

















Original Article

Ecophenotypic Variation of Midas Cichlid, *Amphilophus citrinellus* (Gunther, 1864), in Lake Batur, Bali, Indonesia

Variação ecofenotípica do ciclídeo Midas, *Amphilophus citrinellus* (Gunther, 1864), no Lago Batur, Bali, Indonésia

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Abstract

Cichlid fishes exhibit rapid adaptive radiations with significant diversification rates in response to ecological variability, i.e., ecological opportunity or geographical isolation. The discovery of a Midas cichlid species in Lake Batur, Indonesia's largest volcanic lake, first reported in 2013, could represent such adaptations. Midas cichlids can now be found in a range of habitats in Lake Batur and dominate the lake's fish population by up to 60%. This study aimed to identify the interaction between habitat, water quality, and Midas cichlid in Lake Batur, facilitating morphometric variances in the fish populations. The fish were captured at five locations in Lake Batur using fishing rods, community nets with mesh sizes of 2–3 inches, experimental gillnets with mesh sizes of 1 inch, and fish scoops in floating net cages during August and November 2022. There were 46 fish samples caught from the five stations, all photographed using a digital camera and later measured using the ZEN 2012 software. The fish measurement employed a truss morphometric method using 21 distinct morphometric body features. Canonical analysis was used to determine the distribution of characteristics, while discriminant analysis was used to examine the closeness of association. The measured water quality parameters included pH, DO, temperature, conductivity, and TDS for *in-situ* and TSS, TP, TN, and chlorophyll A for *ex-situ*. The findings revealed morphometric changes among Midas cichlid species in Lake Batur caused by habitat and water quality differences. The distinction can be detected in the anterior and posterior bodies (C1, B1, C3, C6, C5, B3 and B4). Temperature and aquatic plants, *Azolla pinnata*, may detect the station and shape of fish in Lake Batur. Body shape cannot be identified by chlorophyll A, TN, DO, and TDS. Future genetic research could answer why fish groups with varied body types coexist in the same location.

Keywords: phenotypic, plasticity, cichlid, polymorphism, body shape, lake.

Resumo

Os peixes ciclídeos exibem radiações adaptativas rápidas com taxas de diversificação significativas em resposta à variabilidade ecológica, ou seja, oportunidade ecológica ou isolamento geográfico. A descoberta de uma espécie de ciclídeo Midas em Lago Batur, o maior lago vulcânico da Indonésia, relatada pela primeira vez em 2013, poderia representar tais adaptações. Os ciclídeos Midas agora podem ser encontrados em uma variedade de habitats no Lago Batur, onde dominam a população de peixes em até 60%. Este estudo teve como objetivo identificar a interação entre habitat, qualidade da água e ciclídeo Midas no Lago Batur, facilitando variações morfométricas nas populações de peixe. Os peixes foram capturados em cinco locais no Lago Batur usando varas de pesca, redes comunitárias com malhas de 2–3 polegadas, redes de emalhar experimentais com malhas de 1 polegada e colheres de peixe em gaiolas de rede flutuantes, durante agosto e novembro de 2022. Foram capturadas 46 amostras de peixes nas cinco estações, todas fotografadas com câmera digital e posteriormente medidas no software ZEN 2012. A medição dos peixes empregou um método morfométrico de treliça usando 21 características morfométricas distintas do corpo. A análise canônica foi utilizada para determinar a distribuição das características, enquanto a análise discriminante foi empregada para examinar a proximidade da associação. Os parâmetros de qualidade da água medidos incluíram pH, OD, temperatura, condutividade e TDS para *in situ*, e TSS, TP, TN e clorofila A para *ex situ*. As descobertas revelaram mudanças morfométricas entre as espécies de ciclídeos Midas no Lago Batur, causadas por diferenças de habitat e qualidade da água. A distinção pode ser detectada nos corpos anterior e posterior (C1, B1, C3, C6, C5, B3 e B4). A temperatura e as plantas aquáticas, *Azolla pinnata*, podem detectar a estação e o formato dos peixes no Lago Batur. A forma do corpo não pode ser identificada pela clorofila A, TN, OD e TDS. Futuras pesquisas genéticas poderiam responder por que grupos de peixes com tipos corporais variados coexistem no mesmo local.

Palavras-chave: fenotípico, plasticidade, ciclídeo, polimorfismo, formato corporal, lago.

