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Original Article

Sexual Shape Dimorphism in the Two Native Fish Species (*Glossogobius giuris*) and (*Hypseleotris agilis*) in Lake Mainit, Philippines

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Abstract

Previous studies have primarily relied on fluctuating asymmetry analyses, which, although valuable, may not fully capture the subtle shape variations associated with sexual dimorphism. This study aimed to quantify and compare sexual shape dimorphism in *Glossogobius giuris (*Pidjanga*)* and *Hypseleotris agilis* (Bugwan) using geometric morphometric techniques and describe the water quality condition of the lake. A total of 120 sexually mature individuals were analyzed, comprising 60 *G. giuris* and 60 *H. agilis*, with equal representation of males and females. Digital images of specimens were sorted by sex and converted to TPS format using tpsUtil, followed by landmark digitization in *tpsDig2*. Sixteen homologous anatomical landmarks were placed on each specimen to capture body shape variation. Results of the water quality assessment indicate that the parameters are within the acceptable limits set by the Department of Environment and Natural Resources. Multivariate Analysis of Variance revealed significant differences in morphometric parameters for both species (*G. giuris*: Wilks' $\lambda = 0.8249$, $F = 15.03$, $p = 2.19 \times 10^{-13}$; *H. agilis*: Wilks' $\lambda = 0.9097$, $F = 7.03$, $p = 2.81 \times 10^{-6}$), indicating pronounced shape variation associated with sex. These highly significant results demonstrate that the measured morphometric traits collectively contribute to distinguishing shape variation within and between sexes of the two species. Furthermore, principal component analysis and canonical variate analysis elucidated patterns of sexual dimorphism in both fish types. It arises because differences in the reproductive roles of males and females shape selective pressures, ultimately resulting in distinct morphological traits between the sexes.

Keywords: *Body Shape; Freshwater Ecosystem; Geometric Morphometrics; Landmarks; Relative Warps*

Introduction

Species exhibit a wide array of phenotypes as a result of their geographical distribution (Endler, 1986; Wade & Kalisz, 1990; Foster & Endler, 1999). A substantial proportion of this variation can be explained by habitat type, climate, and predation pressure (Losos *et al.*, 1998; Nagel & Schluter, 1998; Schluter, 1996; Langerhans *et al.*, 2007). Phenotypic variation may be associated with several

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factors: (1) distinct genotypes exhibiting different phenotypes in response to changing environmental conditions, (2) populations showing stable phenotypic differences as a result of selection, also known as adaptive differentiation, and (3) mechanisms such as genetic drift and developmental limitations (Price *et al.*, 2003). Importantly, demonstrating how environmental and ecological variables contribute to phenotypic variation can provide valuable insights into evolutionary processes, including environmental speciation and population divergence (Smith, 1966; Schluter, 1996; Rundle & Nosil, 2005). Freshwater fishes have provided some of the most remarkable examples of how environmental diversity influences the expression of phenotypes (Lostrom *et al.*, 2015).

Sexual dimorphism, the systematic difference in morphology between males and females of the same species, is a widespread phenomenon shaped by both ecological pressures and reproductive strategies (Schluter, 1996; Langerhans, 2009). Variations in body size and shape often arise from differential selection associated with mating systems, fecundity, resource use, and habitat preference (Endler, 1986; Foster & Endler, 1999; Price *et al.*, 2003). In fishes, sexual dimorphism is particularly important because it can influence swimming performance, feeding efficiency, predator avoidance, and reproductive success, thereby contributing to population fitness and ecological niche differentiation (Schluter, 1996; Langerhans, 2009; Montaña & Winemiller, 2013). Understanding these differences provides important insights into evolutionary processes, such as adaptive divergence and population structuring. On the other hand, phenotypic variation, including sexual dimorphism, is driven by a combination of genetic, environmental, and developmental factors. Differences may arise from genotype environment interactions, adaptive differentiation under selective pressures, or stochastic processes such as genetic drift (Price *et al.*, 2003). In aquatic systems, environmental variables such as water flow, habitat complexity, predation pressure, and resource availability play an important role in determining fish morphology (Losos *et al.*, 1998; Langerhans *et al.*, 2003). For instance, individuals inhabiting fast-flowing waters tend to develop more streamlined, fusiform bodies that enhance swimming efficiency, whereas those in slower habitats often exhibit deeper body forms associated with maneuverability and predator avoidance (Brinsmead & Fox, 2002; Langerhans, 2009). These environmentally mediated traits may further interact with sex-specific roles, reinforcing morphological divergence between males and females.

Freshwater ecosystems, such as Lake Mainit, one of the largest and deepest lakes in the Philippines, provide a dynamic setting for examining morphological variation due to their environmental heterogeneity and ecological complexity. The lake supports a diverse assemblage of native fishes that experience varying hydrodynamic conditions, resource distributions, and biotic interactions. Among these, *Glossogobius giuris* and *Hypseleotris agilis* were selected as focal species due to their ecological importance, abundance, and contrasting life-history traits within the lake. Both species occupy benthic habitats and are exposed to similar environmental gradients, making them suitable models for investigating how shared environments may differentially shape male and female morphology. Additionally, their economic and ecological relevance underscores the importance of understanding their adaptive characteristics. Previous studies on these species in Lake Mainit have reported morphological variation and developmental instability (e.g., fluctuating asymmetry), suggesting sensitivity to environmental conditions (Ratunil *et al.*, 2019). However, detailed analyses explicitly addressing sexual dimorphism in body shape remain limited. This gap is important because sex-specific morphological traits may reflect differences in reproductive roles, such as egg production in females or mate competition and mobility in males, as well as ecological partitioning that reduces intraspecific competition.

Advances in geometric morphometrics provide a powerful framework for quantifying and visualizing subtle shape differences associated with sexual dimorphism. Unlike traditional morphometrics, this approach captures the geometry of anatomical structures using landmarks and coordinate data, allowing precise comparisons of shape independent of size (Bookstein, 1997). It has proven highly effective in detecting both interspecific and intraspecific variation, including sex-based differences in fish morphology (Ibañez *et al.*, 2007; Cooke & Terhune, 2015). When integrated with meristic data, geometric morphometrics enables a comprehensive assessment of morphological variation and its

ecological and evolutionary implications. In this study, we examine sexual dimorphism in *G. giuris* and *H. agilis* from Lake Mainit using combined meristic and geometric morphometric approaches. Specifically, we aim to (1) quantify and compare body shape differences between males and females, (2) visualize patterns of morphological variation, and (3) explore the potential influence of environmental and biological factors on these differences. By focusing on two co-occurring native species within a shared ecological context, this study provides insights into how sexual dimorphism is shaped by both reproductive demands and environmental conditions. The findings are expected to contribute to a deeper understanding of adaptive strategies in freshwater fishes and to inform conservation and management efforts for native species in Lake Mainit.

