heritability of harvest growth traits and genotype–environment interactions in barramundi, *Lates calcarifer* (Bloch). *Aquaculture* 402–403: 66–75. <https://doi.org/http://doi.org/10.1016/j.aquaculture.2013.03.029>
- Dufflocq P, Lhorente J P, Bangera R, Neira R, Newman S and Yáñez J M. (2017). Correlated response of flesh color to selection for harvest weight in coho salmon (*Oncorhynchus kisutch*). *Aquaculture* 472: 38–43. <https://doi.org/http://doi.org/10.1016/j.aquaculture.2016.08.037>
- Falconer D S and Mackay T F C. (1996). Introduction to Quantitative Genetics. Pearson Education Ltd., Essex, England.
- Firdaus M, Lelono T, Bintoro G, Saleh R and Salim G. (2018). The expression of the body shape in fish species *Harpadon nehereus* (Hamilton, 1822) in the waters of Juata Laut, Tarakan city, North Kalimantan. *AAFL Bioflux* 11. <https://doi.org/10.5281/zonodo.1250264>
- Froese R. (2006). Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* 22(4): 241–253. <https://doi.org/http://doi.org/10.1111/j.1439-0426.2006.00805.x>
- Fu J, Shen Y, Xu X and Li J. (2016). Genetic parameter estimates for growth of grass carp, *Ctenopharyngodon idella*, at 10 and 18 months of age. *Aquaculture* 450: 342–348. <https://doi.org/https://doi.org/10.1016/j.aquaculture.2015.08.018>
- Fulton T. (1904). The Rate of Growth of Fishes. The 22nd annual report of the fishery board of Scotland, Edinburgh, UK.
- Gheyas A A, Woolliams J A, Taggart J B, Sattar M A, Das T K, McAndrew B J and Penman D J. (2009). Heritability estimation of silver carp (*Hypophthalmichthys molitrix*) harvest traits using microsatellite based parentage assignment. *Aquaculture* 294(3–4): 187–193. <https://doi.org/http://doi.org/10.1016/j.aquaculture.2009.06.013>

- Gilmour A R, Gogel B J, Cullis B R, Welham S J and Thompson R. (2002). ASReml User Guide Release 1.0. VSN International Ltd, Hemel Hempstead, UK.
- Graham J H. (2021). Nature, Nurture, and Noise: Developmental Instability, Fluctuating Asymmetry, and the Causes of Phenotypic Variation. *Symmetry* 13(7). <https://doi.org/10.3390/sym13071204>
- Gustiano R, Iskandariah I, Ath-Thar M H F, Huwoyon G H and Radona D. (2022). Domestication of snakeskin gourami (*Trichopodus pectoralis* Regan, 1910) in Indonesia: Characterization, bioreproduction and early development. *Pakistan Journal of Zoology*: 1–8. <https://doi.org/http://doi.org/10.17582/journal.pjz/20220111140146>
- Joshi R, Woolliams J A, Meuwissen T and Gjoen H M. (2018). Maternal, dominance and additive genetic effects in Nile tilapia; influence on growth, fillet yield and body size traits. *Heredity* 120(5): 452-462. <https://doi.org/10.1038/s41437-017-0046-x>
- Kimball S and Mattis P. (2023). GIMP 2.10.36. [www.gimp.org](http://www.gimp.org). (accessed on 10 Nov 2023).
- Knaepkens G, Knapen D, Bervoets L, Hanfling B, Verheyen E and Eens M. (2002). Genetic diversity and condition factor: a significant relationship in Flemish but not in German populations of the European bullhead (*Cottus gobio* L.). *Heredity* 89(4): 280–287. <https://doi.org/http://doi.org/10.1038/sj.hdy.6800133>
- Li Y, Zhang B, Yang Y and Chen S. (2019). Estimation of genetic parameters for juvenile growth performance traits in olive flounder (*Paralichthys olivaceus*). *Aquaculture and Fisheries* 4(2): 48-52. <https://doi.org/10.1016/j.aaf.2018.12.001>
- Lickliter R. (2013). The origins of variation: evolutionary insights from developmental science, In A: Advances in Child Development and Behavior. Elsevier Inc., 193-223.
- Liu F, Zhan W, Xie Q, Lou B, Han M, Xu W and Tao S. (2022). First genetic evaluation of growth traits in *Larimichthys polyactis* to guide the formulation of selective breeding programs. *Aquaculture* 554. <https://doi.org/https://doi.org/10.1016/j.aquaculture.2022.738141>
- Lozano-Jaramillo M, Komen H, Wientjes Y C J, Mulder H A and Bastiaansen J W M. (2020). Optimizing design to estimate genetic correlations between environments with common environmental effects. *Journal of Animal Science* 98(2). <https://doi.org/10.1093/jas/skaa034>
- Luan S, Yang G, Wang J, Luo K, Zhang Y, Gao Q, Hu H and Kong J. (2012). Genetic parameters and response to selection for harvest body weight of the giant freshwater prawn *Macrobrachium rosenbergii*. *Aquaculture* 362–363: 88–96. <https://doi.org/http://doi.org/10.1016/j.aquaculture.2012.05.011>