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1. Introduction

The body features of a fish are important characteristics in determining its interaction with the environment and any resulting biological evolutions. Any changes in the fish's body shapes or characteristics due to evolution can be described briefly via morphometric investigations (Hulse and Wainwright, 2002). Robust high Deoxyribonucleic acid (DNA) analysis through restriction-site-associated DNA sequencing or phylogenetic reconstruction provides greater clarity in revealing potential adaptive radiation in fish, particularly for shallow divergence (Ford et al., 2015). However, some fishes have faster diversity rates and clear body characteristic changes, from which a morphological test could be used to determine if adaptive radiation has occurred. For example, the fish family of Cichlidae has long been recognized for its extraordinary adaptive radiation and phenotypic flexibility and serves as a paradigm in evolutionary and ecological studies (Fryer, 1972; Stiassny, 2001). The fish is an important, affordable protein source, allowing extensive use in freshwater aquaculture (Turner, 2007). While cichlids' extraordinary abilities are advantageous in some aspects of ecological and economic vantage points, these same traits have caused the fish to be characterized as an ecological risk or invasive species (Agostinho et al., 2021; Nico et al., 2007).

Cichlid fishes are predicted to have multiple separate adaptive radiations with high diversification rates and considerable ecological diversification (Burrell, 2015; Elmer et al., 2010; Kusche et al., 2015). These capabilities are also observed in the Midas cichlid, particularly its rapid phenotypic diversification and speciation (Muschick et al., 2011). The species are distributed primarily in Costa Rica and Nicaragua and prefer clear water, lakes, and canals with plenty of shoreline cracks to hide from predators (Barluenga and Meyer, 2010; Torres-Dowdall and Meyer, 2021). The Midas Cichlid enjoys calm, slow-moving waters with depths ranging from 3 to 114 feet (1 to 35 meters) (Barlow, 1976). They are voracious omnivores that primarily consume snails and other benthic things, such as aquatic insects, tiny fishes, and plant and animal excrement stuck to submerged logs, leaves, and rocks (Barlow, 1983). They become quite violent and possessive when reproducing.

In Indonesia, the Midas cichlid sister, the red devil (*Amphilophus labiatus*), was introduced in several freshwater reservoirs starting in 2011 for different reasons (Ohee et al., 2018). Since then, they have been found in natural freshwater in Indonesia, notably in Lake Sentani in Papua New Guinea, which significantly threatens the lake's fish biodiversity (Ohee et al., 2018). Sentosa and Wijaya (2013) were the first to report the presence of a Midas cichlid in Lake Batur, the largest lake on Bali Island, Indonesia. At the time, the Midas cichlid population was only 0.4% of the total fish population compared to 63% of the other non-native species, Nile tilapia. Midas cichlids have become invasive in Lake Batur, dominating 60% of the fish population (Gustiano et al., 2023). The Midas cichlids found in Lake Batur have a variety of colors, including a red/orange or pale/opaque backdrop, black spots running down the back, vertically striped from the back to the abdomen, and reddish, yellowish, and black eyes.

In one of the areas of the lake, three separate Midas cichlid populations were found in Lake Batur near Abangsongan Village, signaling that hybridization between other Cichlid species could have occurred (Gustiano et al., 2023).

Ecosystem diversity drives phenotypic and ecological differentiations (Martin et al., 2015). Some researchers argue that genotype-by-environment interaction best approximates of the potential for phenotypic plasticity to arise. Other researchers claim that the correlation of genotype expression across two contexts is a stronger predictor of this potential (Via and Hawthorne, 2005). For both cases, establishing the impacts of genotypic and phenotypic diversities is crucial information needed to improve population stocks of threatened species and mitigate or prevent the potential spread of invasive and infectious species (Forsman, 2014), including fish. The underlying factors must be identified to assess the population's ability to evolve and adapt to varied or changing settings. The habitat diversity of Lake Batur is likely to influence the morphology, behavior and the recent invasive rate of Midas cichlids. However, this assumption is similar to the conclusion offered by other research studying the rapid spread of Midas cichlids in natural freshwater body Indonesia despite limited to non-existent analyses to support the claim. Therefore, this study aimed to identify the interaction between habitat, water quality, and Midas cichlids, which facilitate morphometric variances and their increasing dominance in the fish populations in Lake Batur.

2. Materials and Methods

2.1. Sampling sites

Lake Batur lies South-East of the active Mount Batur volcano. The lake has a 16.05 km² water surface area, an average depth of 50.8 m, and a water volume of 815.38 million m³ with a catchment area of 105.35 km². The lake gets most of its water from rainfall and seepage from the adjacent mountains. The 21.4 kilometres of Lake Batur's coastline is enveloped with two distinct topographies: an undulating lowland to a mountain (Mount Batur peaked at 1,717 meters above sea level) in the west, and steep hilly terrain to a mountain (Mount Abang peaked at 2,172 meters above sea level) in the North, East, and South.

Five sampling stations were determined based on the study of Juliawan et al. (2020) to represent the four sides and ecosystem variability of Lake Batur equally (Figure 1). The fish were captured at the sampling sites using a combination of fishing rods, community nets with mesh sizes of 2–3 inches, and experimental gillnets with mesh sizes of 1 inch. The sampling was carried out in August and November 2022, and Midas cichlid *Amphilophus citrinellus* (n=46) were successfully gathered.