Materials and Methods

Study Area

Lake Mainit, the fourth largest lake in the Philippines (Figure 1), is located on the island of Mindanao between the provinces of Surigao del Norte and Agusan del Norte (9°20′–9°31′ N latitude and 125°28′ E longitude). It has an estimated surface area of approximately 17,000 hectares, making it one of the country's most significant inland water bodies. The lake is also the deepest in the Philippines, with a mean depth of about 128 meters and a maximum depth reaching approximately 223 meters. Hydrologically, it serves as a vital freshwater resource for surrounding communities, supporting domestic use, irrigation, and small-scale aquaculture. Ecologically and economically, Lake Mainit ranks among the most productive lakes in the country, second only to Laguna de Bay (Balayut, 1983). It supports a rich ichthyofauna, with around 43 recorded fish species (Uy *et al.*, 2015), many of which are of commercial importance. Fisheries in the lake provide a primary source of livelihood for local communities along its shoreline, highlighting its critical role in food security and regional socio-economic stability. In addition, the lake's ecological condition and biodiversity make it an important site for scientific research, particularly in studies of fish diversity, morphometrics, and environmental change.

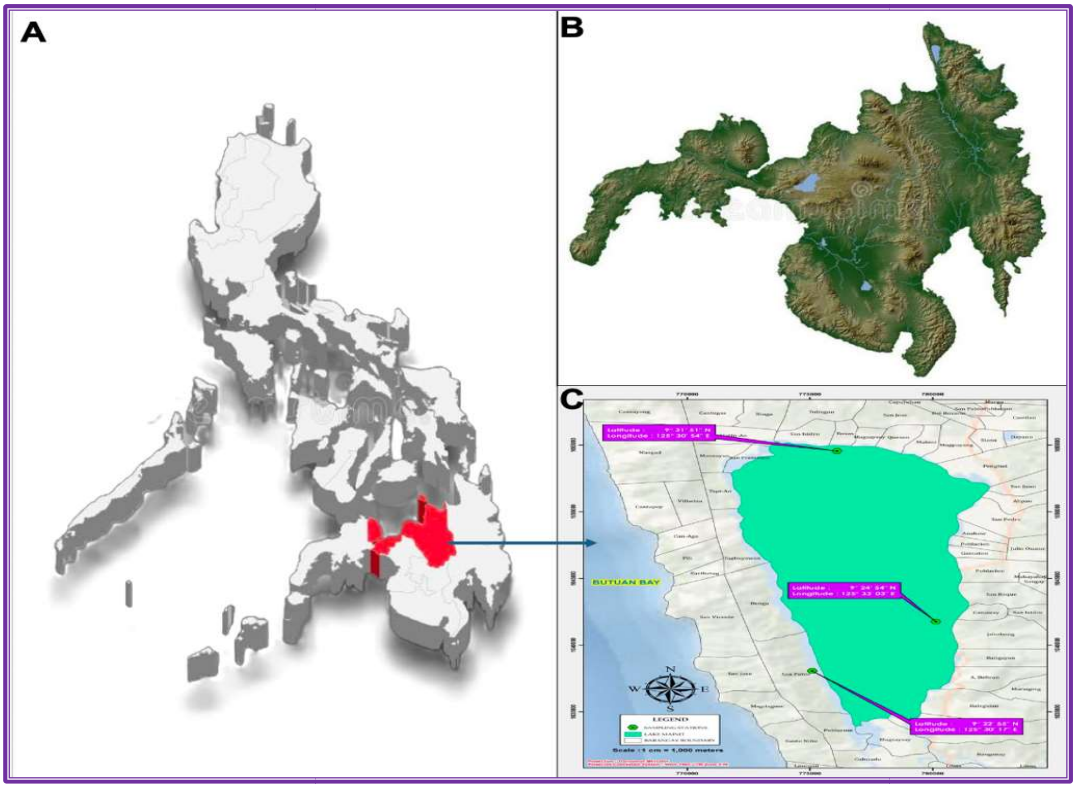

Figure 1: *Map of the Study Area (**A**) Philippines (**B**) Mindanao (**C**) Lake Mainit*

Fish Collection and Processing

Fish samples were collected through netting with the assistance of local fishermen in the study area. Immediately after collection, specimens were sorted by species and sex and subsequently validated to ensure accurate identification of *Glossogobius giuris* and *Hypseleotris agilis*. A total of 120 individuals were obtained, comprising 60 individuals per species, with equal representation of males and females (30 males and 30 females each). All specimens selected were sexually mature and relatively uniform in size to minimize ontogenetic variation. Following sorting and validation, samples were preserved using 10% formalin to maintain structural integrity and prevent post-mortem deformation. For morphometric analysis, each specimen was then mounted on a Styrofoam board, with fins carefully extended and pinned to standardize body posture. Photo documentation was conducted by capturing high-resolution images of both left and right lateral sides of each specimen, with three replicate images taken per side to reduce measurement error. Sex determination was performed through external examination of the genital region, where females were identified by the presence of granular ovaries with yellow to orange pigmentation, while males exhibited smooth, whitish, and granular-free testes.

Landmarks Digitization & Geometric Morphometric Analysis

Specimen photographs were first sorted according to sex (male and female). The images were converted to TPS format using *tpsUtil*, followed by landmark digitization using *tpsDig2.* A total of sixteen (16) anatomical landmarks were used to characterize the body shape of *H. agilis* and *G. giuris* (Figures 2a & 2b). The sixteen landmark points (Table 1) used are standard morphometric characters for evaluating shape variations in this type of fish based on the study ofPaña *et al.* (2015). To determine the relative warp analysis (RWA), the converted TPS files containing the anatomical landmarks were employed to tpsRelw. Histograms were used to illustrate and process the variations between the sexes in patterns of sexual dimorphism and body form. Data analyses, such as Multivariate Analysis of Variance (MANOVA), Principal Component Analysis (PCA), Canonical Variance Analysis (CVA), and Paleontological Statistics (PAST) software, were used to quantify and draw shape differences (Figure 3). Additionally, CVA was employed to represent, in a scatter plot, patterns of variation at the population level.