- Morioka S, Ito S and Kitamura S. (2010). Growth and morphological development of laboratory-reared larval and juvenile snakeskin gourami *Trichogaster pectoralis*. *Ichthyological Research* 57(1): 24–31. <https://doi.org/http://doi.org/10.1007/s10228-009-0118-x>
- Nakharuthai C, Sreebun S, Kabpha A, Phuong T V and Boonanuntanasarn S. (2022). Characterization of *ddx4* and *dnd* homologs in snakeskin gourami (*Trichopodus pectoralis*) and their expression levels during larval development and in gonads of males and females. *Animals* 12(23). <https://doi.org/http://doi.org/10.3390/ani12233415>
- Naval-Sanchez M, McWilliam S, Evans B, Yanez J M, Houston R D and Kijas J W. (2020). Changed Patterns of Genomic Variation Following Recent Domestication: Selection Sweeps in Farmed Atlantic Salmon. *Frontiers in Genetics* 11: 264. <https://doi.org/10.3389/fgene.2020.00264>
- Oyebola O O, Omitoyin S B, Hounhoedo A O O and Agadjihouèdé H. (2022). Length-weight relationship and condition factor revealed possibility of mix strains in *Clarias gariepinus* population of Oueme valley, Benin republic (West Africa). *Total Environment Research Themes* 3–4. <https://doi.org/http://doi.org/10.1016/j.totert.2022.100009>
- Phuc T H, Vu N T, Nga N T K, Ky N T and Nguyen N H. (2021). Assessment of a long-term selective breeding program for giant freshwater prawn *Macrobrachium rosenbergii* since 2007. *Aquaculture* 541. <https://doi.org/https://doi.org/10.1016/j.aquaculture.2021.736745>
- Ragheb E. (2023). Length-weight relationship and well-being factors of 33 fish species caught by gillnets from the Egyptian Mediterranean waters off Alexandria. *The Egyptian Journal of Aquatic Research* 49(3): 361-367. <https://doi.org/http://www.doi.org/10.1016/j.ejar.2023.01.001>
- Reis Neto R V, de Oliveira C A L, Ribeiro R P, de Freitas R T F, Allaman I B and de Oliveira S N. (2014). Genetic parameters and trends of morphometric traits of GIFT tilapia under selection for weight gain. *Scientia Agricola* 71(4): 259-265. <https://doi.org/10.1590/0103-9016-2013-0294>
- Sampantarak U, Promkaew P and Maelim P. (2004). Effects of Stocking Rate on Culture of Sepat Siam, *Trichogaster pectoralis* Regan, 1909 in Peat Swamp Area. Department of Fisheries, Bangkok, Thailand.
- SAS. (2016). Base SAS® 9.4 Procedures Guide: Statistical Procedures, 6<sup>th</sup> ed. SAS Institute Inc., Cary, NC, USA.
- Srimai W, Koonawootrittriron S, Chaivichoo P, Manee-aphai W, Phu-onnim A, Koolboon U and Na-Nakorn U. (2020). Selection response and genetic parameters for growth in North