2.2. Truss morphometric analysis

Truss morphometric analysis was carried out on 46 fish samples. A digital camera was first used to photograph the fish samples for analysis. The ZEN 2012 (Blue edition) software was then used to analyze the fish images (Nur et al., 2023).

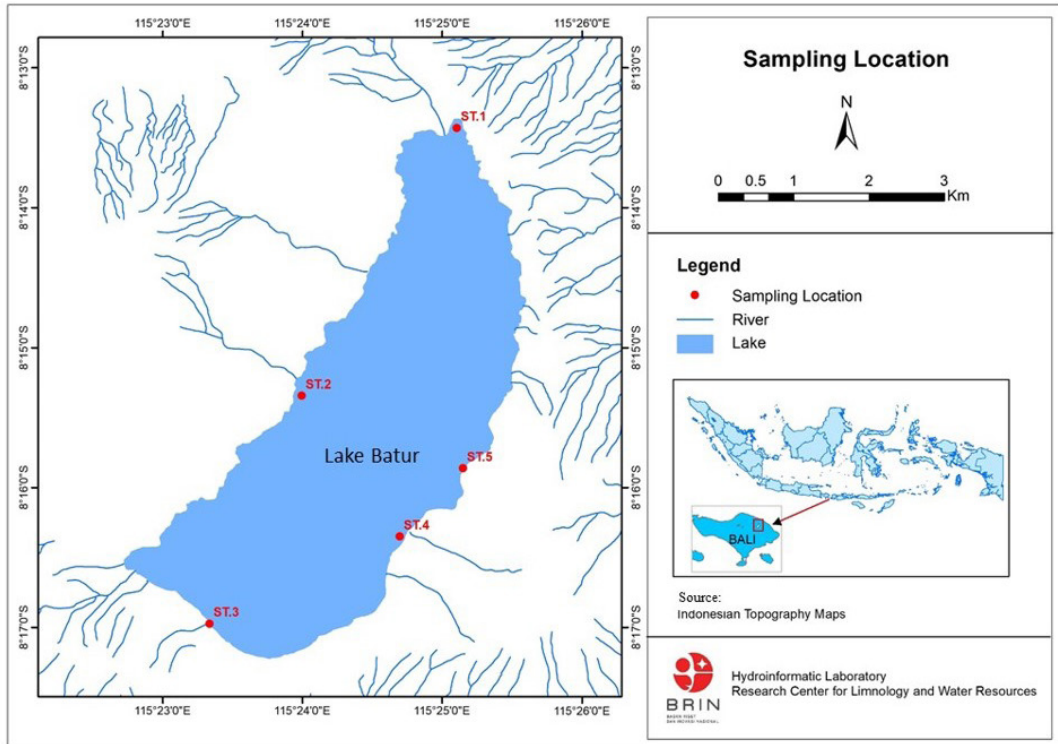


Figure 1. Sampling locations in Lake Batur, Bangli Regency, Bali Province. Station 1: Songan; Station 2: Toya Bungkah; Station 3: Kedisan; Station 4: Abang Songan; and Station 5: Cemara Landung.

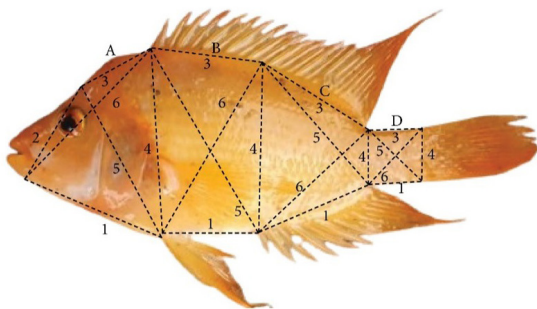


Figure 2. Truss morphometric measurement on Red Midas cichlid. (A) Head: A1: Under posteriormost point of the maxilla - Origin of pelvic fin; A2: Constructed line between posteriormost point of the maxilla - Posteriormost point of the eye; A3: Above posteriormost point of the eye - Origin of dorsal fin; A4: Origin of pelvic fin - Origin of dorsal fin; A5: Origin of pelvic fin - Above posteriormost point of the eye; A6: Under posteriormost point of the maxilla - Origin of dorsal fin; (B) Anterior body: B1: Origin of pelvic fin - Origin of anal fin; B3: Origin of dorsal fin - Origin of soft dorsal fin rays; B4: Origin of soft dorsal fin rays - Origin of anal fin; B5: Origin of dorsal fin - Origin of anal fin; B6: Origin of soft dorsal fin rays - Origin of pelvic fin; (C) Posterior body: C1: Origin of anal fin - End of anal fin base; C3: Origin of soft dorsal fin rays - End of dorsal fin base; C4: End of dorsal fin base - End of anal fin base; C5: Origin of soft dorsal fin rays - End of anal fin base; C6: End of anal fin base - Origin of anal fin base; (D) Caudal Peduncle: D1: End of anal fin base -Ventral anterior of caudal fin; D3: End of dorsal fin base - Dorsal anterior of caudal fin; D4: Dorsal anterior of caudal fin - Ventral anterior of caudal fin; D5: End of dorsal fin base - Ventral anterior of caudal fin; D6: Dorsal anterior of caudal fin - End of anal fin base.