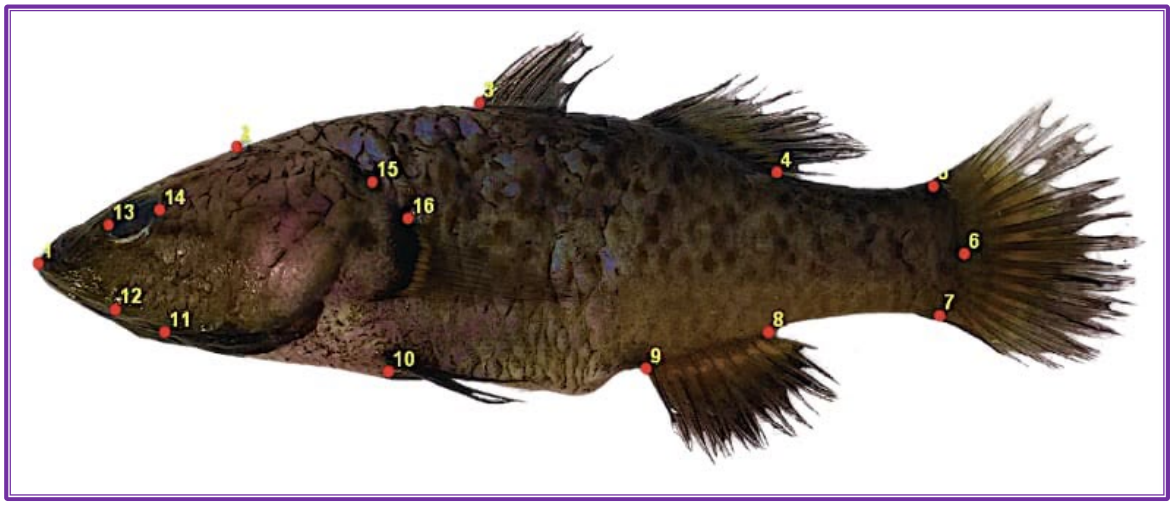

Figure 2a: *Hypseleotris agilis*

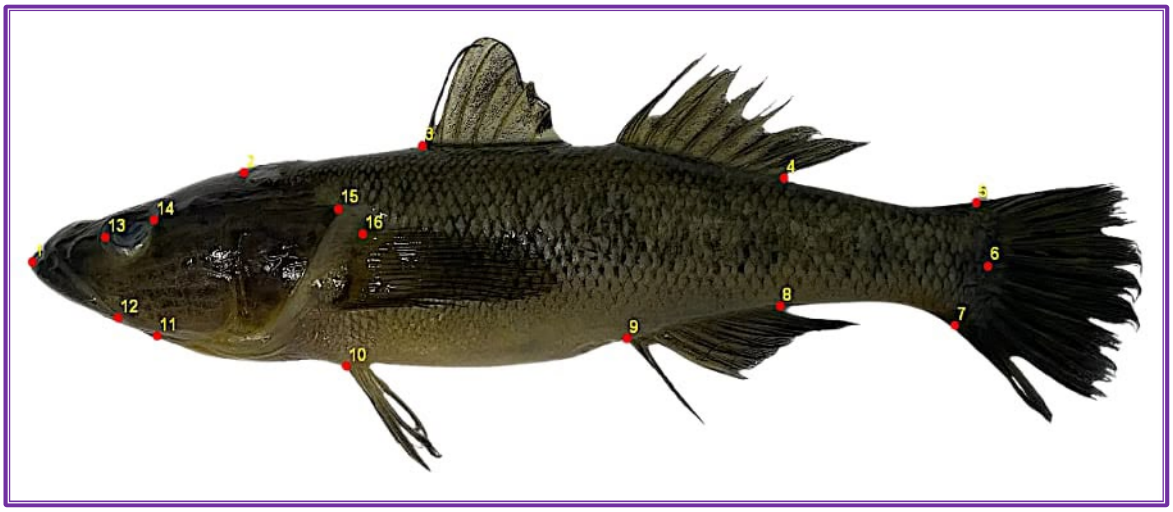

Figure 2b: *Hypseleotris agilis*

Table 1: *Anatomical Landmark Points and Description Used to Describe the Body Shape of G. Giuris and H. agilis*

Landmarks	Description
1	Snout tip
2	Posterior ends of nuchal spine
3	Anterior insertion of dorsal fin
4	Posterior insertion of dorsal fin
5	Dorsal insertion of caudal
6	Midpoint of caudal border of hypural plate
7	Ventral insertion of caudal fin
8	Posterior insertion of anal fin
9	Anterior insertion of anal fin
10	Dorsal bases of pelvic fin
11	Ventral end of lower jaw articulation
12	Posterior ends of maxilla
13	Anterior margins through midline of orbit
14	Posterior margins through midline of orb
15	Dorsal ends of operculum
16	Dorsal bases of pectoral fin

Selection of Morphological Characters

In this study, twelve morphometric parameters were selected out of the nineteen standard measurements commonly used in fish morphometric analyses (Figure 3). The selection was based on their functional relevance, measurability, and ecological interpretability in distinguishing interspecific and intraspecific variations. Morphometric traits that exhibit high reliability, minimal measurement error, and significant environmental or functional importance were prioritized to ensure accurate characterization of shape variation between *H. agilis* and *G. giuris*. The twelve parameters comprising body weight, total length, standard length, head length, head height, body height, tail base height, eye diameter, and lengths of dorsal, ventral, and anal fin bases were chosen because they capture key aspects of body form, swimming performance, and feeding adaptation (Turan, 1999; Bhat, 2004). These traits are known to vary in response to environmental conditions such as current velocity, habitat structure, and trophic niche, thereby serving as robust indicators of ecological and evolutionary differentiation (Ibañez *et al.*, 2007; Stelkens & Seehausen, 2009).

The remaining seven parameters were excluded either due to redundancy or their limited discriminatory power in differentiating shape variation at the species level. Several studies have emphasized that the excessive inclusion of morphometric variables can lead to multicollinearity, thereby obscuring the biological significance of morphometric variation (Bookstein, 1991). Thus,

reducing the parameter set to twelve ensured analytical efficiency, minimized overlapping measurements, and enhanced interpretive clarity. This selective approach aligns with established morphometric practices in fish ecology, where the choice of parameters is tailored to the research objective and the ecological characteristics of the study species (Turan, 1999; Oliveira *et al.,* 2019).

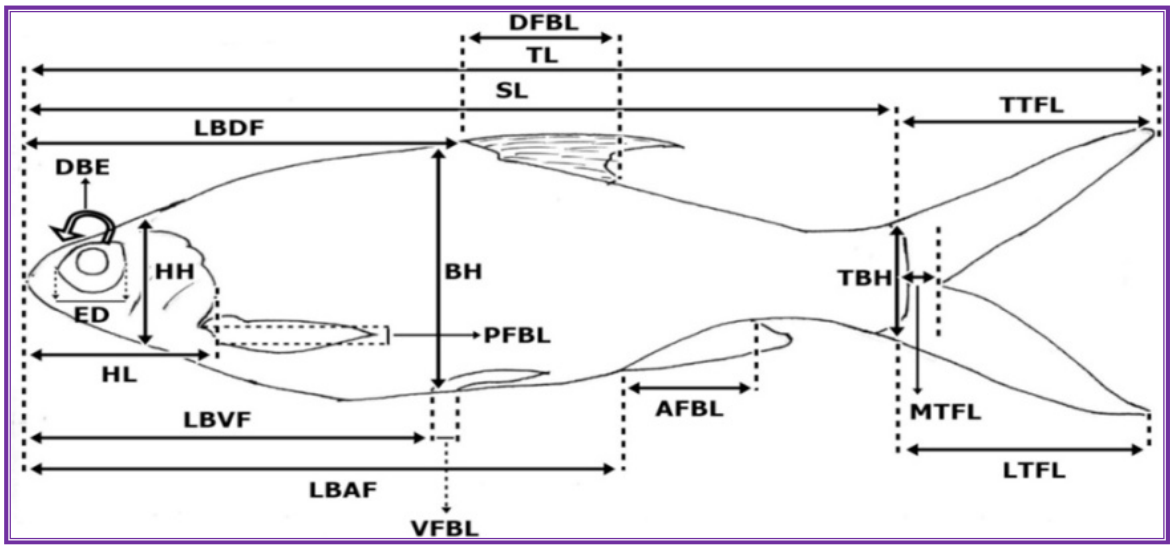

Figure 3: *The Morphometric Characters of the Collected H. agilis and G. Giuris Specimens were Adopted from the Methodology of Samad et al. (2025).*

Physicochemical Parameters

Physicochemical water parameters, including temperature, conductivity, pH, total dissolved solids (TDS), and dissolved oxygen (DO), were measured concurrently with fish sampling at three stations, each with three replicates. These parameters were selected based on the measurement capabilities of the multi-parameter water quality meter (EUTECH PCD) and do not represent a comprehensive assessment of all environmental variables in the study area. At each sampling site, three randomized trials were conducted to ensure measurement reliability. All data were recorded using the probe and subsequently analyzed using Paleontological Statistics Software (PAST), with results expressed as mean ± standard error of the mean (SEM).

