TROPICAL LIFE SCIENCES RESEARCH

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

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HIGHLIGHTS

- Phenotypic variation, sexual dimorphism and genetic parameters of six harvest traits were quantified in 8,345 domesticated snake 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.

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

[1]Onprang Sutthakiet, [1]Thanathip Suwanasopee, [2]Uthairat Na-Nakorn and [1]Skorn Koonawootrittriron*

[1]Department of Animal Science, Faculty of Agriculture, Kasetsart University, Chatuchak, 10900 Bangkok, Thailand
[2]Department of Aquaculture, Faculty of Fisheries, Kasetsart University, Chatuchak, 10900 Bangkok, Thailand

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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 nine 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

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

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 USD17.45 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 flavour 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 (USD1.6/kg–USD2.7/kg) exceeded that of Nile tilapia (*Oreochromis niloticus*, USD1.6/kg–USD2.0/kg) and broadhead catfish (*Clarias macrocephalus*, USD1.1/kg–USD1.4/kg), while the retail price of large, salted-sundried snakeskin gourami was nearly four times higher (USD7.1/kg–USD10.0/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, optimising production and strengthening breeding programs necessitate a comprehensive understanding of phenotypic variation and the interrelationships among economically relevant traits.

As with other whole-body sale fish, consumer preference for snakeskin gourami extends beyond body weight (BW) and total length (TL) to include key body-shape attributes that influence marketability. These traits include corrected length (CL), body thickness (BT) and body depth (BD), which are particularly relevant for processed fish products. Consumers favour a rounded or plump body shape, with BD and CL as the primary determinants of desirability, while BT represents the third dimension 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 the snakeskin gourami, including morphological development (Morioka *et al.* 2010) and genetic characterisation (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 optimising marketable traits. Furthermore, while the market currently categorises 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 optimisation.

MATERIALS AND METHODS

Experimental Fish Population

This study utilised 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 standardised 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 characterised by good health, active behaviour, absence of deformities and overall robust physical condition. Mature males and females used for spawning had an average BW of 111.97 ± 44.51 g and 140.49 ± 68.52 g, respectively. Before 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 h, enabling sequential spawning with multiple females while maintaining natural reproductive behaviour.

After successful spawning, the breeding pairs were removed from the tanks, allowing the fertilised 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 DAH. At this stage, the juveniles were transferred to three identical rearing cages, each measuring 1 m × 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 m × 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^2 to support optimal growth conditions. Fish were reared under these conditions until the harvest age of 270 DAH, receiving a standardised feeding regimen (SFR) throughout the production cycle.

Feeding commenced upon complete yolk sac absorption. From 3 DAH–7 DAH, the fry was provided with an egg-yolk suspension as an initial nutrient source. Subsequently, from 5 DAH–10 DAH, the diet transitioned to live *Moina* spp., a natural zooplankton food source. From 8 DAH–15 DAH, fry was fed a finely ground fish meal containing 60% crude protein to support early growth. At 13 DAH–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 BW 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 (Fig. 1).

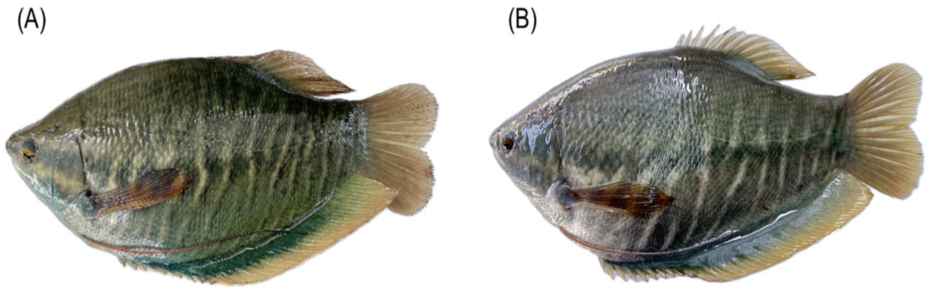

FIGURE 1: Male (A) and female (B) snakeskin gourami.