The truss morphometric measurement was based on the method developed by Brzeski and Doyle (1988), in which the distance between the points of morphometric markers set on the body frame was measured (Figure 2 and Table 1). All character morphometric measurements are divided by standard length. Analysis of variance (one-way ANOVA) was performed on the transformed data to see whether species differences impacted the fish's morphological appearance. Following the observation of an effect, the procedure is carried out using Discriminant Function Analysis to examine associations between species based on their morphological traits and Duncan's multiple range tests to identify the important character between species. The analysis was carried out using SPSS.

2.3. Habitat and water quality

During the sampling campaigns, *in-situ* and *ex-situ*, the water quality parameters were measured, and fish habitat characteristics were observed. The following water quality parameters were measured *in-situ* using a Lutron WA-2017SD water quality checker: pH, dissolved oxygen (DO), temperature, electrical conductivity, and total dissolved solids (TDS). The other water quality parameters were measured *ex-situ* by collecting water samples in a 1 L HDPE bottle, followed by each parameter analysis in the laboratory: total suspended solids (TSS) (gravimetric method), total phosphorus (TP) (4500-P and 4500-PE methods), total nitrogen (TN) (brucine method; APHA, 1975), and chlorophyll A (chl A) (10200 H method).

Table 1. Description of 21 measured morphometric morphological characters.

Truss cells	No	Code	Description
Head	1	A1	Under posterior most point of the maxilla – Origin of pelvic fin
	2	A2	Constructed line between posterior most point of the maxilla – Posterior most point of the eye
	3	A3	
	4	A4	Origin of pelvic fin – Origin of dorsal fin
	5	A5	Origin of pelvic fin – Above posterior most point of the eye
	6	A6	Under posterior most point of the maxilla – Origin of dorsal fin
Anterior body	7	B1	Origin of pelvic fin – Origin of anal fin
	8	B3	Origin of dorsal fin – Origin of soft dorsal fin rays
	9	B4	Origin of soft dorsal fin rays – Origin of anal fin
	10	B5	Origin of dorsal fin – Origin of anal fin
	11	B6	Origin of soft dorsal fin rays – Origin of pelvic fin
Posterior body	12	C1	Origin of anal fin – End of anal fin base
	13	C3	Origin of soft dorsal fin rays – End of dorsal fin base
	14	C4	End of dorsal fin base – End of anal fin base
	15	C5	Origin of soft dorsal fin rays – End of anal fin base
	16	C6	End of anal fin base – Origin of anal fin base
Caudal peduncle	17	D1	End of anal fin base -Ventral anterior of caudal fin
	18	D3	End of dorsal fin base – Dorsal anterior of caudal fin
	19	D4	Dorsal anterior of caudal fin – Ventral anterior of caudal fin
	20	D5	End of dorsal fin base – Ventral anterior of caudal fin
	21	D6	Dorsal anterior of caudal fin – End of anal fin base

Three replicates sampling and measuring of water qualities were done at each station. The water quality data was then analyzed using PCA using Paleontological Statistics software (Hammer and Harper, 2001).

3. Results

3.1. Morphometric analysis

The ANOVA test showed that the differences in population significantly affected the variation in morphological character ($p < 0.05$). Furthermore, Duncan's test revealed that only two characters (A3 and D5) were not significantly different among the population, as shown in Table 2. DFA analysis produced four functions, where Function 1 has an eigenvalue of 6.163, which indicates that 43.8% of the total variance with a significant contribution or high-loading characters include B3, D6, B5 and A3. Meanwhile, Function 3 has 1.669 eigenvalue, showing that 11.9% of the total variance with significant contributing characters were D4, A4, B4, B6, A2, C1, C6, C5, C3 and A6. An eigenvalue of 0.804 was obtained for Function 4, which indicates that 5.7% of the total variance with significant contributing characters include B1, A1, A5, D1, D3, D5 and C4 (Table 3). Table 4 shows that the intrapopulation at each station is 100% based

on shared components. Further examination of Midas cichlids revealed that combining canonical discriminant functions 1 and 2 could separate populations of Midas cichlids from different stations, except for samples from stations 2 and 3 (Figure 3). Cluster analysis of Midas cichlid populations from the five sites revealed that station 1 has the most distant resemblance (Figure 4).