Results

Physico-Chemical Parameters

Table 2 presented the physicochemical parameters measured across three sampling sites in a tributary of Lake Mainit, Philippines. The mean conductivity ranged from 215 to 240 µS/cm, which falls within the acceptable limits set by national water quality standards, indicating compliance with DENR guidelines. The mean dissolved oxygen (DO) concentrations ranged from 3.96 to 7.84 mg/L. Values recorded in the upper and middle reaches (3.96–4.41 mg/L) fall below the DENR minimum standard of 5 mg/L, indicating non-compliance in this parameter, while the lower reach (7.84 mg/L) meets and exceeds the required threshold. The mean pH values ranged from 7.97 to 8.03, remaining within the acceptable range for freshwater systems under DENR standards. Water temperature ranged from 28.0 to 28.7°C, which is within the normal range for tropical freshwater ecosystems and compliant with environmental standards. Total dissolved solids (TDS) ranged from 125 to 131 mg/L, remaining within acceptable limits and indicating low concentrations of dissolved substances.

Table 2: *Physico-chemical Water Parameters Across the Three Sampling Sites in Lake Mainit, Philippines*

Parameters	Standard DENR-DAO 2016-08 (Class AA)	Northern Area	Middle Area	Southern Area	Remarks
Conductivity	Not Specified	215.67 ± 28.61	216 ± 27.74	240 ± 7.02	Within the permissible limits
Dissolve Oxygen	>5mg/L	4.41 ± 0.03	3.96 ± 0.24	7.84 ± 0.14	Within the permissible limits
pH	6.5-8.5	7.98 ± 0.12	7.97 ± 0.01	8.03 ± 0.04	Within the permissible limits
Temperature	26-30 ^{0}C	28.67± 0.33	28.67 ± 0.33	28.00 ± 0.58	Within the permissible limits
Total Dissolve Solids	Not Specified	131.33 ± 1.33	125.33 ± 0.67	126.67 ± 1.76	Within the permissible limits

Morphometric Measurements

Table 3*: Morphometric Characters of H. agilis and G. Giuris Collected in Lake Mainit, Philippines*

Species	BW (g)	TL (cm)	SL (cm)	HL (cm)	HH (cm)	BH (cm)	TBH (cm)	ED (cm)	LBDF (cm)	LBVF (cm)	LBAF (cm)	DFBL (cm)
H. agilis	15.99 ± 0.64*	103.86 ± 1.41*	85.45 ± 1.28*	28.1 ± 0.56*	19 ± 0.51*	22.52 ± 0.64*	11.3 ± 0.36*	5.4 ± 0.13*	42.27 ± 0.60*	31.08 ± 0.47*	56.33 ± 0.88*	7.78 ± 0.31*
G. guiris	39.78 ± 1.13*	152.61 ± 1.70*	130.75 ± 1.52*	34.21 ± 0.83*	21.30 ± 0.30*	26.26 ± 0.63*	12.40 ± 0.26*	6.30 ± 0.17*	54.28 ± 1.42*	46.16 ± 1.30*	83.65 ± 1.36*	15.38 ± 0.35*

Note: **P<0.05, BW=Body Weight; TL=Tail Length; SL=Standard Length; HL=Head Length; HH=Head Height; ED=Eye Diameter; LBDF=Length Before Dorsal Fin; LBVF=Length Before Ventral Fin; LBAF=Length Before Anal Fin; DFBL=Dorsal Fin Base Length*

Table 3 presentedthe morphometric characteristics of *H. agilis* (Bugwan) and *G. giuris* (Pijanga) collected from Lake Mainit, Philippines, based on twelve measured parameters. Significant differences ($P< 0.05$) were observed between the two species across the assessed morphological traits, indicating species-specific body shapes and proportions. These differences likely reflect adaptations to their respective ecological niches, feeding strategies, and locomotor behaviors. For instance, variations in body depth, head size, and fin dimensions may influence swimming performance, foraging efficiency, and reproductive capabilities, highlighting the functional and ecological significance of the observed morphological divergence. The results reveal apparent interspecific differences, with *G. giuris* exhibiting significantly greater mean body weight (39.78 g vs. 15.99 g) and total length (152.61 cm vs. 103.86 cm) compared to *H. agilis*.

Relative Warp Analysis

Table 4: *MANOVA Test between Sexes of G. giuris and H. agilis Collected from Lake Mainit, Philippines.*

Species	Wilks' λ	df1	df2	f-value	P-value
G. giuris	0.8249	5	354	15.03	2.19×10^{-13}
H. agilis	0.9097	5	354	7.027	2.81×10^{-6}

The multivariate analysis of variance (MANOVA) presented in Table 4 revealed statistically significant differences in the morphometric parameters of *G. giuris* (Wilks' $\lambda = 0.8249$, $F_{5,354} = 15.03$, $p = 2.19 \times 10^{-13}$) and *H. agilis* (Wilks' $\lambda = 0.9097$, $F_{5,354} = 7.03$, $p = 2.81 \times 10^{-6}$). These highly significant values indicate that the measured morphometric traits collectively contributed to distinguishing shape

variation within and between populations of the two species. A lower Wilks' Lambda value in *G. giuris* suggests greater variability in its morphometric configuration compared to *H. agilis*, implying stronger morphological diversification possibly influenced by environmental or ecological pressures across Lake Mainit.

Sexual Dimorphism in G. giuris and H. agilis

The Relative Warp Analysis (RWA) in the pooled female and male fish samples is presented in Table 5. It was revealed that the first five relative warps accounted for a substantial proportion of total shape variation in both *G. giuris* (98.43%) and *H. agilis* (98.28%), indicating that sexual shape differences in both species are captured primarily along a limited number of principal morphological axes. In *G. giuris*, RWA 1 alone explained (93.83%) of the total shape variance, with subsequent warps contributing only marginally (≤2.13%). In contrast, *H. agilis* exhibited an even higher proportion of variance explained by RWA 1 (95.79%), with the remaining warps each contributing less than 1.2%.