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

According to Fulton (1904), K 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.

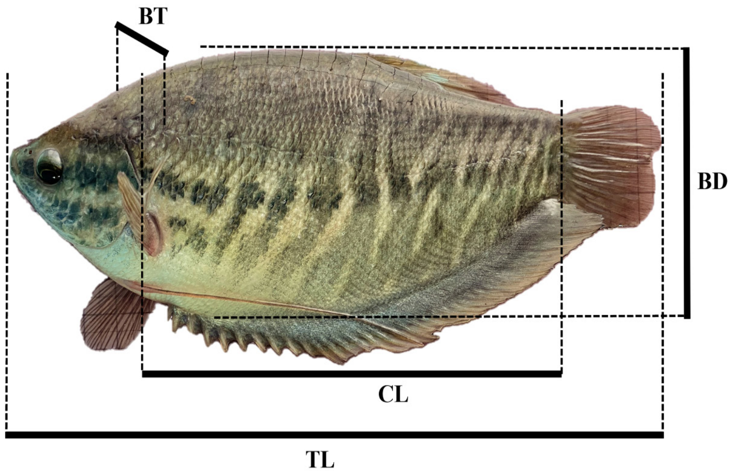

FIGURE 2: Measurement for the total length (TL), corrected length (CL), body thickness (BT) and body depth (BD) of the snakeskin gourami.

Classification of Snakeskin Gourami Sizing

Fresh snakeskin gourami were classified by weight per kilogram, based on a modified system from Yensuk (2005), to facilitate standardised analyses in both research and market contexts. The classification includes seven distinct categories: XXL (≥ 250 g; 3 fish/kg–4 fish/kg), XL (250 g–200 g; 4 fish/kg–5 fish/kg), L (167 g–200 g; 5 fish/kg–6 fish/kg), M (111 g–167 g; 6 fish/kg–9 fish/kg), S (83 g–111 g; 9 fish/kg–12 fish/kg), XS (83 g–62g; 12 fish/kg–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:

$$y_{ijklm} = \mu + Gen_i + Cage_{j(i)} + Sex_k + \mathrm{b}(DAH_l) + e_{ijklm}$$

Where y_{ijkl} represents the phenotypic value of body weight at harvest, μ is the population mean, Gen_i is the fixed effect of generations (i = G_0, G_1 and G_2), $Cage_{j(i)}$ is the collection point at harvest (j = 1, ..., 27), which is nested within generation (Gen_i), Sex_k is the fixed effect of sex (k = male, female), b(DAH_l) is the continuous covariate representing days after hatching (l = 234, 235, ..., 284), where b is the regression coefficient, and e_{ijkl} denotes the residual error.

All results were expressed as least squares means (LSMeans) ± 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 analysed 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 (Gen_i), collection point nested within generation ($Cage_{j(i)}$) and sex (Sex_k)) as well as a continuous covariate (days after hatching (b(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 DAH–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 $h^2 = V_a/V_p = V_a/(V_a + V_c + V_e)$ and $c^2 = Vc/V_p = V_c/(V_a + V_c + V_e)$, respectively.

The genetic correlation ($r_{p/g}$) between all traits was calculated as follows: For $r_{p/g(xy)} = (COV_{p/g(xy)})/(V_{p/g(x)}V_{p/g(y)})$. 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

Characteristics of the Snakeskin Gourami Population

This study analysed 8,345 domesticated snakeskin gouramis, 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% ± 20.16%, with a sex ratio of 1:1.5 favouring females.

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

Least squares mean (LSMeans) of measured traits at harvest indicated significant differences between males and females (Table 1). Females exhibited significantly larger BW (82.24 ± 0.65 g) compared to males (64.03 ± 0.69 g, $P < 0.01$). Similarly, TL was significantly greater in females (16.91 ± 0.04 cm) than in males (16.31 ± 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 ± 0.03 cm) than in males (9.55 ± 0.03 cm, $P < 0.01$).