3.2. Habitat and water quality

Each station has unique features based on the types of environments, substrate, present aquatic plants, depth, and altitude. The surface water temperature measured at the five sampling stations ranged from 23.7 to 27.8°C. All sampling stations have no significant difference in temperature except for station 1, which was significantly different from the other stations ($p < 0.05$) (Table 5). The DO concentration in Lake Batur was typical high altitude and unpolluted lakes ranging from 4.0 to 7.9 mg/L. The statistical comparison of the DO concentration showed that station 2 was considerably different from the other four stations. The pH value, ranging from 7–8, also indicated that the water was in good condition. EC ranged from 1,587 to 3,035 S/cm. The TDS in the water ranged from 1,057 to 1,494 mg/L, indicating the number of dissolved solids in organic ions, compounds, and colloids. The TSS ranged from 2.6 mg/L to 18.5 mg/L. Total N ranged from 0.27 mg/L to 0.60 mg/L, except for stations 4 and 5.

Table 2. Morphometric diversity of 21 character measurement in Midas cichlid populations in Lake Batur, Bali, Indonesia.

Character	Station 1 (n=4)	Station 2 (n=10)	Station 3 (n=9)	Station 4 (n=10)	Station 5 (n=13)
A1	35.58 ± 4.08 ^a	37.82 ± 0.76 ^{bc}	36.47 ± 1.49 ^{ab}	38.29 ± 1.57 ^c	37.54 ± 1.12 ^{bc}
A2	23.85 ± 1.95 ^b	23.10 ± 1.28 ^b	21.55 ± 1.06 ^a	22.67 ± 0.96 ^{ab}	21.56 ± 1.60 ^a
A3	27.59 ± 2.98 ^a	26.91 ± 1.68 ^a	26.57 ± 1.21 ^a	26.04 ± 2.87 ^a	28.27 ± 2.20 ^a
A4	46.92 ± 2.40 ^{ab}	48.09 ± 1.53 ^b	45.72 ± 2.08 ^a	45.25 ± 2.59 ^a	45.30 ± 1.43 ^a
A5	41.37 ± 1.72 ^a	43.83 ± 0.94 ^b	41.91 ± 1.38 ^a	42.00 ± 1.61 ^a	41.54 ± 1.35 ^a
A6	48.71 ± 2.95 ^b	47.11 ± 1.37 ^{ab}	45.25 ± 1.33 ^a	46.18 ± 2.85 ^a	47.35 ± 1.83 ^{ab}
B1	24.10 ± 3.40 ^c	20.33 ± 1.82 ^a	23.78 ± 0.96 ^c	22.30 ± 2.32 ^{bc}	21.13 ± 1.11 ^{ab}
B4	43.91 ± 2.66 ^c	43.65 ± 1.61 ^{bc}	40.39 ± 2.50 ^a	41.00 ± 3.84 ^{ab}	41.18 ± 1.50 ^{ab}
B3	25.42 ± 1.22 ^a	24.82 ± 2.23 ^a	28.25 ± 2.21 ^b	28.25 ± 2.82 ^b	23.22 ± 1.52 ^a
B5	53.24 ± 2.44 ^b	52.71 ± 1.66 ^b	52.32 ± 1.44 ^b	52.55 ± 1.94 ^b	50.26 ± 0.96 ^a
B6	50.27 ± 3.38 ^b	49.20 ± 1.96 ^{ab}	47.66 ± 1.99 ^a	47.19 ± 2.88 ^a	47.19 ± 1.56 ^a
C1	27.54 ± 2.46 ^{ab}	29.49 ± 1.14 ^c	29.10 ± 1.50 ^{bc}	26.21 ± 1.34 ^a	28.49 ± 2.19 ^{bc}
C4	14.22 ± 0.50 ^a	15.11 ± 0.66 ^b	14.52 ± 0.56 ^{bc}	14.46 ± 1.02 ^{bc}	14.91 ± 0.54 ^{bc}
C3	30.01 ± 2.00 ^a	32.90 ± 1.44 ^b	30.51 ± 2.38 ^{ab}	29.95 ± 3.28 ^a	30.70 ± 2.30 ^{ab}
C5	39.31 ± 2.37 ^a	42.39 ± 1.75 ^b	39.24 ± 2.17 ^a	39.11 ± 3.74 ^a	39.81 ± 2.03 ^a
C6	36.69 ± 2.14 ^{ab}	38.47 ± 1.48 ^b	37.56 ± 1.82 ^b	35.37 ± 1.86 ^a	37.64 ± 1.89 ^b
D1	9.83 ± 0.94 ^{ab}	10.03 ± 0.98 ^{ab}	8.72 ± 1.27 ^a	9.67 ± 1.59 ^a	11.12 ± 1.3 ^b
D4	13.55 ± 1.15 ^{ab}	14.50 ± 0.83 ^c	14.09 ± 0.87 ^{bc}	12.77 ± 0.58 ^a	13.35 ± 0.66 ^{ab}
D3	9.74 ± 0.18 ^{ab}	9.95 ± 1.25 ^{ab}	9.10 ± 1.10 ^a	9.74 ± 1.17 ^{ab}	10.48 ± 0.88 ^b
D5	16.77 ± 0.55 ^a	17.74 ± 1.63 ^a	16.76 ± 0.89 ^a	16.82 ± 0.56 ^a	17.31 ± 0.76 ^a
D6	17.09 ± 0.62 ^a	18.09 ± 0.68 ^b	17.24 ± 0.98 ^a	17.02 ± 0.68 ^a	18.40 ± 0.68 ^b