Table 5: *Composition of Relative Warp Analysis in the Pooled Sexes of Glossogobius giuris and Hypseleotris agilis*

Species	Relative Warp Analysis (%)
G. giuris	RWA 1 = 93.83%
	RWA 2 = 2.13%
	RWA 3 = 1.09%
	RWA 4 = 0.78%
	RWA 5= 0.60% **Total: 98.43%**
H. agilis	RWA 1 = 95.79%
	RWA 2= 1.14%
	RWA 3=0.59%
	RWA 4=0.41%
	RWA 5=0.35% **Total: 98.28%**

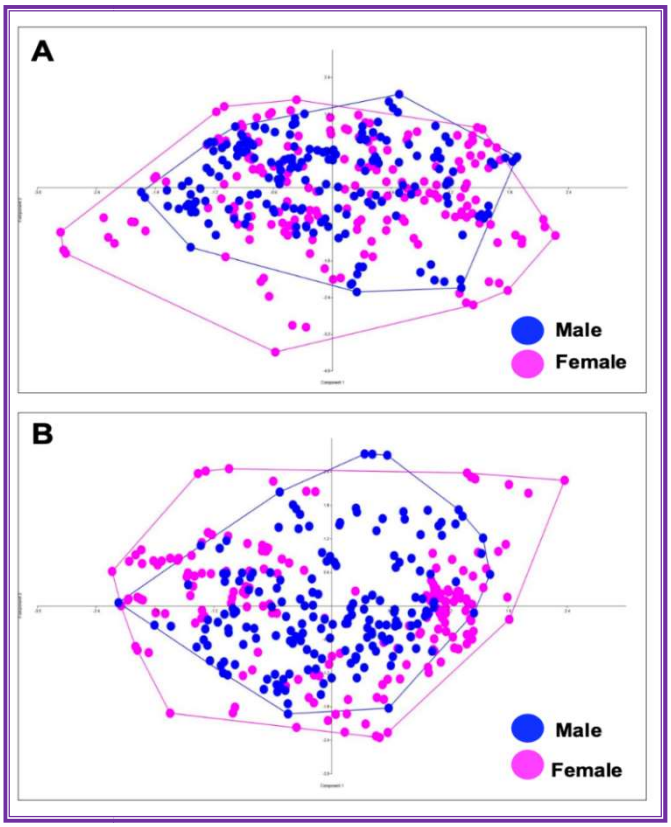

Figure 4: *Canonical Variate Analysis of the Pooled Male and Female Fish Samples. (A) G. Giuris (B) H. agilis*

The scatterplots represented by the Canonical Variate Analysis (Figure 4) and Principal Component Analysis (Figure 5) visually reinforce the patterns of sexual dimorphism summarized in Table 6 by showing partial but distinct clustering of males and females in morphospace. The overlap between male and female distributions suggests that in *G. giuris*, morphological differences are present but not strongly discrete, aligning with the interpretation that variation is driven by a combination of ecological (e.g., foraging-related traits like gape and body shape) and reproductive factors rather than strict sexual segregation. In contrast, *H. agilis* shows a slightly clearer spread and separation between sexes, particularly with females occupying a broader or shifted region of the space, which supports the role of sexual selection and agonistic behavior in shaping more pronounced male traits (e.g., larger head and fin elongation).

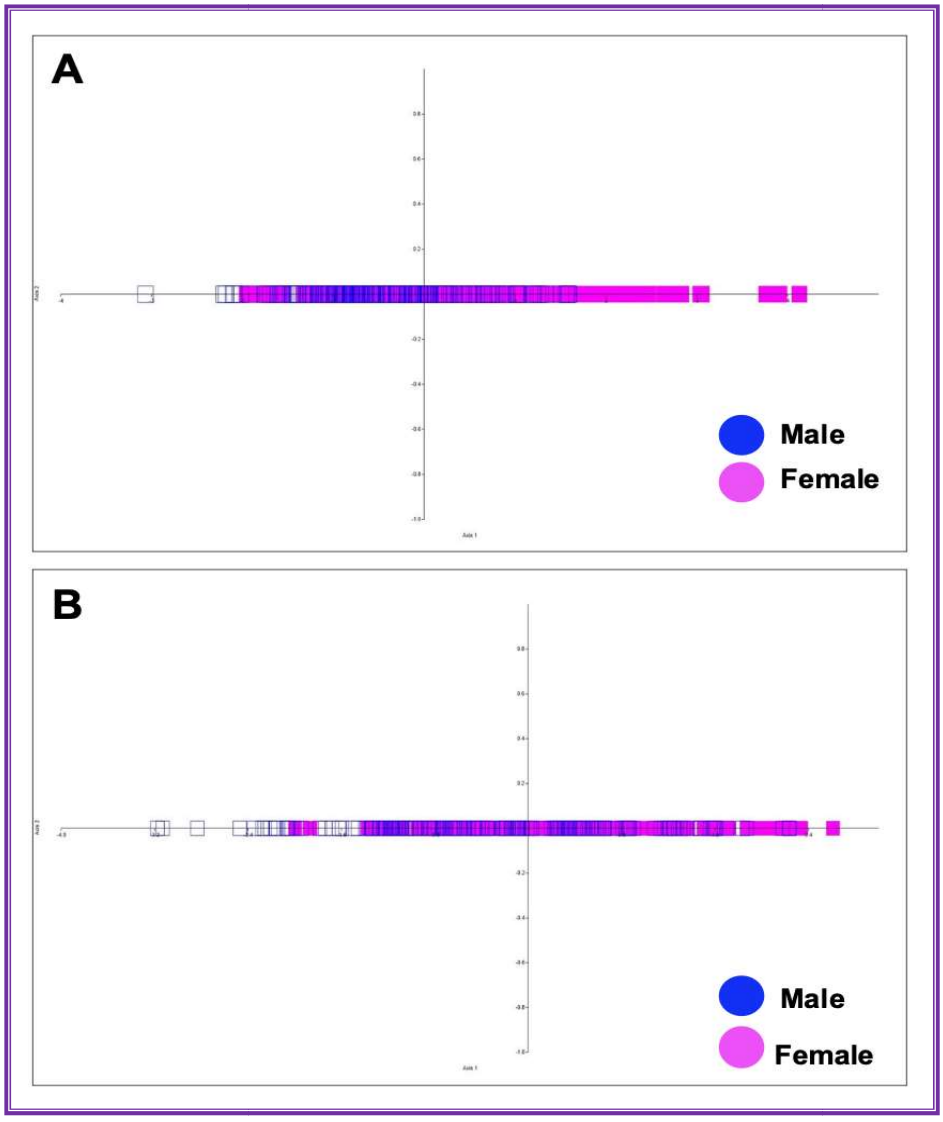

Figure 5: *Principal Component Analysis of the Pooled Male and Female Fish Samples. (**A**) G. Giuris (**B**). H. agilis*

Table 6: *Summary of the Morphological Traits between Sexes of G. giuris and H. agilis*

Feature	***G. giuris* (Pijanga)**	***H. agilis* (Bugwan)**
Male Traits	Longer gape, slender body, larger fin bases	Larger head, elongated dorsal/anal fins
Female Traits	Deeper/stouter body, high abdominal curvature	Deeper belly region (gravid)
Selection Driver	Ecological (Foraging) & Reproductive	Sexual Selection (Agonistic behavior)

Table 6 presented a comparative overview of sexual dimorphism in two fish species, *G. giuris* (Pijanga) and *H. agilis* (Bugwan), highlighting how morphological traits differ between males and females and the evolutionary drivers underlying these differences. In *G. giuris*, males exhibit a longer gape, more slender body, and larger fin bases. These features are typically associated with enhanced foraging efficiency and mobility, suggesting that ecological pressures, particularly feeding strategies, play a major role in shaping male morphology. In contrast, females display a deeper and stouter body with pronounced abdominal curvature, traits commonly linked to increased reproductive capacity, as they allow for greater egg production and storage. For *H. agilis*, male traits such as a larger head and elongated dorsal and anal fins are indicative of adaptations driven by sexual selection. These features may enhance success in agonistic interactions, such as male–male competition or territorial displays. Females, on the other hand, exhibit a deeper belly region, especially when gravid, reflecting reproductive investment similar to that observed in *G. giuris*.