TABLE 1. The least square means ± 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 sexes, male and female snakeskin gourami.

Traits	*N*	Male	*N*	Female
BW (g)	3,344	64.71 ± 0.60^{b}	5,001	84.89 ± 0.56^{a}
TL (cm)	3,241	16.39 ± 0.04^{b}	4,909	16.99 ± 0.04^{a}
CL (cm)	3,070	9.76 ± 0.03^{b}	4,676	10.47 ± 0.03^{a}
BT (cm)	3,344	1.98 ± 0.01^{b}	5,001	2.24 ± 0.01^{a}
BD (cm)	3,190	5.14 ± 0.02^{b}	4,809	5.69 ± 0.02^{a}
K	3,241	1.42 ± 0.01^{b}	4,909	1.62 ± 0.01^{a}

Notes: Least square means comparison was done by the 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 ± 0.01 cm) compared to males (1.98 ± 0.01 cm, $P < 0.01$). Likewise, BD was significantly larger in females (5.71 ± 0.01 cm) than in males (5.16 ± 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 ± 0.01) than in males (1.44 ± 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 categorised into six commercial size groups: XL, L, M, S, XS and XXS (Fig. 3). The size distribution revealed that despite the relatively short cultivation period compared to traditional farming practices (which extend to 12 months–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.

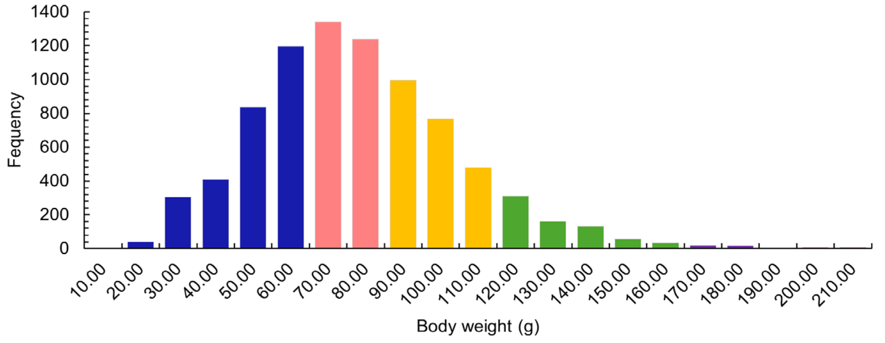

FIGURE 3: A distribution of body weight (g) for the domestic snakeskin gourami population, segmented into various size categories.

Notes: Blue = XXS, pink = XS, yellow = S, green = M, purple = L, red = 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 emphasising 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 optimised 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, optimising stocking densities, and extending rearing periods to maximize profitability. These findings from this study provide a comprehensive characterisation 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. 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 $P < 0.0001$

Table 2 and Fig. 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 (Figs. 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 Fig. 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 (Fig. 4D) and rounder/plum (BD; Fig. 4H) than males of comparable weight, where females consistently demonstrate greater BT (Fig. 4F) and K (Fig. 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.