Mean ± SD at the same row with different superscripts are significantly different (p<0.05).

Table 3. Eigenvalue, percentage of variance, and cumulative percentage of variance of four factors using morphometric truss in Midas cichlid populations in Lake Batur, Bali, Indonesia.

Character	1	2	3	4
Eigenvalue	6.163 ^a	5.441 ^a	1.669 ^a	.804 ^a
% of Variance	43.8	38.7	11.9	5.7
Cumulative %	43.8	82.4	94.3	100.0
B3	-.342*	0.181	0.321	-0.260
D6	.313*	-0.016	-0.158	0.241
B5	-.251*	0.095	-0.226	0.005
A3	.132*	-0.094	-0.068	-0.063
D4	0.078	0.227	-.475*	-0.229
A4	-0.020	0.087	-.432*	0.150
B4	-0.026	-0.028	-.407*	0.208
B6	-0.058	-0.010	-.369*	-0.028
A2	-0.159	-0.047	-.318*	0.274
C1	0.178	0.156	-.311*	-0.258
C6	0.175	0.102	-.299*	-0.124
C5	0.062	0.097	-.294*	0.279
C3	0.066	0.108	-.253*	0.198
A6	0.047	-0.160	-.236*	0.146
B1	-0.186	-0.046	0.133	-.682*
A1	0.022	0.046	0.151	.532*
A5	-0.009	0.191	-0.302	.380*
D1	0.196	-0.164	-0.024	.349*
D3	0.127	-0.106	-0.021	.287*
D5	0.097	0.040	-0.172	.250*
C4	0.136	0.064	-0.113	.230*

*Largest absolute correlation between each variable and any discriminant function.

Table 4. Value sharing component of Midas cichlid populations (%) in Lake Batur, Bali, Indonesia.

	S1_RM	S2_RM	S3_RM	S4_RM	S5_RM	Total
S1_RM	100.0	0.0	0.0	0.0	0.0	100.0
S2_RM	0.0	100.0	0.0	0.0	0.0	100.0
S3_RM	0.0	0.0	100.0	0.0	0.0	100.0
S4_RM	0.0	0.0	0.0	100.0	0.0	100.0
S5_RM	0.0	0.0	0.0	0.0	100.0	100.0

Table 5. Water quality based on sampling locations in Lake Batur, Bali, Indonesia, conducted in August and November 2022.

Location	Temperature (°C)	DO (mg/L)	pH	Conductivity (µS/cm)	TDS (mg/L)	TSS (mg/L)	TN (mg/L)	TP (mg/L)	Chlorophyll A (mg/cm ³)
Station 1	27.3 ± 0.53 ^a	7.0 ± 0.45 ^b	7.9 ± 0.11 ^a	2,780.1 ± 173.40 ^a	1,464.25 ± 30.17 ^a	15.1 ± 3.29 ^a	0.3 ± 0.03 ^a	0.05 ± 0.02 ^a	48.28 ± 3.32 ^a
Station 2	24.8 ± 1.11 ^b	7.7 ± 0.18 ^a	8.0 ± 0.06 ^a	2,311.4 ± 724.07 ^a	1,402.25 ± 11.63 ^b	4.7 ± 2.09 ^a	0.6 ± 0.00 ^b	0.07 ± 0.04 ^a	60.14 ± 0.78 ^b
Station 3	25.8 ± 0.96 ^b	6.0 ± 0.22 ^b	7.9 ± 0.04 ^a	2,755.3 ± 69.8 ^a	1,179.75 ± 122.02 ^c	10.3 ± 3.11 ^a	0.4 ± 0.05 ^c	0.07 ± 0.04 ^a	45.59 ± 3.99 ^a
Station 4	25.3 ± 0.73 ^b	5.8 ± 1.74 ^b	8.0 ± 0.05 ^a	2,815.8 ± 3.01 ^a	1,392.13 ± 3.09 ^b	7.1 ± 1.23 ^a	0.5 ± 0.01 ^d	0.05 ± 0.01 ^a	60.21 ± 4.77 ^b
Station 5	25.3 ± 0.74 ^b	5.8 ± 1.54 ^b	7.6 ± 0.58 ^a	2,830.6 ± 21.22 ^a	1,412.13 ± 13.91 ^b	7.3 ± 4.76 ^a	0.5 ± 0.01 ^d	0.05 ± 0.02 ^a	65.49 ± 0.46 ^c

Note: Different superscripts in the same columns indicate significant differences (p <0.05).