Discussion

Physico-Chemical Parameters

In terms of conductivity, these values reflect moderate ionic concentrations that are typical of freshwater systems. Comparable conductivity levels have been reported in other Philippine rivers, such as the Marilao River and Urdaneta tributaries, where similar ranges were associated with naturally occurring minerals rather than strong anthropogenic inputs (Vicente-Becket, 1992). Minimal variation in conductivity was observed among the sampling stations, suggesting relatively stable ionic conditions throughout the study area. In contrast, dissolved oxygen showed variation across stations, indicating differences in oxygen availability along the stream gradient. Similar patterns have been documented in other freshwater systems, such as the Marilao–Meycauayan–Obando River System, where midstream sections exhibited lower DO levels compared to downstream areas (Pleto *et al.*, 2020). Such spatial variation may be influenced by differences in water flow, aeration, and localized environmental conditions.

Further, pH-neutral, slightly alkaline conditions are typical of many tropical freshwater environments and are consistent with values reported in other Philippine aquatic systems (Obusan *et al.*, 2023). Variation in pH across sampling stations was minimal, indicating a relatively stable acid–base condition throughout the study area. The values of temperature are comparable to those reported in Laguna de Bay and several inland rivers in Mindanao (Magbanua *et al.*, 2017). Temperature variation among stations was also minimal, suggesting uniform thermal conditions during sampling. Additionally, Total Dissolved Solids (TDS) values are comparable to those reported in relatively less impacted upland rivers in Mindanao (Magbanua *et al.*, 2017). The low variation in TDS across stations further suggests consistent water quality conditions in terms of dissolved solids. Overall, the physicochemical profile of the study area generally falls within acceptable DENR standards, except for the dissolved oxygen levels observed in the upper and middle reaches. The parameters measured indicate relatively stable water quality conditions across sampling stations, with only slight spatial variations. These variations may be associated with differences in hydrological and physical characteristics among sites, although further investigation would be necessary to determine specific influencing factors.

On the other hand, variations in physicochemical parameters can significantly impact morphometric variability in fish populations by influencing growth patterns, functional morphology, and ecological performance. Water flow and dissolved oxygen, for instance, are strongly associated with body shape adaptations, where individuals in low-oxygen or slow-flowing environments may develop deeper bodies, while those in well-oxygenated, fast-flowing habitats tend to exhibit more streamlined forms to enhance swimming efficiency (Langerhans, 2009; Brinsmead & Fox, 2002). Temperature is another critical factor affecting metabolic rates and developmental processes, potentially leading to differences in body size and proportions across habitats (Ohlberger *et al.*, 2007). Similarly, pH and conductivity, which reflect the chemical composition of the water, may indirectly influence morphometric traits by affecting food availability, physiological stress, and habitat suitability (Willis *et*

al., 2005; Montaña & Winemiller, 2013). These environmental gradients can drive phenotypic plasticity or local adaptation, resulting in measurable morphological divergence within and among fish populations (Langerhans *et al.*, 2003; Ibañez *et al.*, 2007). Consequently, even subtle variations in water quality parameters across lake ecosystems may contribute to shaping the observed morphometric patterns in freshwater fishes.

Morphometrics Measurements

These variations extend across several dimensions, such as head length, body height, and fin base length, indicating species-specific growth patterns and ecological specializations. The larger, more robust morphology of *G. giuris* may provide advantages in energy storage, reproductive potential, and sustained swimming endurance (Froese *et al.*, 2014), while the smaller and streamlined form of *H. agilis* appears better suited to fast-flowing or shallow habitats where maneuverability and rapid response are crucial for survival (Winemiller, 1991; Ibañez *et al.*, 2007). Similar morphometric differentiation has been documented in sympatric freshwater fish species of Philippine lakes and rivers, illustrating how body form evolves in response to ecological and hydrological gradients (Roy *et al.*, 2020). Ecologically, these size and shape disparities influence habitat use and trophic interactions within the lake. The deeper-bodied *G. giuris* typically occupies benthic or slow-moving zones, where its mass and fin dimensions provide substrate stability and an advantage in bottom-feeding or ambush foraging (Herder *et al.*, 2006; Pusey *et al.*, 2004). In contrast, *H. agilis*, with its slender body and reduced head length, is better adapted to littoral or pelagic microhabitats that favor burst swimming and reduced drag, aiding in predator evasion and planktonic feeding. Such morphological and habitat differentiation minimizes competition and promotes niche partitioning, a pattern well established among tropical freshwater species (Bhat, 2004). In the ever-changing environment of Lake Mainit, where the flow of water, turbidity, and nutrient gradients change from place to place, this kind of adaptive segregation helps species live together and makes the whole community more stable.

Morphometric variation between these species also reflects phenotypic plasticity driven by local environmental pressures. Traits such as body depth, fin base length, and head proportions are known to respond to hydrodynamic and trophic conditions, influencing energy efficiency and swimming performance (Webb, 1984; Peres-Neto & Magnan, 2004). Across tropical freshwater systems, morphological plasticity facilitates adaptive divergence, allowing species to occupy specialized niches and maintain ecological balance (Stelkens & Seehausen, 2009; Oliveira *et al.,* 2019). The functional morphology, especially fin size and body form, further determines locomotor ability and ecological interaction. Plaut (2000) noted that elongated fins can reduce swimming efficiency, making individuals more vulnerable to predation and less competitive in resource-limited environments. In Lake Mainit, these trade-offs likely shape spatial distribution, with *H. agilis* favoring shallow, fast-flowing zones and *G. giuris* thriving in deeper, slower habitats.

Furthermore, the morphometric and population differences observed may also stem from intrinsic biological factors. According to Samad *et al.* (2025), population variation in fish is influenced by ontogenic development, age, sex, gonadal maturity, geographic distribution, and parasitic pressure, all of which interact with environmental variables such as water chemistry, temperature, and resource availability. This interplay contributes to the morphological diversity and ecological adaptability observed in *H. agilis* and *G. giuris*, underscoring their phenotypic flexibility and resilience to environmental change. Overall, the morphometric distinctions between these two species illustrate the combined effects of ecological, hydrological, and evolutionary forces shaping fish community structure in Lake Mainit. These findings emphasize the role of habitat heterogeneity and environmental gradients in driving morphological adaptation, niche differentiation, and biodiversity maintenance in tropical freshwater ecosystems.

Relative Warp Analysis

The pronounced shape differentiation in *G. giuris* may reflect its broader ecological amplitude and adaptability to benthic environments, where hydrodynamic conditions and substrate interactions favor

individuals with deeper bodies and longer fin bases. Such body configurations enhance maneuverability near the substrate, improve station-holding in slow-moving waters, and facilitate foraging efficiency on benthic prey (Herder *et al.*, 2006; Pusey *et al.*, 2004). This morphological plasticity likely enables *G. giuris* to maintain dominance in bottom-associated niches, where competition and spatial heterogeneity drive the diversification of its shape.