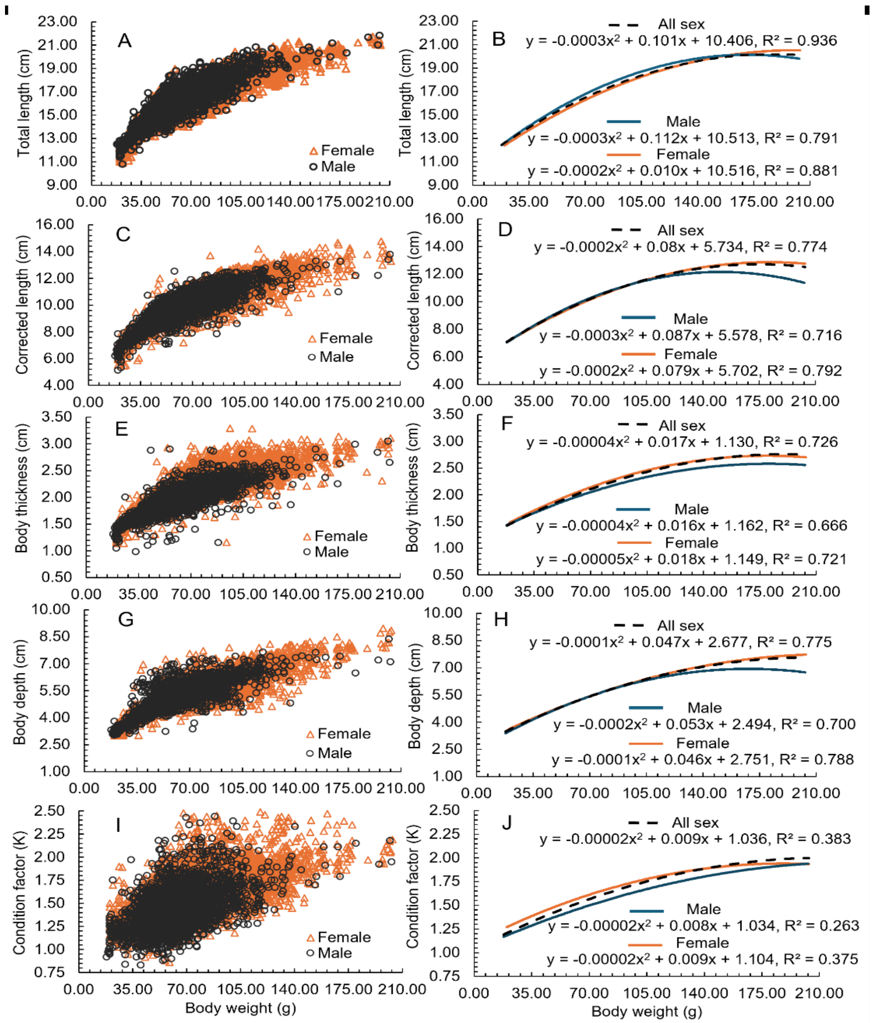

FIGURE 4: The scatter plots and trendlines illustrating the relationship between body weight and total length (A and B), corrected length (C and D), body thickness (E and F), body depth (G and H) and condition factor (I and J) for all sex, male and female.

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 analysed. The heritability for body weight was 0.190 ± 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 ± 0.037 for BT to 0.147 ± 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 ± 0.016 to 0.214 ± 0.035, with low standard errors, highlighting the reliability of these estimations.

TABLE 3. Phenotypic variance (V_p ± SE), additive genetic variance (V_a ± SE), common full-sib family variance (V_c ± SE), heritability (h^2 ± SE) and common environmental effect (c^2 ± 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 ± SE	V_a ± SE	V_c ± SE	h^2 ± SE	c^2 ± SE
BW	461.823 ± 16.460	87.640 ± 36.824	98.869 ± 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 traits 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	

Notes: BW = body weight, TL = total length, CL = corrected length, BT = body thickness, BD = body depth, K = condition factor.

DISCUSSION

The size of the harvested snakeskin gourami in our study, ranging from 13 fish/kg–14 fish/kg, 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^2) compared to the more typical 3 fish/m^2–5 fish/m^2 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 fish/kg–6 fish/kg, 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 (Boonanuntanasarn *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 in males. Behavioural interactions and nutritional factors influence size variation in the 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 labour-intensive grading operations. However, it is essential to recognise that size distributions can be activated in favourable 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; Trọng *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 realised 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 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 minimised.

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 emphasising 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, and 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 ± 0.24. The K value in females showed significantly more rounder/plumper 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 did 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 emphasises 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 unanalysed 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 (Neto *et al.* 2014; Fu *et al.* 2016; Joshi *et al.* 2018).

Although the heritability of growth and related traits is 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 minimise 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 minimise 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 generalisability 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.

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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 conceptualisation and design, genetic and statistical analysis, interpretation of results, supervision and manuscript revision.

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

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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 $P < 0.0001$