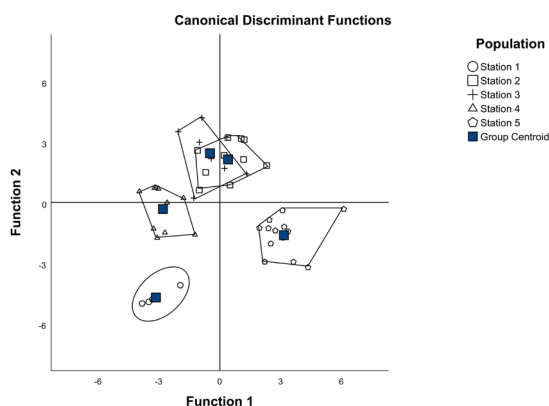


Figure 3. Distribution of five populations of Midas cichlid in Lake Batur, based on truss morphometric.

Meanwhile, total P levels ranged from 0.03 mg/L to 0.1 mg/L. Total N and total P are the primary indicators representing eutrophication in aquatic environments. The chl A content in this study ranged from 41.60 mg/m³ to 65.95 mg/m³. The chl A level at each location revealed that the eutrophication level of this lake was in correlation with the concentration of P and N. Station 5 has the highest chlorophyll abundance (65.49 ± 0.46 mg/cm³) compared to the other four stations (Table 5). Based on the results of the PCA analysis, three clusters were formed where stations one and three were separate while stations two, four and five were in one cluster. Station one is separated due to temperature factors, while stations 2, 4, and 5 are influenced by chl A and TN (Figure 5).

4. Discussion

Morphometric truss analysis has been frequently utilized and successful in differentiating various populations within a species, such as in freshwater catfishes (Gustiano et al., 2021; Kusmini et al., 2019; Miyan et al., 2016) and the Indian Scad sea fish, *Decapterus russelli* (Sen et al., 2011).

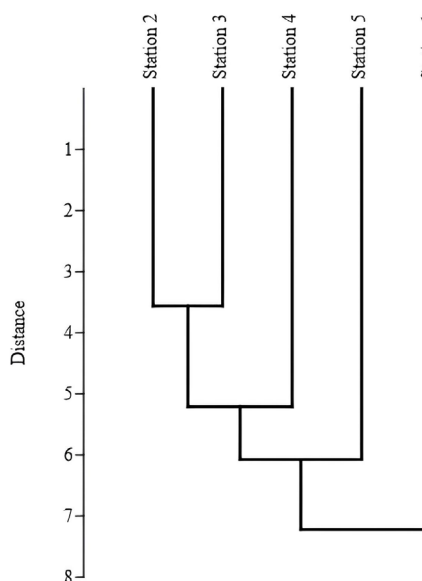


Figure 4. Similarity of Midas cichlid populations in Lake Batur, Bali, Indonesia.

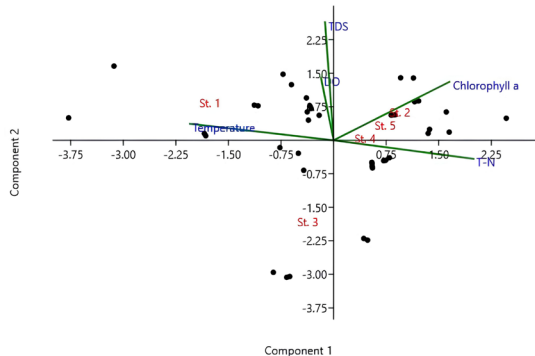


Figure 5. Scatter plot of water quality properties in Lake Batur, Bali, Indonesia.

The Midas cichlid populations in our study can be divided into four groups based on their body shape or characteristics (Figure 4). The fish's intraspecific variation is a phenotypic feature, which Spoljaric and Reimchen (2007) argued can vary substantially within freshwater fish taxa. This morphological variation can be induced by environmental factors, i.e., temperature, turbidity, and water currents (Mir et al., 2013; Yulianto et al., 2020), as well as habitat characteristics (Shuai et al., 2018; Webster et al., 2011). Such morphological changes due to environmental pressure can be accelerated by the fish's inherent phenotypic plasticity (Nur et al., 2022; West-Eberhard, 2008) and geographic isolation (Worsham et al., 2017). In most cases, a sufficient degree of isolation can even result in both morphological and genetic diversity across fish populations within a species (Turan, 2004).