In contrast, *H. agilis* displayed a higher Wilks' Lambda value, indicating more conserved morphometric features. This pattern suggests relatively uniform body shape expression, possibly due to its adaptation to pelagic or littoral habitats characterized by more consistent hydrological conditions. The streamlined body and reduced fin base dimensions of *H. agilis* confer hydrodynamic efficiency, favoring swift movements and predator evasion in open-water zones (Winemiller, 1991; Ibañez *et al.*, 2007). The observed shape uniformity may also reflect environmental filtering, where only morphotypes suited for fast-flowing or shallow-water microhabitats can persist. These findings underscore that body shape formation in *G. giuris* and *H. agilis* is not solely species-specific but also ecologically driven. Changes in the hydrological regimes, substrate types, and feeding strategies in Lake Mainit probably put selective pressure on morphological evolution. Such shape divergence supports ecological partitioning and coexistence within the lake's fish assemblage, an adaptive outcome widely observed in tropical freshwater ecosystems (Bhat, 2004; Stelkens & Seehausen, 2009).

Moreover, studies indicated that *G. giuris* females exhibit a deeper, more robust body form, whereas males generally have a slimmer and more streamlined body profile (Dorado *et al.*, 2012). Additionally, females have a shorter standard length than males, while males exhibit a longer gape length and caudal peduncle. Gape length is a key functional trait associated with differences in feeding strategies among fishes (Kassam *et al.*, 2004). Variation in caudal peduncle length may indicate differences in swimming performance. Such body shape differences do not necessarily reflect phylogenetic relationships but are more likely adaptations to local trophic dynamics and environmental conditions (Corti, Loy & Cataudella, 1996). It was also identified that females displayed a more pronounced body than males, likely due to their fuller abdomens associated with reproductive functions. A similar phenomenon, influenced by size rather than genetics or sexual dimorphism, has been reported in the body shapes of trout (*Salmo trutta*) (Monet *et al.*, 2006). Furthermore, males were found to have comparatively larger bases of the pectoral and anal fins (Dorado *et al.*, 2012). Accordingly, in male *G. guiris*, the caudal peduncle is deeper and the anal fin more elongated, resulting in a more tubular body shape. This configuration, with a narrower shoulder region tapering toward the deeper caudal peduncle, reduces drag and produces a streamlined form that enhances swimming efficiency (Nacua *et al.*, 2010).

At the same time, studies on *H. agilis* have shown notable body shape variations within the population. Males are characterized by an elongated jaw and a deeper head profile, as well as longer bases of the second dorsal and anal fins, while females exhibit a deeper and more extended belly in the trunk region (Nacua *et al.*, 2012). The relatively larger head of males observed aligns with previous reports describing the male population as having a pronounced enlargement of the dorsal head and nape region (Thacker & Unmack, 2005). Elongated dorsal and anal fin rays in males are a diagnostic feature of sexual dimorphism in *Hypseleotris* species. Meanwhile, the fin elongation observed in male *H. agilis* from the previous study increases the span of the fins from the leading edge to the trailing edge tip and alters their aspect ratio. Such elongation is likely driven by sexual selection, as enlarged fins can enhance agonistic displays and serve as effective signals to threaten or deter rivals (Nacua *et al.*, 2012). Also, sexual shape variation in this species has been documented by several authors, with the male population consistently described as having a pronounced enlargement of the dorsal head and nape region. It was also reported that Hypseleotris has a diagnostic sexually dimorphic trait characterized by elongation of the dorsal and anal fin rays in males (Thacker & Unmack, 2005).

Additionally, previous works found that *G. giuris* exhibits significant body shape differences influenced by environmental and reproductive pressures, with females showing greater morphological variability

likely associated with spawning-related energy allocation and environmental stress responses (Cabuga *et al.,* 2025). For instance, a study on teleost fishes demonstrated that male-biased gene expression in sex-related pathways contributes to morphological divergence between the sexes, reinforcing the idea that sexual dimorphism is not only structural but also genetically regulated through sex-linked and autosomal interactions (Beato *et al.*, 2026). Comparably, research on Selenanthias species reported clear secondary sexual dimorphism in body form and coloration, highlighting that reproductive strategies such as protogynous sex change are often associated with pronounced sex-based morphological differences in reef-associated fishes (Nomura *et al.*, 2026). In addition, studies on freshwater loaches have revealed widespread secondary sexual dimorphism, particularly in fin morphology and secondary traits such as tubercles and fin enlargement in males, underscoring that even subtle morphological traits can reliably distinguish the sexes in cypriniform fishes (Bohlen *et al.*, 2025). Complementing these findings, recent work on fin size and shape variation in killifish confirmed that sexual dimorphism frequently manifests in locomotor-related structures, suggesting functional divergence between males and females linked to mating behavior and habitat use (Brockelsby *et al.*, 2026).

Sexual Dimorphism in G. giuris and H. agilis

In geometric morphometric studies, the high percentage of explained variance within the initial relative warps suggests that dominant biological factors such as sexual dimorphism play a significant role in structuring body shape variation (Bookstein, 1991; Zelditch *et al.*, 2012). This dominance of the first relative warp implies a strong, unidirectional pattern of shape differentiation between sexes. In gobiid fishes, sexual dimorphism is frequently expressed through differences in head depth, body elongation, and fin base positioning, which are often linked to reproductive roles and mating behavior (Murdy & Takita, 1999; Huyse *et al.*, 2004). The concentration of variance in RWA 1 suggests that sexual shape differences in *G. giuris* are relatively conservative and structurally integrated, likely reflecting functional constraints associated with benthic lifestyles and ecological generalism (Webb, 1984; Langerhans & Reznick, 2010).

This pattern indicates a highly pronounced primary axis of sexual shape variation. Previous studies on Hypseleotris and related eleotrid–gobiid taxa have consistently reported strong sexual dimorphism, particularly in males, characterized by elongation of the dorsal and anal fins, enlargement of the nape and head region, and overall changes in body depth (Patzner *et al.*, 2011; Thacker & Roje, 2011). These sexually dimorphic traits are typically associated with courtship displays, mate attraction, and intrasexual competition, which tend to produce marked and directionally consistent shape differences (Andersson, 1996; Lim & Kotellat, 1995). The relatively lower contribution of higher-order warps (RWA 2–5) in both species suggests limited subtle or localized shape variation beyond the dominant sexual axis. However, the slightly higher cumulative contribution of minor warps in *G. giuris* compared to *H. agilis* may reflect greater within-sex morphological variability, potentially driven by environmental heterogeneity or broader ecological tolerance (Wimberger, 1992; Villéger *et al.*, 2010). In contrast, the highly constrained shape variation in *H. agilis* supports the notion that sexual selection exerts a more substantial influence on body form than ecological factors in this species. Generally, the RWA results strongly express sexual dimorphism in both species, albeit with differing magnitudes and biological emphases. *G. giuris* appears to exhibit moderate sexual shape differentiation superimposed on a functionally constrained body plan. In contrast, *H. agilis* shows a more pronounced and specialized pattern of sexual dimorphism dominated by secondary sexual traits. These findings are consistent with broader evidence that sexual selection intensity and reproductive behavior play key roles in shaping morphological divergence between sexes in small-bodied freshwater fishes (McGee *et al.*, 2020). Alternatively, sexual dimorphism may arise through ecological selection that operates differently on males and females, promoting sex-specific niche differentiation and consequently leading to divergence in trophic morphology (Spoljaric & Reimchen, 2007; Hedrick & Tameles, 1989).