- African catfish, *Clarias gariepinus* (Burchell, 1822). *Aquaculture* 518. <https://doi.org/http://doi.org/10.1016/j.aquaculture.2019.734843>
- Srimai W, Koonawootrittriron S, Manee-aphai W, Chatchaiphan S, Koolboon U and Na-Nakorn U. (2019). Genetic parameters and genotype-environment interaction for growth traits of North African catfish, *Clarias gariepinus* (Burchell, 1822). *Aquaculture* 501: 104–110. <https://doi.org/https://doi.org/10.1016/j.aquaculture.2018.10.064>
- Sutthakiet O, Koonawootrittriron S, Chatchaiphan S, Thaitungchin C and Na-Nakorn U. (2019). Genetic parameters of a snakeskin gourami (*Trichopodus pectoralis*, Regan 1910) base population created from crossing three hatchery stocks. *Aquaculture* 512: 734358. <https://doi.org/https://doi.org/10.1016/j.aquaculture.2019.734358>
- Sutthakiet O, Koonawootrittriron S, Sukhavachana S, Chatchaiphan S, Thaitungchin C and Na-Nakorn U. (2020). Heritability and genetic correlation of body shape and deformity in snakeskin gourami, *Trichopodus pectoralis* Regan, 1910. *Aquaculture* 523: 735208. <https://doi.org/https://doi.org/10.1016/j.aquaculture.2020.735208>
- Sutthakiet O, Suwanasopee T, Na-Nakorn U and Koonawootrittriron S. (2024). Optimizing growth and production efficiency of snakeskin gourami (*Trichopodus pectoralis*) through intensive cage culture: Impacts of culturing season and sex. *Agriculture and Natural Resources* 058(5): 585-592. <https://doi.org/http://doi.org/10.34044/j.anres.2024.58.5.05>
- Talaad Thai. (2025). Daily Price Fish and Seafood. <https://talaadthai.com/en/products?category=15>. (accessed on 1 Jan 2024).
- Teubner D, Paulus M, Veith M and Klein R. (2015). Biometric parameters of the bream (*Abramis brama*) as indicators for long-term changes in fish health and environmental quality--data from the German ESB. *Environmental Science and Pollution Research* 22(3): 1620-1627. <https://doi.org/10.1007/s11356-014-3008-3>
- Trọng T Q, Mulder H A, van Arendonk J A M and Komen H. (2013). Heritability and genotype by environment interaction estimates for harvest weight, growth rate, and shape of Nile tilapia (*Oreochromis niloticus*) grown in river cage and VAC in Vietnam. *Aquaculture* 384–387: 119–127. <https://doi.org/http://doi.org/10.1016/j.aquaculture.2012.12.022>
- Vu N T, Van Sang N, Phuc T H, Vuong N T and Nguyen N H. (2019). Genetic evaluation of a 15-year selection program for high growth in striped catfish *Pangasianodon hypophthalmus*. *Aquaculture* 509: 221–226. <https://doi.org/http://doi.org/10.1016/j.aquaculture.2019.05.034>
- Waiprib Y, Na-Nakorn U, Jintasataporn O, Runglerdkriangkrai J, Pansawat N, Mookdasanit J, Maneerote J, Thaitungchin C and Jintasataporn O. (2016). Enhancing Aquaculture

Potential and Quality and Safety of Processed Snakeskin Gourami Fish (*Trichogaster pectoralis* Regan) Products. Thailand Science Research and Innovation (TSRI).

Yensuk S. (2005). Production and marketing of snake-skinned gourami (Sepat Siam) and products in Changwat Samut Prakan. MS diss, Kasetsart University.

## APPENDIX

**Table S1** Pearson correlation matrix and p-value for body weight (BW), total length (TL), standard length (SL), body depth (BD), body thickness (TN), corrected length (CL), and condition factor (K) at harvest of all sexes

Traits	TL	SL	BD	TN	CL	K
BW	0.90**	0.91**	0.87**	0.84**	0.86**	0.61**
TL		0.96**	0.81**	0.78**	0.86**	0.26**
SL			0.84**	0.80**	0.91**	0.36**
BD				0.76**	0.83**	0.54**
TN					0.76**	0.55**
CL						0.46**

Note: \*\* represents highly significant at  $P < 0.0001$