Four truss dimensions (B3, D6, B5 and A3) were found to be the main distinguishing characteristics of the Midas cichlid populations in each sampling station. The populations of stations 1, 4, and 5 were distinct from each other, with no observable overlaps. In contrast, the populations of stations 2 and 3 had overlaps, indicating that these fish groups are very similar. Based on the morphometric similarity, the fish populations in the adjacent stations were highly similar to those of the distant stations. It is argued that Midas cichlid populations interact between these stations due to their relatively locational closeness. The influencing populations are notably more substantial from higher altitude stations to the lower ones, such as from station 2 (1,057 m a.s.l) to station 3 (488 m a.s.l) and from station 4 (1,200 m a.s.l) to station 3. The frequent release of sulfur dioxide (sulfur eruption) in many sites of Lake Batur, which is considered an active caldera, could also be attributed to the fish movement between adjacent areas in the lake. For example, waters in Station 2 have a higher concentration of dissolved sulfur dioxide (sulfurous acid water), indicated by plenty of natural hot springs. As such, the fish populations from this area likely move to the adjacent areas, either temporarily or permanently, to avoid exposure to the degraded water conditions. This specific habitat characteristic could be responsible for the higher similarity of fish populations between station 2 and station 3.

Numerous unresolved taxonomic difficulties remain a major problem in the cichlid family. However, regional isolation has been well known to play an important role in the evolution and preservation of phenotypic variation in cichlids in rivers and lakes (Píálek et al., 2012; Seehausen and Magalhaes, 2010). Structured littoral fish species in lakes have more significant color variation than pelagic or deep-water demersal species (Genner and Turner, 2005; Koblmüller et al., 2008). Studies on cichlid populations in African lakes confirmed that populations of stenotopic species, i.e., species with narrow specialization under certain environmental conditions, are often isolated from each other, even by small habitat barriers (Koblmüller et al., 2011; Sefc et al., 2007; Smith and Kornfield, 2002). Geographic isolation certainly facilitates and maintains phenotypic differentiation. Nevertheless, other factors such as genetic predisposition, environmental variation, and mate preference also play important roles in the evolution of allopatric phenotypic differentiation (Maan and Sefc, 2013).

Stations 1 and 5 are the farthest and highest sampling locations, allowing the Midas cichlid populations in these areas to stay isolated or avoid mixing with the other populations. The similarity analysis of water quality parameters produced comparable results to the research conducted by Suryawan et al. (2020). The authors measured water quality parameters and aquatic plant distribution in sampling points close to this study's sampling stations. Stations 1 and 3 are in one group of Suryawan et al.'s (2020) investigation, whereas stations 2, 4, and 5 are in another. As a result, the present station has mostly stayed the same. Possible discrepancies between stations can influence the phenotypic differences that exist. It should be noted that there is no population mixing because of population mobility to other locations.

The variation of water quality parameters between the sampling stations suggested that environmental factors/water quality might have influenced the variety of fish phenotypes developed at the locations. The fish shape and water temperature at station 1 were the two variables that distinguish the station from the others. The temperature at station 1 was higher and significantly different from the other four locations ($P < 0.05$). High temperatures have allowed a particular aquatic plant in station 1, *Azolla pinnata*, known to favor high temperatures (Watanabe and Berja, 1983), to flourish, which was not found in the other stations. The combination of these two components of environmental factors (high temperature and aquatic plants) most likely contributed to the phenotype variation of Midas cichlid at station 1.

Furthermore, some researchers have also reported that water quality could influence morphological variation (El-Zaeem, 2011; Mir et al., 2013; Wimberger, 1992; Yulianto et al., 2020). Differences in water quality parameters other than temperature were observed in this recent study, where the values of chl A, TN, DO, and TDS in station 3 significantly differed from stations 2, 4, and 5. However, the variations of these parameters resulted in no difference in the fish populations' morphology among the sampling stations. Similarly, in separating fish populations from Station 3 and 5, water quality does not alter the phenotype; other factors may be more relevant.

5. Conclusion

The study discovered morphometric differences amongst Midas cichlid species in Lake Batur. The anterior and posterior bodies are distinguished by truss morphometric character (C1, B1, C3, C6, C5, B3, and B4). The differences were likely caused by habitat and water quality differences represented by the presence of *Azolla pinata* and temperature, respectively. The other water parameters, such as chl A, TN, DO, and TDS, could be used to differentiate the environmental condition between the stations but eventually did not influence body form variation between the fish populations. Future research using the genetics approach could sufficiently explain why there are Midas cichlids populations with varying body types in the same location.

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