Specimens from large lakes were found to display more pronounced shape dimorphism, whereas those from small and shallow ponds showed reduced dimorphism. These patterns suggest that such traits function as adaptations reflecting differences in ecological niches between the sexes (Spoljaric

& Reimchen, 2007). A similar observation was reported in wild-caught *Poecilia reticulata*, where females exhibited smaller heads and deeper caudal peduncles than males, a pattern not observed in laboratory-reared specimens (Burns *et al.*, 2009). Selective pressures may modulate sexual shape dimorphism, either amplifying or diminishing it, contingent upon environmental heterogeneity that accommodates the distinct habitat preferences of each sex (Nacua *et al.*, 2012). Any alteration in fin shape or total surface area would primarily affect a fish's maneuverability. Consequently, natural selection on the fins favors adaptations that optimize the fish's efficiency in its preferred behaviors and habitats while minimizing energy expenditure to enhance fitness. Additional functions attributed to these fins should be considered secondary and may either reinforce or diminish these primary traits (Herler *et al.*, 2010; Rundle *et al.*, 2006; McGuigan *et al.*, 2005). Sexual dimorphism in *G. giuris* and *H. agilis* from Lake Mainit was generally subtle but detectable through morphometric analyses. Canonical Variate Analysis (CVA) and Principal Component Analysis revealed that male (blue) and female (pink) clusters largely overlapped, indicating that the sexes share a common fundamental body plan while exhibiting peripheral shape variations (Figures 4 & 5). Female hulls generally occupied a broader morphospace than male hulls, suggesting higher phenotypic plasticity or fluctuating asymmetry in females. The absence of fully discrete clusters demonstrates that sexual dimorphism in both species is continuous rather than categorical. In *G. giuris*, females typically exhibited deeper and stouter bodies with increased ventral curvature, adaptations likely linked to accommodating large egg masses during the spawning season. Males were characterized by longer gape lengths and enlarged pectoral and anal fin bases, traits associated with competitive behaviors such as territory defense and foraging efficiency (Ratunil *et al.*, 2019).

In *H. agilis*, males generally exhibit larger heads and elongated dorsal and anal fins. The enlarged head is likely a result of sexual selection through agonistic behavior, while fin elongation is hypothesized to reflect niche-specific selection pressures. The male population also exhibited a slightly dominant sex ratio (~58.7%). Morphological divergence observed in CVA further reflected energy trade-offs between gonadal maturation and somatic growth, with females showing more robust abdominal regions during peak Gonadosomatic Index (GSI) months, such as December (Libay *et al.*, 2019). Collectively, these patterns suggest that sexual dimorphism in both species is subtle, species-specific, and primarily expressed through functional traits related to reproduction and ecological strategies (Table 6).

Sexual dimorphism may also represent a functional adaptation reflecting differences in behavior and ecological habits between males and females, particularly in body shape. Exposed to varying environmental conditions, fish, like all organisms, can undergo morphological adaptations that enhance survival. The environment is widely recognized as a key factor shaping an organism's morphology during ontogeny. Consequently, the observed shape differences between sexes may also result from ecological or niche-specific selection, reflecting distinct habitat preferences and resource use by males and females. Similarly, it was observed that wild-caught female *Poecilia reticulata* exhibited smaller head sizes and deeper caudal peduncles than males. This pattern was absent in laboratory-reared specimens, underscoring the role of environmental conditions in shaping sexually dimorphic traits (Burns *et al.*, 2009). Accordingly, body shape is a reliable indicator of a fish's swimming performance and habitat preference (Fornai *et al.*, 2021). Body shape, therefore, reflects not only an organism's genetic makeup but also the influence of its environment and behavioral habits.

Body shape variation in the native fishes *G. giuris* and *H.* agilis is shaped by a complex interaction of genetic, ecological, and life-history factors. Body form is widely recognized as a reliable indicator of swimming performance, habitat use, and environmental specialization in fishes (Webb, 1984; Langerhans & Reznick, 2010). In both species, environmental heterogeneity within Lake Mainit, such as variation in water depth, substrate type, and resource availability, likely influences morphological differentiation through phenotypic plasticity during ontogeny (Wimberger, 1992). Additionally, sexual dimorphism contributes to shape variation, as males and females experience different selective pressures related to reproduction, including gonadal investment, mating behavior, and sexual

selection (Andersson, 1996). In *H. agilis*, male-biased traits such as enlarged heads and elongated fins are associated with agonistic behavior and niche-specific selection, whereas females often exhibit deeper abdominal regions linked to reproductive investment (Libay *et al.*, 2019). Similarly, in *G. giuris*, differences in body depth and fin morphology between sexes reflect trade-offs between somatic growth, fecundity, and foraging efficiency. Collectively, these patterns suggest that body shape variation in both species is not solely genetically determined but is strongly mediated by ecological conditions, behavioral strategies, and reproductive roles, emphasizing the adaptive value of morphological diversity in freshwater fishes.

Data Availability

The datasets generated during and/or analyzed during the current study are available in the main author. Readily available upon requests.

Limitations

Despite the statistically significant MANOVA results for both *G. giuris* ($\lambda = 0.8249$, $p < 0.001$) and *H. agilis* ($\lambda = 0.9097$, $p < 0.001$), several limitations remain evident. The persistent overlap in morphospace suggests that, although sex-based differences are detectable at the multivariate level, they are not strongly discrete, which may reflect within-sex variability, size-related (allometric) effects, or unaccounted ecological influences such as habitat variation in Lake Mainit. The analysis is also limited by its reliance on external morphological traits, which may not fully capture functional, behavioral, or reproductive differences, particularly those linked to mating systems or agonistic interactions. Additionally, the lack of explicit control for ontogenetic stages (e.g., juveniles vs. adults) and reproductive conditions (e.g., gravid females) could confound the interpretation of dimorphism.

Future Scope

Future research should address these gaps by incorporating larger and more stratified samples, applying size-correction and allometric analyses, and integrating geometric morphometrics with ecological and behavioral datasets. Longitudinal or seasonal sampling would help clarify how reproductive cycles influence morphology. At the same time, complementary approaches such as genetic, hormonal, or functional performance analyses (e.g., feeding efficiency or swimming capacity) could provide a more mechanistic understanding of the selective pressures shaping sexual dimorphism in these species.

Conclusion

This study demonstrates that both *Glossogobius giuris* and *Hypseleotris agilis* exhibit significant sexual dimorphism in body shape, as revealed through geometric morphometric analyses. These differences are primarily driven by reproductive roles, ecological adaptations, and environmental conditions within Lake Mainit. While both species show distinct morphological patterns between sexes, *F* displays greater variability, whereas *H. agilis* exhibits more conserved shape traits. Overall, the findings highlight the combined influence of ecological and biological factors in shaping fish morphology and provide helpful insights to the conservation and management of these native species. Notably, this study represents one of the few integrative morphometric investigations to jointly apply linear and geometric approaches in elucidating sex-based shape variation in these species within a Philippine freshwater ecosystem.

Authors' Contribution

All authors contributed to the study conception and design. Field works and Laboratory analysis were performed by Cresencio C. Cabuga Jr and Jojean Marie D. Pondang. The Data Generation were performed by Christian James R. Presilda and Mafi Kamille A. Angco. The first draft of the manuscript was written by Cresencio C. Cabuga Jr., Julito A Puebla Jr and Ailene B. Budiongan performed the Statistical Analysis of the Data. All authors read and approved of the final manuscript.

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Conflict of Interest

The authors declare that they have no competing interests.

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